Chapter 5

THE DEEP ATLANTIC OCEAN

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INTRODUCTION

The Atlantic Ocean is a long sinuous ocean which originated during the Mesozoic following the break-up of the supercontinent of Pangea. For most of its length, the eastern and western boundaries are clearly defined by land masses, except where it is separated from the Caribbean Sea and Gulf of Mexico by troughs and trenches. The northern and southern limits are more difficult to define. To the north we consider the Atlantic to include the subpolar Greenland and Norwegian Basins. These are linked hydrographically to the rest of the Atlantic, although they are isolated topographically by the ridge system extending between Greenland and Scotland. To the south, the boundary between the South Atlantic and Southern Ocean is generally defined hydrologically by the Subtropical Convergence around 40ºS (e.g., Webb, 1996).

In this chapter we review current knowledge about the distribution and ecology of organisms on the floor of the Atlantic Ocean from the continental slope to the abyss, and describe the environmental setting that they experience. We focus particularly on the North Atlantic, since the literature for this hemisphere is far more voluminous than for the South Atlantic. As with any large review, we have been selective in our coverage of the regional literature, concentrating on aspects with which we are most familiar, or which have received greatest attention from investigators. Our treatment of the Atlantic intentionally omits hydrothermal vent and seep settings, which are covered in Chapter 4 of this volume. Following a description of the environment of the deep Atlantic, and of the biological communities region by region, we have attempted to synthesize general patterns of faunal density and biomass, community respiration, bioturbation and succession.

Distinctive features of the Atlantic Ocean

The two margins of the Atlantic separated between about 175 and 90 million years ago, making it the youngest of the major world oceans. Because of its relative youth, the Atlantic is a narrow ocean, with a relatively high ratio of margin to open water. The configuration of the eastern and western sides strongly influences the movement of surface currents (Longhurst, 1998) and, ultimately, the nature of the deep-sea biota. Because of the high ratio of margin to open water in the Atlantic, mass wasting events on the margins (involving the collapse and slumping of sediments) affect a considerable fraction of the deep ocean. Earthquake-induced turbidity flows may sequester carbon originally deposited on the shallow margins in deep-sea sediments (Thunell et al., 1999). Regions such as the Madeira Abyssal Plain (Weaver et al., 1992), the Grand Banks abyss (Huggett, 1987), or the Cariaco Basin (Thunell et al., 1999) apparently contain turbidite[1] sediments originating on the margin. Despite the frequency of mass wasting along the margin, the Atlantic is generally less tectonically active than the Pacific. There are fewer subduction zones and trenches, and thus less hadal habitat. Hydrocarbon seeps, which are common along much of the active Pacific margin, are apparently relatively rare in the Atlantic, particularly on the eastern margins (Sibuet and Olu, 1998). Sediment deposition is a dominant process on the broad slope and rise. Strong bottom

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[1] Turbidite sediments are produced by deposition from gravity-driven flows of sediment ‘rivers’. They may be homogeneous, or characterized by fining upward. See Glossary, p. 475.

flows, sometimes reaching storm proportions, are more prevalent in the Atlantic than in other oceans. These play an important role in redistributing sediments and organic matter in deep water, leading to the formation of vast sediment drifts (Hollister et al., 1984).

Atlantic water masses exhibit distinctive properties. There is a strong flow of cold abyssal water from both polar regions, whereas very little deep arctic water directly enters the Pacific Ocean. The North Atlantic is the source of much of the World Ocean's deep water. These young, near-bottom water masses are better oxygenated, and the calcium compensation depth[2] is much deeper, than in the Pacific and Indian Oceans. This affects the distribution of sediment types. Carbonate oozes are the dominant sediments in the Atlantic, and carbonate-free red clays, which cover vast tracts of the deep Pacific, are confined to relatively small areas. Sedimentation rates are higher in the central parts of the Atlantic, and manganese nodule fields are less extensive than in the other oceans. Massive upwelling, characteristic of eastern boundaries in the Pacific and Indian Oceans, is less extensive in the Atlantic, and the intense oxygen-minimum zones that develop in these other oceans are limited to a small area off West Africa.

The processes in the upper water column that drive the timing and magnitude of primary production in the Atlantic are different from those operating in the Pacific (Longhurst, 1995, 1998). The spring bloom is more intense and widespread in the North Atlantic than anywhere else in the oceans, leading to a greater degree of seasonality in surface production and to relatively predictable seasonal inputs of phytodetritus to the deep seabed. Particularly in marginal environments, much of the marine primary production is deposited on the seafloor, making the Atlantic margins highly dynamic settings, with important roles in organic-matter cycling. There is evidence that these inputs are more likely to meet the respiratory demands of the benthos than in the Pacific Ocean.

The youth of the Atlantic may also influence zoogeographic patterns. About a third of the benthic species present in deep water appear to be endemic, and the degree of endemism increases with depth (Vinogradova, 1997). Some major groups are apparently absent or poorly represented in the Atlantic. Different families dominate the demersal fish fauna in the Atlantic (in ranked order, the Macrouridae, Alepocephalidae, Ophidiidae, Gadidae and Ragidae), and the NE Pacific (in ranked order, the Scorpaenidae, Liparidae, Zoarcidae, Ragidae, Pleuronectidae and Macrouridae) (Merrett and Haedrich, 1997). Among the protists, the xenophyophore order Stannomida, which is common and diverse in the Pacific, is represented in the Atlantic by a single species. Atlantic vent faunas have distinctive features as well. Vestimentiferans, common in the Pacific, are absent from the Atlantic, whereas bresiliid shrimps are a dominant element in the Atlantic but not the Pacific (Gebruk et al., 1997). Because many researchers and nations have concentrated their efforts in one ocean or another, there are relatively few investigations that compare deep-sea processes in a global context. Future efforts to compare and contrast the Atlantic with other world oceans and seas will undoubtedly reveal additional unique features, as well as unexpected commonalities.

HISTORY OF RESEARCH

The North Atlantic was a cradle for the development of deep-sea biology both during the latter part of the 19th century and in recent decades. To some extent, this reflects proximity to population centers and academic institutions in western Europe and North America.

By the 1860s, a considerable number of observations, many of them made serendipitously during sounding operations in the North Atlantic, strongly suggested that animals could live on the ocean floor (Rice, 1975; Rice et al., 1976; Mills, 1983). However, the first concerted attempts to sample deep-sea animals by means of dredges were made in the late 1860s in the waters to the north and west of the British Isles, initially from H.M.S. *Lightning* (1868) but principally from H.M.S. *Porcupine* (1869, 1870). The deepest sample taken during these early cruises demonstrated that animal life could flourish at a depth of 4289 m. It was these dredging activities which finally and belatedly disproved the azoic theory of Forbes (1844). They also paved the way for the great world-wide *Challenger* Expedition of 1872–1876, which in turn stimulated other European deep-sea campaigns such as the French *Travailleur* and *Talisman* expeditions in the Northeast Atlantic and Mediterranean, and the work of Albert I of Monaco who introduced many innovative methods into deep-sea biology (Mills, 1983). The

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[2] The calcium carbonate (calcite) compensation depth (CCD) is the depth at which <20% of skeletal carbonate is preserved in the sediment.

Danish Ingolf expeditions of 1895 and 1896 around Greenland, Iceland, and the Færøerne were notable for the use of fine-meshed screens (silk gauze) to sift mud recovered by the trawl and dredge. These residues yielded a diversity of small animals, for example, 70 tanaid species (49 of them new) and 121 isopod species (61 of them new) (Hansen, 1913, 1916).

There were parallel developments on the North American margin. An early pioneer was Pourtáles who dredged to a maximum depth of 494 m in the Florida Straits using the U.S. Coast Guard steamer *Corwin* in the summer of 1867. During the following two years Pourtáles and Louis Agassiz obtained abundant animals down to a maximum depth of 1555 m on the U.S. continental margin between Florida and the Grand Bahama Bank from the steamer *Bibb* (Mills, 1983). A decade later (1877–1880), under the direction of Alexander Agassiz, another U.S. Coast Guard steamer, the *Blake*, undertook a series of biological cruises on the continental margin of the eastern United States, during which animals were dredged from depths down to almost 3000 m (Agassiz, 1888). These studies raised issues that continue to concern deep-sea biologists – not least, the question of food supply to the deep-sea benthos.

After fifty years or so of relative quiescence, deep-sea biology has undergone a renaissance since the 1960s, a period during which national and, more recently, international programs have become more focused on specific areas and issues (Table 5.1; Fig. 5.1). Work conducted in the North Atlantic by American and European scientists has contributed substantially to the tremendous development of deep-sea ecology during this period. Perhaps the most significant advance resulted from the recognition by H.L. Sanders, R.R. Hessler and their colleagues, that smaller animals (macroinfauna – animals residing within the sediment column which are retained on a 0.3 or 0.5 mm mesh) are abundant and highly diverse in the deep sea, a discovery made during the mid-1960s on the continental margin of the northeastern United States using novel sampling techniques (Sanders et al., 1965; Hessler and Sanders, 1967). Although to some extent foreshadowed by earlier observations (for instance, those of Hansen referred to above), this discovery overturned the paradigm of low deep-sea species diversity which had been derived from studying large epibenthic megafaunal animals caught in coarse-meshed bottom nets. Many of the ideas which have developed subsequently regarding the magnitude and geographic patterns of deep-sea species diversity have resulted from research carried out on this intensively studied margin (e.g., Rex, 1983; Grassle and Morse-Porteous, 1987; Grassle and Maciolek, 1992) and elsewhere in the Atlantic Ocean (Rex et al., 1993, 1997; Allen and Sanders, 1996). Two other major developments in deep-sea biology during the last 20 years have been the discovery that the deep-sea floor is subject to seasonal or unpredictable episodic inputs of organic matter which play an important role in structuring benthic communities, and the discovery that certain areas are physically disturbed by periodic strong currents (benthic storms: see Chapter 2). Again, these developments arose largely from work carried out in the North Atlantic Ocean.

The important contribution made by Russian scientists to knowledge of the biology of both the South and North Atlantic Ocean should not be overlooked. Much of the extensive Russian literature on the faunas of the Atlantic slopes and abyssal plains, large-scale faunal distribution patterns, and primary phytoplankton production, is summarized in the English-language volume edited by Gebruk et al. (1997).

GENERAL PHYSICAL AND CHEMICAL CHARACTERISTICS

Seafloor topography and physiography

An excellent and detailed account of the physiography and geology of the Atlantic Ocean has been given by Emery and Uchupi (1984). According to the hypsometric curve of Emery and Uchupi (1984, fig. 9 therein), the mean depth of the Atlantic between 60ºN and 60ºS is 3730 m, very close to the average for the entire World Ocean, with the modal depth lying between 4000 m and 5000 m. The most important first-order feature is the Mid-Atlantic Ridge which divides the ocean longitudinally into two halves, each with a series of major basins delimited by secondary, more or less transverse ridges (Fig. 5.2). The Ridge extends above the 2000 m contour along most of its length and has a major influence on the circulation of near-bottom water masses (Tomczak and Godfrey, 1994). It is interrupted by a series of transform faults including the Romanche Fracture Zone near the equator and the Gibbs Fracture Zone at 53ºN. Both these features provide routes for bottom water to pass from one side of the ocean to the other. Second-order physiographic features include the

Table 5.1
Major national and international research projects and programs in the Atlantic Ocean

	Project	Dates	Study area	Purpose
EUROPE				
Denmark	BIOFAR	1990	Slope SW of Faroes	Faunal survey
France	BIOGAS	1972–1974 1978–1981	Bay of Biscay	Comprehensive environmental and faunal survey, recolonisation experiments, etc.
France	EUMELI	1989–1992	NW African margin	Comparison of faunas under different organic matter input regimes
Germany	BIOTRANS BIO-C-FLUX BIGSET	1984–1989 1989–1994 1996–1999	48º00–48º30ºN 19ºW	Benthic reaction to organic matter flux
Germany	Sondersforschungsbereich 313	1985–1998	Greenland–Norwegian Sea	Particle flux to seafloor and its transformation into paleoceanographic record
The Netherlands	DORA	1984–1986	Porcupine Abyssal Plain	Effect of radioactive waste dumping
UK		1972–present	Rockall Trough	Time series study of macrofauna
UK	IOSDL Porcupine Seabight programme	1977–1986	Porcupine Seabight	Survey of mega-, macro-, meiofauna
European Union (MAST I Framework)	‘Natural variability and the prediction of change in marine benthic ecosystems’	1990–1993	NE Atlantic slope and abyssal plains	Describing environmental and biological variability at different temporal and spatial time scales; investigating effects of disturbance on benthos
European Union (MAST II Framework)	‘Community structure and processes in the deep-sea benthos’	1993–1996	Porcupine, Madeira, Cape Verde Abyssal Plains	Comparison of benthic communities disturbed by phytodetritus with undisturbed communities
European Union (MAST III Framework)	BENGAL: ‘High resolution temporal and spatial study of the benthic biology and geochemistry of a north-eastern Atlantic abyssal locality’	1996–1998	PAP	Flux through water column and modification of flux prior to incorporation in permanent record
European Union (MAST II Framework)	OMEX 1	1992–1996	Transects of continental margin in Goban Spur area	Physical, chemical and biological processes at ocean margins controlling transport of material from shelf into deep sea
U.S.A.				
	Gay Head to Bermuda Transect	1960s	Massachusetts to Bermuda	Quantitative evaluation of deep-sea macrofauna (diversity/abundance)

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Table 5.1, *continued*

Project	Dates	Study area	Purpose
Atlantic Continental Slope and Rise Study (ASCAR) North Atlantic Bight, Mid Atlantic Bight, South Atlantic Bight	1983–1986	NW Atlantic slope and rise: 28ºN to 42ºN	US Minerals Management Service, sediment and faunal surveys, canyon study
Shelf Edge Exchange Processes (SEEP I)	1983–1984	U.S. Mid Atlantic Bight, south of Long Island and New Jersey	Carbon export and transformation within shelf and slope sediments
Shelf Edge Exchange Processes (SEEP II)	19??	U.S., Southern Mid Atlantic Bight	Carbon export and transformation within shelf and slope sediments
High Energy Benthic Boundary Layer Experiment (HEBBLE)	1980–1986	Nova Scotia Rise	Physical, geological, and faunal studies of environment subject to benthic storms

wide continental shelves developed off Newfoundland, southern South America and northwestern Europe, and the continental rises and abyssal aprons which are particularly expansive in the South Atlantic and the northern part of the North Atlantic (Emery and Uchupi, 1984: figs. 10–12 therein). Extensive carbonate platforms are developed in the western Atlantic, notably the Blake Plateau and Bermuda Rise. Unlike those in the Pacific, the continental margins on both sides of the Atlantic are largely passive. However, active margins with deep trenches (maximum depths 8414 m and 8264 m, respectively) are present in the western Atlantic (Puerto Rico Trench) and southern Atlantic (South Sandwich Trench). Smaller-scale (third-order) physiographic features include submarine canyons, which are particularly numerous on the continental margin off the northeastern United States, western Europe and parts of northwestern Africa (Emery and Uchupi, 1984: fig. 37 therein). Some extend into deep-sea channels, probably created by turbidity currents originating from the canyons. These features meander across the continental rises and abyssal plains. Canyons may have an important effect on the composition of associated biological communities.

Deep-water hydrography

The large-scale hydrography of the Atlantic Ocean is dominated by the overall northward movement of warm surface and intermediate water, derived ultimately from the Pacific and Indian Oceans, through the South Atlantic and into the North Atlantic, where it becomes more saline through evaporation (Broecker, 1991; Schmitz, 1995). On reaching the Greenland–Norwegian Sea, this water is subject to intense winter cooling and sinks by vertical convection. The resulting Norwegian Sea deep water spills over the Faroe Bank Channel and the Faroe–Iceland Ridge and entrains resident Atlantic water to form Northeast Atlantic Deep Water (NEADW). This water mass finds its way into the Northwest Atlantic basin where it mixes with bottom water flowing through the Denmark Strait and low–salinity water from the Labrador Sea to form a composite water mass termed North Atlantic Deep Water (NADW). North Atlantic Deep Water flows southwards into the South Atlantic and eventually back into the Indian and Pacific Oceans via the Circumpolar Current (Worthington, 1976; Gage and Tyler, 1991). This 'thermohaline conveyer belt' (Broecker, 1991; Rahmsdorf, 1997) leads to a net transfer of heat from the south to the north ('North Atlantic heat piracy': Berger and Wefer, 1996).

Other water masses are also present in the North Atlantic. The deep (>4500 m) basins off Northwest Africa are occupied by Antarctic Bottom Water (AABW), which enters the North Atlantic via the Vema Gap. At depths greater than 2000 m, the dominant Northeast Atlantic water mass is Mediterranean Water, which flows through the Straits of Gibraltar, around the Northwest European continental margin, and through

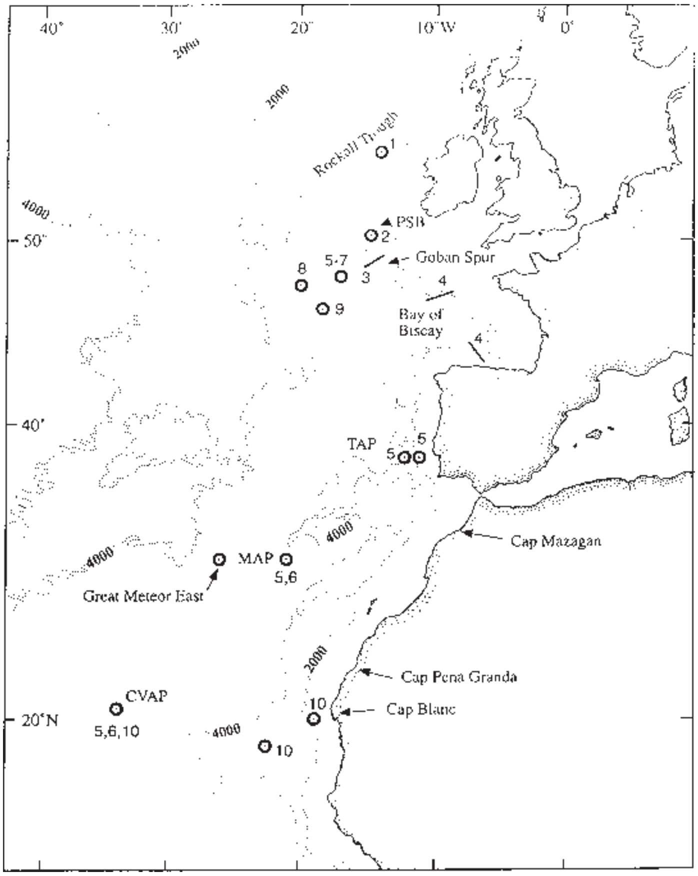

Fig. 5.1. Locations of major sampling programs within the deep Atlantic. CVAP, Cape Verde Abyssal Plain; MAP, Madeira Abyssal Plain; PSB, Porcupine Seabight; TAP, Tagus Abyssal Plain. The numbers identify national and international research projects listed in Table 5.1. (1, Rockall Trough time series; 2, IOSDL Porcupine Seabight Programme; 3, OMEX; 4, BIOGAS; 5, EU MAST I; 6, EU MAST II; 7, EU MAST III; 8, BIOTRANS and its successors; 9, DORA; 10, EUMELI).

the Rockall Trough, becoming progressively diluted as it proceeds northwards. Mediterranean Water is characterized by high density and salinity and by its variable physical properties (Weston, 1985).

The deep bottom water in the South Atlantic lies below the “conveyer belt” and is derived mainly from the Weddell Sea (Mantyla and Reid, 1983; Mackensen et al., 1995). The deep Weddell Sea Bottom Water is too cold and dense to escape from the Antarctic. The AABW which penetrates northwards into the South Atlantic is lighter, and consists of a mixture of three separate water masses, dominated (>50%) by Circumpolar Water (CPW). The AABW flows from the Weddell Sea into the Argentine and Brazil Basins via the Scotia Sea and Georgia Basin, and is characterized by low temperature and salinity and relatively high concentrations of oxygen and nutrients. From the Brazil Basin, it either escapes northwards into the Guiana Basin, or circles eastwards and southwards, via the Romanche Fracture Zone, into the southeastern Atlantic basins.

Bottom-water oxygen concentrations in the Atlantic are generally higher ($>5\,\mathrm{ml}\,\ell^{-1}$) than in the Pacific and Indian Oceans, particularly in water of North Atlantic origin (Mantyla and Reid, 1983; Reid, 1996, fig. 2 therein), and severe oxygen depletion ($<0.2\,\mathrm{ml}\,\ell^{-1}$) is not as extensive as in marginal regions of these other oceans (Diaz and Rosenberg, 1995, fig. 1 therein). Areas of intermediate depth with bottom-water oxygen depletion are associated with upwelling on the eastern side of the Atlantic. The two main areas in the Atlantic are off Northwest Africa, where upwelling is associated with the Canary Current, and off Southwest Africa where it is associated with the Benguela Current

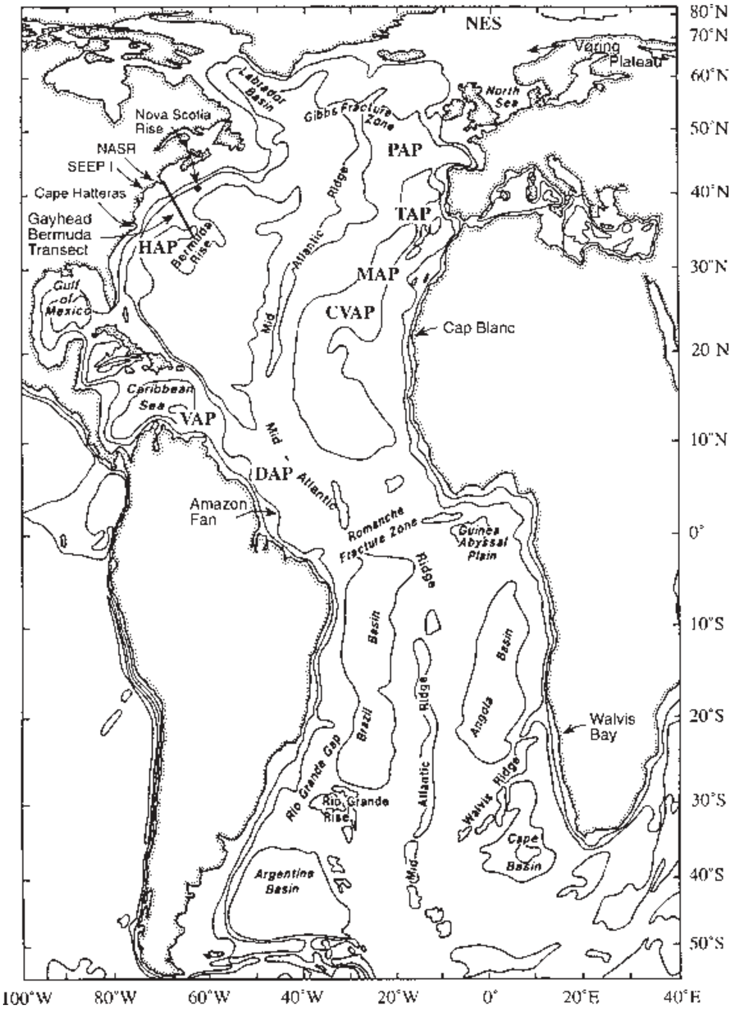

Fig. 5.2. Map of the Atlantic Ocean showing major features and locations discussed in the chapter. CVAP, Cape Verde Abyssal Plain; DAP, Demerara Abyssal Plain; HAP, Hatteras Abyssal Plain; MAP, Madeira Abyssal Plain; NGS, Norwegian–Greenland Sea; PAP, Porcupine Abyssal Plain; VAP, Venezuela Abyssal Plain. Adapted from Tomczak and Godfrey (1994).

(Shannon and Nelson, 1996; Summerhayes et al., 1995; Tomczak and Godfrey, 1994). In both areas, the large organic-matter flux to the seafloor has a profound impact on the structure and function of the underlying benthic communities.

A turbid nepheloid[3] layer often occurs in water several hundred meters above the seabed. In the Atlantic, this layer is best developed where the bottom currents are strongest – that is, beneath strong western boundary currents associated with subtropical gyres (the Gulf Stream and the Brazil Current). Similar features have been described in the Northeast Atlantic, for instance, on the continental slope west of the Porcupine Bank (Dickson and McCave, 1986), on the Feni Drift (van Weering and de Rijk, 1991) and in the foothills of the Mid-Atlantic Ridge next to the Porcupine Abyssal Plain (Nyffeler and Godet, 1986). Where kinetic energy is greatest, mesoscale eddies develop and sediment resuspension occurs. These episodic events, termed ‘abyssal storms’, can erode and redeposit several centimeters of sediment within a short period. Such events have been studied in detail on the Nova Scotia Rise in the Northwest Atlantic (Hollister and McCave, 1984; Brown et al., 1989).

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[3] A *nepheloid* layer is one containing a high concentration of suspended particles. It is often defined optically by turbidity measurements (with a nephelometer).

Sediments and mass movement

The deep Atlantic Ocean floor is covered by sediments deposited by near-shore and volcanic processes, by turbidity currents and related gravity-driven processes, by bottom currents and by pelagic sedimentation (Emery and Uchupi, 1984). Sokolova (1997) considered the extensive Russian literature on sedimentation processes in the North and South Atlantic. Sands and gravels of terrestrial or biogenic origin are generally restricted to the shelf and upper slope. Sediments become progressively finer with increasing depth and distance from land (Emery and Uchupi, 1984; Lampitt et al., 1986), although in some areas submarine canyons channel coarser sediments onto the continental slope and rise (Mart et al., 1979; Auffret, 1985; Weston, 1985). Over much (67%) of the Atlantic Ocean, however, the surface sediments are carbonate oozes ($CaCO_3$ content 30–50%) with a mean particle size of $<100\,\mu m$ (Apostolescu et al., 1978; Emery and Uchupi, 1984; Auffret, 1985; Lampitt et al., 1986; Udintsev, 1990), a sand-sized fraction consisting predominantly of planktonic foraminiferal tests, and an organic-carbon content generally <0.5% (Emery and Uchupi, 1984, fig. 345B therein). In the central South Atlantic, the calcareous oozes are dominated by pteropod shells. Siliceous (diatomaceous) oozes cover about 7% of the Atlantic floor, mainly in the region to the north of the Antarctic continent (Sverdrup et al., 1970), where their accumulation reflects levels of benthic and benthopelagic dissolution rather than an increased flux of opal (biogenic silicate) to the sea floor (Lampitt and Antia, 1997). The principal clay minerals in deep Atlantic sediments are kaolinite and chlorite, with greater proportions of kaolinite beneath the tropics. Off the Amazon and western Sahara Desert, the kaolinite/chlorite ratio is >10, indicating large kaolinite inputs from these sources (Pinet, 1998).

In general, Atlantic sediments have a much higher calcium carbonate content than Pacific sediments. Differences in ocean chemistry result in a calcium carbonate (calcite) compensation depth (CCD) which is much deeper (>5000 m) in the Atlantic, particularly in eastern basins which are less influenced by corrosive AABW, than in the Pacific (Sverdrup et al., 1970; Berger, 1975; Biscaye et al., 1976). As a result, areas where red clay (from which the carbonate has been removed by dissolution) accumulates are restricted to deep, relatively small basins, for example west and northwest of the Cape Verde Islands, under the Sargasso Sea in the central subtropical Atlantic and in the western South Atlantic (Emery and Uchupi, 1984, fig. 341C therein). The aragonite (essentially pteropod-derived) compensation depth is also relatively deep in the Atlantic, normally being located between 2000 and 3000 m (Berger, 1978) but rising to 400 m under the Northwest African upwelling area (Ganssen and Lutze, 1982).

Sedimentation rates for Central Atlantic foraminiferal oozes are generally in the range 1–5 cm ky^{-1} compared with >5 cm ky^{-1} for the largely terrigenous sediments which accumulate around the margins of the North Atlantic (Brown et al., 1989; Pinet, 1998). The sediment drifts (e.g., the Feni Drift) which are developed in parts of the northeastern Atlantic (Johnson and Schneider, 1969) are also characterized by sedimentation rates of >5 cm ky^{-1} (Thomson et al., 1993). These enhanced rates reflect the advection of fine material by bottom currents.

During the recent geological past, large areas around the Atlantic margin have been disturbed by gravity-driven mass movements, including slumps, slides, debris flows and turbidity currents, which have modified the seafloor to a significant extent (Stoker et al., 1998). These categories may be related; for example, some debris flows seem to be associated with turbidity currents (Masson et al., 1996). Mass movements are well documented off Northwest Europe, Northwest Africa, Southern Africa, the United States between New York and Cape Hatteras, and Brazil (Emery and Uchupi, 1984, fig. 43 therein). Massive sediment transport has been intensively studied on the continental rise and abyssal plain off Northwest Africa, an important area for the development of modern ideas about continental-margin sedimentation (Jacobi and Hayes, 1982; Simms et al., 1991; Masson et al., 1996). Here, debris flows, notably the unusually large Canary and Saharan flows (Embley, 1976; Masson et al., 1994, 1996), have occurred on the upper continental rise, transporting 600 km^3 of sediment from the shelf over a very short period, perhaps days or even hours – as much as the southern California basins have received from turbidity currents in a million years. Elsewhere in the Northeast Atlantic, the mid-Norwegian margin (the ‘Storegga’ area, 62ºN) is notable for a series of enormous slides, the most recent of which occurred about 7000 years ago (Bugge et al., 1988). These slides and associated debris flows and turbidity currents have transported 6000 km^3 of sediment from the shelf to depths of 3500 m over horizontal distances of 800 km.

Not surprisingly, turbidite deposition is a very important feature of Atlantic sedimentation and turbidite-formed abyssal plains are present off most of the continents, except the southern part of South America (Brown et al., 1989). The best-documented example is the Madeira Abyssal Plain, which is composed of a sequence of large turbidite deposits separated by thin pelagic layers. The turbidites were derived from several sources on the Northwest African margin, and their emplacement appears to be related to changes in climate and sea-level over the past 700 000 years (Weaver et al., 1992). Despite the prevalence of turbidite deposits, the actual currents have rarely been observed. The best-known turbidity flow occurred in 1929, when an earthquake on Grand Banks, Newfoundland, triggered a sediment slump which developed into a turbidity current extending 800 km from its source across the abyssal plain (Heezen and Ewing, 1952). Thunell et al. (1999) observed a striking increase in near-bottom concentrations of suspended sediment and mass flux through the water column in the Venezuela Basin following a 1997 earthquake. These mass-movement events must have had a devastating impact on the benthic fauna at the time of their emplacement, and may have a continuing effect through their influence on the granulometry (Huggett, 1987) and organic-matter content (Thunell et al., 1999) of the sediment.

While most of the material on the Atlantic seabed is pelagic or terrigenous in origin, authigenic[4] deposits occur in certain areas. Manganese nodules (composed of a mixture of iron and manganese oxides) were first recovered from the Atlantic near the Canary Islands during the *Challenger* Expedition. They are most extensively developed in the Argentine, Brazil and Cape Basins in the South Atlantic and in the Sargasso Sea in the North Atlantic. These Atlantic nodules have a somewhat lower manganese content (16%) and higher iron content (21%) than those in the Pacific and Indian Oceans (Brown et al., 1989). Phosphorites (authigenic calcium phosphate) occur on the shelf off south-west Africa (Price and Calvert, 1978), and unconsolidated phosphatic deposits are found in various areas around the Atlantic margin, including the shelf and upper slope off North Carolina and Northwest Africa (e.g., Riggs et al., 1985; Summerhayes et al., 1972).

ORGANIC-MATTER FLUX AND BENTHOPELAGIC COUPLING

General patterns of primary production

Apart from spatially limited areas of hydrothermal vents and seeps (see Chapter 4), almost all food available to the deep-sea benthos is derived from primary production in the euphotic zone. The ‘Dahlem map’ (Berger, 1989, fig. 11) provides an overview of estimated primary production for the Atlantic Ocean based on previous maps and remote-sensed satellite data. For the North Atlantic, more precise data on new primary production (i.e., production depending on nutrients imported into the euphotic zone) can be derived from surface chlorophyll concentrations determined from satellite imagery (Campbell and Aarup, 1992). Campbell and Aarup identified three areas characterized by different patterns of seasonal production and increasing levels of overall production: (i) a subtropical zone in which production reaches a maximum in the winter and minimum in the late summer (new production = 18 g C m^{-2} y^{-1}), (ii) a mid-latitude zone characterized by a spring bloom followed by oligotrophic conditions throughout the summer (new production = 24 g C m^{-2} y^{-1}), and (iii) a subpolar zone with minimum production in the winter and maximum in the late summer (new production = 43 g C m^{-2} y^{-1}). These three zones represent 20% of the area of the Atlantic and 43% of the North Atlantic, and exclude the entire tropical region where primary production is strongly influenced by upwelling and river inputs.

Longhurst (1995, 1998) and Longhurst et al. (1995) have presented a comprehensive scheme to classify seasonal cycles of primary production and consumption in the World Ocean. Sathyendranath et al. (1995) focused in detail on the Atlantic Ocean. Longhurst and his colleagues recognized four primary ecological domains (three oceanic and one coastal) which have characteristic seasonal cycles of water-column stability, nutrient supply and solar illumination. These are divided into 57 biogeochemical provinces defined on the basis of local features such as currents, fronts and topography. The important Atlantic provinces include, from north to south: North Atlantic Drift (NADR), Subtropical Gyre [STGW (West) and STGW (East)], North Atlantic Tropical Gyre (NATR), Western Tropical Atlantic (WTRA), Eastern Tropical Atlantic (ETRA), and South Atlantic Tropical Gyre (SATG) (Sathyendranath

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[4] *Authigenic*: generated locally (*in situ*), usually by a geochemical reaction (e.g., precipitation of Mn or Fe oxides to form nodules).

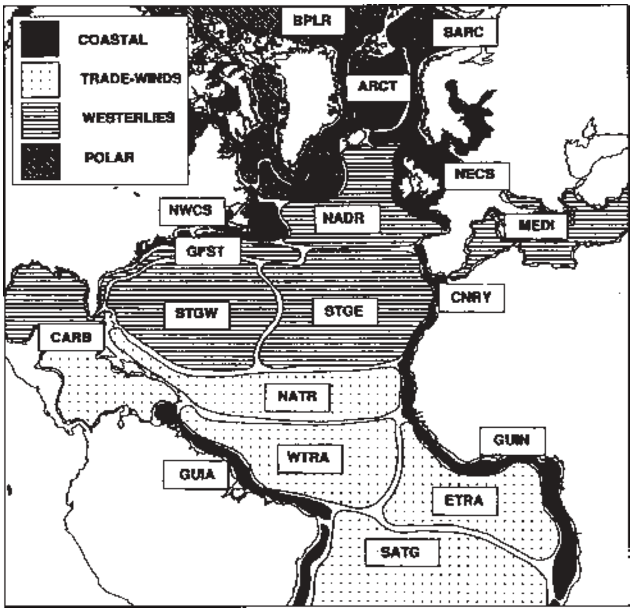

Fig. 5.3. Approximate areas occupied by primary ecological domains and secondary provinces in the Atlantic Ocean. The provinces are as follows. *Coastal Domains*: NW Atlantic (NWCS), NE Atlantic (NECS), E. Atlantic (CNRY), Guinea (GUIN), Guiana (GUIA); *Trade-Wind Domain*: North Atlantic Tropical Gyre (NATR), Western Tropical Atlantic (WTRA), Eastern Tropical Atlantic (ETRA), South Atlantic Tropical Gyre (SATG), Caribbean and Gulf (CARB); *West-Wind Domain*: Gulf Stream (GFST), North Atlantic Drift (NADR), Subtropical Gyre (East and West) (STGE & STGW), Mediterranean (MEDI); *Polar Domain*: Boreal Polar (BPLR), Arctic (ARCT), Subarctic (SARC). From Sathyendranath et al. (1995).

et al., 1995) (Fig. 5.3). The Atlantic pelagic provinces are important because they appear to influence the nature of food flux to the ocean floor, and in particular the variability of the flux over an annual cycle (Lampitt and Antia, 1997). Some correspond, in broad terms, to areas where the food supply to the benthos is seasonally pulsed, others to areas where the benthic food supply is more continuous. The temperate North Atlantic area is unusual among the pelagic provinces of the world in being subject to a distinct spring bloom which is not adequately grazed by zooplankton. This leads to the accumulation of a substantial phytoplankton biomass, and its subsequent aggregation, export from the mixed layer and sedimentation to the ocean floor (Longhurst and Harrison, 1988; Longhurst et al., 1995; Lampitt and Antia, 1997), a process of considerable significance for the underlying benthic communities, as discussed below.

Seasonally pulsed fluxes

The North Atlantic has been an important area for the development of ideas about the delivery of food to the ocean floor (Gooday and Turley, 1990; Rice and Lambshead, 1994). The long-held notion of a uniform (non-seasonal) rain of fine particles was swept aside in the late 1970s and early 1980s by two discoveries. First, it was found that the flux of settling particles may have a distinct seasonal component. Second, in areas of the North Atlantic which experience a strong spring bloom (the Atlantic Westerly Winds biome of Longhurst, 1998), this seasonal flux is dominated by sinking aggregates of phytoplankton detritus (phytodetritus). These escape recycling in the mixed layer of the ocean and settle to the abyssal ocean floor over a period of several weeks (Turley et al., 1995; Lampitt and Antia, 1997). Like many advances in oceanography, these discoveries depended on technological developments, notably of deep-moored sediment traps, long-term photography of the seafloor, and coring devices capable of collecting virtually undisturbed samples. They also reflect the fact that the North Atlantic experiences the strongest and most extensive spring bloom of any oceanic area (Longhurst, 1998).

Some of the earliest sediment-trap studies revealing flux seasonality were made in the North Atlantic. Deuser et al. (1981) and Deuser (1986) studied samples collected between 1978 and 1984 by a trap moored at 3200 m water depth (1000 m above the seafloor) in the Sargasso Sea. The flux of particles of different sizes and compositions fluctuated seasonally and there was also considerable interannual variation in the magnitude and timing of the flux. More recent studies have been carried out in the Northeast Atlantic, a more productive region than the Sargasso Sea, as part of the Biochemical Ocean Flux Study (BOFS). Traps were deployed by Honjo and Manganini (1993) approximately 4000 m, 3200 m and 700 m above the bottom at 48ºN, 21ºW (water depth 5261 m) and 34ºN, 21ºW (water depth 5083 m), and by Newton et al. (1994) 1455 m and 90 m above the bottom at 47ºN, 20ºW (4555 m water depth). In all cases the particulate flux through the water column was distinctly seasonal.

The mass seasonal deposition of aggregated phytodetritus to the ocean floor was first revealed in studies by the Institute of Oceanographic Sciences Deacon Laboratory (IOSDL; now part of the Southampton Oceanography Centre), conducted during the 1980s in the Porcupine Seabight, an embayment of the continental margin southwest of Ireland (50ºN, 13ºW) (Rice et al., 1991). Phytodetritus was photographed on the seabed down to 4000 m during phototransects using the IOSDL epibenthic sledge and collected using the Barnett-Watson multiple corer (Billett et al., 1983; Rice et al., 1986). Subsequently, its arrival on the seafloor during the late spring and early summer, and its subsequent dispersal and disappearance from the seafloor by late summer, were documented by means of the BATHYSNAP time-lapse camera system (Lampitt and Burnham, 1983; Lampitt, 1985). For example, the BATHYSNAP record for 1984 shows a distinct peak in late May (Lampitt et al., 1995), although the timing of the peak and its intensity often varies between years (Newton et al., 1994). Phytodetritus has been observed at a variety of other continental margin sites in the Northeast Atlantic including the Bay of Biscay (Sibuet, 1985), the Norwegian continental margin (Graf, 1989), and at 20ºN off the Northwest African margin. Its deposition is also well documented in more central oceanic regions of the NE Atlantic, in particular the BIOTRANS[5] area, which is centered around 19º40′W, 47º20′N in the foothills of the Mid-Atlantic Ridge (Thiel et al., 1988/89; Pfannkuche, 1993), and on the adjacent Porcupine Abyssal Plain (Rice et al., 1994). On the western side of the North Atlantic, Hecker (1990b) described the occurrence of phytodetritus between 450 m and 2400 m on the continental slope south of New England. Deposits were heaviest between 1000 m and 1500 m, and were observed to move downslope over a five-day period. Phytodetritus was also observed in the Lydonia canyon (2000 m) during April 1996. The delivery of phytodetritus to the seafloor appears to occur in areas of the North Atlantic where the winter thermocline is relatively deep (>500 m on the Porcupine Abyssal Plain), leading to a strong spring bloom and an accumulation of phytoplankton biomass (Rice et al., 1994). This corresponds broadly to the North Atlantic Drift province of Longhurst (1995) and Sathyendranath et al. (1995), and the mid-latitude zone of Campbell and Aarup (1992). There is no evidence for inputs of phytodetritus in more oligotrophic regions such as the Sargasso Sea. Phytodetritus was not observed in core samples or in long-term BATHYSNAP sequences obtained at the Madeira Abyssal Plain (4940 m; 31ºN, 21ºW) and Cape Verde Abyssal Plain (4535 m; 21ºN, 31ºW) sites of the Southampton Oceanography Centre (Rice et al., 1994). Bottom photographs taken by Christiansen and Thiel (1992) at 31º and 34ºN on the Madeira Plain, however, suggest that some deposition may occur in this region.

North Atlantic phytodetritus has the following general characteristics. It is composed of the remains of various organisms derived from the euphotic zone (including Cyanobacteria, small chlorophyte algae, diatoms, coccolithophorids, silicoflagellates, dinoflagellates, tintinnids, radiolarians and Foraminifera), crustacean moults, small fecal pellets (‘minipellets’), bound together in a gelatinous matrix to form aggregates up to about 1 cm in diameter (Billett et al., 1983; Thiel et al., 1988/89). Phytodetritus contains rich populations of bacteria, some of them barophilic[6], as well as active cyanobacteria which originate from surface waters (Lochte and Turley, 1988) and may make good markers for freshly deposited phytodetritus (Pfannkuche and Lochte, 1993). The aggregates form an often extremely patchy layer (from a few mm to several cm in thickness) on the seafloor, and are typically concentrated in depressions or behind mounds and other obstacles (Thiel et al., 1988/89; Rice et al., 1994) (Fig. 5.4). They

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[5] *BIOTRANS*: BIOlogical vertical TRANSport and energetics in the benthic boundary layer of the deep sea. The BIOTRANS study area is bounded by the following coordinates: 47º00′–47º30′N, 19º–20ºW.

[6] Requiring high pressure for growth.

Fig. 5.4. Photograph of phytodetritus in depressions from the Porcupine Abyssal Plain (48.50ºN, 16.30ºW, 4850 m).

are light and easily resuspended and redistributed by currents (Lampitt, 1985; Hecker, 1990b). As a result of degradation during its passage through the water column, the organic-carbon content of phytodetritus is surprisingly low: 0.56–1.28% dry weight in the Porcupine Seabight (1000–4500 m) (Rice et al., 1986) and 0.9–7.8% dry weight in the BIOTRANS area (Thiel et al., 1988/89).

Phytodetrital deposits have also been observed later in the summer. Duineveld et al. (1997) and de Wilde et al. (1998) describe a 'mucus layer' which was present on the surfaces of cores recovered from the lower Celtic margin slope (>3500 m) during late August, 1995. This material was not present at upper-slope sites on the Goban Spur. Unlike 'normal' spring phytodetritus, it could not be resuspended easily. The mucus layer contained large numbers of coccoliths and high concentrations of fresh chloroplastic and other pigments (e.g., peridinin), suggesting recent derivation from an offshore bloom dominated by coccolithophorids but also including dinoflagellates and green algae. Additional and less predictable pulses of particulate organic matter may also be important for Atlantic benthic communities. These include the rapid sedimentation of fecal pellets originating from copepods (Graf, 1989) or salp swarms (Pfannkuche and Lochte, 1993), and the deposition of salp bodies and *Sargassum* (Grassle and Morse-Porteous, 1987).

Benthic responses

Pulses of phytodetritus and other forms of organic matter typically evoke a rapid response by the benthic community and serve to couple processes on the deep-sea floor and in the upper water column (Gooday and Turley, 1990). Pfannkuche (1993) estimated that 1.1% of spring bloom primary production and 9.6% of organic matter exported out of the surface 150 m at the BIOTRANS site was respired during the summer, and that 60–80% of the increased benthic activity (as estimated from concentrations of adenosine triphosphate (ATP), electron-transport activity and sediment community oxygen consumption [SCOC]) during this period was attributable to micro-organisms inhabiting the phytodetrital layer. Pfannkuche et al. (1999) investigated in detail the benthic response, indicated by total adenylates, total phospholipids (reflecting biomass of small organisms including bacteria and meiobenthos), and hydrolytic enzyme activity (reflecting metabolic activity) at this site during the period March to August 1992. They reported a precise and rapid coupling between sedimentation events and metabolic activity in early spring and summer, but very little corresponding biomass increase. Results from a shallower (1430 m) site on the Vøring Plateau (Norwegian continental margin) also imply a very rapid benthic metabolic response to food fluxes. Here, Graf (1989) detected an increase in chlorophyll a, and a corresponding increase in metabolic activity (ATP concentration), within days of the arrival of a pulse of copepod fecal pellets from the euphotic zone. Moreover, the response occurred at depth within the core, not just at the surface; chlorophyll was present down to 9 cm, and ATP peaks were apparent at 6 cm and 8 cm depth in two cores. A deposit of mucus-like phytodetritus sampled in August 1995 on the Celtic margin yielded high RNA and DNA concentrations, indicative of enhanced microbial activity (de Wilde et al., 1998).

A seasonal community response is not always apparent, however. Lampitt et al. (1995) could detect no seasonal variation in SCOC (measured using the hanging-core technique) at a site 2000-m deep in the Porcupine Seabight. Moreover, the oxygen demand of cores without a layer of phytodetritus was not obviously different from that of cores with phytodetritus. Likewise, there was no SCOC response to the spring deposition of phytodetritus on the nearby Goban Spur (Celtic margin) (Duineveld et al., 1997). In this case, the deposit had probably been laterally advected, and was therefore more degraded than material derived from the overlying water column. Similarly, Sayles et al. (1994) reported that sediment oxygen consumption at an oligotrophic site near Bermuda (4400 m water depth) was nearly constant between March 1989 and

October 1992, despite strong seasonal variations in the organic-matter flux to the seafloor.

There is evidence for changes in the abundance and biomass of particular size classes and taxa following organic-matter inputs. In a detailed study of the BIOTRANS area (4550 m depth) of the Northeast Atlantic, Pfannkuche (1992, 1993) and Lochte (1992) found: (a) a doubling of bacterial biomass between March and July, and (b) a switch from dominance of the meiofaunal fraction by metazoans in March and May to dominance by Foraminifera in July and September. Small barophilic flagellates also thrive within organic aggregates (Lochte and Turley, 1988). Thus, the response to phytodetritus at the BIOTRANS site is accounted for mainly by Bacteria and protozoans (see also Pfannkuche and Soltwedel, 1998). Among benthic Foraminifera, the immediate response seems to be largely confined to certain opportunistic species which live mainly in the phytodetrital layer (Gooday, 1988, 1993, 1996b) and undergo rapid population increases during the summer (Gooday and Lambshead, 1989; Gooday and Turley, 1990). The opportunists include *Alabaminella weddellensis* and *Epistominella exigua*, both calcareous forms, and the allogromiid *Tinogullmia riemanni.*

A link between food pulses and metazoan population dynamics has proved more difficult to establish. Unlike Foraminifera and Bacteria, the metazoan meiofauna and macrofauna exhibited no significant increase in either numbers or biomass following phytodetrital deposition at the abyssal BIOTRANS site (Pfannkuche, 1992, 1993) and in the bathyal Porcupine Seabight (Gooday et al., 1996). There is some evidence from the Hebridean margin, however, that meiofaunal densities increase during the summer (Mitchell et al., 1996). Similar results have been obtained in the bathyal Mediterranean (de Bovée et al., 1990). However, direct evidence that phytodetritus may influence growth rates is provided by BATHYSNAP photographs showing a specimen of the barnacle *Poecilasma kaempferi* growing more quickly during and following the deposition of phytodetritus on the Goban Spur (1520 m depth) than prior to the flux event (Lampitt, 1990). Some echinoderms certainly feed on phytodetritus. Pigment analysis of the gut contents of certain holothurian species suggests that they consume phytodetritus almost exclusively when it is present on the seafloor (Billett et al., 1988; Lauerman et al., 1997). There is good evidence from gut contents and sea-floor photographs that the echinoid *Echinus affinis* feeds on fresh phytodetrital deposits (Campos-Creasey et al., 1994), and that this triggers the seasonal growth and reproduction reported in this species (Tyler and Gage, 1984; Gage and Tyler, 1985). Seasonal growth and reproduction reported in a range of other North Atlantic deep-sea invertebrates (sponges, actiniarians, brachiopods, protobranch bivalves, echinoids, asteroids, ophiuroids, spider crabs and hermit crabs) may also be linked to seasonality in food supply, although the evidence is largely circumstantial (Tyler, 1986, 1988, 1995; Gooday and Turley, 1990; Gage and Tyler, 1991; Van-Praet, 1990; Witte, 1996).

REGIONAL DESCRIPTIONS

The Northwest Atlantic continental margin

The Atlantic continental slope and rise (ASCAR region; 28–42ºN, 200–4000 m water depth) off the eastern United States has been studied extensively (Milliman and Wright, 1987). Several large programs (Table 5.1) have focused on aspects of carbon cycling and benthic biological patterns on the slope, though much additional work has taken place on the continental shelf. A dominant physical feature is the warm Gulf Stream, which flows north from the Florida Strait along the slope and then diverges eastwards off Cape Hatteras. The western Boundary undercurrent, associated with North Atlantic deep water, flows southwest along the entire rise below about 2000 m. Colder coastal and slope water, derived from various sources, occurs generally inshore of the Gulf Stream (Schmitz et al., 1987). The direct influence of the Gulf Stream on the bottom can be detected to a depth of over 600 m in some places. Both cold-core (cyclonic) and warm-core (anticyclonic) rings, associated with the Gulf Stream, introduce water with different properties into the major ASCAR water masses. However, ring effects are concentrated in the upper 1000 m (Schmitz et al., 1987).

General discussions of the biological communities of the ASCAR region can be found in Hessler and Sanders (1967), Hecker et al. (1983), Blake et al. (1985, 1987), Maciolek et al. (1987a,b), Wiebe et al. (1987), and articles within Diaz et al. (1994). Many of these reports are the result of extensive surveys made under the auspices of the United States Minerals Management Service, which is charged with evaluating natural resources (e.g., hydrocarbons) and the impact of exploiting these. These reports divide the ASCAR region into the North, Mid and South Atlantic Bights (NAB, MAB and SAB, respectively), covering the United States margin from Georgia to Canada.

Gay Head–Bermuda transect

Historically, perhaps the most important study of Atlantic deep-sea infaunal communities was carried out by Sanders, Hessler and coworkers (Sanders et al., 1965). They sampled sediments along a transect from the Massachusetts shelf (20 m) to Bermuda (1000 m), encompassing the intervening slope, rise and abyssal environments; this is now referred to as the Gay Head–Bermuda transect. Quantitative samples were taken with an anchor dredge and washed through a 0.42 mm mesh. They revealed much higher faunal densities and diversity than expected (Hessler and Sanders, 1967), and initiated a persistent fascination with the quantification and explanation of high diversity in the deep sea (Rex, 1983; Grassle, 1989; Rex et al., 1997). Macrofaunal densities decreased with both depth and distance from land (Sanders et al., 1965; Hessler and Sanders, 1967; Sanders and Hessler, 1969), and each region along the transect was found to support characteristic faunal densities (individuals m^{-2}): the outer continental shelf 6000–13 000; the upper slope 6000–23 000; the lower slope 1500–3000, the continental rise 500–1200; the abyss beneath the Gulf Stream 150–270; the abyss in the Sargasso Sea 30–130; the lower Bermuda Slope 120–300 and the upper Bermuda slope 500–750 (Sanders et al., 1965). Polychaetes formed 34–84%, crustaceans 3.5–50% and bivalves 1–24% of these faunal assemblages. The best-represented polychaete families were the Ampharetidae, Maldanidae, Paraonidae, Phyllodocidae, Spionidae and Syllidae, which together accounted for 88 of the 266 polychaete species present (Sanders et al., 1965). Bivalves were mainly Eulamellibranchiata and Protobranchiata (93% of total). No consistent relationship was observed between animal densities and the organic-carbon or nitrogen content of the sediments, and it was noted that some of the highest densities occurred on the upper slope where organic-carbon values were low (Sanders et al., 1965). Sanders et al. (1965) proposed that the absence of correlation was related to the refractory nature of sedimentary organic matter, an idea substantiated by later studies on the northwest margin (references in Diaz et al., 1994).

Epibenthic sled samples taken along the Gay Head–Bermuda transect yielded a spectrum of species different from that given by the anchor dredge, but substantiated the finding of high faunal diversity in individual samples (Hessler and Sanders, 1967; Sanders and Hessler, 1969). Along the transect, sharp faunal breaks were observed for polychaetes, bivalves and crustaceans at the shelf–slope boundary (100 to 300 m), a region taken as the upper limit of the deep-sea benthos in this part of the Atlantic. Despite an absence of abrupt boundaries at bathyal or abyssal depths, Sanders and Hessler (1969) considered depth to be a primary determinant of species composition. They pointed out that, while 48% of bivalve species were shared between a 1400-m station on the Gay Head–Bermuda transect and a 1700-m station off West Africa, an 800-m change in depth on the Northwest Atlantic margin (along the Gay Head–Bermuda transect) produced much greater differences in species composition. Sanders and Hessler (1969) also argued that depth change has a greater impact on densities than distance from land. For example, densities at their 4500 m and 5000 m stations were less than at 200 m by a factor of 50–390, despite surface productivity being half as great at the deeper stations.

Studies of the respiration of the benthic community, conducted along the Gay Head–Bermuda transect with grab respirometers (Smith, 1978), indicated decreasing oxygen consumption by the sediment community with increasing water depth and distance from shore (Smith and Hinga, 1983). Respiration varied by a factor of 25 from the shallowest station (1850 m) to the deepest (5200 m). Smith (1978) formulated a predictive equation for sediment-community oxygen consumption (SCOC) which explained 92.4% of the variation in measurements. Depth alone accounted for 83.1% of this, with sediment nitrogen content, C:N ratio, faunal biomass and water temperature also contributing.

Nova Scotia rise

The Nova Scotia rise is the best-studied high-energy habitat in the deep Atlantic Ocean. An area centered around 40º27′N, 62º20′W (4600 to 4800 m) experiences episodic, intense sediment-transport events. This was the site of the High Energy Benthic Boundary Layer Experiment (HEBBLE), which focused on the physical aspects, sediment transport and biological dynamics of this energetic benthic environment. Currents within 59 m of the seabed, measured over a 4.5 year period, exhibited increased speeds (15–23 cm sec^{-1}) during periods termed benthic storms. These occurred approximately every 21 days, and lasted on average for 7 days. Every 10 months there was a storm with average velocity $>23\,\mathrm{cm\,sec^{-1}}$ (Aller, 1989). The storms caused the following sequence of events: (a) erosion, in which surface sediment, surficial organic matter, bacteria, larvae and juveniles were swept away; (b) intermediate current velocity, during which there was deposition of fresh organic matter, removal of metabolites, and mechanical stimulation of microbes; and (c) decelerating currents, involving deposition of several centimeters of sediment, burial of organisms and infilling of burrows. Maximal foraminiferal and metazoan abundances were observed during this period (Aller, 1989).

At the HEBBLE site the sediments support unusually high densities of bacteria, polychaetes, bivalves, isopods and tanaids relative to other locations at comparable depths (Thistle et al., 1985, 1991). Thistle et al. (1991) suggested that this indicated a fairly high flux of food to the seafloor. Community structure is distinct, in that macrofaunal assemblages are dominated by 2 species of ampharetid polychaetes, which comprise over 60% of the individuals collected. A predominance in the macrofauna of juveniles, rather than adults (as is more typical of abyssal sites), suggests that the fauna is continually responding to disturbance (Thistle et al., 1985). Comparable ‘opportunistic’ characteristics were observed in deep-sea recolonization experiments carried out at a depth of around 2000 m by Grassle (1977) and Desbruyères et al. (1980). The macrofaunal taxa at the HEBBLE site are mainly deposit feeders which can take advantage of organic matter deposited on the sediment surface (Thistle et al., 1985). They appear to mix sediments actively (DeMaster et al., 1991).

Densities of nematodes and harpacticoid copepods at the HEBBLE site, and diversity of copepods, did not differ from those reported in other abyssal areas (Thistle et al., 1985, 1991). Thistle and Sherman (1985) suggested that some nematodes use long retractable tails to avoid resuspension, but in general the nematode fauna exhibited few of the adaptations normally found in nematodes from high-energy, coarse-grained environments.

Taxa residing in surficial sediment (isopods, nematodes and harpacticoid copepods) exhibited variation in abundance over time that was attributed to erosion by storms (Thistle, 1988; Thistle et al., 1991). Standing stocks of polychaetes, bivalves, and tanaids, many of which burrow, remained relatively constant during the study (Thistle et al., 1991). Thistle and Wilson (1987, 1996) observed that surface-dwelling isopods, presumably exposed to erosion, were much less common at the HEBBLE site than in other, more quiescent, deep-sea regions.

North-Atlantic (NAB) and Mid-Atlantic Bights (MAB)

Continental slope and rise: Hecker (1990a) examined variation in the megafauna with depth and geographic location on the continental margin south of New England, on the eastern and western edges of Georges Bank, and along the SEEP I transect (34 m to 2394 m) (Fig. 5.2). In this region, 80% of the continental slope consists of gully and ridge morphology (Scanlon, 1984). Hecker (1990a) described four megafaunal zones with fairly abrupt boundaries. The upper slope was dominated by solitary scleractinians and quill worms (*Hyalinoecia artifex*), and the lower slope by the brittlestar *Ophiomusium lymani*, cerianthid anemones, sea pens and the urchin *Echinus affinis*. These two regions exhibited highest densities. The upper mid-slope was occupied by lower numbers of red crabs and fishes, and the transition zone by cerianthids, sea pens and ophiuroids. Animal distributions were controlled by effects of local topography on currents, and accompanying effects on food availability. The mid-slope, where densities were lowest, is a broad depositional band; higher currents are present on the upper and lower slopes where megafaunal densities were greatest.

Comparable studies of megafaunal zonation in the Mid-Atlantic Bight were carried out by Hecker et al. (1983) on the continental margin (100 m to 2300 m) east of New Jersey. Five major zones were observed, with faunal breaks at 400 m, 750 m, 1450 m and 1600 m. The megafauna between 200 and 400 m comprised mainly crabs (*Cancer* spp., *Munida iris*), sea pens (*Stylatula elegans*), and anemones (*Cerianthus borealis*). Between 400 m and 750 m dominants were the red crab (*Geryon quinquedens*), the anemone *Bolocera tuediae*, quill worms (*Hyalinoecia artifex*), rattails (*Nezumia* spp.) and hake (*Urophycis chesteri*). Between 700 m and 1400 m the eel *Synaphobranchus* spp. became dominant. From 1400 m to 2300 m *Ophiomusium lymani* and *Echinus affinis,* cerianthid anemones and the sea pen *Distichoptilum gracile* were dominant. As in the North Atlantic Bight, megafaunal abundances were highest in the shallower (<600 m) and deeper (>1400 m) parts of the margin. Species richness was higher in areas with boulders, outcrops and cliffs than in primarily muddy areas (Hecker et al., 1983).

Surveys of the macrofauna on the North Atlantic and Mid-Atlantic Bight margins have been carried out by Wigley and Theroux (1981), Rowe et al. (1974, 1982), and Maciolek et al. (1987a,b). Wigley and Theroux (1981) reported on a study carried out in the 1960s of macrobenthic invertebrates (>1 mm) in the Mid-Atlantic Bight between Boston and Cape Hatteras at 563 locations, at depths from 4 m to 3080 m. Macrofaunal densities averaged 293 individuals m^{-2} at 400–999 m, 72 individuals m^{-2} from 1000–1999 m, and 46 individuals m^{-2} from 2000–3080 m. These low densities were probably a result of the large mesh size and sampling bias of the grab samplers used. Corresponding biomass values were 12, 7 and 8 g m^{-2}, respectively. Densities were generally higher off southern New England than in the New York or Chesapeake Bight areas. A number of groups, including pogonophorans, thyasirid bivalves, hyalinoecid polychaetes, selected ophiuroids, and scaphopods, were most abundant at slope and rise depths.

Rowe et al. (1974) reported average densities and biomass on the continental slope south of New England (550–2080 m) to be 3325 individuals m^{-2} and 5.93 g m^{-2}, respectively. Values for the continental rise (2425–3923 m) were 789 individuals m^{-2} and 0.69 g m^{-2}; values for the abyssal plain (4901–4950 m) were 175 individuals m^{-2} and 0.22 g m^{-2}. These slope values were 3 times the densities and 10 times the biomass observed at comparable depths by Rowe et al. (1974) in the Gulf of Mexico.

Rowe et al. (1982) observed that, on the margin off New England, densities and biomass of macrofauna (>420 μm) showed significant declines with increasing water depth ($r^2 = 0.59$, $P < 0.01$, and $r^2 = 0.56$, $P < 0.01$, respectively). Considerable overlap was observed between upper-slope assemblages and those characteristic of shallower waters in the Gulf of Maine. The sharpest faunal boundaries were observed at depths of 1400–1700 m. Dominant taxa were oligochaetes (30%) from 203 to 570 m; polychaetes (*Cossura longocirrata* and *Heteromastis filiformis* – 27%) from 1141 to 1437 m; bivalves and polychaetes (*Deminucula cancellata* and *Poecilochaetus fulgoris* – 19%) from 1707 to 1815 m (DOS I), polychaetes, oligochaetes and aplacophorans (*Glycera capitata*, oligochaete spp. and *Prochaetoderma* sp. – 17%) from 2341 to 2673 m (DWD 106), sipunculans and spionid and oweniid polychaetes (20%) from 2749 to 3264 m (Hudson Rise) and scaphopods and the polychaete *Ophelina abranchiata* (15%) at 3659 m (DOS II). Diversity was greatest at mid-slope depths.

Detailed surveys of the macrofauna (>0.3 mm) in the North, Mid- and South Atlantic Bights were carried out by the United States Minerals Management Service as part of an oil exploration effort (Maciolek et al., 1987a,b; Blake et al., 1985). The North Atlantic Bight study examined stations between 255 and 2180 m from the United States/Canada border to the region south of Georges Bank off New England (Maciolek et al., 1987a). The Mid-Atlantic Bight study examined stations from 1500 to 2505 m off New Jersey, near Dump Site 106, and in a test drilling area (Maciolek et al., 1987b). The South Atlantic Bight results are discussed below. Faunas of the North Atlantic Bight and Mid-Atlantic Bight were remarkably similar. Polychaetes comprised 44–47% of the total macrofauna, arthropods 22% and molluscs 14%. Sipunculans and pogonophorans were common as well, particularly at the 1220–1350 m station in the North Atlantic Bight and the 2100 m station in the Mid-Atlantic Bight. Cirratulid, dorvilleid, paraonid and spionid polychaetes were among the most abundant taxa. Diversities were maximal at 1220–1350 m in the North Atlantic Bight and 1500–1600 m in the Mid-Atlantic Bight.

Densities in the North Atlantic Bight ranged from a high of 18 778 individuals m^{-2} at 255 m to a low of 3078 individuals m^{-2} at 2100 m. Dominant taxa included the bivalve *Thyasira ferruginea* at 255 m (overall the most abundant in the North Atlantic Bight study), the polychaetes *Prionospio aluta* and *Tharyx* spp. at 550 m, the sipunculans *Aspidosiphon zinni* and *Golfingia (Nephasoma) daphanes* at 1220–1350 m, and the polychaete *Aurospio dibranchiata* at 2100 m (Maciolek et al., 1987a). In the Mid-Atlantic Bight (1500–2505 m) dominant taxa were polychaetes (*Aurospio dibranchiata* [6.6%], *Pholoe anoculata* [4.4%], *Tharyx* sp. 1 [4.1%], and *Prionospio* sp. [3%]) and 2 prochaetadermatid aplacophorans [together 7%] (Maciolek et al., 1987b).

Canyons: The continental margin of the Northwest Atlantic is heavily carved by submarine canyons and gullies. Submarine canyons offer a highly heterogeneous substratum relative to similar depths on slopes. Several investigations have focused on the benthic faunas of these canyons and the adjacent slope areas, often with differing results. Rowe (1971b) reported that Hatteras Canyon, studied with camera and trawl samples, exhibited reduced abundances of some megafaunal species relative to slope habitats, but that other taxa were unique to the canyon. Haedrich et al. (1975, 1980) and Valentine et al. (1980), on the other hand, found that megafaunal assemblages in Alvin, Hudson and Oceanographer Canyons were similar to those on nearby slopes. Houston and Haedrich (1984) studied the macrofauna (>0.52 mm) within and outside Carson submarine canyon (76–1129 m) on the Grand Banks. They found no difference in abundance, biomass or average body size (weight) inside or outside the canyon, or with water depth. They noted unexpectedly low abundance and biomass values, which they attributed to low organic-carbon content of the sediment (0.3%). Rowe et al. (1982), in studies of the Hudson Canyon off New York, found that macrofaunal composition did not differ inside the canyon from the adjacent slope. Macrofaunal densities were higher within the canyon head only at upper continental slope depths, most likely a result of trapping of labile organic matter. Canyon densities in deeper regions were comparable to those on the outer slope.

Maciolek et al. (1987a) examined macrofauna within and outside Lydonia Canyon (40º20′N, 67º40′W) at 550 and 2100 m during three cruises. At the shallower station, macrofauna were more abundant within the canyon, owing in part to high densities of the polychaetes *Tharyx annulosus* (32% of total fauna) and *Prionospio aluta* (8.3% of total fauna). Over half of the dominant species exhibited significant density differences at the canyon stations. No macrofaunal differences between the canyon and slope were observed at the deeper station, however.

A series of seven cruises examined the megafauna of the canyons and slopes of the North Atlantic and Mid-Atlantic Bights, using bathymetric profiling, a towed camera sled, and submersible observations (Hecker et al., 1983). Lydonia Canyon in the North Atlantic Bight was studied in detail. At most depths (300–2100 m), densities of megafauna in the canyon were greater than on the slope. Between 300 and 400 m this difference resulted from dense assemblages of the sea pen *Pennatula aculeata* and the brittle star *Ophiura* sp. in the sediment-covered axis, to the coral *Eunephthya florida* on cliffs and to the quill worm *Hyalinoecia artifex* on the lower flanks. Between 500 and 1500 m the canyon contained 38–614 individuals m^{-2}, consisting largely of localized, dense populations of corals, sponges and shrimps. The sponge *Asbestopluma* sp. was especially abundant between 800 and 950 m. Below 1500 m the brittle star *Ophiomusium lymani* became very abundant in Lydonia Canyon and on the slope. In the canyon, maximum *O. lymani* densities occurred between 1750 and 1800 m, and the species remained dominant to at least 2350 m. Other common taxa within Lydonia Canyon and on the nearby slope were the decapod crustaceans *Cancer borealis*, *C. irroratus* and *Geryon quinquedens,* and a several species of hake (*Urophycis* spp.) and grenadier (*Coryphaenoides carpinus*, *C. rupestris* and *Nezumia aequalis/bairdii*). At least two species, the longfin hake (*U. chesteri*) and the red crab (*G. quinquedens*), occurred at higher abundances on the slope outside the canyon. Filter feeders and scavengers dominated the canyon fauna at depths less than 1000 m, while deposit feeders (mainly *Ophiomusium lymani*) were dominant below 1500 m. In general, Hecker et al. (1983) found faunal patterns to be more complex and megafaunal assemblages less cohesive within Lydonia Canyon than on the slope.

Baltimore Canyon (38º5′N, 73º40′W) in the Mid-Atlantic Bight was compared to two slope areas located on the continental margin east of New Jersey (Hecker et al., 1983). Consistent elevation of megafaunal densities was not observed within Baltimore Canyon relative to the comparison slope sites, as was the case in Lydonia Canyon. However, densities from Hedrickson Canyon were consistently higher than at comparable depths on the slope (Hecker et al., 1983). At depths greater than 500 m, dense aggregations of anemones (*Halcurias pilatus* and *Hormathia nodosa*) occurred on the canyon walls. Several dominants on the slope, including a burrowing brittle star (*Amphilimna* spp.), a sea pen (*Stylatula elegans*) and a scleractinian (*Desmosmilia lymani*), were less abundant in the canyon. In the Mid-Atlantic Bight, as in the North Atlantic Bight, crabs and hake were dominant within canyons and on the surrounding slope, but they did not differentiate between these habitats. The rattail *Coryphaenoides rupestris* was the dominant grenadier within Baltimore and Hendrickson Canyons, and appears to be a canyon ‘indicator’ species. The holothurian *Peniagone* sp. and the sea pen *Distichoptilum gracile* were especially abundant within Hendrickson Canyon. In Baltimore Canyon, scavengers and carnivores dominated the megafauna above a depth of 1400 m, filter feeders dominated between 1400 and 1600 m and deposit feeders dominated below 1600 m (Hecker et al., 1983).

The extent to which canyon faunas appear distinct from those on the surrounding slope is a function

Table 5.2
Sedimentary and biological characteristics of 3 sites located at 850 m on the North Carolina continental slope[1] (mean ± 1 SD)

	SITE I (32º52′N, 76º27′W)	SITE II (34º15′N, 75º44′W)	SITE III (35º24′N, 74º48′W)
% Organic carbon	1.2	2.1	1.7
Sediment accumulation rate (cm ky^{-1})	6.7	160	<1100
Organic C deposition (g m^{-2} y^{-1})	10	37	<170
Organic C accumulation (g m^{-2} y–^{1})	0.65	20	<150
D_b (Th-234) (cm^2 y^{-1})	6.0±6.2	4.6±5.2	109±11
Σ CO$_2$ flux (μmol m^{-2} d^{-1})	2.2±0.2	3.8±0.4	4.7±0.4
Methane	Absent	Absent	Present
Macrofaunal abundance (ind m^{-2}; 300 μm)	9400±3100	21 400±5000	55 400±15 000
% of most abundant macrofaunal species	15.8	14.3	26.3
Macrofaunal biomass (g wet wt m^{-2})	7.19±5.51	8.16±3.99	54.52±14.44
Polychaete diversity (H') (base e)	4.66±0.81	4.57±0.75	2.76±0.54
Megafaunal density (ind m^{-2}) 700–1599 m	0.49±0.08	2.65±0.95	0.88±0.15
Dominant surface features	Sand ripples, arborescent foraminifera	Pits and mounds	*Bathysiphon filiformis* tubes

[1] Data are from Schaff et al. (1992), DeMaster et al. (1994), Blair et al. (1994), and Hecker (1994).

of sampling technique and canyon attributes (Hecker et al., 1983). Canyons with low topographic relief and little exposed hard substratum are most likely to resemble open-slope environments. Similarly, trawl sampling is less effective in regions with high topographic relief, but obtains more sediment-dwelling fauna, again causing samples to resemble muddy-slope faunas.

South Atlantic Bight (SAB)

The North American continental shelf and slope between West Palm Beach, Florida, and Cape Hatteras, North Carolina, constitute the South Atlantic Bight (Atkinson and Menzel, 1985). Early studies of the deep benthic faunas of this area were carried out by Frankenberg (1971), Rowe and Menzies (1969), Rowe (1971a,b) and Grassle et al. (1975). The continental-slope environment off North and South Carolina has been particularly well studied, partly because of interest in the potential effects of mining the oil and gas reserves in the region (Diaz et al., 1994). The Carolina slope and rise exhibit remarkable variability in sedimentary and biological features because of the interaction of topography, ocean currents and major estuarine inputs. The Charleston Bump deflects the Gulf Stream producing a gyre, behind which are some of the most species-rich benthic assemblages known in the marine environment (Blake and Grassle, 1994; Blake and Hilbig, 1994). The slope of the South Atlantic Bight is deeply cut by canyons and gullies. Some of these, such as the Wilmington Canyon, are the result of fluvial drainage across the shelf and slope during times of lower sea level. But many of the steep canyons off Cape Hatteras are thought to result from mass wasting and slumping, and to be maintained presently by headwall and sidewall submarine erosion, with significant sediment drape deposited on crests during the Quaternary (Mellor and Paull, 1994).

Studies of three intensely investigated North Carolina mid-slope sites (each at a depth of 850 m) spaced 150 to 180 km apart, demonstrate the extent of geochemical and biological heterogeneity that can occur in margin settings (Table 5.2). Organic-carbon content of the sediments, consisting of fairly refractory material, varies little at the three sites, but measures of organic-matter flux into the seabed and rates of accumulation of organic carbon differ among stations by factors of from 4 to 200 (Blair et al., 1994; DeMaster et al., 1994). These differences are associated with strong gradients in rates of carbon remineralization (CO$_2$ flux), macrobenthic and megafaunal densities, species diversity patterns and bioturbation rates (Table 5.2). Cross-margin transects into greater depths off Capes Hatteras, Lookout, Fear and Charleston also indicate considerable regional heterogeneity off the Carolinas (Blake and Grassle, 1994).

Comparisons of macrofauna from four transects in the South Atlantic Bight with comparable data from the North and Mid-Atlantic Bights, indicate that both the highest and lowest macrofaunal diversities can be found in the South Atlantic Bight. Generally it is mid-slope depths (1220 to 1500 m) that exhibit highest species richness and evenness, but in the South Atlantic Bight some stations at 800 m and 3000 m were diverse. The low-diversity assemblages found off Cape Hatteras (Blake and Grassle, 1994) are discussed below.

Analyses of macrofaunal species composition for 146 quantitative boxcore samples collected from depths of 600–3500 m between Cape Hatteras and Charleston Bump yielded 1300 species, of which over 30% were new to science (Hilbig, 1994). Half of these were polychaetes, 22% were crustaceans and 16% were molluscs. This study found that the zoogeographic barrier reported to occur between Capes Lookout and Hatteras (Cutler, 1975) was non-existent for bivalves, but was confirmed for most cumaceans, some aplacophorans and many polychaetes (Hilbig, 1994).

Cape Hatteras: The slope off Cape Hatteras appears to be atypical with respect to the rest of the Western Atlantic slope in terms of sedimentation and benthic standing stocks (Table 5.2). It has been suggested that the sedimentary/nutrient regime is more typical of estuarine or shelf environments (Rhoads and Hecker, 1994). The Cape Hatteras region receives high input of organic matter comparable to that occurring in coastal estuaries (DeMaster et al., 1994). The high inputs are associated with high sedimentation rates resulting from outwelling from nearshore embayments and topographic funneling of nutrients from the shelf out to the slope (Blake and Diaz, 1994). The Gulf Stream and Virginia currents converge in this region. This convergence, combined with the topographic position of the Cape on the outer edge of the shelf, leads to a funneling of water masses and their constituents offshore (Rhoads and Hecker, 1994). Thus, much of the organic input in this region is terrigenous, coming from Chesapeake and Delaware Bays to the north, North Carolina sounds, and the shelf. Evidence for terrigenous inputs comes from lighter δ^{13}C values for sediments (−21.2) than is observed at sites further south (−18.7 to −19.6) (Blair et al., 1994). The composition of fatty acids and sterols are typical of refractory shelf and estuarine sediments (Harvey, 1994). The concentrations of chlorophyll a in sediments at depths from 530 m to 2003 m averaged 19.9 mg m^{-2}, a value much higher than observed elsewhere on the eastern continental slope of the United States. Viable diatoms present in cores up to 14 cm below the surface suggest high rates of bioturbation (Cahoon et al., 1994). Observations of rapid subduction of diatoms by maldanid polychaetes at this site support this idea (Levin et al., 1997, 1999), as do other experimental studies of particle mixing (DeMaster et al., 1994; Blair et al., 1996; Fornes et al., 1999). Analyses of fatty acids and sterols suggest that diatoms and dinoflagellates are the principal source of labile organic matter to the sediments, with a minor input of vascular-plant material (Harvey, 1994).

The Cape Hatteras margin supports extraordinarily large numbers of megafauna (Hecker, 1994) and dense infaunal assemblages with unusually low species diversity (Schaff et al., 1992; Blake and Grassle, 1994; Blake and Hilbig, 1994). The abundant megafauna includes large populations of brittle stars and asteroids, the foraminiferan *Bathysiphon filiformis*, three demersal fish, two eelpouts and a large anemone (Fig. 5.5) (Hecker, 1994). These taxa attain much higher population densities off Cape Hatteras than at any other site on the eastern margin of the United States (Hecker, 1994).

Macrofaunal densities at depths between 530 and 850 m off Cape Hatteras are also extraordinarily high (46 000–89 000 individuals m^{-2}), about 2–9 times higher than at comparable depths elsewhere on the eastern United States slope (Blake and Hilbig, 1994; Blake and Grassle, 1994; Schaff et al., 1992). These densities are typical of those found in shallow water, and some of the species are characteristic of shelf depths (Schaff et al., 1992; Blake and Grassle, 1994). Bioturbation activity in this area is much higher than in other regions of the Northwest Atlantic margin (Schaff et al., 1992; Diaz et al., 1994; DeMaster et al., 1994; Levin et al., 1997; Fornes et al., 1999).

The diversity and evenness of benthic foraminiferal assemblages (the fraction >63 μm – i.e., within the meiofaunal size range) at depths between 600 m and 2000 m off Cape Hatteras are reported by Cutter et al. (1994) to be high ($H' = 4.02$–4.42, $\log_e$). About 9% of the species present are those characteristic of shelf environments (Cutter et al., 1994), comparable to values from the metazoan macrobenthos. These data, however, refer to ‘total’ assemblages – that is, there was no discrimination between ‘dead’ and ‘live’ individuals (the ‘live’ being those stained with rose Bengal). Gooday et al. (2001) found that large Foraminifera (the fraction >300 μm – i.e., within the

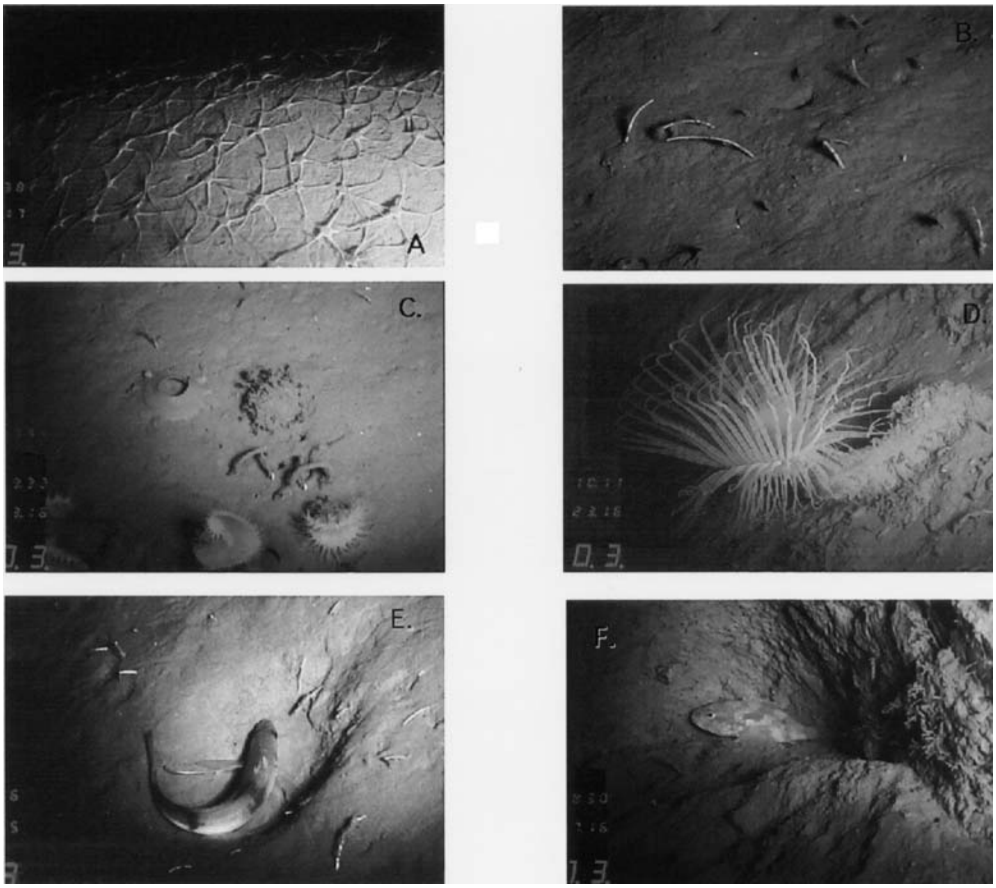

Fig. 5.5. Photographs of epifauna on the North Carolina continental margin off Cape Hatteras, NW Atlantic Ocean. (a) Aggregation of brittle stars (*Ophiura sarsi*) and unidentified asteroids atop a ridge, 600 m; (b) the foraminiferan *Bathysiphon filiformis* (white tubes) and polychaete tubes, ~800 m; (c) anemones (*Actinauge verrillii*), eel pout (*Lycenchelys verrillii*), and egg case at 850 m; (d) anemone on steep gully wall, 850 m; (e) *Phycis chesteri* (hake) and *Bathysiphon filiformis* tubes at 850 m; (f) *Helicolenus dactylopterus* off Cape Hatteras at 350 m. Note dense polychaete tubes protruding from the gully wall.

macrobenthic size range) were more abundant (15.7–24.0 stained individuals cm^{-2}) at Site III of Schaff et al. (1992) off Cape Hatteras (850 m) than at Sites I (4.3–8.7 individuals cm^{-2}) and II (8.6 individuals cm^{-2}) off Cape Fear and Cape Lookout, respectively. However, the faunas were substantially less diverse at Site III (31–42 species) compared to Sites I (64–90 species) and II (67 species). In all cases, these data are derived from the 0–15 cm layer.

Blake Plateau and Spur: It is clear from bottom photographs that certain areas of the deep ocean are eroded by strong near-bottom currents. Substrata in these high-energy regions can be sediment-covered, where particles are periodically resuspended and deposited, or moved as bedload (Hollister et al., 1984) or sediment-free rock, as sometimes found on seamounts, in canyons and at the base of plateaus (Genin et al., 1992).

Genin et al. (1992) studied the benthic fauna at depths between 3300 and 3900 m on the flanks of the Blake Escarpment off the southeastern United States. Here the bottom has steep, exposed limestone cliffs covered with manganese oxide alternating with sediment-covered slopes. The Western Boundary Undercurrent passes along the face of the escarpment and is associated with a southward flow at a speed sometimes exceeding 30 cm sec^{-1} (Lai, 1984). Analyses of over 2000 photographs revealed domination of the community by massive demosponges (Lithistidae), several species of gorgonian corals, and brisingid asteroids. Megafauna cover averaged 10% on hard substrata, and sometimes covered as much as 25% of the bottom. Megafaunal abundance at this site is several orders of magnitude higher than that reported for other sediment-free (non-reducing) sites of comparable depth. Genin et al. (1992) attributed these high abundances to an increased rate of food supply resulting from the high particle flux generated by the current, as surface productivity in the area is not known to be especially large.

Northwest Atlantic Abyss and trenches

The abyssal and hadal environments of the Northwest Atlantic have received minimal attention. By far the best-studied are the Hatteras Abyssal Plain (Fig. 5.2) and the Puerto Rico Trench, but even for these areas there are only a handful of reports, with the emphasis largely on meiofauna.

Hatteras and Nares abyssal plains

The relations between metazoan meiofaunal abundance and biomass, bacterial abundance and particulate flux were examined at a depth of 5411 m on the Hatteras Abyssal Plain (32ºN, 70ºW) (HAP), and compared to values in the Puerto Rico Trench (PRT) (Tietjen et al., 1989). Meiofaunal abundance on the Hatteras Abyssal Plain was 11.4±2.6 individuals cm^{-2}, and the biomass was 3.84 micrograms C cm^{-2}. Although nematodes comprised 75% of the individuals, harpacticoid copepods made up 85% of the biomass. Most of the meiofaunal biomass was present below the 0–2 cm layer. Comparisons with the Puerto Rico Trench indicate higher meiofaunal densities, biomass and even bioturbation rates on the Hatteras Abyssal Plain than in the Puerto Rico Trench (7460–8189 m). Nematode faunas at the same two sites, and at a bathyal silty-sand site in the Puerto Rico Trench (2217 m), were largely dominated by species of *Acantholaimus, Halalaimus* and *Theristus,* with some additional genera (*Camaicolaimus, Desmodora, Greeffiella, Leptolaimus, Setoplectus* and *Tricoma*) also important at the bathyal silty-sand site (Tietjen, 1989). Many species were endemic – 67% in the Hatteras Abyssal Plain area and 77% in the Puerto Rico Trench area.

Foraminiferal faunas on the Nares Abyssal Plain have been described by Schröder (1986) and Schröder et al. (1989). The assemblage at a 5800 m site located below the calcium compensation depth is dominated by fragile agglutinated taxa, komokiaceans being particularly abundant and diverse. More than 70% of the 54 species (komokiaceans excluded) recognized here are also present in the central North Pacific, reflecting the wide occurrence of many abyssal agglutinated foraminiferal species (Schröder et al., 1988).

Puerto Rico Trench

Early, non-quantitative reports of the fauna of the Puerto Rico Trench focused on taxonomic descriptions and provided little general information about the benthic community (Nybelin, 1951; Bruun, 1957; Péres, 1965; Staiger, 1972). Recent sampling has demonstrated that, in contrast to the typical view that trenches support abundant, low-diversity assemblages, the Puerto Rico Trench has a depauperate benthic assemblage (Richardson et al., 1995). Three 0.25 m^2 boxcores collecting macrofauna (>297 μm) along the central axis of the trench (8371–8376 m) collected only 21 specimens (= 28 individuals m^{-2}) belonging to 13 species, with a biomass of only 0.079 g wet wt m^{-2} (Richardson et al., 1995). Polychaetes and tanaids accounted for 54% of the individuals and 96% of the wet biomass. Slightly higher faunal biomass (0.3–0.42 g m^{-2}) was estimated for the Puerto Rico Trench by Pasternak et al. (1975) using dredge samples. Metazoan meiofaunal abundance also was extremely low: 69±10.8 individuals 10 cm^{-2}. Nematodes made up 95% of the total meiofauna; harpacticoid copepods were 2.3% and ostracods were 1.0%. George and Higgins (1979) reported even lower meiofaunal densities of 17.1–17.3 individuals 10 cm^{-2} from 8560 m in the Puerto Rico Trench, but used a 63 μm rather than 42 μm mesh net. Their otter trawls contained deposit-feeding holothurians, isopods, amphipods and cumaceans. The presence of depositional laminae of fine silt visible in *x*-radiographs is considered indicative of low sediment mixing in the Puerto Rico Trench (Richardson et al., 1995). This observation is in agreement with the very low biomass of bioturbating taxa.

The faunal values for the Puerto Rico Trench are among the lowest reported for abyssal or hadal environments. This is attributed to low food flux and poor nutrient value (0.74% organic C) of the food supply. Disturbance by turbidity flows may also contribute to the depauperate nature of the benthic assemblages (Richardson et al., 1995).

Northeast Atlantic

The deep-sea fauna along the northeast Atlantic continental margin, first sampled during the 1860s and

1870s, is perhaps better known than that of any other deep-sea region in the world. Recently, this margin and the adjacent abyssal plains have been the focus for a number of national (e.g., British, Dutch, French and German) programs, and international ones, mainly funded by the European Union (Table 5.1) which have influenced the development of modern themes in deep-sea biology.

Le Danois (1948) provided a valuable synoptic account of early studies of larger animals along the northwest European margin (Bay of Biscay, Porcupine Seabight, Rockall Trough). Comprehensive reviews of meiofauna in the deep northeast Atlantic (their abundance, faunal composition, bathymetric and latitudinal patterns, vertical distribution within the sediment, temporal patterns) have been compiled by Thiel (1983) and Vincx et al. (1994). Gooday et al. (1998) have provided a synopsis of Northeast Atlantic foraminiferal diversity data.

Norwegian–Greenland Sea (NGS)

The benthic systems of this subarctic region have been investigated as part of a large-scale interdisciplinary study ('Sonderforschungsbereich 313') by the University of Kiel of particle flux to the seafloor and its transformation into the paleoceanographic record. Multiple corer samples taken over a wide area of the Norwegian–Greenland Sea were used to analyze the pigment content (chlorophyll equivalents) of the sediment (Graf et al., 1995). The highest concentrations were encountered close to the ice edge off Greenland, in samples from the Kolbeinsey Ridge (800–950 m), and particularly at the 'FLUFF' station, southwest of Jan Mayen Island, where a phytodetritus layer 1 to 2 cm thick was observed during 1989. Pigment concentrations on the Barents Sea slope (380–2500 m) were also high, probably owing to lateral advection from the adjacent shelf, but they were lower on the Vøring Plateau (950–1450 m), and particularly at two deep stations in the East Greenland Basin (3000 m) and the Lofoten Basin (3300 m).

The Vøring Plateau, a bathyal (1200–1600 m) terrace on the Norwegian continental margin, was a particular focus of interest during this project. A site in this area, 1240-m deep, was visited on eight cruises; samples were obtained during seven different months (February, May to October), albeit in different years (Graf et al., 1995, table 1 therein). Chlorophyll equivalents were unmeasurable during mid-May, but increased dramatically in late May and June 1986 before declining during July. A second, lower peak occurred in September 1988. Pigment concentrations were puzzlingly high in February 1987, possibly as a result of some unusual sedimentation event. Data for sediment oxygen demand (SOD) are available for the period from May to September and show two peaks of activity in June and August. Graf et al. (1995) pointed out that fluctuations in the pigment concentrations and sediment oxygen demand match patterns of organic-matter flux, as determined from sediment-trap records. The July peaks correspond to the spring input of particulate organic carbon (POC) and the August/September peaks to the maximum flux of particulate organic nitrogen (PON). A pulse of copepod fecal pellets at the end of May 1986 at a somewhat deeper site (1430 m) led to a rapid increase in concentrations of chlorophyll a in the sediment. Within a period of only 11 days (May 24th to June 4th), the chlorophyll had been incorporated to a depth of 9 cm by the sipunculan *Golfingia (Nephasoma)*. Correspondingly enhanced metabolic activity was indicated by increased ATP concentrations, with subsurface peaks reflecting the feeding activities of *Golfingia (Nephasoma)* and the enteropneust *Stereobalanus canadensis*. These and other large infauna are discussed below.

Sibuet (1985) studied megafaunal echinoderms from the Norwegian, Lofoten and Greenland Basins (depth range 2500–3700 m) where holothurians were exceptionally abundant, occurring in densities of 5779, 4971 and 7232 individuals ha^{-1}. Populations were dominated by *Elpidia glacialis,* a small species <25 mm in size.

Romero-Wetzel and Gerlach (1991) have presented an overview of macrofaunal abundance, species composition, and biomass on the Vøring Plateau based on the >500 μm fraction of 17 boxcores collected from depths between 1200 and 1500 m. Of the 70 species recognized, only the following were present in half or more of the samples: *Malletia obtusa* (bivalve), *Aricidea abranchiata*, *Chaetozone setosa*, *Myriochele* sp. 1, *M. fragilis*, *Notomastus latericeus*, *Paramphinome jeffreysii* (polychaetes), *Golfingia (Nephasoma)* sp. 1 (sipunculan), *Ophiocten gracilis* (ophiuroid), and *Stereobalanus canadensis* (enteropneust). They recognized three categories of macrofauna: smaller and larger infauna, and epifauna (all sizes), which have mean densities of 531, 34 and 56 individuals m^{-2} and biomass values of 1.28, 2.26 and 0.52 g wet weight m^{-2}, respectively (Romero-Wetzel and Gerlach, 1991). These authors also emphasized the contribution of large (10–1000 mg individual biomass) and very large macrofauna (1–100 g) to benthic biomass on the Vøring Plateau. The very large animals in particular were rarely caught in core samples, but were estimated to contribute as much as 70% of total macrofaunal biomass.

Burrowing organisms may play an important role in geochemical processes and sediment bioturbation on the Vøring Plateau. Romero-Wetzel (1987) described a network of very narrow (0.2–0.5 mm diameter), predominantly vertical burrows which penetrated to a depth of 50 cm and intersected the sediment surface as tiny, inconspicuous openings. These are constructed by the sipunculan *Golfingia (Nephasoma)* and may be extremely abundant (up to 20 000 m^{-2}). The sipunculan draws organic matter down into its burrow and ejects feces back onto the sediment surface. Elaborate burrow systems are constructed within the top 10 cm of sediment by the enteropneust *Stereobalanus canadensis* (Romero-Wetzel, 1989). The burrows are 5–6 mm in diameter, and include vertical shafts to the surface as well as extensive, dichotomously branched horizontal galleries. Individual burrow systems may contain several individuals of *S. canadensis* as well as masses of their fecal pellets (Jensen, 1992b). Like its shallow-water relatives, *S. canadensis* secretes brominated phenols. These toxins deter colonization of the burrow wall by metazoan meiofauna, although foraminifers (mainly *Lagena* sp.) appear resistant to their effects (Jensen et al., 1992a). Another large infaunal inhabitant of the Vøring Plateau (at depths of 1244–2926 m), the anemone *Cerianthus* (Anthozoa), occupies a horizontal, branched tube 12–40 cm below the sediment surface in densities of up to 3.5 individuals m^{-2}(Jensen, 1992a). Jensen suggested that the tube systems act as a ‘gas pipeline’ for methane and hydrogen sulfide derived from deeper in the sediment column. He speculated that the gases might support endosymbiotic bacteria or bacteria living in the tube lining.

Jensen et al. (1992b) discovered distinct difference between the meio- and macrofauna on opposite sides on a ridge on the Vøring Plateau. The side exposed to sediment advection (Expo-stations) had generally higher oxygen consumption rates, lower meiofaunal biomass and lower maximum depth of penetration of meiofauna than the other side where sediment was being accumulated (Impo-stations). Taxa which were more abundant at the Impo-stations included larger nematodes (e.g., *Pararaeolaimus rumohri* and various desmoscolecids) and several pogonophore species (i.e. infaunal worms); those found mainly at the Expo-stations included smaller nematodes (*Acantholaimus elegans, Desmodora pilosa*, *Rhabdodemania* sp. and *Sabatieria* sp.), sipunculans, sponges and hydroids (i.e. suspension and deposit-feeders). Jensen et al. (1992b) concluded that a distinctive pogonophore and nematode fauna occupies areas of the Vøring Plateau which experience high levels of sediment and organic-carbon accumulation.

Foraminifera are an important component of the Norwegian–Greenland Sea benthos. On the Vøring Plateau, Romero-Wetzel and Gerlach (1991) estimated that they constituted 41.6% of the biomass of ‘larger meiofauna’ (wet weight 1–100 micrograms), in addition to an unknown proportion of the ‘small meiofauna’. Thies (1991) described ‘live’ (Rose Bengal stained) and dead foraminiferal faunas (>250 µm fraction) in 81 box cores from areas between Greenland and Spitzbergen (Svalbard) and between Greenland and Norway (depth range 81 to 3695 m). A total of 102 species were recognized, but the faunas were of low diversity, particularly in the deep basins where only 3–5 species were present in the >250 µm fraction. Thies (1991) recognized a low-diversity fauna on the lower slope and in the basins, dominated by *Cibicidoides wuellerstorfi, Cribrostomoides subglobosa, Crithionina hispida* and *Pyrgo rotaliaria.* This contrasts with a more diverse fauna (up to 19 species) on the upper slope and shelf characterized by *Cibicides lobatulus, Cribrostomoides subglobosa, Reophax difflugiformis* and *R. scorpiurus* She concluded that food supply exerted a decisive influence on the foraminiferal faunas. This is in accordance with the observations of Heeger (1990; reviewed by Gooday et al., 1992) that many of the Foraminifera in the Norwegian–Greenland Sea feed on fresh phytodetritus. Moreover, ingested food can be converted into biomass very rapidly (Heeger, 1990), within a period of days in experimental systems (Altenbach, 1992; Linke et al., 1995). Some species (*C. subglobosa, Pyrgo murrhina*, *Rhabdammina abyssorum*), show corresponding physiological adaptations to a fluctuating food supply. Rapidly fluctuating ATP content and heat production indicate that they can survive periods of starvation by metabolizing their own protoplasm, while the ability to phosphorylate adenosine monophosphate (AMP) to adenosine triphosphate (ATP) allows a rapid physiological reawakening to occur when the Foraminifera are presented with a sudden food pulse (Linke, 1992; Linke et al., 1995).

British continental margin

Recent work has concentrated in three main areas of the Celtic margin of Britain: the Rockall Trough, the Porcupine Seabight, and the Goban Spur – localities which are convenient to reach from British ports and relatively easy to sample.

Rockall Trough (RT): This elongate basin lies between Scotland and the northern part of Ireland on the one hand, and the Rockall Bank on the other, and deepens from the Wyville Thomson Ridge in the north to the Porcupine Abyssal Plain in the south. It has been intensively studied for over 20 years by J.D. Gage and his colleagues at the Scottish Marine Biological Association/Scottish Association for Marine Science in Oban. They have compiled a data set from two deep Permanent Stations, one situated at 2200 m depth, the other at 2900 m – the longest time series available anywhere in the deep ocean. Mean standing crop of macrofauna (>420 μm, excluding Foraminifera), sampled using replicate 0.25 m^2 box cores, was 1716 individuals m^{-2}, with a wet weight of 14.92 g m^{-2} (Gage, 1979). Polychaetes (59.1% of the individuals) were the dominant taxon followed by tanaids (10.3%), bivalves (10.1%), isopods (4.4%), scaphopods (3.9%), amphipods (3.3%) and nemertines (3.3%). The proportions of various taxa were remarkably similar in box cores taken at 1800 m, 2000 m, 2500 m and 2900 m in other parts of the Rockall Trough; only isopods tended to be relatively more abundant at the Permanent Station. The isopod fauna includes 79 species, dominated by the Eurycopidae, Haploniscidae, Ilyarachnidae, and Ischnomesidae (Harrison, 1988). The bivalves consist predominantly (80%) of members of the Nuculanidae. The macrofauna at the Permanent Station was also sampled using an epibenthic sledge fitted with a 500 μm-mesh net (Gage et al., 1980). These catches were dominated by polychaetes, bivalves and ophiuroids, although there was considerable variation between individual catches, caused in particular by summer recruitment of juveniles of the ophiuroid *Ophiura ljungmani.*

Gage (1986) reviewed knowledge of the invertebrate megafauna of the Rockall Trough based on catches from Agassiz trawls or large, single- or twin-warp trawls. The faunas are generally similar to those found in the Bay of Biscay and Porcupine Seabight. Echinoderms predominate at all depths, and species are zoned bathymetrically, the greatest rates of faunal change occurring between 800 and 1200 m and (particularly in the case of ophiuroids) around 1800 m. Other invertebrates, particularly cnidarians and crustaceans, are also important. The cnidarians include the deep-water coral *Lophelia pertusa*, a widespread inhabitant of the upper slope along the European continental margin, and associated with areas of steady current around the Rockall Trough (Wilson, 1979). The influence of currents on the megafauna is particularly evident on the Feni Ridge on the western flank of the Rockall Trough, where suspension feeders are more common than they are at tranquil sites on the eastern side of the Trough. As well as bathymetry and current velocity, megafaunal composition seems to reflect sediment type and bottom water-mass distribution. Thus, the zone of rapid change in the echinoderm fauna between 800 and 1200 m occurs within a distinctive water mass of Mediterranean origin, and also spans the permanent thermocline. Gage (1986) attributed differences in the depths of zones of maximum faunal change between the Rockall Trough and sites in the Northwest Atlantic and Northeast Pacific to such local influences superimposed on bathymetric and other trends which apply globally.

The availability of extensive time-series material allowed Gage and his colleagues to analyse the demography and reproductive dynamics among animals in the Rockall Trough (reviewed by Tyler, 1988; Gage, 1991; Gage and Tyler, 1991). This has led to the recognition of taxa displaying seasonal reproduction, leading to the production of juveniles in the spring, coincident with phytodetrital pulses (Gage and Tyler, 1991). Seasonally breeding taxa include isopods, the protobranch bivalves *Ledella pustulosa* and *Yoldiella jeffreysi,* and the echinoderms *Echinus affinis, Ophiura ljungmani, Plutonaster bifrons* and possibly *Dytaster insignis, Ophiocten gracilis* and *Ophiomusium lymani.* Other echinoderms have non-seasonal (continuous) reproduction with large or intermediate egg size and low or intermediate fecundity. Classical growth-rate studies based on size distributions have been carried out for *E. affinis, L. pustulosa*, *Ophiomusium lymani*, *Ophiura ljungmani* and *Y. jeffreysi.* In the case of *Ophiomusium lymani,* it was impossible to disentangle the individual cohorts present within the single unimodal size peak. In this species, and in *Ophiura ljungmani* and the crinoids *Annacrinus wyvillethomsoni* and *Bathycrinus carpenteri,* growth rates have been determined by analyzing growth zones in skeletal plates (Duco and Roux, 1981). These studies suggest that the two crinoid species have growth and mortality patterns similar to those of near-shore species. The echinoid *Echinus affinis*, however, appears to live longer (up to 28 years) and grow more slowly than related shallow-water species, although some other echinoderm species may grow faster (Gage and Tyler, 1985).

Porcupine Seabight (PSB): This embayment of the continental slope, lying southwest of Ireland and south of the Rockall Trough, is bounded by the Porcupine Bank to the west, the Irish shelf to the east and the Goban Spur to the south (Fig. 5.1). It is connected to the Porcupine Abyssal Plain by a narrow southwestern opening. An excellent general account of the topography, sedimentology, geology and hydrography of the Porcupine Seabight has been given by Rice et al. (1991). To the north and west the slopes are fairly gentle but the eastern side is cut by canyons; this makes conventional sampling gear difficult to use. An important feature is the Gollum Channel System, which runs through the axis of the Seabight and out onto the Porcupine Abyssal Plain. Recent submersible observations suggest that the upper part of the channel system (down to at least 940 m depth) is active, but that at 3000 m depth bottom currents are too weak to resuspend fine-grained sediments (Tudhope and Scoffin, 1995).

Between 1977 and 1986, the Porcupine Seabight was subject to an extensive sampling program by the Institute of Oceanographic Sciences (U.K.), summarized by Rice et al. (1991). The main focus was on the megafauna, but the meiofauna (including the Foraminifera) was also studied. This program yielded some important results, the most notable being the discovery of phytodetritus deposition (Billett et al., 1983), described elsewhere in this chapter (p. 121).

The invertebrate megafauna was sampled with a semi-balloon otter trawl and an epibenthic sledge, and photographed *in situ* using a camera attached to the sledge. Rice et al. (1982) used an epibenthic sledge fitted with an odometer wheel, and simultaneously obtained seafloor photographs, to quantify the megafauna in the Porcupine Seabight. Despite various shortcomings, a combination of sampling and photography provided reasonably accurate estimates of densities for some non-sessile taxa such as the larger echinoderms. For example, the holothurian *Benthogone rosea* had a mean density of 0.098 and 0.114 individuals m^{-2} (photographic and catch data respectively) in a haul taken at 1400 m. Dense aggregations of the small holothurian *Kolga hyalina* are occasionally observed in the Porcupine Seabight. Billett and Hansen (1982) counted 50 individuals m^{-2} in photographs taken around a depth of 3700 m, and 34 individuals m^{-2} around 4000 m depth, these high densities being associated with the Gollum Channel System. Specimens caught at particular stations were small and had a narrow size distribution, suggesting periodic synchronous reproduction and other opportunistic life-history characteristics. Large numbers of possibly opportunistic holothurians have also been observed in some Northwest Atlantic canyons (Rowe, 1971b).

Megafaunal biomass in the Porcupine Seabight is between two and five times greater than in the Bay of Biscay (Billett, 1991). Despite considerable scatter, total biomass values (whether measured as wet weight, dry weight, or ash-free dry weight [AFDW]) show a clear logarithmic decrease between 500 and 4100 m depth, with echinoderm biomass decreasing less steeply with depth than the biomass of crustaceans and ‘other phyla’ (Lampitt et al., 1986). On the upper slope (200–1000 m), the main megafaunal animals are crustaceans (particularly the crab *Geryon tridens* and other decapods), sponges and cnidarians. Echinoderms predominate at greater depths, constituting >75% and sometimes >90% of the invertebrate megafaunal AFDW at 1500 m, 2000 m, 2500 m, 3500 m and 4000 m depth (Billett, 1991). Holothurians are always the most important taxon, except around 2500 m depth in the center of the Seabight where the megafauna is dominated by asteroids. Billett (1991) has summarized the bathymetric distribution of holothurian species in the Porcupine Seabight based on epibenthic sledge catches (Fig. 5.6). He recognized three zones: the upper and middle slope where species occupy relatively narrow depth bands related to changing hydrographic conditions, the middle and lower slope, where holothurians are uncommon for poorly understood reasons, and areas beyond the base of the slope where bathymetric distributions are relatively broad.

Lampitt et al. (1986) repeatedly sampled a station at a depth of 1300 m using an epibenthic sledge. Differences in megafaunal biomass between samples collected at this site on a single cruise spanned an order of magnitude, from $<0.1\ g\,m^{-2}$ to $>1\ g\,m^{-2}$ ash-free dry weight. These disparities were due entirely to variations in the abundance of *Pheronema carpenteri.* This hexactinellid sponge is abundant along parts of the Northwest European margin and forms dense aggregations between 1000 m and 1300 m in the Porcupine

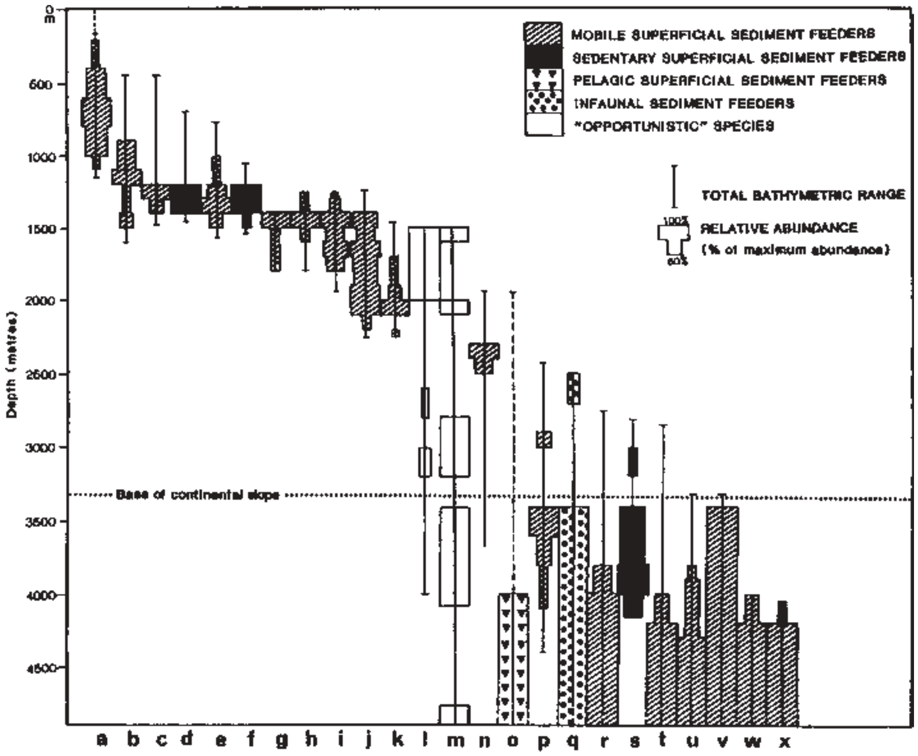

Fig. 5.6. Bathymetric distribution of the 24 most common holothurians in the Porcupine Seabight showing total range and relative abundance of each species at various depths. Feeding types are also indicated. From Billett (1991).

Seabight (Rice et al., 1990). The density and biomass of these populations were analysed from photographs by Rice et al. (1990). Maximum sponge densities in 10-m depth horizons ranged from 0.8 to 1.6 individuals m^{-2} (biomass 199–453 $g\,m^{-2}$) but reached values of 2.5 to 5.0 individuals m^{-2} (biomass 498 to 1131 $g\,m^{-2}$) in single photographs. These dense populations lie below a zone on the upper slope where near-bottom tidal current velocities are enhanced by topographic effects. Rice et al. (1990) suggested that *Pheronema* avoids the regions of highest current velocity but populates nearby downslope areas in order to benefit from the availability of an enhanced load of suspended material. Mats of *Pheronema* spicules cover about a third of the seafloor in the sponge zone. Macrofaunal densities were an order of magnitude higher in a spicule-dominated box core from 1250 m than in box cores from outside the sponge zone (Bett and Rice, 1992).

Meiofauna in the Porcupine Seabight was sampled using the Barnett–Watson multiple corer. Pfannkuche (1985) studied samples taken at 500-m intervals along a transect of the Seabight extending from a depth of 500 m to 4850 m. Metazoan meiofaunal abundance (individuals 10 cm^{-2}) decreased rapidly from 2604 to 1492 between depths of 500 and 1500 m, but more gradually from 828 to 315 below 2000 m. Biomass (AFDW), declined correspondingly from 1.16 mg 10 cm^{-2} at 500 m to 0.61 at 1500 m, and then from 0.6 at 2000 m to 0.35 at 4850 m. Both biomass and abundance were closely related to the concentrations of chloroplastic pigments measured in a parallel set of samples. The foraminiferal meiofauna at a bathyal station 1320–1340 m deep has been described by Gooday (1986). Foraminifera accounted for 46–59% of all the meiofauna, and were highly diverse (95–124 species). This was one of the earliest studies to describe the vertical distribution of foraminiferal species within the sediments. Some species were more or less restricted to the upper 1 cm, while others lived infaunally. In a later study, Gooday and Lambshead (1989) and Lambshead and Gooday (1990), described population fluctuations among foraminiferal species in relation to phytodetritus deposition. Some species, particularly those associated with phytodetrital aggregates, were substantially more abundant during July, when phytodetritus was present on the seafloor, than during April before its arrival. In contrast, few seasonal changes were observed among the metazoan meiofauna at this site (Gooday et al., 1996).

Goban Spur: The Goban Spur is a gently sloping stepped platform which forms the southeastern flank of the Porcupine Seabight. Together with the Meriadzek Terrace (a plateau-like feature on the continental margin to the southeast of the Goban Spur; see Fig. 5.1). This region was studied intensively as part of the OMEX project funded by the European Union, which addressed the role of the Northwest European continental margin in the global carbon cycle (van Weering et al., 1998).

Total benthic biomass on the Goban Spur was dominated by small organisms: Bacteria, Fungi, flagellates, Foraminifera, and small metazoan meiofauna. The percentage contribution of these groups to the total benthic biomass increased with water depth from 90% on the shelf to 97–98% at bathyal and abyssal depths (Pfannkuche and Soltwedel, 1998). Soltwedel et al. (1996) studied trends in the metazoan meiofauna along a transect extending down the Goban Spur and onto the Porcupine Abyssal Plain (182–4470 m). Abundances (individuals cm^{-2}) varied as follows: 33.5 (182 m), 38.1 (410 m), 19.1 (1013 m), 6.6 (2084 m), 4.3 (3552 m), 6.4 (3889 m), 12.4 (4470 m). Nematodes made up between 66% (at 182 m) and 93% (at 3552 m) of the fauna and, below depths of 2000 m, showed a clear decrease in size with increasing bathymetric depth, as observed previously by Pfannkuche (1985) in the Porcupine Seabight and Soetaert and Heip (1989) in the Mediterranean. These observations support the hypothesis of Thiel (1975) that organisms tend to become smaller with increasing bathymetric depth as a result of food limitation.

Flach and Heip (1996a) analysed macrofauna (>500 μm; no. ind. m^{-2}) in box cores taken along a similar transect (208–4470 m) during October 1993, May 1994 and August 1995, and related the differences observed to seasonal and interannual variations in organic-matter inputs. Flach and Heip (1996b) have reported on the vertical distribution of macrofauna within the upper 15 cm of sediment in the May 1994 samples. One of the main findings of these studies is that there are clear seasonal and interannual variations in the macrofauna on the Goban Spur only above about 1500 m depth. Macrofaunal densities decreased exponentially with increasing bathymetric depth, but they also showed substantial seasonal and interannual differences. In particular, densities were significantly higher on the upper part of the slope (down to 1500 m) during May than in August and October, mainly as a result of the presence of large numbers of juvenile echinoderms including the echinoid *Echinus affinis* and the ophiuroid *Ophiocten gracilis,* both seasonal breeders. These fluctuations probably reflect interannular differences in the intensity of phytodetrital pulses. Polychaetes were always the most important macrofaunal taxon. Their numbers declined fairly regularly along the transect, and were significantly higher at the two shallowest stations (208–231 m, 670–693 m) during May. Crustaceans were most abundant at mid-slope depths (670–2256 m), significantly more so in August. Biomass (mg m^{-2}) also tended to decline with depth, but was consistently higher (1021) at 1034 m (station B), owing to the predominance of relatively large animals, and low (1425) at 1457 m (station II) where the animals were relatively small. Sedimentary organic carbon peaked at station B, suggesting that this site received substantial inputs of labile phytodetritus. Biomass values were somewhat higher in May at the three shallowest stations (208–1034 m) and higher in August at mid-slope stations (1425–2256 m), but these seasonal differences were not significant. Macrofaunal community respiration rates, estimated from individual weights and biomass values, were high in May between 208 m and 1034 m, but much lower at the deeper stations. At mid-slope depths (2200 m), however, rates were higher in August than in May. Between 40% and 80% of the macrofauna occurred in the 0–1 cm layer of sediment and the stations of intermediate depth (670 m, 1034 m and 1425 m) showed the highest proportions within this upper layer.

The numerical density of the megafauna undergoes a steady decrease along the OMEX transect, but biomass values are more irregular (Duineveld et al., 1997). Low values are found around the shelf break (200 m) and upper slope (700 m) (1913 and 1914 g wet weight 1000 m^{-2}, respectively) and Pendragon Escarpment (2200 m; 1188 g 1000 m^{-2}), while the highest values occur at 1450 m (4076 g 1000 m^{-2}) and 3650 m (3789 g 1000 m^{-2}). These irregularities reflect the changing taxonomic composition of the megafauna, which is dominated at different depths by crinoids (200 m), echinoids (700 m), holothurians (100 m, 3650 m, 4500 m) and poriferans (1450 m).

Among the megafauna, macrofauna and Foraminifera (>150 μm fraction), the proportion of deposit feeders generally increased with increasing water depth across the Goban Spur transect (Flach et al., 1998). The densities of suspension feeders, however, were particularly high within a zone on the upper slope (1000–1500 m water depth) subject to high current velocities. Submersible observations indicate that suspension-feeding megafauna are also common on hard steep substrates (<1000 m depth) to the west of the Porcupine Bank and Goban Spur (Tyler and Zibrowius, 1992). The most common taxa observed by Tyler and Zibrowius (1992) were sponges, cnidarians (actiniarians, corals, zoantharians, ceriantharians, antipatharians, alcyonarians and particularly gorgonians) and echinoderms (mainly crinoids, asteroids and ophiuroids). A crinoid-dominated zone between 2100 and 2600 m depth was associated with a northward-flowing water mass reaching velocities of 7 cm s^{-1}.

French and Iberian margins

Bay of Biscay: There has been a long history of French research along the Bay of Biscay continental margin and on the adjacent abyssal plain, starting in the 1880s with the *Travailleur* and *Talisman* campaigns (Le Danois, 1948; Rice, 1980). A century later, the eleven cruises organized by Biologie Gascogne (BIOGAS) between 1972 and 1981 yielded a considerable body of quantitative information on many aspects of the Biscay benthos (Sibuet, 1977; Laubier and Sibuet, 1979; Laubier and Monniot, 1985). The megafauna was sampled using a large beam trawl and evaluated photographically; macro- and meiofauna and bacteria were sampled using an epibenthic sled, and Reineck and USNEL box corers. The extensive BIOGAS collections were studied by numerous scientists from many countries, resulting in a long list of publications. In particular, the volume edited by Laubier and Monniot (1985) includes data on different faunal groups (from bacteria to megafauna), necrophages, and particular higher taxa, as well as processes such as sediment recolonization and particle fluxes. Laubier and Monniot (1985) have also given a comprehensive list of BIOGAS publications, which include both taxonomic and ecological studies.

The BIOGAS program centered around six intensively worked stations, four located in the northern part of the Bay (stations 1–4: 1920–4825 m depth) and two in the southern part (stations 5–6: 1894–4475 m depth), extending from the continental slope out onto the continental rise and abyssal plain (Laubier and Sibuet, 1979). Sibuet and Segonzac (1985) reported on the 'megafauna' from trawl samples, although they examined the fraction >1 mm and therefore included animals more appropriately considered as macrofauna. The megafauna show greater heterogeneity, both across the Bay and at particular stations, than do the meiofauna and macrofauna. Densities decreased by a factor of 9 from the shallowest to the deepest station along the northern transect (2924 individuals m^{-2} to 321 individuals m^{-2}). The shallowest station (#1: 1920–2245 m), on the Meriadzek Terrace was particularly rich and diverse, with cnidarians (actiniarians) and echinoderms making up about two-thirds of the fauna. Molluscs were abundant (34%) at station 3 (4134–4240 m), and ascidians became fairly important (up to 14% of the fauna) at the deepest station (#4: 4706–4825 m). Fewer animals were present at the two southern stations; for example, at station 5 on the continental slope (1894–1995 m) the faunal density was 440 individuals ha^{-1}, much lower than at comparable depths on the Meriadzek Terrace (2924 individuals ha^{-1}). In the south, too, echinoderms (mainly holothurians), were relatively more important than on the northern margin (Sibuet, 1977; Sibuet and Segonzac, 1985). These north-to-south differences in assemblages of larger invertebrates within the Bay of Biscay probably reflect the greater terrigenous input (including plant material) in the southern area, much of it presumably channeled down submarine canyons.

Biogenic traces visible in seafloor photographs showed a good correlation with abundance of animals (>1 mm) across bathymetric gradients, and, in agreement with animal densities, were more prevalent at the northern than at the southern sites (Mauviel and Sibuet, 1985). Trace densities were greatest on the Meriadzek Terrace, but their diversity was highest at station 3, close to the lower end of the Shamrock Canyon, where 23 of the 29 categories recognized by Mauviel and Sibuet (1985) occurred. The traces included a wide variety of tracks, burrows, and mounds, as well as holothurian fecal casts.

Data on the macrofauna, both *sensu strictu* (>250 μm fraction, macrofaunal taxa only) and *sensu lato* (>250 μm fraction, all taxa), from BIOGAS stations 1–3 in the northern Bay of Biscay (2100–4100 m) are given by Dinet et al. (1985). At 2800 m and 4150 m, the macrofauna appears to be fairly abundant. Although the comparison is complicated by differences in mesh sizes, densities at the 2800 m BIOGAS station (4635 individuals m^{-2}, for the >250 μm fraction) are most similar to values from 1800 m (4320 individuals m^{-2}, for the >420 μm fraction) and 2000 m

(4156 individuals m^{-2}, for the >420 μm fraction) in the Rockall Trough (Dinet et al., 1985, table 5). More data are available for the metazoan meiofauna, particularly the nematodes, from the six BIOGAS stations. Dinet and Vivier (1977) found that total meiofaunal densities declined with increasing bathymetric depth, as did the proportion of the fauna present in the upper 1 cm of sediment. Densities also showed considerable spatial variability at both bathyal and abyssal sites, and particularly at stations 1, 2 and 4 to the north and station 5 to the south. Dinet and Vivier (1977) attributed this variability to the physico-chemical heterogeneity of the sediments. Interestingly, they could find no seasonal variation in total meiofaunal densities, or any correlation between densities and the organic-carbon content of the sediments. In a second study, Dinet and Vivier (1979) investigated the nematode fauna at the species level. The populations were very diverse, most species being represented by only one or a few individuals. The minimum and maximum diversity values occurred at the two southern sites (from about 50 species at station 5 to about 128 species at station 6) with the four stations of the northern transect yielding approximately 82–115 species (Dinet and Vivier, 1979, fig. 5 therein). Analysis of faunal similarity indicates an approximate separation between stations on the continental slope and those on the continental rise. However, there were no consistent differences between northern (1–4) and southern (5–6) sites; stations 1 and 6 showed a fairly close affinity, while station 5 showed little similarity to other sites. According to Soetaert and Heip's (1995) analysis of these and other literature data, the nematode faunas of the continental rise and the abyssal plain in the Bay of Biscay closely resemble those from the Hatteras Abyssal Plain, the HEBBLE site and the Puerto Rico Trench at the generic level. In terms of trophic groups, they are dominated by selective and non-selective deposit feeders and epistrate feeders; predatory/scavenging forms are uncommon (<10%).

Iberian margin: Gage et al. (1995) and Lamont et al. (1995) described macrofaunal sediment communities at two contrasting localities off Portugal, a presumed high-energy site in the Setubal Canyon (3356–3776 m), which is believed to experience periods of elevated current activity, and a tranquil site on the adjacent Tagus Abyssal Plain (5038 m). In both cases, the samples were dominated by agglutinated Foraminifera, and the metazoan fauna comprised nematodes, polychaetes, peracarid crustaceans, molluscs and echinoderms in descending order of numerical importance. Mean macrofaunal densities (300 μm individuals m^{-2}) were an order of magnitude higher in the canyon (mean 459.2, s.d. 208.6) than on the Tagus Abyssal Plain (mean 10.55, s.d. 22.24). On the other hand, species diversity for bivalves, tanaids and agglutinated Foraminifera was higher on the abyssal plain. There is some evidence that the fauna is more aggregated on the scale of tens of meters (between cores) in the canyon than on the abyssal plain, although the evidence for this is not conclusive. In general, the results of these studies suggest that hydrodynamic disturbance tends to diminish species diversity and increase the spatial heterogeneity of assemblages.

Northwest African margin

Studies carried out during the 1970s by the Institut für Hydrobiologie und Fischereiwissenschaft (IHF), Hamburg, and the Institute of Oceanographic Sciences (IOS), Wormley, have contributed greatly to knowledge of the benthos under the upwelling region and in other areas of the Northwest African margin. Downslope transects were worked by IHF off Cap Blanc (21ºN), near the center of the main upwelling area where primary production reaches 200 g C m^{-2} yr^{-1}, as well as off Morocco (Cape Mazagan, 35ºN) and Western Sahara (Cabo Peña Grande, 24–26ºN) to the north and off the Mauretanian coast (17ºN) to the south. General results have been reviewed by Thiel (1978, 1979, 1982, 1983); Pfannkuche et al. (1983) presented data from the Moroccan transect where upwelling intensity is low.

In general, the benthic system is strongly influenced by upwelling intensity, and hence surface primary production, and by hydrographic conditions (Thiel, 1978; Pfannkuche et al., 1983). Concentrations of chloroplastic pigments (chlorophyll breakdown products), which indicate organic-matter inputs, are two orders of magnitude higher off Cap Blanc than off Morocco; the Western Saharan transect yielded intermediate values (Thiel, 1978, fig. 4 therein). Along the Cap Blanc transect, pigment concentrations are high on the shelf, low on the upper slope (200 m) and then increase to much higher values between 400 and 1500 m before diminishing gradually with increasing depth. The low values at 200 m are believed to reflect the influence of a high-energy benthic boundary layer on the sedimentation of organic matter. Off Morocco, there is no increase on the lower slope. Instead, pigment intensities peak at the shelf edge, decline rapidly to 1200 m, and then remain relatively constant down to 3000 m.

Meiofaunal densities are higher at all depths off Cap Blanc (21ºN) than off Morocco (35ºN), presumably reflecting the increased organic-matter input in this highly productive region. Moreover, the abundance profiles along these transects are distinctly different, corresponding fairly closely to pigment concentrations. At 21ºN, meiofaunal abundances are highest on the shelf, drop to a distinct minimum at 200 m, followed by maximum values between 400 and 1000 m and declining numbers in deeper samples. At 35ºN, high abundances are also found on the shelf (2656 individuals m^{-2}) and at 400 m (2480 individuals m^{-2}) with a minimum at 200 m (1778 individuals m^{-2}). However, below 400 m, meiofaunal numbers fall fairly steeply down to 1200 m (631 individuals m^{-2}), below which they decline only slightly down to 3000 m (557 individuals m^{-2}). Meiofaunal biomass along the Moroccan transect follows a similar trend. Macrofaunal densities and biomass are also much higher at 21ºN and 17ºN than they are at 35ºN. The difference is particularly apparent above a depth of 1000 m. Along the deeper parts of the two southerly transects, the decrease in macrofaunal abundance is much steeper than off the Moroccan coast. Pfannkuche et al. (1983) also determined rates of benthic respiration and the activity of the electron transport system (ETS) (a measure of metabolic activity) along the Moroccan transect, in both cases using a shipboard technique. Respiration was highest at 130 m and 400 m, fell sharply between 400 and 800 m and then decreased slightly down to 3000 m. Electron transport activity also decreased with depth, and was substantially lower than values reported by Christensen and Packard (1977) from 21ºN, particularly at the shelf and slope sites above 500 m.

Sibuet et al. (1993), Cosson et al. (1997), and Galeron et al. (2000) have presented faunal data for their eutrophic, mesotrophic and oligotrophic EUMELI stations (sites E, M and O) located at 1700 m depth on the slope off Cap Blanc, 3100 m on the continental rise southwest of Cap Blanc, and 4700 m on the Cape Verde Abyssal Plain, respectively (Fig. 5.1). Densities of macrofauna (>500 μm) were 5403 individuals m^{-2} at site E and 1856 individuals m^{-2} at site M – high values which reflect the substantial organic-matter inputs at these stations. In contrast, only 231 individuals m^{-2} were recovered at site O. Polychaetes were the most abundant macrofaunal group (56% at site E, 67% at site M and 64% at site O) but tanaidaceans (12.7%, 10.0%, 11.9%), isopods (10.6%, 8.6%, 7.6%) and bivalves (8.2%, 1.9%, 6.5%) were also important. The spatial distribution of macrofauna tended to be patchy at the two shallower stations and particularly at site E, but much more homogeneous at site O. Cosson et al. (1997) attributed the aggregated faunal distributions at site E to the heterogeneous deposition of organic matter associated with upwelling, strong near-bottom currents, and the generation of small-scale sedimentary structure by macrofaunal activity. There was no evidence for temporal (seasonal) variability among the macrofauna at either station, although this may have reflected inadequate sampling. The densities of other faunal categories followed trends similar to those for the macrofauna (Sibuet et al., 1993). Densities of meiofauna (>40 μm; multiple and box-core samples) were 55.2±4.6, 27.7±2.3, 6.9±0.5 cm^{-2}, and those of megafauna (>2 mm; trawl samples) were 8624, 702 and 33 ha^{-1} at sites E, M and O, respectively. Xenophyophores (giant protists) were an important component of the megafauna in photographs from site M (Auffret et al., 1992).

Megafauna on the Northwest African margin have been sampled using various types of trawl, including an IOSDL epibenthic sledge equipped with a camera (Aldred et al., 1976; Rice et al., 1979). Unusually large populations of megafaunal organisms occur at various places on the continental slope and rise. At 2000 m off Cap Blanc (21ºN), sledge catches were dominated numerically by the suspension-feeding anemone *Actinoscyphia aurelia* and the irregular spatangoid echinoid *Pourtalesia miranda* (Rice et al., 1979). The anemone is abundant (>1 m^{-2}) in both the catches and photographs obtained between 1000 and 2000 m in this area (Aldred et al., 1979). At 4000 m off Cap Blanc, virtually the only organism visible in bottom photographs was the xenophyophore *Reticulammina labyrinthica* (Rice et al., 1979; Tendal and Gooday, 1981). Individual specimens reached 6 cm maximum dimension (Gooday and Tendal, 1988), considerably larger than specimens of the same species from the Porcupine Abyssal Plain (Gooday, 1996a). Further north, off the Moroccan coast, the hexactinellid sponge *Pheronema carpenteri* occurs in overall densities of up to 0.17 individuals m^{-2} at depths between 740 and 820 m (Barthel et al., 1996). Although considerably lower than the *Pheronema* densities recorded in the

Porcupine Seabight (Rice et al., 1990), local densities off Morocco may reach up to 6 individuals m^{-2} in single photographs. Of particular interest was the distribution of live and dead sponges, which suggested a progressive upslope movement of the population, possibly in search of a richer food supply.

Galeron et al. (2000), observed that total metazoan density and biomass (megafauna, macrofauna, and meiofauna) decreased with increasing depth and decreasing food supply across the EUMELI stations. However, each faunal component studied responded differently to the variation in food input. Overall, the megafauna dominated biomass at the most eutrophic site, macrofauna dominated at intermediate food conditions, and meiofauna dominated at the most oligotrophic site. However, within metazoan size groups, some taxa (e.g., sponges, tunicates and holothuroids) did not follow this pattern, implying that food availability is not the sole control on community structure.

There is a close relation between benthic foraminiferal biomass and surface primary production along the Northwest African margin (Altenbach, 1988; Altenbach and Sarnthein, 1989). The species composition of foraminiferal assemblages is also controlled, at least partly, by organic-matter fluxes (Lutze, 1980; Lutze and Coulbourne, 1984). In particular, a *Uvigerina peregrina* biofacies predominates in areas to the south of 22ºN (near Cap Blanc) where the annual flux rate exceeds 2–3 g C m^{-2}, whereas a *Cibicidoides wuellerstorfi/C. kullenbergi* biofacies occupies lower-productivity areas to the north (Lutze and Coulbourne, 1984; Altenbach, 1988). Other factors influencing foraminiferal faunas along this margin include bathymetry, sediment granulometry and bottom-water oxygen concentrations.

Northeast Atlantic abyssal plains

The faunas of Northeast Atlantic abyssal plains are known in varying degrees of detail as a result of recent national and international sampling programs (Table 5.1). The Porcupine Abyssal Plain has been particularly well studied within the framework of BENGAL and earlier projects funded by the European Union. Many of the biological and geochemical results of the BENGAL Project have appeared in a recent special volume (Billett, 2002).

Megafauna: Thurston et al. (1994) have provided a detailed account of the megafauna (>4 mm) of the Porcupine Abyssal Plain, Madeira Abyssal Plain (MAP) and Great Meteor East region (GME) and have summarized comparable published data (derived from net catches and *in situ* photographs) from other abyssal plains (Table 5.3). One of the most striking conclusions of this analysis is that megafaunal biomass is much greater (16–39×) at 48ºN on the Porcupine Abyssal Plain than it is in the Madeira Abyssal Plain and the Great Meteor East region areas (both at 31ºN); there is a corresponding but much smaller disparity in density values. The biomass differences are mirrored in the taxonomic composition of the megafauna in regions to the north of 40ºN and south of 33ºN. Holothurians, actiniarians, and to a lesser extent asteroids, constitute a major proportion of the invertebrate megafauna, both in terms of abundance and (particularly for holothurians) biomass, on the Porcupine Abyssal Plain (Thurston et al., 1994) and Iberian Abyssal Plains (Feldt et al., 1989). On the Madeira Abyssal Plain and in the Great Meteor East area (i.e. to the south of 33ºN) the megafauna is dominated by asteroids and natant decapods, with holothurians constituting a relatively small proportion of the fauna. Similarly, the Cape Verde Abyssal Plain (CVAP) harbors a sparse megafauna (0.00052 individuals m^{-2}) (Bett et al., 1995). One may note that values for megafaunal density from the Cape Verde Abyssal Plain given by Sibuet et al. (1993), which are an order of magnitude greater than those of Bett et al. (1995), are based on the >1mm fraction and therefore include animals normally considered as macrofauna. Thurston et al. (1994) have suggested that the large holothurian-dominated biomass on the Porcupine Abyssal Plain is supported by the phytodetritus flux which occurs in this area but not to the south of 33ºN.

Sibuet (1985) has presented a survey of the echinoderm fauna of deep Atlantic basins, mainly abyssal plains but including some continental-margin regions. Echinoderms constitute a highly variable proportion of the total megafauna in samples from >4000 m: 12% (Angola Basin, 5250 m), 33% (Cape Basin, 4650 m), 63% (Demerara Plain near the Amazon cone, 4420 m), 19% (Demerara Plain, 4850 m), 20% (Vema fracture zone, 5100 m), 3% (Cape Verde Abyssal Plain, 5190 m), 48% (southern Bay of Biscay, 4450 m), 20% (northern Bay of Biscay, 4750 m), 17% (northern Bay of Biscay, 4200 m), 75% (Porcupine Abyssal Plain, 4820 m). The dominant classes are always either holothurians (Angola Basin, Demerara Abyssal Plain, Vema fracture zone, Cape Verde Abyssal Plain, northern Bay of Biscay) or ophiuroids (Cape Basin, southern Bay of Biscay, Porcupine Abyssal Plain). Maximum

Table 5.3
Biomass and abundance of selected benthos in the deep Atlantic Ocean[1]

Location	Water depth (m)	Meiofauna		Macrofauna		Megafauna		References
		Density (m^{-2})	Biomass[2] ($g\,m^{-2}$)	Density (m^{-2})	Biomass[2] ($g\,m^{-2}$)	Density (m^{-2})	Biomass[2] ($g\,m^{-2}$)	
NORWEGIAN–GREENLAND SEA								
Vøring Plateau	1200–1500	110000	0.89	610 (500 µm)	3.28	4 (top 3 taxa)	7	Romero-Wetzel and Gerlach (1991)
export stn	1325–1424		0.20–0.57		13.06–25.48			Jensen et al. (1992b)
import stn	1325–1424		0.6–1.00		17.21–32.10			Jensen et al. (1992b)
	1245	172000	0.007 (C)					Jensen (1988)
	1255	204000	0.006 (C)					Jensen (1988)
	1426	107000	0.010 (C)					Jensen (1988)
Norwegian Basin	2725			6440				Dahl et al. (1976)
	2992			1848				Dahl et al. (1976)
	2998			1026				Dahl et al. (1976)
	3665			54–74				Dahl et al. (1976)
	2600–3600	71000		740		0.61		Sibuet et al. (1989)
	3062	200000	0.010					Jensen (1988)
SE Jan Mayen	2133	60000	0.004					Jensen (1988)
Lofoten Basin	2957			187–264 (250 µm)				Dahl et al. (1976)
	3213			422				Dahl et al. (1976)
	3294	20000	0.003					Jensen (1988)
Spitzbergen Basin	3203			355				Dahl et al. (1976)
	3209			3188				Dahl et al. (1976)
Greenland Basin	2465			288				Dahl et al. (1976)
	2492			829				Dahl et al. (1976)
	2904			1944				Dahl et al. (1976)
	2941			759				Dahl et al. (1976)
	3294			1292				Dahl et al. (1976)
	3306			4509				Dahl et al. (1976)
	3606			388				Dahl et al. (1976)
	3718			4654				Dahl et al. (1976)

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Table 5.3, *continued*

Location	Water depth (m)	Meiofauna		Macrofauna		Megafauna		References
		Density (m^{-2})	Biomass^2 ($g\,m^{-2}$)	Density (m^{-2})	Biomass^2 ($g\,m^{-2}$)	Density (m^{-2})	Biomass^2 ($g\,m^{-2}$)	
Norwegian Shelf	970	138 000	0.073					Jensen (1988)
NORTHEASTERN ATLANTIC								
Iceland Basin	2880					0.91–9.38	1.27–15.56	Christiansen and Thiel (1992)
Rockall Trough	1800			4320 (420 μm)	4.80 (wet)			Gage (1978)
	1800			1636 (420 μm)	3.72 (wet)			Gage (1978)
	2000			4156	4.156			Gage (1978)
	2500			1332	3.08			Gage (1978)
	2900			3052	4.08			Gage (1978)
	2875			2903 (297 μm)	0.92 (dry)			Gage (1977)

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Table 5.3, *continued*

Location	Water depth (m)	Meiofauna		Macrofauna		Megafauna		References
		Density (m^{-2})	Biomass ^{2} ($g\,m^{-2}$)	Density (m^{-2})	Biomass ^{2} ($g\,m^{-2}$)	Density (m^{-2})	Biomass ^{2} ($g\,m^{-2}$)	
Porcupine Seabight	2650	54 500		1180		1.0		Sibuet et al. (1989)
	4820	50 000		420		0.31		Sibuet et al. (1989)
	300	502 000 (42 μm)						Vanreusel et al. (1995b)
	600	1 410 000						Vanreusel et al. (1995b)
	900	1 523 000						Vanreusel et al. (1995b)
	1200	1 500 000						Vanreusel et al. (1995b)
	1500	1 283 000						Vanreusel et al. (1995b)
	500					1	5.0	Lampitt et al. (1986)
	500	2 604 000 (42 μm)	1160 (AFDW)					Pfannkuche (1985)
	510	1 963 000	0.093					Pfannkuche (1985)
	960	1 593 000	0.075				Pfannkuche (1985)	
	1492	943 000	0.061					Pfannkuche (1985)
	2000	828 000	0.060					Pfannkuche (1985)
	2510	744 000	0.059					Pfannkuche (1985)
	2785	900 000	0.063					Pfannkuche (1985)
	3567	663 000	0.055					Pfannkuche (1985)
	4167	528 000	0.051					Pfannkuche (1985)
	4500	362 000	0.036					Pfannkuche (1985)
	4850	315 000	0.036					Pfannkuche (1985)
	4100					0.01	0.05–0.07	Lampitt et al. (1986)

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Table 5.3, *continued*

Location	Water depth (m)	Meiofauna		Macrofauna		Megafauna		References
		Density (m^{-2})	Biomass^2 ($g\,m^{-2}$)	Density (m^{-2})	Biomass^2 ($g\,m^{-2}$)	Density (m^{-2})	Biomass^2 ($g\,m^{-2}$)	
Porcupine Abyssal Plain	4850					0.014 (4.5 mm)	0.169	Thurston et al. (1994)
	4850					0.008 (otter trawl)	0.189	Thurston et al. (1994)
	4000–4800					0.004 (10 mm)	0.081	Rutgers van der Loeff and Lavaleye (1986)
	??					0.002 (30mm)	0.054	Feldt et al. (1989)
	4500–4550					0.194 (>20 mm)		Christiansen and Thiel (1992)
	4350–4750					0.093 (>30 mm)		Sibuet and Coic (1989)
Bay of Biscay (BIOGAS)	2100			2783 (250 µm)				Dinet et al. (1985)
	2900	[39 000]		4635 (250 µm)		0.020		Tietjen (1992)
	4100			3612				Tietjen (1992)
Bay of Biscay (NW)	2150			2783	0.21 (dry)			Tietjen (1992)
	1920–2245					0.292 (1 mm)		Sibuet and Segonzac (1985)
	2878–3380					0.069		Sibuet and Segonzac (1985)
	4134–4240					0.048		Sibuet and Segonzac (1985)
	4706–4825					0.032		Sibuet and Segonzac (1985)
Bay of Biscay (SE)	1895–1995					0.044		Sibuet and Segonzac (1985)
	4434–4475					0.021		Sibuet and Segonzac (1985)
BIOTRANS Site	3800–4590	320 000	0.007 [C]	2000	0.106	1.07–4.14	0.20–2.18	Pfannkuche (1992)
Madeira Abyssal Plain	5400–5450					0.0035 (>4.5 mm)	0.004	Thurston et al. (1994)
	5400–5450					0.002 (>18.5 mm)	0.011	Thurston et al. (1994)

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Table 5.3, *continued*

Location	Water depth (m)	Meiofauna		Macrofauna		Megafauna		References
		Density (m^{-2})	Biomass^2 ($g\,m^{-2}$)	Density (m^{-2})	Biomass^2 ($g\,m^{-2}$)	Density (m^{-2})	Biomass^2 ($g\,m^{-2}$)	
Iberian Abyssal Plain	5200					0.001 (>30 mm)	0.007	Feldt et al. (1989)
NORTHEAST TROPICAL ATLANTIC								
EUMELI	1700	1 041 514 (40 μm)		2568 (500 μm)		0.8624 (>2 cm)		Sibuet et al. (1993)
	1700			5403 (250 μm)				Cosson et al. (1997)
	3100	479 247		1124 (500 μm)		0.0702		Sibuet et al. (1993)
	4600	130 189		88 (500 μm)		0.0033		Sibuet et al. (1993)
	3100			1856 (250 μm)				Cosson et al. (1997)
	4600					5.2 ha^{-1}		Bett et al. (1995)
Vema Fracture Zone	5100			860	0.08 (dry)			Khripounoff et al. (1980)
	5100	130 000		200		0.033		Sibuet et al. (1989)
Demerara Abyssal Plain	4420	278 000	0.010 [C]	2159	0.09 (dry) 0.039 [C]	0.011	0.010 [C]	Sibuet et al. (1984, 1989)
	4800		0.005 [C]		0.014 [C]		0.0265 [C]	
Off N. Morocco	400	2 480 000		1265	1.12			Pfannkuche et al. (1983)
	600	1 465 000		1546	1.99			Pfannkuche et al. (1983)
	800	1 175 000		1132	1.76			Pfannkuche et al. (1983)
	1200	631 000		932	1.75			Pfannkuche et al. (1983)
	1500	620 000		1004	1.30			Pfannkuche et al. (1983)
	2000	570 000		832	0.82			Pfannkuche et al. (1983)
	2435	550 000						Pfannkuche et al. (1983)
	3000	447 000		352	0.45			Pfannkuche et al. (1983)
Cape Verde Basin (Cape Verde Abyssal Plain)	4950	62 000		95		0.012		Sibuet et al. (1989)
	5190	87 000		100		0.007		Sibuet et al. (1989)
	4700			232				Cosson et al. (1997)

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Table 5.3, *continued*

Location	Water depth (m)	Meiofauna		Macrofauna		Megafauna		References
		Density (m^{-2})	Biomass^2 (g m^{-2})	Density (m^{-2})	Biomass^2 (g m^{-2})	Density (m^{-2})	Biomass^2 (g m^{-2})	
WESTERN ATLANTIC								
Hatteras Abyssal Plain	5300		0.038 [C]		0.0064 [C]			Tietjen et al. (1989)
Venezuela Basin	3450	131 000	0.0394 [C]	678	0.0152 [C]	0.0025	0.0010 [C]	Tietjen (1992)
(Caribbean Sea)	3950	81 000	0.0173 [C]	263	0.0026 [C]	0.0031	0.0012 [C]	Tietjen (1992)
	5050	49 000	0.0132 [C]	238	0.0053 [C]	0.0016	.0064 [C]	Tietjen (1992)
NORTHWEST ATLANTIC								
Gayhead–Bermuda Transect	1110–1180			3070–4430	0.845–1.216 (420 μm)			Rowe et al. (1974)
DOS-1	1850			3218	9.45			Smith (1978)
	1900			2020	15.60			Rowe et al. (1974)
	2080			700	0.325			Rowe et al. (1974)
DWD	2200			22 988	0.556			Smith (1978)
	2425			1344	0.871			Rowe et al. (1974)
	2710			1089; 742	0.485, 0.529			Rowe et al. (1974)
ADS	2750			8764	2.143			Smith (1978)
	2885–2950			309–1150	0.154–1.485			Rowe et al. (1974)
HH	3000			2143	0.653			Smith (1978)
DOS-2	3650			1632	0.771			Smith (1978)
	3923			466	0.158			Rowe et al. (1974)
JJ	4670			753	0.220			Smith (1978)
KK	4830			285	0.180			Smith (1978)
	4901–4950			175	0.218			Rowe et al. (1974)
NN	5080			117	0.078			Smith (1978)
MM Sargasso	5200			259	0.142			Smith (1978)

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Table 5.3, *continued*

Location	Water depth (m)	Meiofauna		Macrofauna		Megafauna		References
		Density (m^{-2})	Biomass^2 ($g\,m^{-2}$)	Density (m^{-2})	Biomass^2 ($g\,m^{-2}$)	Density (m^{-2})	Biomass^2 ($g\,m^{-2}$)	
Cape Hatteras								
1985	500–1599					0.88		Hecker (1994)
	604			46 255 (300 μm)				Blake and Grassle (1994)
1988–91	850			55 500 (300 μm)	54.52			Schaff et al. (1992)
1985	2003			8950				Blake and Grassle (1994)
1992	500–1599			37 282 (300 μm)		2.65		Hecker (1994); Blake and Hilbig (1994)
	580–2000					9.93–12.41 (>2 mm)		Brown (1991)
	3000					1.015		Brown (1991)
	3500					0.786		Brown (1991)
Long Bay	600–1799					0.93		Brown (1991)
Cape Lookout	700–1599					0.49		Brown (1991)
1983–4	583			16 337 (300 μm)				Blake and Grassle (1994)
1988–91	850			21 400 (300 μm)	8.16			Schaff et al. (1992)
	1000			9130 (300 μm)				Blake and Grassle (1994)
	1500			5017				Blake and Grassle (1994)
	2000			5622				Blake and Grassle (1994)
	3006			870				Blake and Grassle (1994)
	3494			1000				Blake and Grassle (1994)
Cape Fear	850			9439 (300 μm)	7.19			Schaff et al. (1992)
Hatteras canyon	800–1599					0.29		Hecker (1994)

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Table 5.3, *continued*

Location	Water depth (m)	Meiofauna		Macrofauna		Megafauna		References
		Density (m^{-2})	Biomass[2] ($g\,m^{-2}$)	Density (m^{-2})	Biomass[2] ($g\,m^{-2}$)	Density (m^{-2})	Biomass[2] ($g\,m^{-2}$)	
New Jersey	600–1499					0.46		Hecker (1994)
	600–1499					0.24		Hecker (1994)
	1263				1.47 (300 μm)			Hathaway (1971)
	2132				5.5 (300 μm)			Hathaway (1971)
Carson canyon	1129			370.4	3.61 (520 μm)			Houston and Haedrich (1984)
U.S./Canada boundary	500–1300					2.61		Hecker (1994)
Scotian rise	4620	23 500		2215				Thistle et al. (1985)

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[1] Mesh size is given between parentheses where available.

[2] Biomasses are wet wt unless indicated otherwise.

densities for individual classes do not exceed 64 individuals m^{-2}, except at the Porcupine Abyssal Plain site where holothurian and ophiuroid densities reach 363 and 965 m^{-2}, respectively. Holothurian abundance was found to correlate well with organic-carbon flux.

Variations in megafaunal composition may have a temporal as well as a spatial aspect. Results from the BENGAL Project suggest that a striking and persistent shift in the composition of the megafauna occurred on the Porcupine Abyssal Plain during the 1990s (Billett et al., 2002). The holothurian *Amperima rosea* exhibited a massive increase in abundance, and *Ellipinion* cf *molle* (holothurian) and *Ophiocten hastatum* (ophiuroid) also showed substantial increases between 1989–1994 and 1996–1999. Billett et al. (2002) have argued that long-term changes in the quantity and/or quality of the organic-matter supply to the seafloor may underlie these fluctuations.

Megafaunal behavior can be addressed by means of seafloor photography. Examples of this approach being used in the Atlantic include determination of rates of movement in echinoderms in the Porcupine Seabight and Porcupine Abyssal Plain areas (Lampitt and Billett, 1985; Smith et al., 1997b), and feeding activities in an echiuran on the Cape Verde Abyssal Plain (Bett and Rice, 1993). In addition, a BATHYSNAP sequence obtained on the Madeira Abyssal Plain has provided remarkable documentation of test development in giant testate protists. The sequence shows three specimens of the xenophyophore *Reticulammina labyrinthica* undergoing a 3–10-fold increase in volume over an 8-month period. Growth occurred episodically and in distinct phases, each lasting about two days, during which sediment was collected and incorporated into the test. The growth phases were separated by periods of about two months during which the external appearance of the tests changed little. Gooday et al. (1993) suggested that the xenophyophores used the accumulated sediment as a source of both food and particles for test construction, thereby combining growth with deposit feeding.

Macrofauna: Macrobenthic density and biomass are also substantially higher on the Porcupine Abyssal Plain than on the Madeira Abyssal Plain, by factors of approximately 5 and 35, respectively (Rice, 1993). Macrofaunal densities on the Cape Verde Abyssal Plain are very low, only 88 individuals m^{-2} of which 59% are polychaetes (Sibuet et al., 1993). Apart from protobranch bivalves (Allen and Sanders, 1996), polychaetes are the only macrofaunal group to have been studied in any detail. Paterson et al. (1994a,b) compared polychaete populations at sites on three Northeast Atlantic abyssal plains (Porcupine, Madeira, Tagus) with those from other regions in the Atlantic and Pacific Oceans. Polychaetes were more abundant on the Porcupine Abyssal Plain (302 individuals m^{-2}) than on the Tagus Abyssal Plain (169 individuals m^{-2}) and Madeira Abyssal Plain (178 individuals m^{-2}); these densities represented 17%, 27% and 25%, respectively, of all metazoans >300 μm and 35%, 58% and 49% of the macrofaunal taxa >300 μm. The Porcupine Abyssal Plain yielded 32 species and the Tagus Abyssal Plain only 11 species. Several undescribed species of *Aphelochaeta, Prionospio* and *Sigambra* were represented at all three sites. The five most abundant families on the Porcupine Abyssal Plain were the Spionidae (25%), Cirratulidae (22%), Sabellidae (10%), Ophelliidae (8%) and Paraonidae (8%); on the Tagus Abyssal Plain the Cirratulidae (24%), Spionidae (17%), Pilargidae (11%), Ophelliidae (11%) and Paraonidae (9%); on the Madeira Abyssal Plain the Sabellidae (24%), Flabelligeridae (20%), Paraonidae (16%), Spionidae (8%) and Pisionidae (6%). Rarefaction curves indicated that family richness was higher on the Porcupine Abyssal Plain and the Tagus Abyssal Plain than on the Madeira Abyssal Plain.

Meiofauna: Vincx et al. (1994) provides an overview of meiofauna from the Northeast Atlantic, including the Porcupine Abyssal Plain, the Madeira Abyssal Plain, the Cape Verde Abyssal Plain, the Iberian Abyssal Plain and the BIOTRANS area (Figs. 5.1, 5.2); additional data on the nematode component are provided by Vanreusel et al. (1995a) and Lambshead et al. (1995). Total meiofaunal and nematode densities are higher at northern abyssal sites (e.g., BIOTRANS, Porcupine Abyssal Plain; 45–48ºN) than on the Madeira Abyssal Plain (30ºN) and Cape Verde Abyssal Plain (21ºN); for example, total densities are almost five times higher on the Porcupine Abyssal Plain than on the Cape Verde Abyssal Plain (Vanreusel et al., 1995a). Other differences are apparent among the nematode fauna. In particular, there is a substantially higher proportion of nematodes inhabiting the upper centimeter of sediment on the Madeira Abyssal Plain compared to the Porcupine Abyssal Plain (Lambshead et al., 1995), and mean individual nematode body weight is significantly lower on the Cape Verde Abyssal Plain compared to the Porcupine Abyssal Plain, mainly due to the greater abundance of large nematodes at the more northerly site (Vanreusel et al., 1995a). These contrasts are believed to reflect differences in the supply of organic matter to the seafloor, in particular the fact that the deposition of aggregated phytodetritus is restricted to the northern part of the Northeast Atlantic (Porcupine Abyssal Plain and BIOTRANS area).

Gooday (1996b) has given a detailed analysis at the species level of foraminiferal assemblages in multiple-corer samples (top 1 cm of sediment) collected from the Porcupine Abyssal Plain, Madeira Abyssal Plain and Cape Verde Abyssal Plain during August, 1989. Foraminifera accounted for 61–76% of the total meiofauna in these samples. Densities were higher on the Porcupine Abyssal Plain than at the two southern sites, and part of the difference is accounted for by specimens inhabiting the phytodetrital layer, present only at on the Porcupine Abyssal Plain. The phytodetrital foraminiferal populations were of low diversity and dominated by a few apparently opportunistic species (e.g., *Epistominella exigua*). These species are typically much less common in the underlying sediment, so that the phytodetrital assemblages can be regarded as being to some extent 'decoupled' from those in the underlying sediment. Total populations, from the phytodetritus plus the 0–1 cm sediment layer, are highly diverse (123–167 species) and broadly similar in their species composition. However, in addition to the phytodetritus-exploiting species, some sediment-dwelling species of *'Hyperammina', Lagenammina, Leptohalysis* and *Reophax* were more abundant at the Porcupine Abyssal Plain site whereas a few, such as *Lagenammina tubulata* and *Subreophax aduncus*, were more abundant at the southern sites.

Northeast Atlantic Seamounts

Seamounts are abundant in the deep Atlantic (Epp and Smoot, 1989), but there have been few ecological descriptions of their benthic communities (Rogers, 1994). The best studied are the Meteor and Vema Seamounts, but even here the papers are few, and mostly are taxonomic in nature (citations within Rogers, 1994). Thiel (1970, 1975) studied the meiofaunal communities of the Meteor Seamount, 1600 km from the coast of Africa, and the Josephine Seamount, 300 miles west of southern Portugal in a region of higher primary productivity. Samples taken from the summit plateaus at depths of 206–355 m and 292–350 m yielded mean densities of 40.3 ± 14.0 individuals cm^{-2} and 22.7 ± 7.4 individuals cm^{-2} on Josephine and Meteor, respectively. Samples taken by Rachor (1975) just southwest of the Josephine Seamount were much lower. The Meteor data suggest little difference in meiofauna between the shallow seamount and the Iberian Abyssal Plain 5000 m deeper, although primary productivity may be twice as much above the Iberian deep sea. Heavy predation pressure by fishes and strong currents above the Great Meteor Seamount may have reduced meiofaunal densities (Thiel, 1975). In the South Atlantic, Russian investigations have contributed to knowledge of the seamount faunas, for example, on the Valdivia Seamount (Kamenskaya, 1988).

North Atlantic necrophages

Necrophages (animals which scavenge dead carcasses) play an important role in the cycling of organic matter on the deep-sea floor (Haedrich and Rowe, 1977; Smith, 1985a). Megafaunal necrophages usually congregate around large carcasses within hours of the carcass reaching the seabed, and are capable of consuming all but the bones within days (Hargrave, 1985). Among the commonest necrophages in the deep Atlantic are fish (particularly macrourids, ophidioids and synaphobranchiid eels), natantian decapods, and amphipods (almost entirely lysianassids). These highly mobile benthopelagic animals appear to be concentrated within, at most, a few meters of the deep-sea floor, but can swim up hundreds or even thousands of meters into the overlying water column (Smith et al., 1979; Thurston, 1990; Sainte-Marie, 1992). In particular, the amphipod *Eurythenes gryllus* undergoes an ontogenetic migration hundreds of meters up into the water column (Charmasson and Calmet, 1987; Christiansen et al., 1990; Christiansen, 1996). It is notable that dominant scavengers in the Pacific, such as hagfish, sablefish and ophiuroids (Smith, 1985a), are not observed at bait in the deep Atlantic.

The existence of necrophages in the deep sea was first revealed in the Northeast Atlantic when amphipods were caught in baited traps deployed from the Prince of Monaco's yacht *L'Hirondelle* during its campaign of 1888 (Chevreux, 1900; Richard, 1934). Baited traps are the most effective means of sampling scavenging amphipods (Thurston, 1979; Hargrave, 1985; Hargrave et al., 1995), whereas larger animals such as fish and decapods are best documented by means of baited cameras (Isaacs, 1969). Both fish and amphipods attracted to bait include opportunistic generalist feeders as well as the more specialized scavengers (Thurston, 1979; Thurston et al., 1994). However, in the case of both amphipods and fish, the scavengers which are abundant around bait represent only a small proportion of the species known to be present in the deep sea (Thurston, 1979, 1990; Merrett and Haedrich, 1997).

Although still limited, information on the taxonomic composition, distribution and ecology of Atlantic necrophage faunas is growing. Many species are widely distributed in the Northeast and Tropical Atlantic. According to Thurston (1990), the region between 8ºN and 50ºN supports a 'single faunal entity'. Most of the amphipods caught and photographed on the Iberian Abyssal Plain (4885 m) by a baited fish trap equipped with a camera belonged to the genera *Orchomene* and *Paralicella*. The photographic record revealed a slow increase in numbers of amphipods present on the bait, and subsequent fluctuations in abundance which may have been related to the presence of fish in the trap and to current activity. These interactions were examined further by Lampitt et al. (1983), who used methods similar to those of Thurston (1979) at a site 4009 m deep close to the mouth of the Porcupine Seabight. Fluctuations in the numbers of amphipods visible on the bait could be related to tidal cycles and to the presence of small black fish (probably *Paraliparis bathybius*). Amphipods were most abundant when current velocities were low. However, appearances of the black fish coincided with the flood tide (i.e., higher current velocities) and also with a marked decline in numbers of visible amphipods, suggesting that the fish preyed on the amphipods.

In situ studies of feeding and digestion by *Eurythenes gryllus*, conducted on the Nares Abyssal Plain (3421 m) using time-lapse photography, revealed rapid consumption of bait (1.8 g individual^{-1} h^{-1}) by large amphipods (3–6 cm). These crustaceans ingested 30–60% of their body weight within 12 h (Hargrave, 1985). From studies on the Nares and Sohm Abyssal Plains using traps which allowed timed exposure to bait, it was established that, once *E. gryllus* starts to feed on carrion, digestion is rapid, with 0.4–1.0% of the gut contents lost per hour and 95% digested in 1–10 days (Hargrave et al., 1995). *Eurythenes* has mandibles and a gut adapted to rapid gluttonous feeding; it apparently can survive long periods between meals. Other lysianassid scavengers (e.g., *Orchomene*) have smaller guts and seem to process food in a more continuous manner (Sainte-Marie, 1992). Sainte-Marie (1992) suggested that none of the deep scavenging amphipods are completely obligate necrophages, and that foraging in the water column is required to compensate for scarce resources (see also Thurston, 1990).

Photographic records obtained on the Porcupine and Madeira Abyssal Plains using a baited time-lapse camera system (BATHYSNACK) revealed that decapods are also common scavengers in the deep Atlantic (Thurston et al., 1994). On the Porcupine Abyssal Plain, the dominant necrophages identifiable in photographs were fish, mainly *Coryphaenoides (Nematonurus) armatus* and *Pachycara bulbiceps*, and the decapod *Munidopsis* spp. Another decapod, the shrimp *Plesiopenaeus armatus*, dominated necrophages photographed on the Madeira and Cape Verde Abyssal Plains but was very rarely photographed at bait on the Porcupine Abyssal Plain, despite being present in trawl samples taken at this site. These latitudinal differences between necrophages on Northeast Atlantic abyssal plains are striking, and possibly linked to differences in food availability. The greater abundance of scavenging fish on the Porcupine Abyssal Plain than on the Madeira or and Cape Verde Abyssal Plains may reflect higher densities of large animals present in the pelagic community, and hence of carrion on the seafloor, on the Porcupine Abyssal Plain (Merrett, 1987). *Plesiopenaeus armatus* appears to be a facultative necrophage which is deterred from scavenging on the Porcupine Abyssal Plain by the presence of large fish, but is able to do so at the southern sites where fish are scarcer (Thurston et al., 1994). A species of *Plesiopenaeus* was also attracted, together with macrourid and ophidiid fish, to a baited camera system deployed at 4850m on the Demerara Abyssal Plain (Rowe et al., 1986).

As part of the BIOGAS program, Desbruyères et al. (1985b) studied necrophages with baited traps along a bathymetric transect between 200 m and 4700 m across the continental margin in the northern Bay of Biscay. They also deployed baited cameras 7 m, 100 m and 200 m above the seafloor at three stations deeper than 4000 m. Necrophages caught in the traps were dominated by reptant decapods (*Geryon, Munida*) and isopods (Gnathiidae) between 200m and 1800 m and by fish and amphipods below this depth. Fish were not observed at all above 1800 m. Among the fish, sharks were the main group attracted to bait on the Meriadzek Terrace (1800–3000 m) and the Le Danois Bank (1980 m), while rattails (macrourids) dominated below 4000 m. Desbruyères et al. (1985b) noted a correlation between maximum current velocities and the highest abundances of macrourids at their 4700 m station. They also observed that an attack on the bait by a single fish provoked an immediate concentration of congeneric individuals around the bait.

Unique information about the biology of abyssal scavenging fish in the Atlantic and Pacific Oceans has been obtained using AUDOS, a free vehicle which attracts fish to bait in which small transponders are embedded (e.g., Priede et al., 1990, 1991, 1994a,b; Armstrong et al., 1992; reviewed by Merrett and Haedrich, 1997). The fish readily ingest these transponders along with the bait. The transponders report back acoustically to a sonar on the central AUDOS vehicle, allowing the movements of the fish on the ocean floor to be tracked over a range of up to 500 m. The AUDOS experiments have demonstrated that benthopelagic species living in the water near the seafloor do not sit and wait for carcasses, as previously believed, but actively search for them. The first fish to arrive at bait in the Northeast Atlantic were *Coryphaenoides armatus* and *Histiobranchus bathybius*. Having ingested the bait (and transponder), the fish generally wandered slowly away from the food source, usually disappearing from the range of the AUDOS sonar within a period of twelve hours. Recent observations made on the Porcupine Abyssal Plain suggest that there were no significant differences in the arrival times or swimming speeds of fish before and after the arrival of phytodetritus at this site (Smith et al., 1997a). These results contrast with the observation that macrourids arrived more slowly at bait in the North Pacific Ocean before the spring bloom than they did later in the year following a pulsed input of organic matter (Priede et al., 1994a).

Equatorial and South Atlantic

Compared with the North Atlantic, the deep-sea benthos of the Equatorial Atlantic, and particularly the South Atlantic, is rather poorly known. Most studies have concerned the abundance, diversity and distribution of particular groups, in some cases as part of an ocean-wide study of distribution and diversity patterns. Examples include ascidians (Monniot and Monniot, 1978; Monniot, 1979), protobranch bivalves (Allen and Sanders, 1996) and echinoderms (Sibuet, 1979, 1985). Russian expeditions have also contributed much to knowledge of the taxonomy and distribution of animals in the deep South Atlantic (e.g., volumes edited by Vinogradova, 1990, 1993; see also Vinogradova, 1997). A synthesis of meiofaunal, macrofaunal and megafaunal densities in the Angola and Cape Basins (Southeast Atlantic), the Demerara Abyssal Plain and the Vema Fracture Zone (Equatorial Atlantic) as well as in North Atlantic basins has been presented by Sibuet et al. (1989). More recently, Rex et al. (1993) have analyzed latitudinal trends in diversity among macrofaunal bivalves, gastropods and isopods from the Greenland–Norwegian Sea in the north to the Argentine Basin in the south. Southern Hemisphere sites include the Brazil, Angola and Cape Basins in addition to the Argentine Basin.

Relatively few studies, however, have addressed smaller-size fractions of the benthic fauna at particular sites in the South Atlantic. One of the few is that of Sanders (1969), who presented data for macrofauna ($>420\,\mu$m) from a transect through the oxygen minimum zone (OMZ) off Walvis Bay, Namibia. At depths of 100 m, where the oxygen content of the bottom water was <2% saturation, faunal density was low (125 individuals m^{-2}). Species richness was low as well, comparable to that found at 5000 m under the oligotrophic Sargasso Sea. At 200 m (11% oxygen saturation), densities were exceptionally high (30 000 individuals m^{-2}), but diversity was only slightly increased. At 300 m (15% saturation) diversity remained low, but densities dropped to 8000 individuals m^{-2}. Densities at 450 m, 630 m, 975 m and 2140 m were 2300, 5400, 4750, and 4140 individuals m^{-2}, respectively. Diversity, estimated by rarefaction, increased with depth and increasing oxygen saturation through the 975 m station, but declined again at 2140 m. Sanders (1969) noted that macrofaunal patterns along the Walvis Bay transect, a gradient of oxygen stress, resemble those observed along gradients of organic or chemical pollution. Maximal densities combined with low diversity are observed at the edge of the stressed conditions.

In a recent study, Soltwedel (1997) described meiofauna on the shelf, slope and abyssal plains (27–4601 m) off the tropical West African coast between Guinea (10ºN) and Angola (17ºS). This part of the eastern equatorial Atlantic is subject to coastal upwelling, which varies seasonally and geographically but is never sufficiently intense to result in the formation of an oxygen minimum zone. Meiofaunal abundance and biomass generally decrease fairly regularly with increasing water depth. However, the rate of increase varies in different parts of the margin, and is usually fairly well correlated with upwelling intensity, as indicated by concentrations of chloroplastic pigments in the sediments. In some regions away from the main upwelling centers, densities are relatively low, despite fairly high pigment concentrations. This discrepancy may be due to the degradation of phytodetrital fluxes during lateral advection by subsurface currents.

MICROBIAL PROCESSES

The earliest direct observations of bacterial populations in the deep sea were made in the nineteenth century on samples taken at 5100 m in the Mediterranean by the French vessel *Talisman* (Certes, 1884), while the first quantitative data on the rates of microbial activity were obtained in the Pacific Ocean during the 1950s (Morita and Zobell, 1955; Zobell and Morita, 1957a,b). During the last three decades, however, work carried out in the North Atlantic has contributed enormously to the rapid development of ideas about deep-sea bacterial ecology (Deming and Baross, 1993). In this section we highlight some of these advances.

A landmark event in the history of modern deep-sea microbiology was the sinking of the DSV[7] *Alvin* off New England at a depth of 1540 m in 1968, and the subsequent recovery of its relatively undegraded lunch nearly a year later. Microbiologists interpreted the lack of decomposition in the lunch to indicate that metabolic rates of deep-sea microbes were much slower than those in shallow water (Jannasch et al., 1971). To a great extent, the results of this 'experiment' were misleading. The lack of substantial decomposition can be largely explained by the way in which the lunches were sealed, and therefore insulated from the deep-sea scavengers and bacteria, rather than to slow rates of deep-sea microbial activity (Sieburth and Dietz, 1972). Nevertheless, the *Alvin* lunch incident strongly influenced the direction of deep-sea biology, and initiated a generation of microbiological experiments based on work with *in situ* free vehicles or submersibles (Jannasch and Wirsen, 1973, 1983; Wirsen and Jannasch, 1986).

An important theme in deep-sea microbiological studies has been quantification of the abundance and ecological role of bacteria. Much of this work has been conducted in the North Atlantic (e.g., Deming, 1985; Lochte and Turley, 1988; Turley and Lochte, 1990; Meyer-Reil and Köster, 1992; Lochte, 1992; Deming and Yager, 1992; Deming and Baross, 1993; Boetius and Lochte, 1994, 1996; Turley et al., 1995; Turley, 2000; Turley and Dixon, 2002). Bacterial densities and production tend to decrease with water depth, but the correlation is weak. Flux of particulate organic matter (POC) to the seafloor seems to exert a stronger influence on bacterial populations. Both biomass and the rate of utilization of dissolved organic carbon (DOC) are particularly high at high latitudes, where organic-matter inputs are substantial and seasonally variable. The highest bacterial densities ever recorded in deep-sea sediments were near the HEBBLE site in the Northwest Atlantic, an area which receives an abundant food supply from the activity of currents (Thistle et al., 1985, 1991). The relation observed between bacterial abundance and POC flux is consistent with evidence which emerged during the 1980s that microbial processes can operate at much faster rates than suggested by earlier studies, such as the *Alvin* lunch 'experiment' (Deming, 1985; Lochte and Turley, 1988; Gooday and Turley, 1990; Turley and Lochte, 1990).

Microbial decomposition rates are often substantially enhanced in food-rich microhabitats such as those provided by vertebrate and invertebrate carcasses, phytodetrital aggregates, benthic feces, animal burrows and particularly within animal guts which are hot-spots of barophilic activity. For example, experiments and observations conducted within the past decade in the North Atlantic (notably the BIOTRANS area), indicate that freshly deposited phytodetritus is subjected to intense microbial activity, and that remineralization of the labile component occurs rapidly within a period of about 5 days (e.g., Gooday and Turley, 1990; Poremba, 1994). Degradation is carried out by extracellular hydrolytic enzymes (Boetius and Lochte, 1994), which originate from a mixture of barotolerant bacteria conveyed from the upper water column on sinking aggregates and from indigenous barophilic bacteria (Lochte and Turley, 1988; Turley and Lochte, 1990; Turley et al., 1995). Small (3.5–6.0 μm long) barophilic bodonid flagellates are also associated with decomposing phytodetritus both in natural systems (Lochte and Turley, 1988) and in experimental systems (Turley et al., 1988), and may help to regulate the size of associated bacterial populations.

Remineralization rates depend on the quality or freshness of the sedimenting organic matter, which

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[7] *DSV*: Deep Submergence Vehicle.

depends in turn on the rapidity of transport from the euphotic zone. Seasonal variation in bacterial numbers and biomass have been recorded at the BIOTRANS area, presumably in response to seasonal phytodetritus deposition (Lochte, 1992), although such increases do not always accompany microbial degradation of phytodetritus (Boetius and Lochte, 1994). Insights derived from naturally or experimentally enriched samples, however, are not applicable to bacterial populations in oligotrophic deep-sea regions where activity is likely to be much slower.

ANIMAL TRACES

The Atlantic seabed is covered with surficial sediment features such as pits, burrows, mounds, tracks, fecal casts and resting traces. Many of these result from movement, burrowing, feeding, defecation or dwelling-construction by benthic invertebrates and fishes (Hollister et al., 1975). Detailed surveys of these features have been carried out in the Bay of Biscay (Mauviel and Sibuet, 1985), on the Northwest Atlantic continental margin (Hecker, 1994; Diaz et al., 1994), in the Porcupine Seabight (de Vaugelas, 1989), the Porcupine Abyssal Plain (Bett and Rice, 1993), the Cape Verde Abyssal Plain (Bett et al., 1995) and the Bahama Outer Ridge (Hollister et al., 1974).

Lebensspuren (traces of animal activity) often provide the main evidence for large organisms on abyssal plains and elsewhere in the deep sea, and may be particularly useful for quantifying buried megainfauna (large animals living within the sediments). These organisms, which are very difficult to sample using conventional methods, potentially play a major role in deep-sea community ecology and in the structuring of the deep-sea sedimentary environment (Romero-Wetzel and Gerlach, 1991; Bett et al., 1995). Bett et al. (1995) have provided a survey of *Lebensspuren* photographed on the Cape Verde Abyssal Plain using a wide-angle survey photographic system (WASP) and a camera attached to the epibenthic sledge. They found that the density of traces on this oligotrophic abyssal plain were two orders of magnitude greater than animal densities estimated from the same photographic records (8.72×10^{-2} traces vs 5.2×10^{-4} individuals m^{-2}). The traces were dominated by various kinds of spoke burrows, similar in form to those generally attributed to echiurans. Bett et al. (1995) estimated that the abundance of the spoke-burrow producers is of the order of 0.001 individuals m^{-2}, considerably greater than the density of surface-dwelling megabenthos. Similar traces occur on the Madeira Abyssal Plain (Huggett, 1987). Young et al. (1985) found no strong correlation of megafaunal diversity and trace diversity in the deep Caribbean. However, because the persistence of these features varies with both the physical environment and biological activity (Gage and Tyler, 1991), it is difficult to interpret animal densities directly from quantification of *Lebensspuren.*

Sediment properties can influence the composition of *Lebensspuren*. Huggett (1987) observed striking differences in categories of feeding traces present between areas of the Madeira Abyssal Plain underlain by turbidite deposits and those underlain by pelagic deposits. In particular, meandering traces, and small spokes, were virtually confined to the turbidites, while irregular traces were more common on the pelagic deposits. Huggett (1987) attributed these differences to the greater amounts of organic matter contained within turbidite deposits. Thus, *Lebensspuren* may have the potential to provide geologists with a simple visual method for mapping the distribution of turbidites and pelagic deposits.

DEMERSAL FISH

Merrett and Haedrich (1997) have provided an excellent overview of the biology of deep-sea demersal fish; Haedrich (1997) described their distribution and population ecology. Because some species are familiar and commercially important, the biology of demersal fish (e.g., their diets, reproduction and growth rates) is better understood than that of megafaunal invertebrates, particularly in the continental-slope settings that are now accessible to fisheries. The abundance of fish and invertebrates is not often compared. In the Porcupine Seabight they have roughly comparable biomass values and show a similar decrease with bathymetric depth (Merrett and Haedrich, 1997, figs. 4.3, 4.4 therein). On the Cape Verde Abyssal Plain, the density of the invertebrate megafauna is about three times the density of the fish (Bett et al., 1995).

The taxonomy and biogeography of bottom-dwelling fish are probably better known in the North Atlantic than in any other ocean. Regions like the Rockall Trough are particularly well studied (e.g., Gordon and Duncan, 1985, 1987a,b). Overall, the dominant deep-sea families are the Alepocephalidae (slickheads), Macrouridae (grenadiers) and Ophidiidae (cusk eels). The macrourids are particularly well represented at all depths from the upper slope to the abyss, and the ophidiids are unusual because the number of species increases with bathymetric depth, both absolutely and relative to the total number of fish species (Haedrich and Merrett, 1988; Merrett and Haedrich, 1997). The 505 species belonging to 72 families recorded from areas beyond the 200 m contour in the North Atlantic represent 39% of all deep-sea species (Merrett, 1994). Taxonomically, the North Atlantic fauna is most similar to the Indian Ocean fauna (40% of genera in common) and least similar to the Northeast Pacific fauna (14% of genera in common) (Merrett and Haedrich, 1997). As in the case of many invertebrate taxa, fish diversity is greatest on the middle and lower parts of the slope. In the North Atlantic, the species/family ratio, a useful measure of diversity, is lowest in the depth ranges 200–399 m (species/family ratio = 2.5) and >4000 m (species/family ratio = 2.9) and highest between 400 and 1999 m (species/family ratio = 6.0) (Merrett and Haedrich, 1997, table 2.1 therein). However, it is useful to be reminded (Merrett and Haedrich, 1997) that deep-sea fish are not a particularly diverse group compared with the small invertebrates on which perceptions of high deep-sea diversity are based.

Haedrich and Merrett (1988) have summarized the distribution of species in different bathymetric zones at a series of localities around the North Atlantic continental margin (slope and rise), the region where most demersal fish species occur. Their compilation indicates that two species, the synaphobranchiid eel *Synaphobranchus kaupi* and the grenadier *Coryphaenoides armatus,* are particularly widespread. On the other hand, many other species have restricted geographical ranges, leading Haedrich and Merrett (1988, 1990) to conclude that it is impossible to recognize real demersal fish communities in the deep North Atlantic. Like some invertebrate megafauna (e.g., Billett, 1991), fish species have well-defined bathymetric ranges on North Atlantic continental margins. However, these ranges are often different in different parts of the North Atlantic, and the impression they convey of vertically zoned communities are merely artifacts of species replacement patterns (Haedrich, 1997; Merrett and Haedrich, 1997). Most demersal species probably do not interact ecologically with each other to any great extent.

Truly oceanic abyssal demersal fish faunas (4000–6000 m) are less well documented than those from the continental margin. Nevertheless, the faunas of the Northeast Atlantic basins are reasonably well sampled, and their characteristics can be related to the structure of the overlying water column and patterns of primary production. Merrett (1987) recognized a northern assemblage (Porcupine Abyssal Plain, 49ºN) dominated by three grenadier species (two in the subgenus *Coryphaenoides* (*Chalinura*) and one in the subgenus *C.* (*Nematonurus*)) and the synaphobranchiid *Histiobranchus bathybius,* and a southern assemblage (Madeira Abyssal Plain, 30ºN) dominated by ipnopids (*Bathymicrops regis* and *Bathypterois longipes*) and the rattail *Echinomacrurus mollis*. The northern species are large benthopelagic fish with functional swim bladders and robust musculature, which imply considerable mobility and hence the ability to catch relatively large prey. Limited data suggest that fecundity is high. The southern species are small, microphagous fish which are either negatively buoyant, or able to maintain neutral buoyancy only by reducing ossification and musculature and therefore mobility. Limited data suggest that fecundity is low. Merrett (1987) advanced the hypothesis that these characteristics reflect the switch from the seasonal deposition of phytodetritus at the Porcupine Abyssal Plain site to the more oligotrophic, non-seasonal system which prevails on the Madeira Abyssal Plain. Subsequent sampling has modified this picture somewhat, with the recognition of two assemblages between 31–38ºN and another southern assemblage off the Northwest African margin around 20–22ºN (Merrett, 1992; Merrett and Haedrich, 1997). The latter appears to be related to high productivity associated with the main upwelling zone off Cap Blanc, referred to above (p. 139). Merrett and Haedrich (1997) suggested that, in abyssal open-ocean settings, trophic inputs derived from primary production in the overlying photic zone usually exert a strong influence on the distribution of demersal species. On the other hand, along continental margins, vertical water-column fluxes are obscured by food inputs derived from upwelling, terrigenous sources, currents, shelf production, and interactions between horizontally distributed pelagic organisms and the continental slope. In such areas, these factors have the most decisive effect on distribution patterns.

BASIN-WIDE BIOLOGICAL PATTERNS AND PROCESSES

Though many studies of deep-sea benthos are regional in nature, a few have tried to draw global or basin-wide comparisons in an attempt to evaluate the relative importance of factors controlling biological pattern in the deep sea. In the sections below we review the conclusions of such studies, and, because we found large gaps in treatment of these issues, have attempted to create our own syntheses. We focus on patterns of density and biomass, community respiration, bioturbation and succession, in the belief that much, though certainly not all, of the accumulated knowledge about the deep Atlantic fauna addresses these issues.

Density and biomass

Most early investigations of density and biomass patterns of Atlantic benthos examined the effects of water depth. Investigators usually treat meiofauna, macrofauna, or megafauna, but rarely all three (Table 5.3; but see Galeron et al., 2000). In most places monotonic, sometimes exponential, declines in density and biomass were observed with increasing water depth for each group (Thiel, 1983; figs. 6, 7 therein; Rowe, 1983; fig. 3 therein; Vincx et al., 1994; table 3 therein). Lampitt et al. (1986) reported a logarithmic decline in megafaunal biomass along a depth gradient in the Porcupine Seabight, with a reduction by a factor of 30 between 500 and 4100 m. They observed no significant change in average body weight with depth. Declines in macrofaunal density with depth are also evident along most depth transects in the Northwest Atlantic (Hessler and Sanders, 1967; Rowe et al., 1974; Smith, 1978; Blake and Grassle, 1994; Blake and Hilbig, 1994).

Less regular patterns have been reported beneath upwelling regions, where oxygen minima at intermediate depths depress density (Sanders, 1969; Thiel, 1978; Pfannkuche et al., 1983), where fluxes of organic matter to deep water are very high, as in the Norwegian–Greenland Sea (Thiel, 1983: fig. 9 therein), and in regions subject to hydrodynamic disturbance (Hecker, 1990b). Where hydrodynamic reworking is intense, as in the Rockall Trough and Goban Spur, maximal densities and biomass sometimes occur at mid-slope depths (Gage, 1978; Flach and Heip, 1996b). These patterns may be modified by seasonal and interannual variation (Flach and Heip, 1996b).

A more recent emphasis has been on the comparison of abundance and biomass at sites differing in organic-matter flux (Sibuet et al., 1989, 1993; Rowe et al., 1991; Thurston et al., 1994; Paterson et al., 1994a,b; Vanreusel et al., 1995a; Gooday, 1996b; Cosson et al., 1997; Galeron et al., 2000). These studies have invariably found that flux of particulate organic carbon (POC) is the first-order parameter controlling macrofaunal and meiofaunal abundances in the deep Atlantic (Thiel, 1983; Sibuet et al., 1989; Rowe et al., 1991). Regions of the Atlantic with highest organic flux support the greatest infaunal densities and biomass. Particularly notable hot-spots in this regard are the Norwegian–Greenland Sea (Romero-Wetzel and Gerlach, 1991), the continental margin off Cap Blanc, Northwest Africa (Cosson et al., 1997; Galeron et al., 2000), and off Cape Hatteras, North Carolina. In the latter area, macrofaunal densities at 850 m depth exceed 40 000 individuals m^{-2} (Schaff et al., 1992; Blake and Hilbig, 1994).

A similar correlation is often apparent along bathymetric transects. Work by Pfannkuche et al. (1983) off Morocco (35°N) and Pfannkuche (1985) in the Porcupine Seabight indicates that meiofaunal abundances are strongly linked to surface productivity regimes and sediment chloroplastic pigments, but do not necessarily decrease exponentially downslope. For example, on the Moroccan transect, meiofaunal maxima were observed between 400 and 1200 m. Thiel (1978) reported meiofaunal densities to be fairly constant with depth at sites beneath upwelling areas off Northwest Africa, with densities sometimes exceeding 10^6 m^{-2}. Vanreusel et al. (1995a) documented lower nematode density and biomass in oligotrophic waters off Mauritania (EUMELI 3) than at the Porcupine Abyssal Plain site, which experiences seasonal phytodetrital pulses. Larger nematode body size was observed on the Porcupine Abyssal Plain. In some cases, the macrofaunal and meiofaunal trends appear linked to patterns of bacterial biomass and density (Rowe et al., 1991; Vanreusel et al., 1995b), which are in turn dependent on the primary productivity of overlying waters (Morita, 1979; Tan and Ruger, 1989). Rowe et al. (1991) suggested that the importance of bacteria in the pool of living carbon (relative to macro and meiofauna) increases with depth.

Patterns of density and biomass generally track one another; regions of highest density often exhibit high biomass. However, for macrofauna, biomass declines more rapidly with depth than does abundance because body size declines with depth (Rowe et al., 1974; Thiel, 1975). Based on a comparison of data for macrofauna in the Northwest with data for meiofauna in the Northeast Atlantic, Thiel (1983) reported that the slope of density decline with water depth is steeper for macrofauna than for meiofauna by a factor of 2. A reasonable explanation is that smaller-sized organisms (the meiofauna) are better able to cope with declining food inputs at greater depths. However, east–west differences in patterns of carbon flux with depth may have influenced the outcome of this analysis.

Several authors have suggested that megafauna are more sensitive to changes in food supply than are smaller organisms (Sibuet et al., 1984; Lampitt et al., 1986). Sibuet et al. (1989) have reported that there is a constant proportional relationship between metazoan meiofauna, macrofauna, and megafauna, but that the relation of particulate organic matter to abundance of megafauna differs from that of the other groups. Galeron et al. (2000) found that megafaunal biomass in the tropical Northeast Atlantic exceeded that of macrofauna and meiofauna only at the most eutrophic of the three EUMELI sites. Grassle et al. (1975) estimated that, in the Northwest Atlantic, megafauna were three orders of magnitude less abundant than the macrofauna at 1850 m, whereas biomass for the two size groups was about equal (Haedrich and Rowe, 1977). Megafauna appear to dominate where food input is high (e.g., off Cape Hatteras, off Northwest Africa, or on the Amazon Cone), or where advective transport enhances particle flux (e.g., the Rockall Trough). They appear less important in systems where food supply is lower, although their role in these ecosystems may not be accurately reflected by counts (Lampitt et al., 1986).

There have been no systematic comparisons of the western and eastern Atlantic Ocean in terms of benthic abundance or biomass in deep waters. Too few meiofaunal data exist, and methods are too variable to draw valid comparisons between the two sides of the Atlantic, although they have been discussed by Thiel (1983).

Regressions of macrofaunal density against water depth reveal higher densities in the Northwest than Northeast Atlantic at bathyal depths (Fig. 5.7A). The Northwest Atlantic macrofauna show a strong exponential decline in density with depth (exponential fit: $r^2 = 0.70$; $P < 0.0001$); this relationship is much weaker in the Northeast Atlantic (exponential fit: $r^2 = 0.16$; $P = 0.007$), where the density relationship with depth is more linear ($r^2 = 0.31$; $P < 0.0001$). The regression lines for the two areas cross just below 4000 m (Fig. 5.7A), suggesting that, at abyssal depths, the macrofauna may be more abundant in the Northeast than the Northwest Atlantic. It is possible that these differences, driven largely by high margin densities in the South Atlantic Bight, are due to activities of the western boundary current (Gulf Stream) in focusing organic-matter inputs. However, the same trends are not evident for macrofaunal biomass which, on the basis of limited data (Fig. 5.7B, Table 5.3), appears to be greater in the Northeast than in the Northwest Atlantic.

Strong regional variation is evident in the Atlantic. The Porcupine Seabight yielded invertebrate megafaunal biomass eighteen times and ten times higher, respectively, than depths of 500 m and 4000 m on the slope off southern New England, prompting Lampitt et al. (1986) to suggest that there is higher megafaunal biomass in the Northeast than in the Northwest Atlantic. Megafaunal biomass on the Demerara Abyssal Plain (4.5 mg dry wt. m^{-2}) was less than half that on the Porcupine Seabight (11.7 mg m^{-2}), while the margin off the Amazon had more than twice as much biomass as the Porcupine Seabight. Ocean-wide comparisons of megafaunal biomass, of the sort carried out above for the macrofauna, are made difficult by the broad range of methods and variable minimum body sizes considered in megafaunal investigations (Thurston et al., 1994) (Table 5.3).

Community respiration

Sediment community respiration, also termed sediment community oxygen consumption (SCOC), is of interest because it represents a highly integrated measure of activity levels of aerobic bacteria, protozoans and metazoans. This activity is believed to be strongly controlled by the flux of particulate organic carbon (i.e., food availability) at the sea floor. Sediment community oxygen consumption has been measured using several approaches (Smith and Hinga, 1983). These include (a) *in situ* respirometry, which is based on loss of dissolved oxygen in water overlying enclosed sediments, with measurements made within the seabed or in cores suspended just above the bottom; (b) shipboard core incubations, which also measure changes in dissolved oxygen; (c) biochemical assay of the respiratory electron-transport system (ETS) activity in the laboratory; and (d) calculations of oxygen consumption derived from oxygen concentration gradients in sediment pore-waters. Several other approaches include measurement of chemical oxygen demand with inhibitors and poisons, and ATP analyses (Graf and Linke, 1992). Data collected to date indicate a strong link between surface primary production and *in*

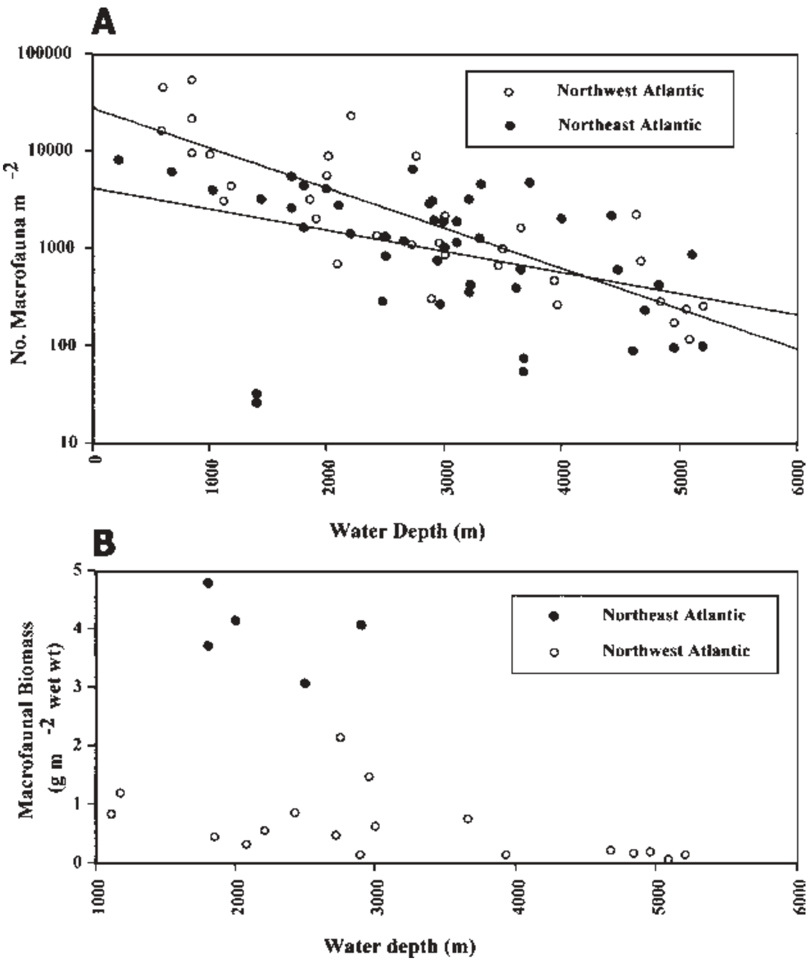

Fig. 5.7. Regression of macrofaunal standing stock against depth for NW and NE Atlantic stations. A, densities; B, biomass.

situ measures of sediment oxygen consumption. This link is mediated by water depth and distance from shore, which, in concert with seasonality and mass transport, control the proportion of surface production that reaches the seabed – that is, organic-carbon flux.

Western Atlantic

Total SCOC in the Northwest Atlantic spans three orders of magnitude, from a low of 0.02 ml O_2 m^{-2} hr^{-1} at 5200 m in the Sargasso Sea near Bermuda to 1.31 ml O_2 m^{-2} hr^{-1} at 1345 m on the continental slope north of the Blake Plateau. On the Blake Plateau at a depth of 1345 m (Hinga et al., 1979), SCOC was twice that at the shallowest slope station (1850 m) along the Gay Head–Bermuda transect (Smith, 1978). Smith and Hinga (1983), using data from nine stations along the Gay Head–Bermuda transect, were able to account for 96% of the variation of *in situ* SCOC with the following regression equation:

$$Y = 0.9421 - 0.0001621D - 0.001252PP,$$

where Y = SCOC in ml O_2 m^{-2} hr^{-1}, D = water depth in meters, and PP = annual primary productivity in g C $m^{-2} y^{-1}$.

In situ measurements of SCOC were reported by Smith and Hinga (1983) in the western tropical Atlantic, in the Straits of Florida at the base of the Blake Plateau (675 m) and in the Tongue of the Ocean station (TOTO) (2000 m) near the Bahamas. Values were 2.95 and 3.10 ml O_2 m^{-2} h^{-1}, respectively – much higher than any reported in the Northwestern Atlantic. Smith and Hinga (1983) suggested that these high respiration rates might result from proximity to land, both to the west and east, and associated channeling into the sites of organic matter from terrestrial and shallow marine sources. Respiration requirements exceeded measured fluxes of particulate organic carbon in the Straits of Florida and the TOTO site by a factor of 5, leading various investigators to suggest that macrophytic algae and seagrass may have supplied some of the missing material (Wiebe et al., 1976). A time series of nine SCOC measurements made by benthic lander at an abyssal station 83 km southeast of Bermuda (BATS), during a period of three years, indicated remarkable constancy ($0.030\pm0.0035\ \mu\mathrm{mol\ cm^{-2}\ d^{-1}}$) with no seasonal variation.

Eastern Atlantic

Measurements made in the Gulf of Guinea off Northwest Africa indicate very high SCOC ($3.93\ \mathrm{ml\ O_2\ m^{-2}\ h^{-1}}$) at 278 m and much reduced values at 4000 m ($0.65\ \mathrm{ml\ O_2\ m^{-2}\ h^{-1}}$). Both are probably elevated by upwelling, and the shallow site may be influenced by terrigenous input from nearby rivers (Hinga et al., 1979). Patching et al. (1986) measured SCOC at depths of 2880 m in the Rockall Trough and 4980 m on the Porcupine Abyssal Plain. Mean values were 2.2 times greater in Rockall Trough ($99–203\ \mu\mathrm{mol\ O_2\ m^{-2}\ h^{-1}}$) than on the Porcupine Abyssal Plain ($58–77\ \mu\mathrm{mol\ O_2\ m^{-2}\ h^{-1}}$). The high rates observed might be related to the timing of the measurements, which were taken just after the spring phytoplankton bloom in surface waters, or to methodology bias (Patching et al., 1986). Seasonal measurements made *in situ* in the Porcupine Seabight (2000 m) by Lampitt et al. (1995) yielded SCOC values between those in the Rockall Trough and on the Porcupine Abyssal Plain ($74–125\ \mu\mathrm{mol\ O_2\ m^{-2}\ h^{-1}}$), but indicated no evidence of seasonal variation. Cores with phytodetritus visible on the surface did not yield SCOC values different from those lacking this material, indicating either degradation so rapid that it was missed or very long community response times (Lampitt et al., 1995). Measurements in June 1985 of around $30\ \mu\mathrm{mol\ O_2\ m^{-2}\ h^{-1}}$, made on the Porcupine Abyssal Plain by Lampitt et al. (1995), were half those made earlier in the year (May 1980, April 1982) by Patching et al. (1986) in the same region. Pfannkuche (1992, 1993) obtained comparable SCOC values slightly further south at the BIOTRANS site (4590 m), where values ranged from 15 to $38\ \mu\mathrm{mol\ O_2\ m^{-2}\ h^{-1}}$ during spring and summer. He reported higher SCOC values in July and August than in spring.

Overview

In general, bathyal and abyssal SCOC data from the eastern Atlantic seem to be higher than *in situ* values at equivalent depths from the northwestern Atlantic, although SCOC measurements made on the Hatteras Abyssal Plain were comparable to those on the Porcupine Abyssal Plain and at the BIOTRANS Site (Table 5.4). The Northwest Atlantic margin off Cape Hatteras experiences extremely high carbon flux (Blair et al., 1994), and this influence may extend to the adjacent abyssal areas. The few data available suggest that the organic-carbon input to the Northeast Atlantic seabed may be subject to more seasonal variation than in the Northwest Atlantic. Both the increased SCOC rates and greater variability may be related to heavy, pulsed input of phytodetritus to the seabed during spring blooms in the northeastern section of the Atlantic. Seasonality of SCOC has been documented in both the Atlantic (Pfannkuche, 1992) and the Pacific (Smith et al., 1994). However, the Atlantic and Pacific differ in the extent to which measured fluxes of particulate organic carbon appear to meet the respiratory demands of the benthic community. Evidence to date suggests that this flux in the North Atlantic is more than sufficient to account for the SCOC (Smith and Hinga, 1983), whereas this is not the case in the Pacific (Smith, 1987).

Bioturbation

Most quantitative estimates of bioturbation in deep-sea sediments are based on a diffusive mixing coefficient (D_b) derived from profiles of radiotracers scavenged on particles in the seabed. D_b is calculated from the following steady-state, unidirectional equation as derived by Nozaki et al. (1977):

$$D_b \frac{\partial^2 N}{\partial x^2} - S\frac{\partial N}{\partial x} + P - \lambda N = 0,$$

where N, radiotracer concentration in bulk sediment (atoms $\mathrm{g^{-1}}$); ∂, bulk sediment density ($\mathrm{g\ cm^{-3}}$); S, sedimentation rate ($\mathrm{cm\ sec^{-1}}$); D_b, mixing coefficient ($\mathrm{cm^2\ sec^{-1}}$); P, production rate of radiotracer (atoms $\mathrm{g^{-1}\ sec^{-1}}$); λ, decay constant of tracer ($\mathrm{sec^{-1}}$).

Most estimates of D_b for sediments of the continental rise and abyss in the Atlantic have been based on ^{210}Pb profiles with a half life of 22 years (Boudreau, 1994). Values determined for marine sediments at depths between 1410 and 5160 m consistently fall between 0.02 and $1.0\ \mathrm{cm^2\ yr^{-1}}$ (Table 5.5, Fig. 5.8A). These values are several orders of magnitude lower than those observed in shallow water. Compilation of

Table 5.4
In situ measurements of sediment community oxygen consumption (SCOC) in the Atlantic ocean[1]

Station	Water depth (m)	SCOC		Reference
		ml O_2 m^{-2} h^{-1}	μmol O_2 m^{-2} h^{-1}	
WESTERN ATLANTIC				
Gayhead–Bermuda Transect	1850	0.50	22.8	Smith and Teal (1973)
	2200	0.46	20.5	Smith (1978)
	2750	0.35	15.6	Smith (1978)
	3000	0.20	8.9	Smith (1978)
	3650	0.21	9.4	Smith (1978)
	4670	0.09	4.0	Smith (1978)
	4830	0.04	1.8	Smith (1978)
	5080	0.07	3.1	Smith (1978)
	5200	0.02	0.9	Smith (1978)
Mid Atlantic Bight	2159	1.17[2]	52.41[2]	Hales et al. (1994)
	4236	0.69	30.82	Hales et al. (1994)
	4501	0.54	23.97	Hales et al. (1994)
	5210	0.31	13.70	Hales et al. (1994)
	5380	0.33	14.84	Hales et al. (1994)
North of Blake Plateau	1345	1.31	58.5	Hinga et al. (1979)
Florida Strait	675	2.95	131.7	Smith and Hinga (1983)
Tongue of the Ocean	2000	3.10	138.4	Smith and Hinga (1983)
Bermuda (BATS)	4400	0.28	12.5	Sayles et al. (1994)
EASTERN ATLANTIC				
Rockall Trough	2280	1.50[3]	67[3]	Patching et al. (1986)
Porcupine Seabight	2000	2.12[3]	94.58[3]	Lampitt et al. (1995)
Porcupine Abyssal Plain	4980	1.39[3]	62.00[3]	Patching et al. (1986)
	4000	0.66[3]	29.75[3]	Lampitt et al. (1995)
BIOTRANS	4590	0.40 (April 88)	17.9	Pfannkuche (1992)
	4590	0.86 (July 86)	38.4	Pfannkuche (1992)
	4590	0.81 (Aug 89)	36.3	Pfannkuche (1992)
Gulf of Guinea	278	3.93	175.5	Hinga et al. (1979)
	4000	0.65	29.0	Hinga et al. (1979)

[1] All measurements are based on grab respirometry unless indicated otherwise.
[2] Porewater oxygen profiles made *in situ* by microelectrodes.
[3] Suspended core methods.

mixing-coefficient data from sites in the Northwest, Northeast and South Atlantic suggest several patterns that bear further investigation. The D_b data from the Northwest Atlantic show an exponential decline with water depth ($r^2 = 0.634$) which is not evident in the Northeast Atlantic (Fig. 5.8A), where maximal D_b values were observed on the lower rise in the Cape Verde and Porcupine Seabight regions. The South Atlantic may exhibit lower mixing than the North Atlantic, but the data are few. Latitude appears to have little influence on mixing as estimated from D_b values (Fig. 5.8B).

Recent estimates of diffusive mixing coefficients made in more dynamic environments with ^{234}Th, a shorter-lived radiotracer (24-d half-life), are much higher. Thorium estimates of mixing rate range from

Table 5.5
Estimates of bioturbation rates and mixed layer depth in deep Atlantic sediments

Region	Latitude	D_b (cm^2 y^{-1}) (mixed layer)[1]	Water depth (m)	Tracer	Reference
CONTINENTAL SLOPE					
Northwest Atlantic					
North Carolina (off Cape Hatteras)	35ºN	19±11.0 (x±1 SD)	850	Th-234	DeMaster et al. (1994)
		7.4±4.7 (x±1 SD)	850	glass beads	DeMaster et al. (1994)
North Carolina (off Cape Lookout)	34ºN	4.6±5.2 (x±1 SD)	850	Th-234	DeMaster et al. (1994)
		0.84±0.65 (x±1 SD)	850	glass beads	DeMaster et al. (1994)
North Carolina (off Cape Fear)	32ºN	6.0±6.2 (x±1 SD)	850	Th-234	DeMaster et al. (1994)
		0.29		glass beads	DeMaster et al. (1994)
Nova Scotian Rise	40ºN	1–33	4800	Th-234	DeMaster et al. (1991)
Newfoundland slope	50ºN	0.1–1.0	1500	Pb-210	Smith and Schafer (1984)
North Atlantic	21ºN	0.25	1410	Pu-230	Guinasso and Schink (1975)
Northwest Atlantic		0.19	2705	Pb-210	Turekian et al. (1975)
	37ºN	0.7–1.2 (8)	1170	Pb-210	Tanaka et al. (1991)
	38ºN	30	2800	Th-234	Aller and DeMaster (1984)
	39ºN	0.42	501	Pb-210	Anderson et al. (1988)
		1.03	553	Pb-210	Anderson et al. (1988)
		0.77	869	Pb-210	Anderson et al. (1988)
		0.45	1126	Pb-210	Anderson et al. (1988)
		0.14, 0.49	1170	Pb-210	Anderson et al. (1988)
		0.92	1275	Pb-210	Anderson et al. (1988)
		0.75	1359	Pb-210	Anderson et al. (1988)
		0.20	1643	Pb-210	Anderson et al. (1988)
		0.71	2362	Pb-210	Anderson et al. (1988)
		0.60, 0.73	2700	Pb-210	Anderson et al. (1988)
Northeast Atlantic					
Northeast Atlantic	51ºN	0.046	2365	Pb-210	Thomson et al. (1993)
BOFS		0.042	4150	Pb-210	Conte et al. (1994)
EUMELI	21ºN	0.142	2050	Pb-210	Reyss et al. (1993)
BIOGAS	47ºN	0.183 (7)	2100	Pb-210	Mauviel and Sibuet (1985)
	47ºN	0.189, 0.167 (6,10)	2800	Pb-210	Mauviel and Sibuet (1985)
Southwest Atlantic	9ºS	0.10	1345	Pu-239	Guinasso and Schink (1975)
Mediterannean		0.8–1.6	1200	Cs-137, luminophores	Gerino et al. (1993)
MID ATLANTIC RIDGE					
Mid Atlantic Ridge		0.19 (8)	2500	Pb-210	Nozaki et al. (1977)

continued on next page

Table 5.5, *continued*

Region	Latitude	D_b (cm^2 y^{-1}) (mixed layer)[1]	Water depth (m)	Tracer	Reference
ABYSSAL PLAINS					
Northeast Atlantic	50°N 21°W	0.66	3547	Pb-210	Thomson et al. (1993)
	52°N 22°W	0.66	4005	Pb-210	Thomson et al. (1993)
	49°N 21°W	0.21	4067	Pb-210	Thomson et al. (1993)
	~45°N 17°W	0.1	4000–5000	Pb-210	Smith et al. (1986/87)
Northwest Atlantic: Hatteras	32°	0.022, 0.037 (5)	5200	Pb-210	Stordal et al. (1985)
North Atlantic	39°N 42°W	0.220	4810	Pu-239	Guinasso and Schink (1975)
EUMELI	21°N 31°W	0.02	4550	Pb-210	Reyss et al. (1993)
Cape Verde Abyssal Plain	18°N	0.875 (9)	3374	Pb-210	Stordal et al. (1985)
	22°N	0.040 (5)	4660	Pb-210	Stordal et al. (1985)
	22°N	0.19, 0.220 (4)	5032	Pb-210	Stordal et al. (1985)
Madeira Abyssal Plain	35°N 20°W	0.126 (3.7)	5161	Pb-210	Kershaw (1985)
Southwest Atlantic	41°S 20°E	0.04	4910	Pb-120	DeMaster and Cochran (1982)
Southeast Atlantic	29°S 4°E	0.14	4920	Pu-239	Guinasso and Schink (1975)
South Atlantic		0.063	4910	Pb-210	Turekian et al. (1975)
TRENCHES					
Puerto Rico Trench	19°N	0.025	8100	Pb-210	Stordal et al. (1985)

[1] Mixed layer depth in cm, where available, is given in parentheses.

1 to 33 cm^2 y^{-1}. The most intense mixing has been observed on the continental margin at 850 m off Cape Hatteras (DeMaster et al., 1994), and in a high-energy region on the Scotian Rise at 4800 m subject to benthic storms (the HEBBLE site) (DeMaster et al., 1991). The region off Cape Hatteras is a focus for sediment accumulation, and fluxes of organic carbon are among the highest reported for slope environments. At the HEBBLE site, organic-carbon input to the seabed is elevated by benthic storms. In both cases, benthic macrofaunal densities and biomass are also very high (Thistle et al., 1991; Schaff et al., 1992), supporting the idea that vertical and advective carbon flux, faunal abundance and bioturbation are correlated (Berner, 1980; Aller, 1982; Smith, 1992).

Smith et al. (1993) have suggested that the higher mixing rates associated with ^{234}Th (relative to ^{210}Pb) reflect age-dependent mixing, in which younger particles (associated with ^{234}Th) are mixed preferentially compared to older particles (associated with most ^{210}Pb). Atlantic sites have not yielded strong evidence for this phenomenon. However, at three sites on the Northwest Atlantic margin off North Carolina, reduced mixing of experimentally emplaced sand-sized glass beads relative to fine particles tracked by ^{234}Th suggests that mixing rates may depend on particle quality or size (DeMaster et al., 1994; Fornes et al., 1999).

Diffusive mixing models provide accurate estimates of bioturbation only when radiotracer profiles exhibit exponential declines in activity down-core. However, in almost every study of radiotracer profiles in Atlantic

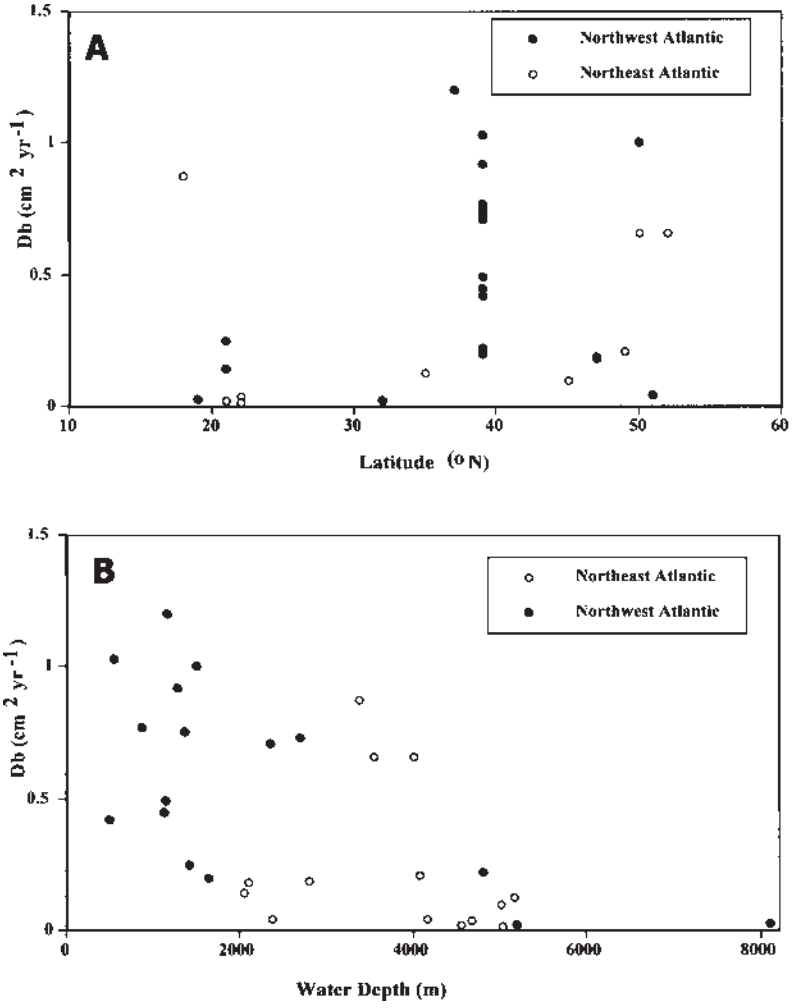

Fig. 5.8. Particle mixing coefficients (D_b) as a function of (A) water depth and (B) latitude.

slope, rise and abyssal sediments, some cores exhibit subsurface maxima or shoulders underlying sharp surface gradients. These are indicative of non-local transport of surface material by animals to depth in the sediment (Smith et al., 1986/87; Brand and Shimmield, 1991; Thomson et al., 1993; Levin et al., 1997; Fornes et al., 1999). Sometimes, downward transport is so intense that subsurface inventories of Pb-210 can be higher than in surface sediments (Thomson et al., 1993). Significant spatial heterogeneity has been observed in both the Northeast and Northwest Atlantic among profiles generated from subcores within a single box-core (Smith and Schafer, 1984; Smith et al., 1986/87; DeMaster et al., 1991). Significant temporal variation in mixing regimes and non-steady-state conditions have been observed at a very dynamic site (HEBBLE) subject to benthic storms (DeMaster et al., 1991).

Subsurface maxima observed in profiles of chlorophyll (Graf, 1989) and experimentally placed diatoms labeled with ^{13}C (Levin et al., 1997, 1999) reveal that subduction of freshly deposited material can be rapid (within days), and may occur deep within the sediment column (9–13 cm). Deposit-feeding organisms implicated in subduction and generation of subsurface maxima in the Atlantic Ocean include sipunculans (J.N. Smith et al., 1986/87; Romero-Wetzel, 1987; Graf, 1989), maldanid, paraonid, and nereid polychaetes (Blair et al., 1996; Levin et al., 1997, 1999), burrowing anemones and decapods (Smith and Schafer, 1984). It may be that much of the mixing recorded on time scales of 100 days or 100 years by use of particle reactive radiotracers such as ^{234}Th or ^{210}Pb actually occurs within hours or days after reactive particles reach the seabed. Levin et al. (1997), for example, estimated that mixing by maldanid polychaetes observed on the Northwest Atlantic slope (at a depth of 850 m) within 1.5 days after diatom deposition could account for 25–100% of the mixing below 5 cm estimated from naturally occurring ^{234}Th (100-day time scale). Rapid downward transport of particles within the sediment column also can result from infilling of vacant burrows. Trapping of reactive organic matter within burrows on the Nova Scotian Rise (4800 m) was shown by Aller and Aller (1986) to cause intensive decomposition and to generate hot-spots of enhanced microbial, meiofaunal and macrofaunal activity in otherwise organic-poor sediment.

Disturbance, colonization and succession

Present understanding of the responses of macrobenthic communities in the Atlantic to disturbance is derived from experiments in which defaunated sediments (rendered azoic by freezing and thawing), plant material, fish or wood were placed in or on the seabed, and subsequent colonization was observed at varying time intervals (Smith and Hessler, 1987).

Initial investigations of infaunal succession were carried out in the Atlantic by deploying deep-sea sediments in trays lying on the seabed. Grassle's (1977) observations of faunal colonization after 2 and 26 months in trays at a depth of 1760 m (Station DOS-1) in the Northwest Atlantic were the first to suggest that recovery rates following disturbance are very slow for the naturally occurring macrobenthic communities. Numbers of colonizing individuals were low, and most belonged to species not previously reported from the study area. Among the commonest were dorvilleid and capitellid polychaetes, priapulids, wood-boring bivalves and snails ectoparasitic on echinoderms. Later tray recolonization studies in the Northwest Atlantic conducted by Grassle and Morse-Porteous (1987) at DOS-1, and at 3600 m (DOS-2), for periods ranging from 2 to 59 months, supported initial findings of slow recovery. Even after 59 months, faunal densities did not attain those in background sediments. Screening of tray sediments revealed enhanced colonizer densities, and led to the speculation that predation may control rates of succession (Grassle and Morse-Porteous, 1987).

Sediment-tray experiments conducted for 6 and 11 months at depths of 2160 m and 4150 m in the Bay of Biscay also indicated very slow colonization by macrofauna (Desbruyères et al., 1985a). However, in an earlier experiment Desbruyères et al. (1980) reported much more rapid colonization of defaunated sediments at 2160 m after 6 months' exposure, with densities in organically enriched sediments overshooting those of control sediments. As in Grassle's experiments, many of the recruits in the Bay of Biscay belonged to species absent from control samples.

These early sediment-tray experiments were fraught with hydrodynamic artifacts, and deemed unrealistic because the experimental substrata were separated from natural sediments (Smith, 1985b; Snelgrove et al., 1995). However, they were very important in revealing the availability in the deep Atlantic of opportunistic colonizers highly adapted to disturbed or enriched settings. Subsequent deployments of hydrodynamically unbiased colonization trays were made by Snelgrove et al. (1992, 1994, 1996) for 23 days and 28 months at a depth of 900 m near St. Croix, U.S. Virgin Islands in the equatorial West Atlantic. These experiments indicated that colonizing macrofauna can attain or exceed ambient densities in 2+ years, but again the colonists were species relatively rare in background sediments (Snelgrove et al., 1996). This trend was even more evident in organically enriched treatments, which were colonized by large numbers of capitellid and hesionid polychaetes, cumaceans and leptostracans that were not observed in control treatments. The characteristic response of specialized, opportunistic species to disturbance in the deep Atlantic has not been observed in the few comparable colonization studies carried out for Pacific macrobenthos. In the eastern Pacific the initial respondents to non-reducing sediment disturbance appear to be species relatively common in the background community (Levin and Smith, 1984; Kukert and Smith, 1992; Levin and DiBacco, 1995). Opportunists such as *Capitella* have not been reported from deep-water experiments in the Pacific, though *Capitella* and leptostracans are known to colonize detritus in shallow submarine canyons (Vetter and Dayton, 1998). Too few sites and forms of disturbance have been examined to determine whether the Atlantic is really distinct from the Pacific in the distribution of deep-sea opportunists, or to permit speculation about the causes.

Enrichment of experimental sediments deployed in recolonization trays have produced colonizer assemblages distinct from the fauna of surrounding sediments and control trays in all Atlantic studies (Desbruyères et al., 1980; Grassle and Morse-Porteous, 1987; Snelgrove et al., 1992, 1996). These experiments, along with those in which direct enrichment of the bottom has been achieved by placement of fish carcasses, wood, or marine algae on the seabed (Grassle and Morse-Porteous, 1987; Snelgrove et al., 1994) indicate the importance of patchy organic inputs to the structure of benthic communities. Sediments near experimentally emplaced wood blocks yielded high densities of mussels (*Idasola argentea*) and wood borers (*Xyloredo* sp.), while sediments containing *Sargassum* exhibited elevated densities of amphipods and several polychaetes including *Capitella* spp. and *Ophryotrocha* sp. Patterns of species richness, dominance, taxonomic composition and abundance all seem to be affected by the supply of organic matter to the seabed (Gooday and Turley, 1990; Rice and Lambshead, 1994; Grassle and Grassle, 1994). In recent decades it has become clear that persistent heterogeneity of this supply results from falling carcasses of fish and mammals, macroalgae and phytodetritus, and from the interaction of accumulating particles with biogenic structures such as depressions, tests, mounds, tracks, fecal casts and traces, which impose roughness on the seabed.

CONCLUSIONS

The Atlantic Ocean has, without question, played a focal role in the development of deep-sea biology. Recent discoveries and long-term, time-series investigations have yielded the unexpected, making it clear that the Atlantic is a dynamic ocean whose inhabitants experience environmental variation over a wide range of spatial and temporal scales. The consequences of this forcing, in terms of taxonomic makeup, population dynamics and ecology, are clearly documented for microbial and protozoan forms, but these consequences are less clear for certain higher taxa. Within the Atlantic, the continental margins are among the most heterogeneous and biologically productive settings. They continue to be most heavily studied because of their proximity to population centers and their commercial potential (e.g., exploitation of fisheries, hydrocarbon resources). Despite this, knowledge of species composition and basic functional attributes is lacking for most places within the Atlantic, especially south of the equator. Given that the Atlantic is the best studied of the Oceans, this is true for all of the deep sea. It is evident that the Western and Eastern sides of the Atlantic have been studied independently, with a few notable exceptions. Similarly, the megabenthos, macrobenthos and meiobenthos, as well as the various taxonomic groups of benthic fauna, have been studied in isolation. Often the research focus and methodologies have differed. As a result, except for the issue of species diversity (see Stuart et al., Chapter 10, this volume), there have been only a few whole-basin syntheses for the Atlantic Ocean (see Sibuet et al., 1989; Rowe et al., 1991). Even patterns of species diversity have been addressed primarily for the macrofauna. This should change with increased potential for remote measurement in the deep sea, acquisition of large-scale synoptic data, dramatic technological advances in measurement capabilities *in situ,* and the tremendous improvement in speed and ease of communication between scientists in distant places. As with diversity, ocean-scale considerations of productivity, hydrodynamics, historical, geological, and chemical influences, as well as integration among biological components (micro, meio-, macro- and megafaunal; procaryotic and eucaryotic; microbial, invertebrate and ichthyofaunal) will certainly yield better understanding of the processes underlying biological pattern in this remarkable ocean.

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