Annu. Rev. Ecol. Syst. 2001. 32:51–93

ENVIRONMENTAL INFLUENCES ON REGIONAL DEEP-SEA SPECIES DIVERSITY*

Lisa A. Levin,[1] Ron J. Etter,[2] Michael A. Rex,[2] Andrew J. Gooday,[3] Craig R. Smith,[4] Jesús Pineda,[5] Carol T. Stuart,[2] Robert R. Hessler,[1] and David Pawson[6]

[1]Scripps Institution of Oceanography, University of California, San Diego, La Jolla, California 92093-0218; e-mail: llevin@ucsd.edu; rhessler@ucsd.edu
[2]Department of Biology, University of Massachusetts, Boston, Massachusetts 02125; e-mail: ron.etter@umb.edu; michael.rex@umb.edu; carol.stuart@umb.edu
[3]Southampton Oceanography Centre, European Way, Southampton SO14 3ZH United Kingdom; e-mail: ang@soc.soton.ac.uk
[4]Department of Oceanography, University of Hawaii, Honolulu, Hawaii 96822; e-mail: csmith@soest.hawaii.edu
[5]Department of Biology, MS 34, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543; e-mail: jpineda@whoi.edu
[6]National Museum of Natural History, Smithsonian Institution, MRC 106, Washington, DC 20560; e-mail: pawson.david@nmnh.si.edu

Key Words Biodiversity, benthos, environmental gradients, depth gradients, diversity measures, bathyal, abyssal, sediments

■ **Abstract** Most of our knowledge of biodiversity and its causes in the deep-sea benthos derives from regional-scale sampling studies of the macrofauna. Improved sampling methods and the expansion of investigations into a wide variety of habitats have revolutionized our understanding of the deep sea. Local species diversity shows clear geographic variation on spatial scales of 100–1000 km. Recent sampling programs have revealed unexpected complexity in community structure at the landscape level that is associated with large-scale oceanographic processes and their environmental consequences. We review the relationships between variation in local species diversity and the regional-scale phenomena of boundary constraints, gradients of productivity, sediment heterogeneity, oxygen availability, hydrodynamic regimes, and catastrophic physical disturbance. We present a conceptual model of how these interdependent environmental factors shape regional-scale variation in local diversity. Local communities in the deep sea may be composed of species that exist as metapopulations whose regional distribution depends on a balance among global-scale, landscape-scale, and small-scale dynamics. Environmental gradients may form geographic patterns of diversity by influencing local processes such as predation, resource partitioning, competitive exclusion,

---

*The US Government has the right to retain a nonexclusive, royalty-free license in and to any copyright covering this paper.

and facilitation that determine species coexistence. The measurement of deep-sea species diversity remains a vital issue in comparing geographic patterns and evaluating their potential causes. Recent assessments of diversity using species accumulation curves with randomly pooled samples confirm the often-disputed claim that the deep sea supports higher diversity than the continental shelf. However, more intensive quantitative sampling is required to fully characterize the diversity of deep-sea sediments, the most extensive habitat on Earth. Once considered to be constant, spatially uniform, and isolated, deep-sea sediments are now recognized as a dynamic, richly textured environment that is inextricably linked to the global biosphere. Regional studies of the last two decades provide the empirical background necessary to formulate and test specific hypotheses of causality by controlled sampling designs and experimental approaches.

INTRODUCTION

Regional-scale sampling studies have provided the primary evidence for spatial patterns of deep-sea community structure and their causes. There has been no synoptic review of regional diversity patterns published since the early 1980s (Rex 1981, 1983). During the last two decades, our knowledge has expanded dramatically from descriptions of geographic gradients in diversity and indirect inferences about the biotic and abiotic factors that may shape them, to more precise understanding of associations between diversity and specific environmental conditions. These findings have transformed our understanding of the deep-sea ecosystem. The deep-sea, soft-sediment environment is highly complex at the landscape level of biodiversity as well as at the local community level, and is dynamically linked to oceanographic processes at the surface.

Here we summarize regional-scale geographic trends of deep-sea species diversity and propose a conceptual model to explain their causes. We are primarily concerned with ecological structuring agents that function on generational rather than evolutionary time scales. The stochasticity or patchiness observed at very small scales in deep-sea communities (Jumars & Eckman 1983, Grassle & Morse-Porteous 1987, Grassle & Maciolek 1992) becomes resolved at larger scales into measurable geographic patterns. The key to understanding deep-sea species diversity lies in documenting these patterns and in discerning the scales at which various causes operate to generate them. Patterns of diversity in the deep sea are much more complicated than previously thought. Early attention centered on bathymetric gradients in the western North Atlantic, the most intensively sampled region of the deep sea. Qualitative (Rex 1981) and quantitative (Etter & Grassle 1992) sampling studies indicated that diversity-depth patterns in the deep sea are unimodal with a peak at intermediate depths and depressed diversity at upper bathyal and abyssal depths. However, unimodal patterns do not appear to be universal (Rex et al. 1997, Stuart et al. 2001), and where they do occur in other basins have been attributed to varied environmental gradients (Paterson & Lambshead 1995, Cosson-Sarradin et al. 1998). Also, a variety of unanticipated oceanographic conditions at specific depths interrupt and modify bathymetric horizontal diversity trends (Gage 1997, Levin & Gage 1998, Vetter & Dayton 1998).

We relate diversity patterns to the regional-scale phenomena of geographic boundary effects, variation in sediment grain size, productivity gradients, oxygen minimum zones, current regimes, and catastrophic disturbances. Regional gradients of diversity represent the combined effects of these ecological factors in governing the rates of local processes. Regional-scale processes are, in turn, a consequence of global oceanography and climate. Compared to other major ecosystems, deep-sea communities appear to be controlled by the same basic mechanisms of energy availability, biological interactions, disturbance, and heterogeneity, but exerted through a very distinctive set of environmental circumstances that is new to ecology. We then consider the important issue of measuring diversity in the deep sea—a basic and persistent problem in comparisons among deep-sea studies and between deep-sea and surface environments (Gage & May 1993, Rex et al. 2000). Finally, a conceptual model is offered to explain how environmental factors interact with biotic processes to generate observed regional patterns.

It is difficult to define, in general terms, a physically or biologically meaningful regional scale in the deep sea. A region is often envisioned topographically as a major deep basin, such as the North American Basin of the North Atlantic that is bounded by the North American Continent and the mid-Atlantic Ridge system (Stuart & Rex 1994). However, deep basins are confluent at considerable depths and connected by the deep thermohaline circulation. Their faunas are not entirely or even largely endemic, suggesting that they neither have distinctive ecologies nor act as isolated theaters of evolution. For our purposes, regions represent areas of roughly 100s to 1000s km^2 that have been well sampled and encompass potentially significant and measurable environmental gradients or ecotones. Most regional studies have taken place at bathyal depths (200–4000 m) on continental margins; much less is known about large-scale spatial variation in abyssal ($>$4000 m) communities.

We focus on the deep-sea macrofauna of soft sediments because it is the most diverse and well-studied component of the benthos. The macrofauna is composed of animals retained on a 300 μm sieve. It includes most familiar invertebrate phyla, and is dominated particularly by polychaete worms, peracarid crustaceans, and mollusks (Gage & Tyler 1991). Where there are sufficient data, we also include the smaller meiofaunal elements. We do not consider reducing environments (hydrothermal vents and seeps); Van Dover (2000) provides an excellent and extensive treatment of these remarkable deep-sea habitats and their ecology.

This review developed from discussion by the Working Group on Deep-Sea Biodiversity supported by the National Center of Ecological Analysis and Synthesis (NCEAS). The Working Group's main objectives are to integrate pattern and scale of biodiversity in deep-sea benthic communities and to apply this to the design of future research programs. Mechanisms of species coexistence on local scales ($<$1 m^2) are addressed for the Working Group by P. V. Snelgrove & C. R. Smith (unpublished manuscript). Later reviews will cover the historical development and global spread of deep-sea faunas and propose strategies for conservation based on our current understanding of pattern and scale.

PATTERNS AND CAUSES OF DIVERSITY

Boundary Constraints and Species Ranges

Deep-sea ecology has focused primarily on the role of local processes in regulating community structure. Explaining species coexistence at small scales in the deep sea remains a major challenge to ecological theory (Gage 1996; P. V. Snelgrove & C. R. Smith, unpublished manuscript). It has proven difficult to extend mechanisms of local community structure to regional patterns in any ecological system (Ricklefs 1987). An alternative approach is to view diversity within regions as a composite of overlapping species distributional ranges (MacArthur 1972, Stevens 1989). Recently, there has been considerable interest in how physiographic and physiological boundaries affect species ranges and consequently patterns of diversity within geographic domains (Colwell & Hurtt 1994, Pineda & Caswell 1998, Willig & Lyons 1998, Lees et al. 1999, Colwell & Lees 2000). Interestingly, a stochastic placement of geographic ranges between boundaries will produce within the bounded region a unimodal pattern of diversity (Colwell & Hurtt 1994) similar to bathymetric gradients found in the deep sea (Figure 1). It is therefore possible to construct null models to test whether observed species diversity gradients depart significantly from those generated randomly by boundary constraints alone. If not, there is little justification for invoking an environmental gradient as the cause.

Pineda (1993) and Pineda & Caswell (1998) applied the geometric constraints model to patterns of deep-sea species diversity along depth gradients in the western North Atlantic. As noted earlier, the macrofauna of this region tend to show unimodal patterns of diversity with depth. The frequency distribution of bathymetric ranges of marine species resembles latitudinal ranges found in terrestrial taxa (Pineda 1993, Brown et al. 1996). Are unimodal diversity depth trends caused solely by boundary constraints imposed by the sea-air interface and the abyssal plain? Pineda & Caswell (1998) tested this possibility for gastropods and polychaetes by using a null model that randomly placed species ranges between the presumed upper and lower boundaries. Actual and randomly simulated diversities were compared for three components of the unimodal pattern: position of peak diversity along the depth gradients, peakedness of the diversity curve, and height of the peak. The null model explained only one aspect of the diversity pattern for each taxon, suggesting that whereas boundaries may affect the general shape of diversity-depth patterns, many important features of the patterns were decidedly nonrandom and attributable to other processes associated with depth.

Sediment Heterogeneity

The remarkable number of species that coexist within deep-sea assemblages is surprising when one realizes that the overwhelming majority of these species are deposit feeders that rely on organic detritus for food (Jumars & Eckman 1983). How can so many species coexist while exploiting the same limited resource? Because the primary food resource is detritus, the nature of the sediments ought

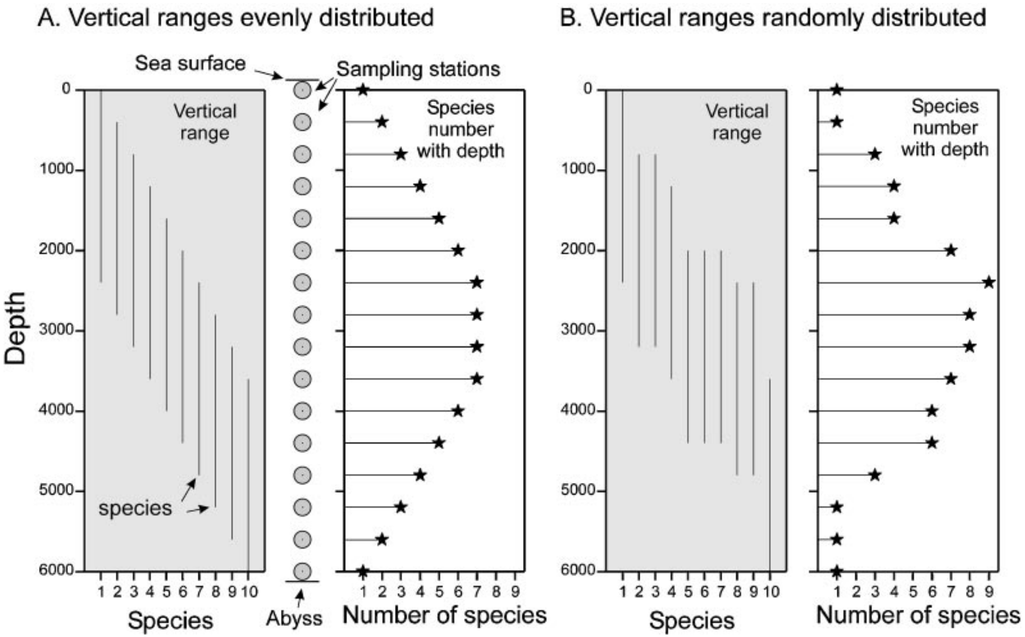

Figure 1 Schematic representation of the potential effects of boundaries on bathymetric patterns in species diversity. The gray panels show ten species evenly and randomly distributed with depth, from 0 to 6000 m (to the left and to the right, respectively). In this representation, all species have a vertical range of 2400 m. Sampling these distributions every 400 m (gray circles) yields bathymetric patterns in species diversity peaking at intermediate depths.

to play an important role in structuring deep-sea communities. Numerous studies have shown that the structure and composition of soft-sediment communities are related to sediment characteristics (e.g., Petersen 1913, Sanders 1968, Rhoads 1974, Gray 1981), but the explanations for these relationships are varied and remain controversial (Snelgrove & Butman 1994).

On the northwest Atlantic slope, spatiotemporal variation in species diversity is correlated with the heterogeneity of sediment grain size across a wide variety of spatial scales (Etter & Grassle 1992). Where sediment grain size is more varied, more species coexist. This is consistent with the hypothesis that species partition the sediments with respect to size. There is abundant evidence that deposit feeders selectively ingest sediments of particular size classes (Taghon 1982, Whitlatch 1980, Wheatcroft & Jumars 1987, Self & Jumars 1988, Wheatcroft 1992). In addition, several species exhibit interspecific differences in particle size preference (Fenchel et al. 1975, Fenchel & Kofoed 1976, Whitlatch 1980), suggesting that the sediments may be partitioned by size in some shallow-water communities. However, this has not been tested for deep-sea species.

The strong correlation between species diversity and sediment heterogeneity does not imply causality. The relationship may be spurious or reflect more important proximal factors. For example, the activities of more diverse communities might actually increase sediment heterogeneity. Also, the size ranges used by Etter & Grassle (1992) in the correlations were of disaggregated grains, and thus may bear little resemblance to food diversity or to the aggregated sediments organisms experience in situ. Definitive answers will require manipulative experiments that tease apart the various potential mediating processes.

Productivity and Food Supply

Spatial gradients in productivity are widely believed to influence species diversity (Waide et al. 1999). In terrestrial systems, the number of animal and plant species often appear to vary unimodally with productivity or nutrient availability (e.g., Tilman 1982, Rosenzweig & Abramsky 1993, Rosenzweig 1995). Diversity within a functional group or taxon increases from regions of low to moderate productivity, and then declines toward regions of higher productivity. Similarly, the unimodal species diversity-depth gradient that attends the exponential decrease in benthic standing stock with depth has been attributed to productivity and its potential mediation of biological interactions (Rex 1973, 1976, 1981).

The deep sea lacks in situ primary production, apart from chemoautotrophic production in reducing environments such as hydrothermal vent and seep habitats (Van Dover 2000). Most food material sinks from the euphotic zone to the benthos in the form of small particles. Particulate organic-carbon (POC) flux can be measured directly with sediment traps, and records integrating annual time scales now exist for at least 37 sites in the open ocean (Lampitt & Antia 1997). Energy availability in deep-sea benthic habitats is also positively correlated with, in order of decreasing strength: 1. sediment-community respiration (Jahnke 1996, Berelson et al. 1997), 2. rate of organic carbon burial within the sediment (Jahnke 1996), 3. benthic biomass and abundance (Rowe et al. 1991, Smith et al. 1997, Cosson et al. 1997), and 4. overlying primary productivity (Deuser et al. 1990, Watts et al. 1992, Lampitt & Antia 1998). It is negatively correlated with depth of water through which phytodetrital food sinks (Suess 1980, Martin et al. 1987). In some cases, the concentrations of organic carbon and chlorophyll a in surface sediments may be directly related to the flux of particulate organic carbon to the seafloor (Emerson 1985, Stephens et al. 1997). But these positive relationships are not necessarily maintained, and may even reverse, over large spatial scales (Jahnke 1996).

A number of productivity gradients have been characterized in the deep sea. There is a general decrease in POC flux (as well as sediment-community respiration and benthic standing crop) from shelf depths to the abyssal plain (Smith & Hinga 1983, Rowe et al. 1991). This depth-related decrease in productivity is well substantiated for gradually sloping and well oxygenated margins such as in the northwest Atlantic (Rowe et al. 1991), but becomes more complicated on irregular slopes or where oxygen minimum zones intersect continental margin (Reimers et al. 1992) and seamounts (Levin et al. 1991). A second productivity gradient is the decrease in seafloor POC flux from the productive coastal zone to the open ocean (Smith & Hinga 1983, Cosson et al. 1997). A third is the reduction in POC flux, sediment-community respiration, and standing crop observed at the abyssal seafloor from the Pacific equatorial zone and its associated nutrient upwelling northward or southward into the oligotrophic central gyres (Smith et al. 1997). Of these three productivity gradients, only that in the abyssal equatorial Pacific varies independently of many other variables that may influence diversity such as the hydrodynamic regime, bottom-water oxygen concentration, and physical environmental stability.

As in other environments (Waide et al. 1999), the relationships between POC flux or proxy variables for productivity and diversity are complicated and scale-dependent. POC flux and sediment-community respiration drop roughly fivefold at the abyssal seafloor from 0°N to 23°N latitude in the central Pacific Ocean (Smith et al. 1997). Mean local nematode diversity, expressed as the number of species rarefied to 51 individuals, exhibits a significant monotonic decline with decreasing POC flux along this gradient [P. J. D. Lambshead, C. J. Brown et al., unpublished manuscript) (Figure 2)]. Within this same general equatorial region, polychaete species richness, normalized to 163 individuals, was weakly positively correlated with total polychaete density, and by inference, POC flux (A. Glover, C. Smith, et al., unpublished manuscript, Figure 2). Neither taxon exhibits a unimodal diversity pattern comparable to those documented for terrestrial productivity gradients (Rosenzweig 1995). However, it is unclear from a comparative standpoint whether we are examining diversity along the ascending or descending part of the diversity-productivity curve, and diversity has been assessed for only one meiofaunal taxon and one macrofaunal group at the family level. Whereas productivity levels beneath central-gyre waters (e.g., 23°N) are extremely low, the productivity levels attained beneath equatorial upwelling are still moderate by deep-sea standards, so

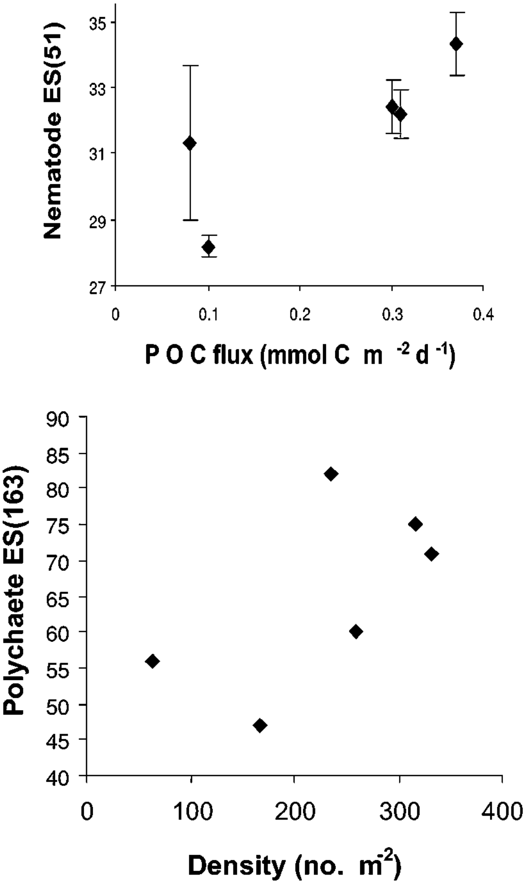

Figure 2 *Top*: Mean local rarefaction species richness (normalized to 51 individuals) as a function of POC flux for nematode samples collected along the equatorial Pacific POC flux gradient. Stations were located at water depths ranging from 4300 to 5000 m, 0°N 140°W; 2°N 140°W; 5°N 140°W; 9°N 140°W; and 23°N 158°W. The correlation between POC flux and rarefaction diversity is high ($r = 0.83$) but not statistically significant ($P = 0.09$) most likely due to small sample size ($n = 5$). Data from Lambshead et al. (2001a, in press). *Bottom*: Rarefaction diversity for macrofaunal polychaetes (normalized to 163 individuals) as a function of polychaete numerical density in the equatorial Pacific. Polychaete density is used as a proxy for POC flux and benthic productivity. Data are for pooled box-core samples (3 to 47 per station) collected from depths of 4300–5000 m at the following locations: 0°N 140°W; 2°N 140°W; 5°N 140°W; 8°27′N 150°47′W; 12°57′N 128°19′W; and 14°40′N 126°25′W. For these data, $r = 0.616$, and $P = 0.193$. Data from A. Glover, C. Smith, et al. (unpublished manuscript).

it is quite conceivable that we are examining diversity along the ascending portion of a more general unimodal diversity-productivity curve.

Cosson-Sarradin et al. (1998) studied polychaete species diversity along a transect of three stations from the continental shelf (<100 m depth) to the abyss (4600 m) off the west coast of central Africa. POC flux varied more than 16-fold from the shelf site to the oligotrophic abyssal station. Local polychaete diversity, based on the Shannon-Wiener index, exhibited a unimodal pattern as a function of POC flux, with a peak in diversity occurring at the mid-slope site (1700 m). However, this transect also represents a strong gradient in physical disturbance resulting from current scour, and possibly physiological stress from organic loading on the continental shelf. Paterson et al. (1998) studied local polychaete diversity (using rarefaction) at six abyssal stations in the Atlantic and Pacific with presumed (but unmeasured) differences in seafloor POC flux. Whereas polychaete abundance covaried with putative POC flux, species diversity showed no obvious relationship. Tietjen (1984, 1989) evaluated local nematode species diversity at six sites in the deep northwest Atlantic. The highest nematode diversity occurred at the sites presumed to have the highest POC flux and productivity.

On the North Carolina slope, the burial rate of organic carbon varies roughly 80-fold along the 850-m contour (Schaff et al. 1992, Blair et al. 1994, Levin et al. 1999). Schaff et al. (1992) and Levin et al. (1994b) examined local polychaete diversity at three stations spaced equidistantly along this productivity gradient and found reduced macrofaunal rarefaction diversity at the station with the highest carbon burial rate. Similar patterns were observed for macrofaunal foraminifera ($>300\ \mu$m) (Gooday et al. 2001). Levin & Gage (1998) used sedimentary organic-matter content as a proxy of food availability to examine diversity-productivity relationships within existing data sets from the deep Indo-Pacific. Their study included a broad range in sedimentary organic carbon ($<0.5\%$ to $>6\%$), and, presumably, habitat productivity. They found negative correlations between sedimentary organic-carbon concentrations and the local diversity of total macrofauna and polychaetes. Dominance in particular, was positively correlated with sediment POC concentrations, suggesting that competitive interactions may shift along POC gradients.

Sampling studies in the western North Atlantic provide, by far, the largest and most geographically extensive database available to examine diversity-productivity relationships. The unimodal diversity-depth patterns revealed by 1. rarefying large qualitative samples (Rex 1981) and 2. tabulations of species number from intensive quantitative sampling (Etter & Grassle 1992) parallel an exponential decline in benthic standing stock with increased depth. As mentioned above, benthic biomass and abundance are assumed to reflect the rate of nutrient input to the seafloor, but this has not been directly measured (Smith et al. 1997). Rex (1973) suggested that depressed diversity in the abyss was imposed by extremely low population densities, essentially as a chronic Allee Effect. There seems to be general agreement among ecologists that this kind of mechanism is responsible for low diversity at very low productivity (Rosenzweig & Abramsky 1993). The drop in diversity in the upper bathyal zone, close to high surface production and terrestrial runoff, could be driven by pulsed nutrient inputs and its potential to accelerate competitive exclusion (Rex 1976, Huston 1979).

Diversity trends in deep-sea microfossils over geological time scales mirror some of the spatial patterns described for modern productivity gradients and corroborate the inference that energy supply can regulate species diversity. Fluctuations in Shannon Wiener (H′) diversity of benthic ostracods correspond to orbitally driven glaciation cycles over a 550,000 year period in the late Pliocene in the North Atlantic (Cronin & Raymo 1997). Diversity was highest during interglacial periods and declined during glacial advances, when surface production may have been lower in the North Atlantic. Thomas & Gooday (1996) proposed that the establishment of a Southern Hemisphere latitudinal gradient in foraminiferan diversity in the late Eocene around 38 my ago, which persists today (Culver & Buzas 1998, 2000), was created by an increase in the seasonally pulsed organic flux that accompanied high latitude, Southern Hemisphere cooling, and the buildup of ice on the Antarctic continent. This temporal diversity pattern was driven by fluctuating dominance of opportunistic foraminifera that consume sinking phytodetritus.

The recent studies discussed above that use direct measures of productivity, such as POC flux, sediment organic content, and carbon burial rates, appear to give conflicting results; diversity varies positively, negatively, or unimodally with productivity. However, these findings are not necessarily contradictory. The productivity/input gradients examined may represent ranges of food availability that occupy different segments of a unimodal diversity-productivity relationship. The increase in diversity from areas of low to high POC flux in the abyssal equatorial Pacific may correspond to the ascending part of the diversity-productivity curve, much as proposed for the elevation of diversity from abyssal to the bathyal regions in the western North Atlantic. The pattern reported for the eastern tropical Atlantic spans a large vertical and horizontal geographic range that may experience productivity inputs broad enough to realize the full unimodal trend. Regions that include exceptionally high nutrient input, such as the North Carolina slope, may fall on the descending part of the curve where diversity and productivity are negatively correlated. Other observations suggest that depressed diversity in the deep sea is associated with periodic high organic loading such as might be associated with areas subject to intense upwelling (Sanders 1969), deposition from lateral transport of nutrients (Blake & Hilbig 1994), benthic storms that expose reactive sediments (Aller 1997), or bottom topography that concentrates food (Jumars & Hessler 1976, Vetter & Dayton 1998). However, all involve multiple factors that could affect diversity, and because the level and variation of production may covary, it is difficult to separate their influence. In general, a unimodal relationship between diversity and productivity at large scales in the deep sea is plausible, but is not well substantiated. Just as in other environments (Waide et al. 1999), it has proven difficult to accurately place available studies on a continuous productivity gradient and to identify clearly the underlying mechanisms through which productivity influences species diversity.

At low levels of productivity, food limitation is thought to constrain the number of species that can survive. Declines in diversity at higher productivity levels may result from four possible causes. 1. Differential numerical responses among species to nutrient loading (varying population growth rates) such that a small number of opportunistic species take over. This will elevate dominance and lower diversity measures that incorporate evenness. In many cases local species richness may not change much (see Levin et al. 2000). 2. Faster rates of competitive exclusion as envisioned by Huston (1979). 3. Increased variability in productivity, which is often correlated with amount of productivity. This variability may bring about declines due to demographic stochasticity. 4. Excess oxygen demand creating hypoxia and leading to declines in both richness and evenness due to physiological stress.

Bottom-Water Oxygen

Bottom-water oxygen concentrations in the deep oceans vary from near 0 to over 7 ml/l (Tyler 1995). Although much of the ocean has oxygen values near saturation, there are extensive midwater regions where oxygen is depleted; these typically occur between 100 and 1200 m depth. They are usually formed beneath highly productive, upwelled waters by degradation of organic matter. The resulting hypoxic zones, referred to as oxygen minimum zones (OMZs) and operationally defined as areas where $O_2 < 0.5$ ml/l, persist over geologic time. OMZs occur in much of the eastern Pacific Ocean, in the Arabian Sea, and off West Africa (Kamykowski & Zentara 1990). Certain deep basins (e.g., off southern California) and fjords also contain permanently hypoxic or anoxic waters. Where these low oxygen regions intercept the continental seabed, the benthos experiences either permanent hypoxia or an oxygen gradient, which may fluctuate daily with internal tides (e.g., Levin et al. 1991), interannually (e.g., with ENSO events, Arntz et al. 1991, Gallardo 1985), or over geologic time (den Dulk et al. 1998, Rogers 2000).

Sediments having oxygen-depleted overlying bottom water typically exhibit substantially reduced macrofaunal diversity. Within OMZs the macrofauna exhibit low species richness and very high dominance (Table 1). This pattern was first reported on the West African margin off Walvis Bay by Sanders (1969), and has since been observed in the eastern Pacific on a seamount off Mexico (Levin et al. 1991), on the Peru and Chile margins (Levin et al. unpublished data), and in the NW Arabian Sea off Oman (Levin et al. 1997b, 2000). Among the macrofauna, many molluscs, crustaceans, echinoderms, and cnidarians appear less tolerant of hypoxia than other taxa (Diaz & Rosenberg 1995), although there are exceptions (Levin & Gage 1998). No single taxon dominates the macrofauna of low oxygen settings, although annelid species are often prevalent. At upper slope depths, within the least oxygenated portions of OMZs, dominance of the most abundant species typically ranges from 40% to 85% (Levin & Gage 1998) (Table 1). Less information is available concerning the diversity responses to reduced oxygen concentrations of bacteria, small protists (nanofauna), meiofauna, or megafauna. Smaller organisms

TABLE 1 Community structure of macrofauna and foraminifera at hypoxic sites within oxygen minimum zones of the eastern Pacific and Indian Oceans

Location	Depth (m)	Bottom-water oxygen (ml/l)	Dominant taxon	R1D (%)	$E_{s\,(100)}$	H'	Density	Reference
Oman margin	400	0.13	Spionidae (Polychaeta)	63	5.6	1.45 ($\log_2$)	12,362 m^{-2}	Levin et al. 2000
Oman margin	412	0.13	Foraminifera >125 μm, 0–1 cm	27	23.9	1.23 ($\log_{10}$)	2533 10 cm^{-2}	Gooday et al. 2000
Santa Barbara Basin	550	0.06	Tubificidae (Oligochaeta)	44	N/A	1.77 ($\log_2$)	1,691 m^{-2}	Levin et al. unpublished
Santa Barbara Basin	590 610	0.05 0.15	Foraminifera >63 μm, 0–1 cm	49 25	8.9 21.4	0.72 ($\log_{10}$) 1.10 ($\log_{10}$)	N/A	Gooday et al. 2000
Volcano 7, Mexico	750	0.08	Aplacophora (Mollusca)	47	10.8	2.59 ($\log_2$)	1,854 m^{-2}	Levin et al. 1991
Peru margin	300	0.02	Tubificidae (Oligochaeta)	83	4.7	0.84 ($\log_2$)	13,539 m^{-2}	Levin et al. unpublished
N. Chile margin (Iquique)	300	0.26	Dorvilleidae (Polychaeta)	73	N/A	N/A	1,834 m^{-2}	Levin et al. unpublished
Central Chile margin (Concepcion)	364	0.52	Amphinomidae (Polychaeta)	31	17.6	2.46 ($\log_2$)	14,206 m^{-2}	Gallardo et al. unpublished

living entirely within the sediments and with no access to the surface may be confined to hypoxic or even anoxic pore-waters, even when the overlying bottom water is oxic (Corliss & Emerson 1990, Jorissen et al. 1998). Yet foraminifera and a variety of larger metazoans (polychaetes, crustaceans, molluscs, echinoderms) all display abundance peaks close to OMZ boundaries (Mullins et al. 1985, Levin et al. 1991).

Where a range of faunal size groups have been compared, larger taxa (megafauna and macrofauna) exhibit density reductions within the most hypoxic portions of OMZs (Wishner et al. 1990, Levin et al. 1991, 2000) that are not evident in bacteria and metazoan meiofauna (Levin et al. 1991, Cook et al. 2000, Neira et al. in press). Metazoan meiofauna of the eastern Pacific OMZ exhibit loss of harpacticoid copepods, and dominance by nematodes (Levin et al. 1991, Neira et al. 2001), but diversities have not been recorded. Foraminiferal assemblages characterized by high dominance and few species are reported from modern, low-oxygen basins in the eastern Pacific and elsewhere (Phleger & Soutar 1973, Douglas et al. 1980, Hermelin & Schimmield 1990, SenGupta & Machain-Castillo 1993, Bernhard et al. 1997). The fossil record yields evidence for similar responses among ancient deep-sea faunas (e.g., den Dulk et al. 1998, Jorissen 1999). However, precise diversity data are rarely reported. At a site within the NW Arabian Sea OMZ, foraminifera exhibited reduced species richness and elevated dominance compared with assemblages from a deep site below the OMZ (Gooday et al. 2000). These low-oxygen faunas consisted largely of small calcareous forms, a trend observed in the OMZ off Peru as well (A. Rathburn, unpublished manuscript). In contrast to fully oxic deep-sea sites, monothalamous and other delicate agglutinated and allogromiid taxa are rare compared to calcareous forms within OMZs (Gooday et al. 2000).

These limited deep-sea observations are consistent with field (Josefson & Widbom 1988, Murrell & Fleeger 1989, Radziejewska & Maslowski 1997, Luth & Luth 1997) and experimental (Moodley et al. 1997) studies conducted in shallow water that suggest that meiofauna, particularly nematodes and foraminifera, are less affected by hypoxia than the macrofauna, at least at higher taxonomic levels. There are, however, shallow-water examples in which nematode diversity is reduced by severe hypoxia (Keller 1986, Austin &Widbom 1991).

Historical records support a role for oxygenation in control of deep-sea diversity. In the northern Arabian Sea, foraminiferal diversity appears to have been strongly influenced during the Quaternary by changes in the flux and quality of organic matter to the seafloor, which led to variations in the thickness and intensity of the oxygen minimum zone (Hermelin & Shimmield 1995, den Dulk 2000). den Dulk et al. (1998) studied a 120,000 years-long Quaternary record from the Pakistan margin in the Northern Arabian Sea. Two foraminiferal assemblages were recognized. A low diversity assemblage with high dominance recurred every 23,000 years, possibly as a result of enhanced summer surface productivity and therefore intensified OMZ development, linked to the precessional component of orbital forcing. A more sustained period of low diversity occurred under glacial conditions, perhaps reflecting a strengthening of the NE monsoon, leading to higher winter productivity. In a detailed multiproxy study of shorter cores (spanning the last 30,000 y) from the same margin, von Rad et al. (1999) detected a switch from low to high foraminiferal diversity on the Pakistan margin during brief, late Quaternary to early Holocene climatic oscillations (Younger Dryas, Heinrich events 1 and 2) when surface productivity was unusually low and presumably the OMZ intensity diminished. Evidence for a close coupling between foraminiferal benthic community structure (including dominance) and bottom-water oxygenation is seen in the Santa Barbara Basin on even shorter time scales. There, fluctuations on decadal to millennial time scales are associated with major climate oscillations that change thermolhine circulation and ventilation (Cannariato et al. 1999).

During the Late Cretaceous, anoxia sometimes occurred on a much larger scale than in modern oceans, and caused widespread benthic mortality (Rogers 2000). Most of these events are far too ancient to have any residual effect on modern diversity patterns. A possible exception occurs in the eastern Mediterranean, which was subject to repeated episodes of basin-wide, deep-water anoxia during the Late Quaternary and most recently around 6000 years ago. Anoxic episodes, represented in the sedimentary record by clearly defined, dark horizons (sapropels), had a profound effect on the benthic foraminiferal faunas (Jorissen 1999). Distinct regional-scale differences in foraminiferal species richness and composition between the eastern and western Mediterranean basins may reflect these major disturbances in the recent geological past (de Rijk et al. 1999).

There is a difficulty with interpreting diversity responses to bottom-water oxygen conditions that derives from the tight linkage between bottom-water oxygen concentration and organic matter inputs in the deep sea (Levin & Gage 1998). Multiple regression analyses of a large macrofaunal data set from the Indian and eastern Pacific Oceans suggest that oxygen exerts a strong effect on species richness, although organic matter availability (evaluated from sediment POC) has a greater influence on dominance (Levin & Gage 1998). Together, these factors lower diversity within OMZs. Although food availability may affect diversity over a broad range of oxygen values, significant reduction of macrofaunal species richness by low oxygen may not occur until concentrations fall below 0.4 or 0.3 ml l^{-1} (Figure 3); this value may be even lower for annelids, the taxon most tolerant to hypoxia. Sulfides, which are toxic at high concentrations to most marine organisms (Bagarinao 1992), are associated with high inputs of labile organic matter, and also vary inversely with oxygen concentration. Their role in reducing diversity within OMZs has yet to be explored.

A major challenge is unraveling the relative importance of physiological stress and biotic interactions in creating deep-sea responses to low oxygen. Although stress may cause loss of species and dominate diversity responses at the lowest oxygen levels, facilitation may also be important. Animal structures such as tubes or burrows that conduct seawater into the sediments, or irrigation activities that mix solutes may enhance oxygen availability and dilute sulfides, facilitating colonization by other taxa. At higher oxygen levels, competitive abilities and predation may regulate diversity.

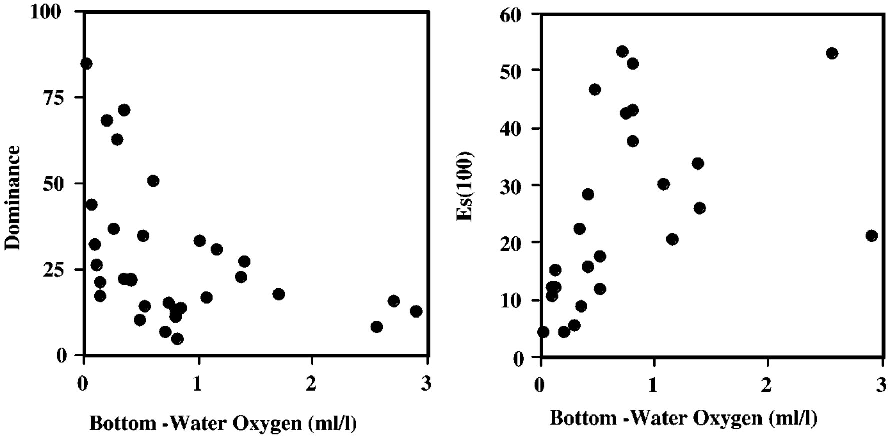

Figure 3 Macrofaunal Rank 1 dominance (% of the total accounted for by the top ranked species) and species richness (E[S_{100}]) plotted as a function of bottom-water oxygen concentration for bathyal stations within and beneath oxygen minimum zones in the eastern Pacific and northern Indian Oceans.

Deep-Sea Currents

Near-bottom flow rates in the deep ocean are typically a few cm/sec, too weak to erode the seabed (Munk 1970, Tyler 1995). The ocean floor is not uniformly quiescent, however, and numerous areas are subject to currents strong enough to erode and transport sediments and disturb soft-bottom communities on scales of 10s or 100s of km, (Heezen & Hollister 1971, Hollister et al. 1984). Episodic benthic storms characterize areas beneath western boundary currents where surface kinetic energy is transmitted through the water column to the sea floor; near-bottom currents reach speeds of 15–40 cm/sec and persist for several days (Gross & Williams 1991, Hollister & Nowell 1991, Aller 1997, Weatherley & Kelley 1985). First described in the HEBBLE area on the Nova Scotian continental rise, benthic storms occur along the western margins of the North and South Atlantic, around South Africa, and in regions around the Antarctic continent (Rowe & Menzies 1968, Flood & Shor 1988, Hollister & Nowell 1991, Richardson et al. 1993). Similar transient, high-energy episodes have been reported in abyssal areas distant from continental margins, for example in the NE Atlantic (Klein 1988) and NE Tropical Pacific (Koutar & Sokov 1994).

There are many other sources of strong current activity in the deep sea. Thermohaline-driven bottom currents transport vast amounts of sediment around the deep ocean, depositing them as huge sediment drifts (contourites), for example, west of Scotland (Hollister et al. 1984, Stow & Holbrook 1984, Kidd & Hill 1986, Stow & Faugères 1993, Viana et al. 1998). In the Rockall Trough, current speeds >15 cm/sec are frequently recorded by current meters moored on the upper slope above 1000 m (Paterson & Lambshead 1995) with peak flows reaching 48 cm/sec (Viana et al. 1998). Along continental margins, more localized hydrographic phenomena such as internal tides, water column instability, and storm-driven eddies may create strong, erosional currents on the upper slope (Dickson & McCave 1986, Pingree & New 1989, Rice et al. 1990, Gage 1997). Complex interactions between steeply sloping topographic features and local hydrography create regions of intensified near-bottom flow on seamounts (Noble & Mullineaux 1989), as well as in canyons (Shepard et al. 1979, Gage et al. 1995, Gage 1997) where turbidity currents also may be active (Jorissen et al. 1994).

Near-bottom currents are among the agents of disturbance that can modify the structure and composition of benthic faunas (Hall 1994). As Levin et al. (1994a) emphasize, however, the critical factor may be sediment mobility, which depends on sedimentary characteristics as well as the current flow itself. Gage et al. (1995) and Gage (1997) demonstrate with rarefaction curves, rank abundance plots, and univariate diversity indices that polychaete diversity is highest at tranquil sites on the Tagus Abyssal Plain and in the central North Pacific, lower in the Rockall Trough and in the hydrodynamically active Sebutal Canyon, and much reduced at the HEBBLE site. Bivalve diversity exhibits a similar trend, although the differences are much less pronounced. Foraminifera at the main (Mid) HEBBLE site were significantly less diverse (H') than at the relatively tranquil shallow site (Kaminski 1985). Allen & Sanders (1996) attribute anomalously low protobranch bivalve mollusc diversity in the North American Basin to possible benthic storms. Paterson & Lambshead (1995) observed a strong linear relationship between the frequency of current velocities >15 m/sec in the Rockall Trough and the equitability statistic V for polychaetes. Negative values of V, indicating high dominance, were associated with high current speeds on the upper slope in the Rockall Trough. As at HEBBLE, polychaete taxa generally considered to be opportunists predominated in parts of the Rockall Trough where physical disturbance was high. On Fieberling Guyot, Shannon-Wiener (H') values for macrofauna were very similar at contrasting sites with daily and infrequent, episodic sediment transport, but species richness measured by rarefaction was somewhat higher at the more stable SPR site (Levin et al. 1994a, see also Levin & DiBacco 1995).

In the case of meiofaunal taxa, strong erosive currents do not necessarily depress diversity. Thistle (1983) found no difference in harpacticoid copepod diversity in samples from the energetic HEBBLE site and the tranquil San Diego Trough. Contrary to his initial expectation, Thistle (1998) observed that harpacticoid copepod diversity was actually higher at the Fieberling Guyot WSS site, where the *Globigerina* sands are mobile on a daily basis, than at the more stable SPR site. Nematode diversity was very similar at three stations (545 m, 835 m, 1474 m depth) in the Rockall Trough and at 1050 m in the San Diego Trough, despite differences in current velocities both between these two basins and with depth within the Rockall Trough (Lambshead et al. 1994). Severe benthic storms do appear, however, to depress nematode species richness [measured as $E(S_{51})$] at the HEBBLE site compared with values from relatively tranquil localities on the Porcupine and Hatteras

Abyssal Plains (Lambshead et al. 2001). This may reflect a greater intensity of current disturbance at HEBBLE than in the Rockall Trough.

The observations reviewed above suggest that currents can modify benthic diversity both locally and regionally, although the mechanisms involved are not well understood. The effects can be either positive or negative, and there are indications that macrofauna are more strongly impacted than meiofauna. Possible mechanisms can be divided into those having a direct impact and those having an indirect impact on diversity. Strong currents may depress diversity directly by eroding surficial sediments and carrying away the animals living in them (Aller 1997). Observations at the HEBBLE site (Thistle et al. 1985, 1991, Lambshead et al. 2001) and the WSS site subject to daily sediment transport on Fieberling Guyot (Levin & DiBacco 1995) suggest that episodic disturbance by erosive flow creates repeated opportunities for recolonization. Constant reworking of the sediment ensures that the benthic fauna remains in an early successional state, favoring opportunists, and keeping diversity low.

Near-bottom currents have the potential to impact benthic faunal diversity in a variety of indirect ways. Moderate currents can enhance the food supply by delivering organic matter and stimulating bacterial production (Thistle et al. 1985, Aller 1989). As long as these inputs are not excessive, they should lead to an increase in both abundance and diversity of macro- and meiofauna. Currents may also entrain larval and subadult organisms, allowing animals to colonize disturbed patches of sediment and enhance local diversity. Moderate flow conditions may potentially increase sediment heterogeneity by creating sedimentary structures and by concentrating organic matter in localized patches. At the White Sand Swale (WSS) site on Fieberling Guyot, active ripples generate heterogeneity by successively burying and exposing organic matter accumulated in the troughs. This process may explain why harpacticoid copepod diversity was higher at WSS than at the more stable Sea Pen Rim site (Thistle 1998). When flow velocities were enhanced experimentally at WSS for a 6-week period, however, there was no detectable change in harpacticoid or total macrofaunal diversity or equitability, possibly because the assemblages were already adapted to strong erosive flow (Levin et al. 1994a, Thistle & Levin 1998).

As indicated above, near-bottom flows in excess of 20–25 cm/s can potentially depress diversity by eroding epifaunal species, but they may also impact diversity indirectly by smoothing out and reducing physical heterogeneity. On a regional scale, erosive bottom currents will tend to homogenize the fauna by dispersing juveniles and subadults. Given the large areas of seafloor swept by erosive currents (Hollister et al. 1994, Hollister & Nowell 1991), the impact of hydrodynamics on regional deep-sea species diversity and biogeography may be considerable.

Hydrodynamic processes are probably involved in the creation of larger habitat patches that increase seafloor heterogeneity. On the upper slope around the NW European continental margin, interactions between the seafloor and internal tides and waves are apparently linked to conspicuous concentrations of hexactinellid sponges (Rice et al. 1990) and corals (Fredrickson et al. 1992). In the Porcupine

Seabight (1000–1300 m water depth), sponges and spicule mats derived from them enhance the abundance and modify the taxonomic composition of the macrofauna (Bett & Rice 1992). Both corals and sponges have numerous associated organisms (Klitgaard 1995, Jensen & Frederiksen 1992, Bartel & Gutt 1992). However, at least in the NE Atlantic, most of the associated organisms are also present in the background community (Klitgaard 1995, Jensen & Frederiksen 1992), suggesting that regional diversity may not be increased substantially by the presence of these large, habitat-creating organisms.

Catastrophic Disturbance

Over geological time scales, continental margin sediments have been disrupted by gravity-driven mass movements, including slumps, slides, debris flows, and turbidity currents (Masson et al. 1994, 1996). At their distal extremities, disturbance by turbidity currents is probably similar to that caused by severe erosive currents such as benthic storms. In the Atlantic Ocean, mass movements are well documented off NW Europe, NW Africa, southern Africa, the United States between New York and Cape Hatteras, and Brazil (Emery & Uchupi 1984). Off NW Africa debris flows, particularly the unusually large Canary and Saharan flows (Jacobi & Hayes 1982, Simms et al. 1991, Embley 1976, Masson et al. 1994, Masson 1996), have displaced 600 km^3 of sediment on the upper continental rise. Elsewhere in the NE Atlantic, the mid-Norwegian margin (the "Storegga" area; 62°N) is notable for a series of enormous slides, the most recent of which occurred about 7000 years ago (Bugge et al. 1987). 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. The flanks of volcanic islands such as the Hawaiian Islands in the Pacific and the Canary Islands in the Atlantic are prone to catastrophic collapses that give rise to massive avalanche deposits on the adjacent deep-sea floor (Lipman et al. 1988, Moore et al. 1989, Cochonat et al. 1990, Masson 1996). These mass movements of sediments are often associated with turbidite deposition, an important mechanism in the formation of abyssal plains adjacent to continents. The best known modern turbidity flow occurred in 1929 when an earthquake on Grand Banks, Newfoundland, triggered a sediment slump that developed into a turbidity current extending 800 km from its source across the abyssal plain. More recently, Thunnell et al. (1999) provided the first direct, real-time documentation of earthquake-generated suspended sediment flows.

Although major mass movements of sediment must devastate the benthic fauna, most of these events occurred thousands of years ago and are unlikely to affect modern faunas directly. Indirect effects, however, may persist for much longer. Debris avalanches and similar chaotic deposits will introduce long-lasting physical heterogeneity on spatial scales up to kilometers (Masson 1996). Turbidites have granulometric characteristics and total organic carbon (TOC) values that differ from those of pelagic sediments (Huggett 1987) and can potentially influence diversity. There is evidence for such an effect at a location on the Madeira Abyssal Plain (MAP; 4950 m water depth) that was swept by a turbidite about 1000 years ago. Here, polychaetes exhibit lower abundance, much lower species richness [expressed as $E(S_n)$ and per unit area], and higher dominance compared to other abyssal NE Atlantic sites, including the equally oligotrophic EUMELI site, where sedimentation is entirely pelagic (Glover et al. 2001). The sedimentary characteristics of the turbidite deposit, which is overlain by only a thin veneer of pelagic sediment, may have confined recolonization to a relatively small suite of opportunistic polychaete species. Nematodes, which lack a dispersive larval phase, also exhibit lower diversity [$E(S_{51})$] at the MAP than at nonturbidite sites on the Porcupine and Hatteras Abyssal Plains (Lambshead et al. 2001b in press). Foraminiferal diversity, on the other hand, is not noticeably depressed at the MAP (Gooday 1996). There is no evidence for low nematode diversity at a site in the Venezuela Basin (5054 m depth) subject to periodic turbidite impacts. This is probably because the sedimentation rate ($7.2 \text{ cm} \cdot \text{ky}^{-1}$) is much higher and the turbidites are older in the Venezuela Basin than in the MAP (Lambshead et al. 2001b in press).

Submarine and subaerial volcanic eruptions may impact deep-sea benthic faunas directly, through deposition of lava or ash layers (Cita & Podenzani 1980), and indirectly through changes in climate and water column stratification (Genin et al. 1995). Fossil foraminiferal evidence from the eastern Mediterranean suggests that the benthic fauna was obliterated by an ash deposit 35,000 years ago but that a very similar assemblage reestablished rapidly (Cita & Podenzani 1980). We are aware of only one species-level study of the effect of a modern ashfall in the deep sea on a benthic taxon (Hess & Kuhnt 1996). During 1991, an ash layer >2 cm thick was deposited over 36,000 km^2 in the South China Sea following the eruption of Mt. Pinatubo, Philippines. Rarefaction curves based on data from Hess & Kuhnt (1996) indicate that foraminiferal assemblages were severely affected by a 6 cm ash deposit at 2503–2506 m; most foraminifera died, although epifaunal specimens found below the ash layer may have survived for some time in a starved, quiescent state. After almost three years, the ash layer had been recolonized by a low-diversity assemblage of infaunal opportunists. In a 2-cm deep ash deposit at 4226 m, however, many mobile infaunal taxa survived and species richness decreased only slightly.

MEASURING THE LEVEL OF DEEP-SEA SPECIES DIVERSITY

Very basic questions remain about how diversity should be measured and interpreted. A wide variety of diversity measures exist that incorporate both richness and evenness but differ in how these components of diversity influence the magnitude of the index (Magurran 1988). Because most diversity indices are sensitive to both evenness and richness, differences can reflect changes in either or both; changes in evenness should not be interpreted as changes in richness. The choice of an index depends on the nature of the question and the type of data available. In most cases, it will be useful to use a variety of indices that together provide greater insight into how and why diversity varies than does a single index.

The most widely used measure of diversity in deep-sea ecology is $E_{(Sn)}$, the Expected Number of Species (Sanders 1968, Hurlbert 1971). This index estimates the number of species in samples normalized (rarefied) to successively smaller sample sizes, providing an interpolated curve of the relationship between the number of species (S) and the number of individuals (N) based on resampling the relative abundance distribution of an actual sample. It is sensitive to both evenness and richness (Gage & May 1993), and was originally designed to allow comparisons of nonquantitative samples taken by epibenthic sleds. The sleds are towed from a surface vessel for a variable distance of about a kilometer and are apt to bounce along the bottom. The only way to compare diversity among such samples is by normalizing them to the same number of individuals, typically the lowest common number of individuals. Quantitative coring devices (Hessler & Jumars 1974) sample a precise area of bottom and accurately measure faunal density. Should quantitative samples be rarefied? This is problematic if the habitats sampled differ greatly in density, which they often do. For example, a boxcore may yield 10,000 individuals from a continental shelf habitat, but fewer than 100 at greater bathyal depths. Normalizing the two samples to 100 individuals effectively compares the number of species at 9 cm^2 on the shelf to 900 cm^2 in the deep sea. This procedure will mask the differences in density between sites, which may be critical for understanding why diversity differs. Because no shallow-water samples may yield as few as 100 individuals, the number of species is predicted from the lower portion of the species-individuals curve where the slope is steepest and the error for estimating S is largest. Finally, because rarefaction assumes a random distribution between S and N, replicate samples from a site are often pooled (e.g., Grassle & Maciolek 1992, Etter & Grassle 1992). This obscures the actual relationship between S and N at the sampling scale, and how differences in heterogeneity among sites may contribute to variation in diversity. Rarefaction has been an important and useful tool for quantifying and comparing community structure, but for a comprehensive understanding of regional patterns of diversity it should be used in combination with other measures.

A better approach for comparing regional species richness with quantitative samples is species accumulation curves with randomly pooled samples (Etter & Mullineaux 2000). This requires replicate samples at each location, but maintains the relationship between S and N, which preserves differences in heterogeneity and allows one to compare diversity based on the number of individuals or area sampled. Most importantly, it can be used to estimate the asymptotic S (the number of species in the community if it were completely sampled) and how well the community has been sampled (the position on the species accumulation curve), both of which are crucial for comparing and interpreting differences in S. Randomized species accumulation curves will typically be lower than rarefaction curves (Figure 4) because they maintain the nonrandom distribution of S and N at the scale of the sampling device. The difference between the two curves reflects the amount of heterogeneity at the scale of the sampler. Two programs that allow one easily to

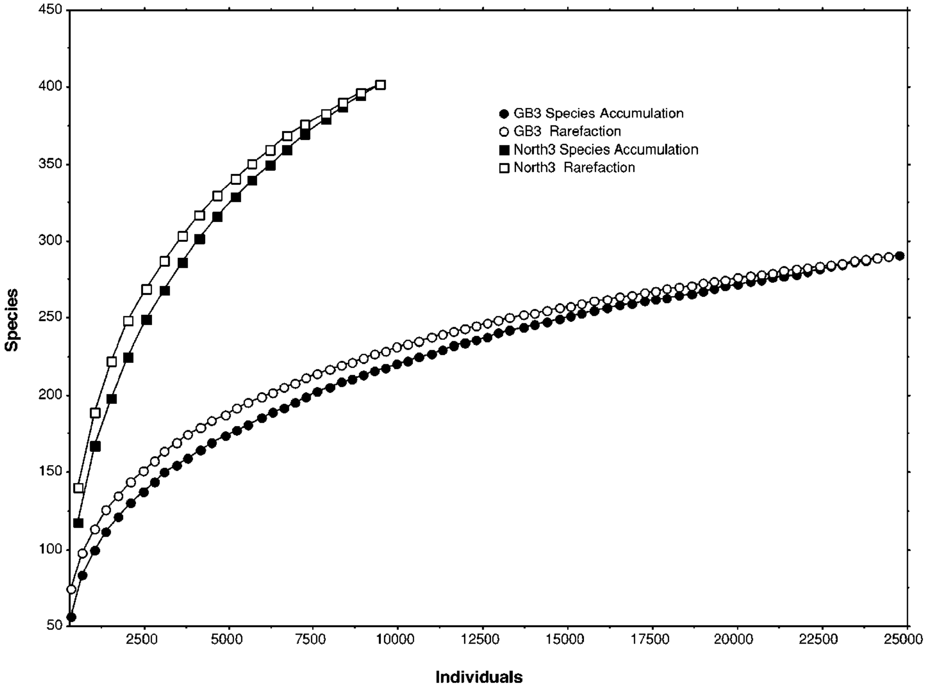

Figure 4 Randomized species accumulation and rarefaction curves for Station 3 on Georges Bank (GB3, 100 m, 40°53.7′N, 66°46.5′W) and Station 3 from the North ACSAR (Atlantic Continental Slope and Rise) (North 3, 1350 m, 41°1.40′N, 66°20.20′W). The randomized species accumulation curves are the average cumulative number of species from 50 randomizations of pooling successively larger numbers of replicates at each station. Data are from Maciolek et al. (1985) and Maciolek et al. (1987b).

compute randomized species accumulation curves are Estimate S (Colwell 1997) and Rosenzweig's (1995).

Gray (1994) and Gray et al. (1997) provide a recent example of the problems encountered when comparing diversity among habitats. Benthic samples from a variety of shallow-water habitats (<200 m) were compared to those collected from the deep northwest Atlantic by Grassle & Maciolek (1992) to argue that shallow-water and deep-sea communities may be quite similar in diversity. However, these comparisons were confounded by the shallow-water samples being collected from broader geographic areas (Gray 1994) at different latitudes and by using different sieve sizes (1 mm rather than 300 μm), both of which can influence diversity (Bachelet 1990, Warwick & Clarke 1996, Rex et al. 1993). More importantly, because estimates of species richness are highly sensitive to sampling effort (May 1975, Colwell & Coddington 1994, Rozenzweig 1995), comparisons should be made only at the asymptote of a species accumulation curve. Although the shallow-water samples of Gray et al. (1997) approach an asymptote, the deep-sea samples show no sign of leveling off (Grassle & Maciolek 1992). The problem of assessing diversity when no asymptote has been reached is often overlooked in spatial and temporal comparative studies of richness. Rarefying the samples to a common number of individuals does not eliminate the sensitivity of richness estimates to sampling effort. For example, samples of 100 individuals in one community may contain 90% of the species, although another may contain only 10%. The only way to overcome this potential artifact is to restrict comparisons of S to the asymptotic S.

To reexamine the question of whether deep-sea habitats support more species than shallow-water habitats, we can compare diversity between a series of deep-water samples collected off the coast of Massachusetts [the North data collected as part of the Atlantic Continental Slope and Rise Study (ACSAR)] (Maciolek et al. 1987b) to a very similar set of samples collected from the nearby shallow waters of Georges Bank (Maciolek et al. 1985). This comparison was selected because the shallow and deep samples are geographically adjacent (both just off the coast of Massachusetts), were collected in a similar way, were sorted by sieves of the same size, have consistent taxonomy (done by the same individuals), and represent the entire macrofaunal community. The Georges Bank samples were collected with 0.04 m^2 Ekman grabs from 38 to 167 m. The ACSAR samples were collected with 0.25 m^2 boxcores from 250 to 2500 m, but only the center 0.09 m^2 was used for community analysis. No other shallow- and deep-water data bases are as comparable.

For the deep-water samples (those >200 m), on average 278 species coexist in an area of 1 m^2 and the expected number of species was 156 when normalized to 1000 individuals (ES_{1000}). In contrast, the shallow-water samples produced an average of only 165 species m^{-2} and 68.8 species per 1000 individuals (Table 2).

TABLE 2 Average measures of diversity and density for the Georges Bank and the ACSAR samples. $E_{(S1000)}$ are Hurlbert's (1971) expected number of species normalized to 1000 individuals. ACSAR North (130 m) are averages based only on samples collected between 1220–1350 m from the North. Data are from Maciolek et al. (1987b) and Maciolek-Blake et al. (1985)

	Georges Bank	**ASCAR North**	**ASCAR North (130 m)**
Samples	1149	191	63
Depth Range (m)	38–167	250–2180	1220–1350
Individuals	680,600	95,140	27,906
Species m^{-2}	165	278	319
$E_{(S1000)}$	68.8	156	188
Shannon Wiener Index ($\log_2$)	4.09	5.59	6.70
Species Richness	680	952	599

This comparison of averages is conservative because the deep-sea samples span a 2000-m depth gradient and include relatively shallow depths that are lower in diversity. If the deep-sea samples are restricted to a 130-m depth interval (similar to the range of Georges Bank samples) centered at 1300 m, the differences are even more pronounced (Table 2). Randomized species accumulation curves based on either individuals or area also indicate that diversity is greater in the deep-sea samples (Figure 5). Asymptotic S values estimated from the species accumulation curves at each site using Chao1 (Colwell & Coddington 1994) indicate that richness varies unimodally with depth (Figure 6), as suggested previously based on rarefied qualitative (Rex 1981, 1983) and quantitative samples (Etter & Grassle 1992).

Pooling the ACSAR samples and Georges Bank samples by depth produces estimates of species richness that are quite similar (Table 2), as Gray [(1994), Gray et al. (1997)] suggested for his studies. In fact, when pooled over 130 m, richness appears to be greater on Georges Bank, but the species accumulation curves (Figure 7) clearly show that the shallow-water estimates are near an asymptote

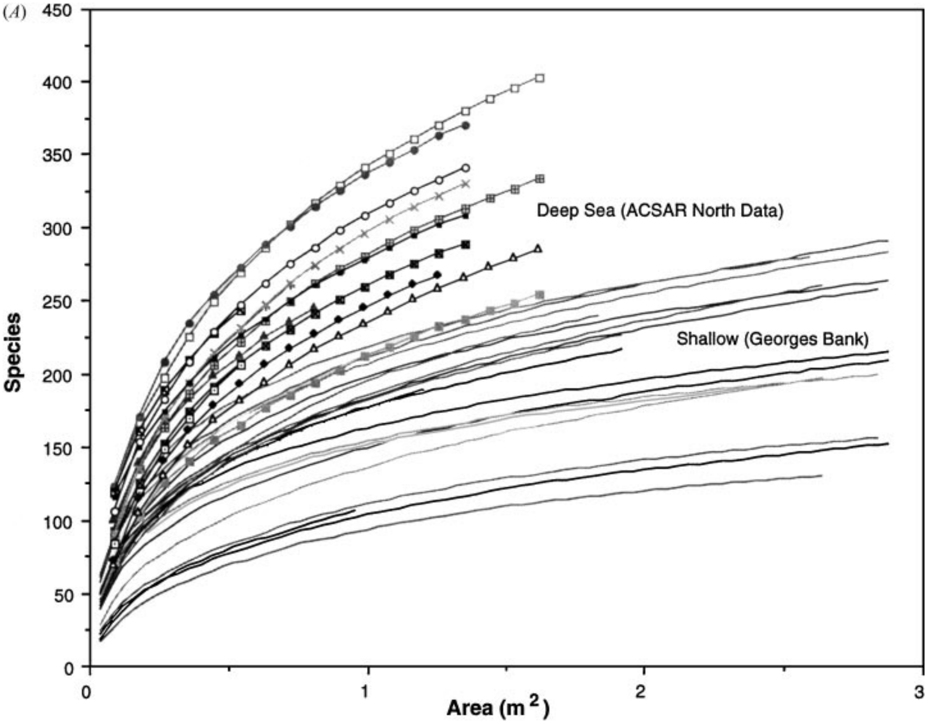

Figure 5 Randomized species accumulation curves for all North (ACSAR) and Georges Bank stations as a function of (A) area sampled and (B) numbers of individuals. The Georges Bank curves lack symbols while the North stations have symbols. Data are from Maciolek et al. (1985) and Maciolek et al. (1987b).

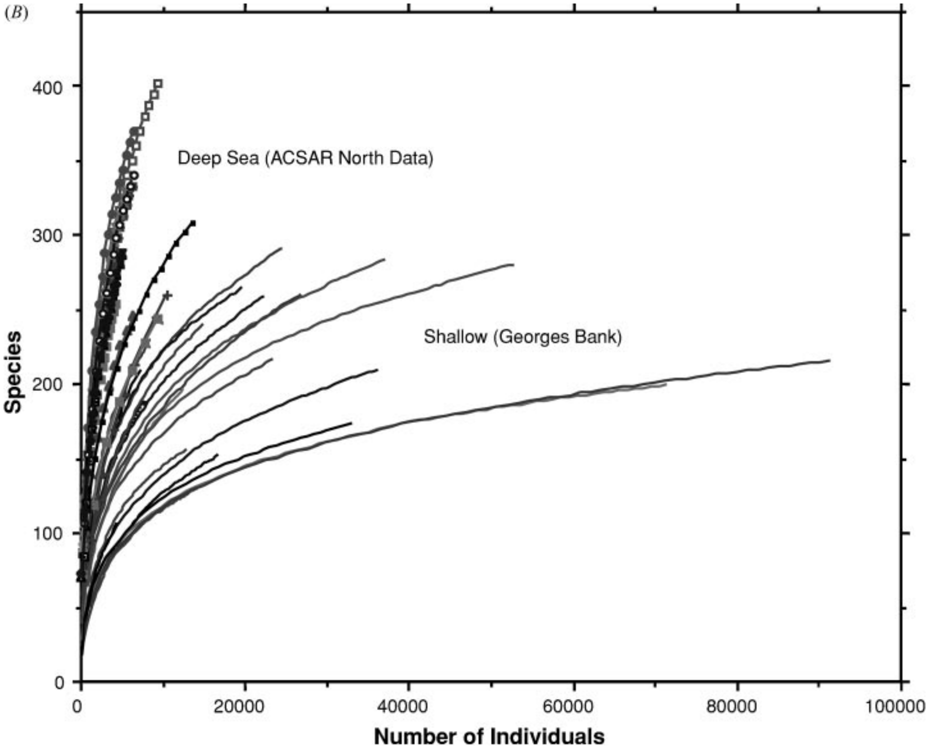

Figure 5 (*Continued*)

although the deep-sea samples are not. This demonstrates the fallacy of comparing richness among locations while ignoring how well each community has been sampled (location on species accumulation curve). When comparisons are restricted to contiguous geographic regions, sampled in similar ways, as are the Georges Bank and North (ACSAR) data, diversity (richness, species/area, species/individual) is much lower on the shelf than at bathyal depths. Although the diversity of shallow-water communities in some parts of the World Ocean may equal or exceed that of the deep sea, if comparisons are not controlled geographically, taxonomically, by habitat, and by sampling methods, they can tell us little about what forces are shaping species diversity in marine ecosystems.

INTERRELATIONSHIPS OF LOCAL AND REGIONAL DIVERSITY

Spatiotemporal variation in deep-sea species diversity represents an integration of ecological and evolutionary processes that operate at different spatial and temporal scales (Figure 8). Smaller-scale processes are embedded hierarchically within

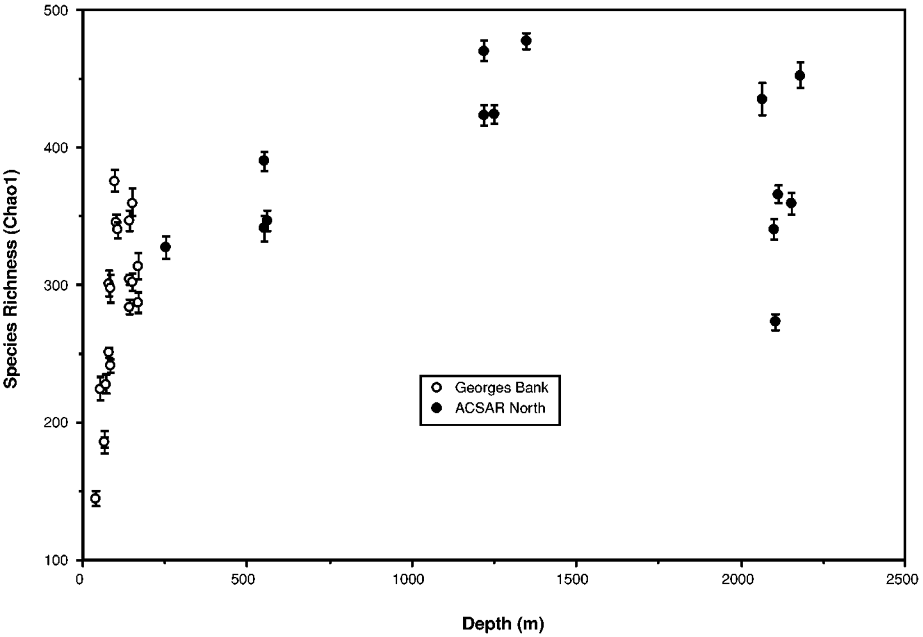

Figure 6 Asymptotic species richness estimated by Chao1 (Estimate S [Colwell 1997]) as a function of depth for Georges Bank and ACSAR North stations. Error bars are 95% confidence limits. Data are from Maciolek et al. (1985) and Maciolek et al. (1987b).

larger-scale processes, and tend to occur at faster rates. Species within a local assemblage (1–10 m^2) are controlled by small-scale processes involving resource partitioning, competitive exclusion, predation, facilitation, physical disturbance, recruitment, and physiological tolerances, all of which are mediated by the nature and degree of heterogeneity. How these processes might regulate local diversity has been reviewed elsewhere (Etter & Mullineaux 2000, P. V. Snelgrove & C. R. Smith, unpublished manuscript), but they will tend to occur on much shorter times scales than landscape or regional-level changes examined here. At regional scales of 100s to 1000s of m, several environmental gradients, dispersal, metapopulation dynamics, and gradients in habitat heterogeneity are likely to be important (Figure 8). We suggest that the environmental gradients discussed in this paper essentially control variation in local diversity by accelerating or decelerating local processes (e.g., patch dynamics). We describe in more detail below how each gradient may influence these local processes. Dispersal among patches will also be important at landscape or regional scales because it determines the potential for membership in local assemblages and plays a critical role in metapopulation dynamics and species persistence at local and larger scales (Caswell & Cohen 1993, Caswell & Etter 1999). For instance, low dispersal rates can decrease the intensity of biological interactions (Menge & Sutherland 1987) and potentially foster coexistence through recruitment limitation (Tilman 1994, Hubbell et al. 1999). At regional

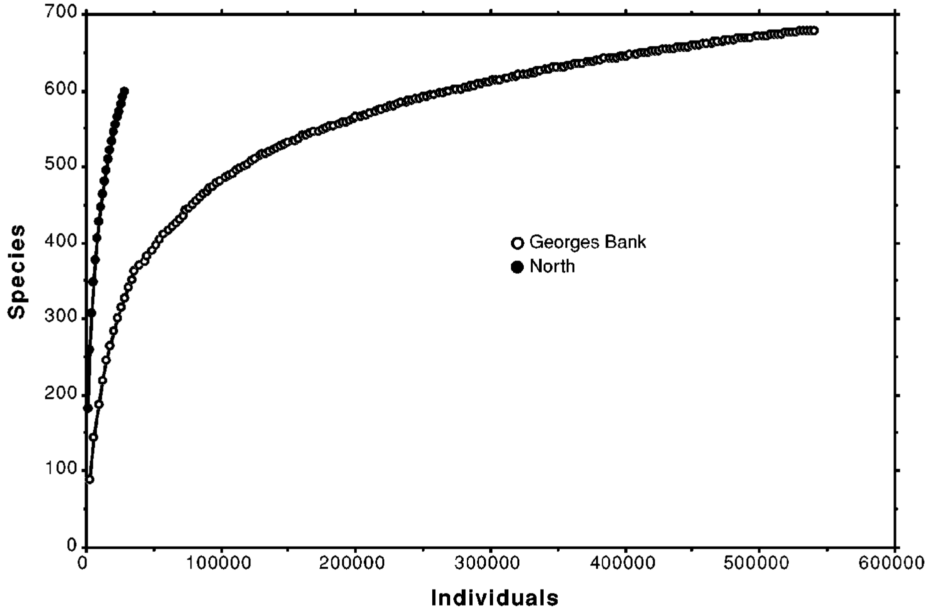

Figure 7 Species accumulation curves for pooled samples over a depth range of 130 m for Georges Bank and ACSAR North studies. The North samples were pooled from stations between 1220–1350 m to compare to a similar depth span in the Georges Bank study. All Georges Bank samples were used (38–167 m). See Table 2 for other diversity metrics comparing these pooled samples.

scales, many species will exist as metapopulations; their presence locally or regionally will be determined by local dynamics, dispersal among patches, and the degree of reproductive asynchrony among populations (e.g., Hanski 1998).Variation in local diversity within regions is also likely to be influenced by the number and different types of habitats at intermediate scales (e.g., 1–10 km) through a mass effect (Shmida & Wilson 1985). We know little about how mass effects contribute to local diversity, but the large number of singletons (species represented by a single individual) within natural deep-sea assemblages suggests that it may be extensive.

It is clear from the foregoing discussion that local diversity varies regionally along environmental gradients in the deep sea. How the numerous environmental factors act to control local diversity is not well understood, but we have developed a conceptual model of how they may directly and indirectly regulate the number of species within communities (Figure 9). These environmental factors do not work in isolation; they are often very interdependent such that changes in one precipitate changes in others, producing cascade effects, all of which modify the rates of local processes.

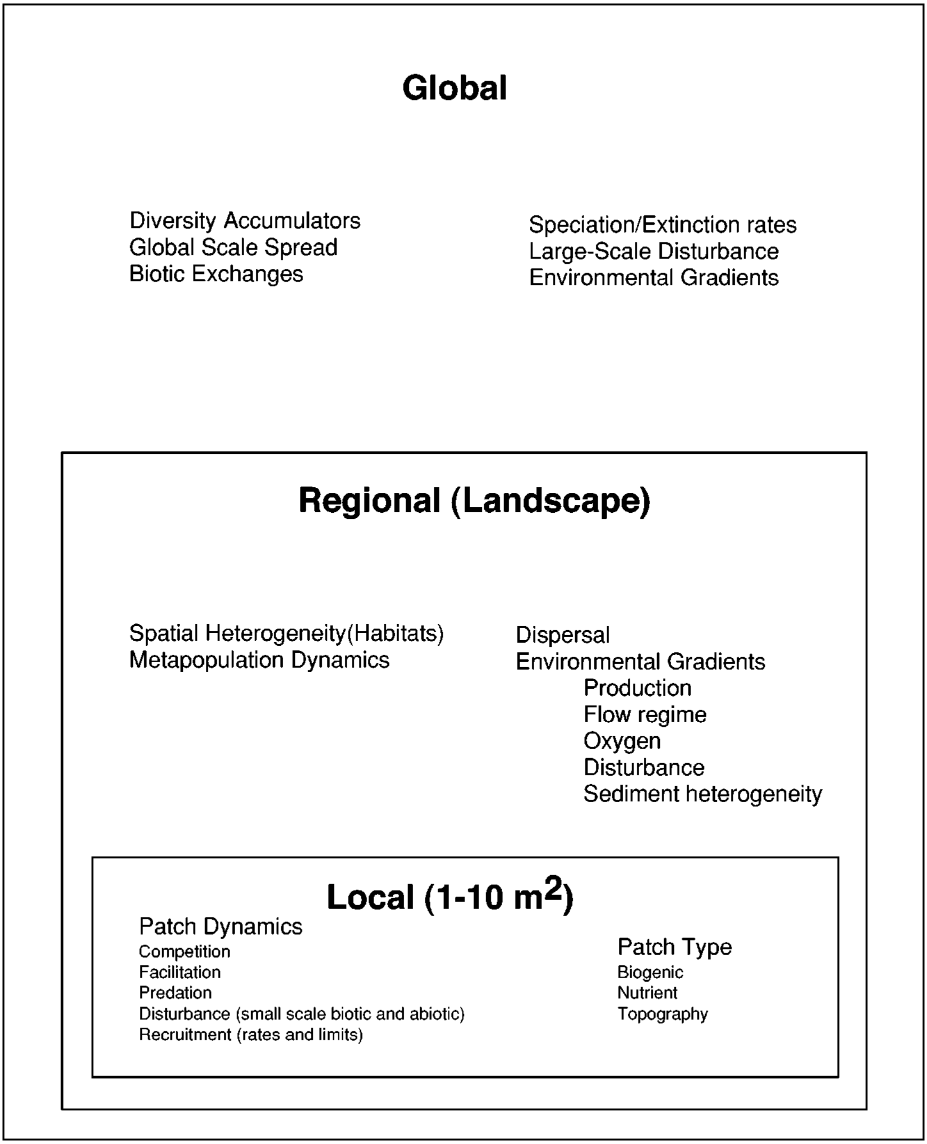

Figure 8 Processes regulating species diversity at local, regional, and global scales. Each box represents one scale and is embedded within the larger scales.

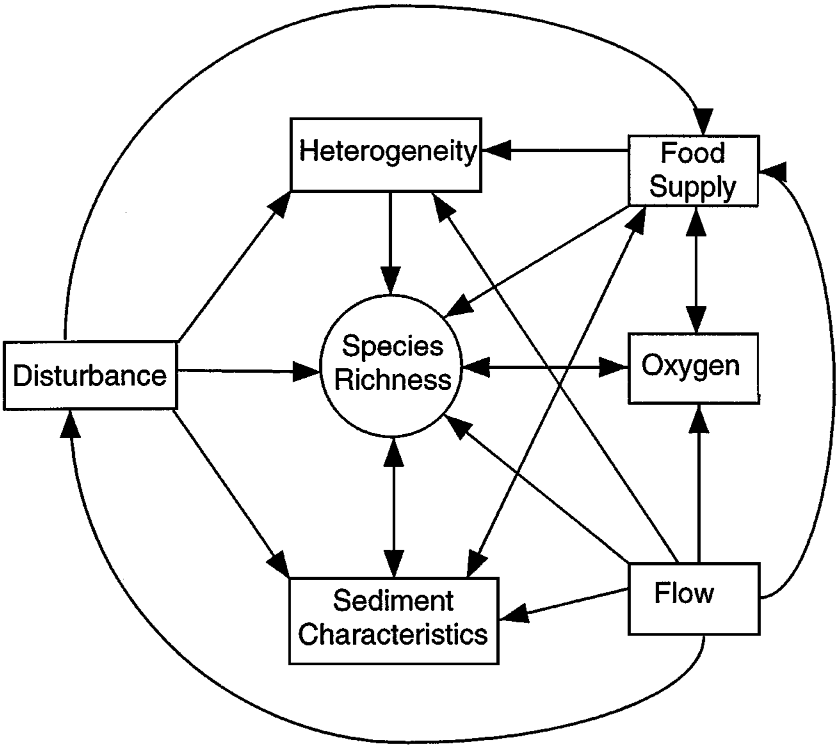

Figure 9 Conceptual model indicating direct and indirect effects of various environmental factors on species richness of local communities.

Near-bottom flow has pervasive effects; it can influence the number of species directly as well as indirectly through modification of other environmental factors (Gage 1997). Near-bottom current speed can directly control species number through larval supply, and at sufficiently high speeds will erode the sediments and many of the organisms on or within them. As current speeds vary, they can also indirectly influence diversity by changing food supply (POM flux and bacterial production), sediment characteristics, oxygen levels above and within the seabed, spatial heterogeneity, and levels of biotic and abiotic disturbance (Figure 9). Each of these factors can also affect the number of species within communities directly as well as indirectly.

Hydrodynamic influences on diversity can be extensive and involve numerous paths of different length and intensity. A unimodal relationship between diversity and flow strength is predicted (Figure 10), but has not been well documented. Low flows may be associated with depositional regimes and reduced sediment heterogeneity. Very strong flows are expected to reduce effectiveness of predators, and eliminate heterogeneity in particle size and surface features such as ripples.

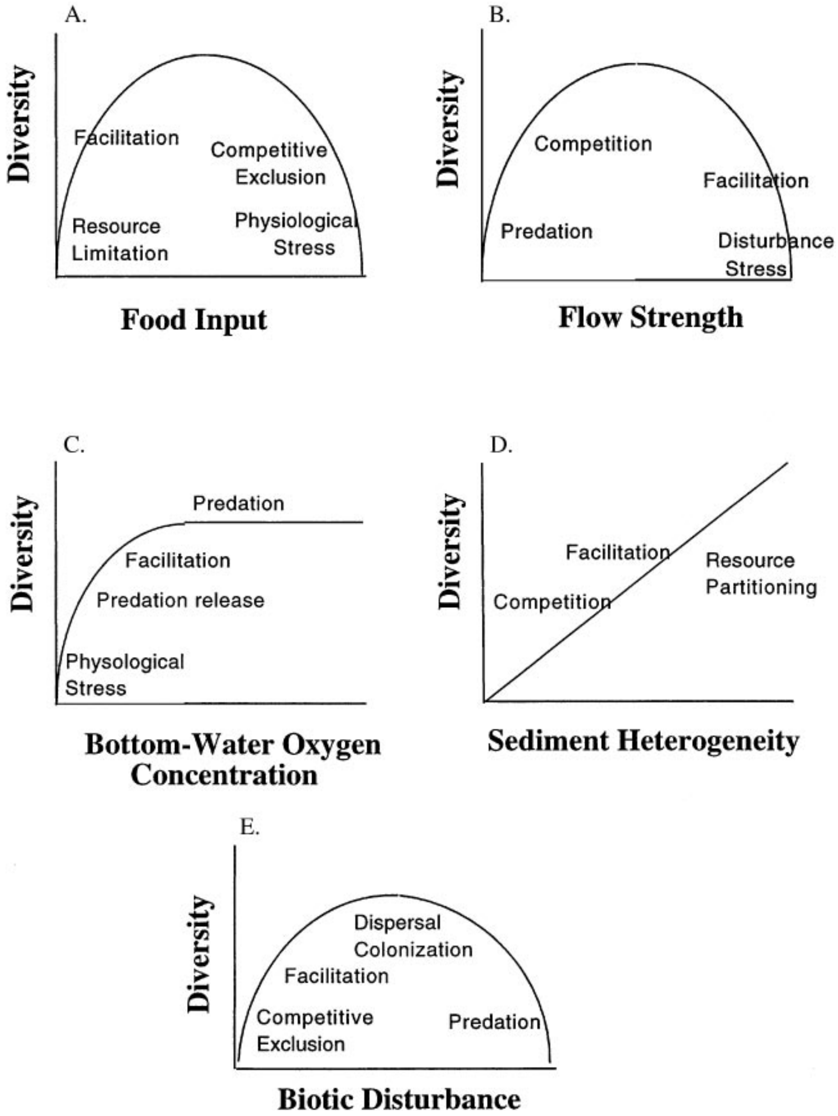

Figure 10 Patterns of diversity change along environmental gradients in the deep sea and biotic interactions hypothesized to be responsible for generating diversity patterns. (A) Productivity, (B) Flow, (C) Bottom-water oxygen concentration, (D) Sediment heterogeneity, (E) Biotic disturbance.

Disturbance resulting from substrate instability or the stress of maintaining feeding activities and dwelling position are likely to reduce species richness and evenness when currents are sufficiently strong to resuspend sediments, although these effects may be ameliorated by large or stabilizing biogenic structures. Intermediate or variable flows are expected to promote maximal diversity through resource partitioning that is maximized by interactions of food and larval supply (particle flux) and sediment heterogeneity.

POM flux or food supply may ultimately play the most significant role in regulating the number of species. As with flow, effects may be direct or be mediated through currents, sediments, disturbance, or hydrologic properties (Figure 9). At low food levels, diversity will be low because there are insufficient resources to support viable populations of many species. As food supply increases, diversity will increase because more species can maintain viable populations. As food availability continues to increase, diversity may decline, producing a unimodal relationship between diversity and food inputs (Figure 10). Why diversity declines at high levels of food supply is not well understood but may reflect a decrease in habitat heterogeneity, differential numerical responses leading to increased dominance by a few species (Rosenzweig & Abramsky 1993, Waide et al. 1999), and/or increased physiological stress due to oxygen limitation or sulfide toxicity. A strong negative correlation of evenness with sediment POC (Levin & Gage 1998) may provide some clues about the importance of species interactions in reducing diversity. Because increases in food supply are often coupled with variability (seasonality) in supply, decline may also reflect increased extinction rates of more specialized forms, due to either demographic instabilities or accelerating rates of competitive exclusion (Rex 1976).

If deposit feeders select sediment particles according to characteristics such as their size, shape, composition, and quality, as has been argued by Wheatcroft et al. (1990), Etter & Grassle (1992), and Smith et al. (1993), diversity will respond positively to increased sediment heterogeneity (Figure 10). Any environmental or biotic factor that alters sediment structure (hydrodynamics, bioturbation, disturbance) has the potential to regulate diversity indirectly. The distribution of particle sizes within the sediments also influences organic content (Milliman 1994); thus changes in diversity due to alterations of sediment heterogeneity may be mediated through food resources.

Oxygen is a requirement for most metazoan life; reduced oxygen availability can exert both direct and indirect negative effects on diversity (Figures 9, 10). At low oxygen concentrations, species richness may be reduced directly through differential tolerance to hypoxia or to the sulfides that build up in organic-rich hypoxic sediments (Diaz & Rosenberg 1995, Bagarinao 1992). Hypoxic conditions may impose habitat homogeneity, contributing to spatially uniform assemblages of low species richness (Levin et al. 2000). Such effects probably occur mainly at bottom-water oxygen concentrations $\ll$0.5 ml/l (Levin & Gage 1998). Differential numerical responses and competitive exclusion may explain increased dominance and reduced species richness where oxygen is low but food availability remains high. Tolerance to hypoxia varies with body size; meiofauna are much more tolerant to low oxygen than most macrofauna or megafauna. Organisms that oxygenate sediments or reduce sulfide concentrations through feeding, dwelling structures, and burrowing may indirectly facilitate other organisms, ameliorating physiological stress and potentially elevating diversity (e.g., Reise 1982, Aller & Aller 1986). Predation pressure and its potential diversifying effects (Hall et al. 1994, Dayton & Hessler 1972) are expected to increase with increasing oxygen saturation.

The processes of disturbance and positive interactions (facilitation) pervade the environmental factors considered above and merit further consideration. Disturbance, a well-known mechanism regulating community structure in other ecosystems (Connell 1978, Petraitis et al. 1989, Pickett & White 1985), undoubtedly plays a similar role in the deep sea. Disturbance to the seafloor is manifested through a variety of biotic and abiotic factors that can affect diversity by regulating levels of competition, predation, and physiological stress. Indirectly, disturbance can increase heterogeneity at low levels and reduce it at high levels by smoothing out biogenic or topographic structures or by inducing stress. Disturbance can also alter the structure of the sediments and thus can influence diversity indirectly through the generation or removal of habitat heterogeneity (Figure 9).

Facilitative interactions, like disturbance, can be important over a range of conditions and are predicted to have strong diversifying effects where conditions are most extreme (Bertness & Callaway 1994). We hypothesize that these effects are especially important in marine sediments, where animal feeding, dwelling, and respiratory activities alter the surrounding milieu. When food is scarce, animal activities that enhance or redistribute food may elevate species richness (Bianchi et al. 1989, Levin et al. 1997a). Stress or disturbance associated with low redox conditions may be ameliorated by infaunal activities (solute pumping, burrowing) that oxygenate sediments (Aller 1982), thereby allowing more species to persist (Reise 1982). Structures formed by animals can provide shelter and a stable substrate, and may serve as hotspots of diversity under strong flow conditions (e.g., tests of xenophyophores on seamounts, Levin et al. 1988).

CONCLUSIONS

Two important conclusions result from our survey of diversity patterns at regional scales. First, the deep-sea ecosystem, long known to support high local species diversity, also shows high biodiversity at the landscape level. High diversity is related to environmental gradients and habitat shifts. Second, there appear to be multiple forces that shape patterns of diversity on regional scales. Variation in species diversity is associated with large-scale variation in sediment grain size diversity, nutrient input, and productivity as well as oxygen availability, hydrologic conditions, and catastrophic events. Disturbance and facilitation are predicted to be agents of particular importance in mediating environmental effects on diversity in the deep sea. These environmental factors are highly interdependent and ultimately reflect global-scale oceanographic processes and climate. It seems likely that regional-scale phenomena interact in complex ways to form biogeographic patterns of local diversity by controlling gradients of ecological opportunity that affect population dynamics at small scales. Exactly how this occurs is uncertain, but, as shown here, the basic features of the regional ecological system are becoming clearer. Importantly, the recognition of conspicuous variation in biodiversity at the landscape level and the discovery of how relevant processes are geographically distributed now make it possible to design controlled sampling studies and manipulative, experimental approaches to better understand the causality underlying regional diversity trends.

Although several large data sets on the composition of deep-sea communities are available, taxonomic and geographic coverage is still very limited. Most large-scale studies of deep-sea species diversity have taken place in the Atlantic. It is reasonable to expect that new biogeographic patterns and ecological forces of fundamental importance will continue to be discovered. The vast majority of diversity studies center on the macrofauna and are often restricted to one or a few taxa. Much less is known about the meiofauna and megafauna. Meiofauna and annelids often demonstrate parallel trends along gradients of oxygen and organic matter (e.g., Cook et al. 2000, Gooday et al. 2000, Gooday et al. 2001), although other groups may respond to environmental pressures in different ways (Lambshead et al. 2001a in press). Thus, whereas recent regional studies provide important direction for mechanistic studies of diversity in the deep sea, documenting the structure and function of whole deep-sea communities on a planet-wide basis remains an important priority.

Sampling methodology and the measurement of species diversity have important implications for conceptualizing patterns of deep-sea diversity and how they compare to those of other environments. Rarefaction, when critically applied, can be a useful way to estimate relative diversity from samples collected by large qualitative trawls and epibenthic sleds. Because the deep-sea fauna is sparsely distributed, large samples are vital for taxonomic discrimination of species and for assessing regional species pools. However, quantitative sampling with sufficient replication to adequately characterize local communities is necessary to measure the actual number of species, standing stock, and the environmental parameters that appear to influence diversity directly. The first controlled comparison of this kind, between the continental shelf and upper bathyal zone, confirms that the deep sea in the Northwest Atlantic region supports considerably higher species richness than in shelf communities. Although the shelf fauna is fairly well sampled, the level of replication at bathyal depths is still inadequate to reveal an asymptote in the species accumulation curve. An important objective for future sampling designs is to determine the level and spatial scale of replication necessary to represent local diversity. Also, because rarefaction of large qualitative samples suggests a marked decline in diversity at abyssal depths (e.g., in the western North Atlantic), quantitative sampling should be extended to the lower bathyal zone and abyssal plain to firmly establish a diversity-depth gradient.

Contemporary ecological theory is based exclusively on the history of observations made in terrestrial, aquatic, and surface marine systems. Most of Earth's largest environment, the deep sea, remains unexplored. It is a vast world of extreme physical circumstances, novel adaptations, and very basic permutations of the carbon cycle that support all life (Gage & Tyler 1991, Rowe & Pariente 1992, Van Dover 2000). Explaining the extraordinarily high level of species coexistence encountered at very small scales in the deep sea remains a fundamental problem (P. V. Snelgrove & C. R. Smith, unpublished manuscript; Etter & Mullineaux 2000). Although the regional studies reviewed here represent scattered areas of the deep sea, they significantly enrich our knowledge of global biodiversity at the landscape level, and should ultimately contribute to a comprehensive theoretical understanding of community structure and function.

ACKNOWLEDGMENTS

The Deep-Sea Biodiversity Working Group is supported by the National Center for Ecological Analysis and Synthesis, a Center funded by the National Science Foundation (DEB-94–21535), the University of California, Santa Barbara, and the State of California. The authors' research is supported by the National Science Foundation grants OCE-9811925 (RJE and MAR), OCE 98-03861 (LAL), OCE 99–86627 (JP), OCE-9811925 (RJE), OPP 98–15823 (CRS), and the NOAA National Undersea Research Program grant UAF 00–0050 (LAL). We thank D. Morrow for assistance with manuscript preparation.

LITERATURE CITED

Allen JA, Sanders HL. 1996. The zoogeography, diversity and origin of the deep-sea protobranch bivalves of the Atlantic: the epilogue. *Prog. Oceanog.* 38:95–153

Aller J, Aller R. 1986. Evidence for localized enhancement of biological activity associated with tube and burrow structures in deep-sea sediments at the Hebble site; western North Atlantic. *Deep-Sea Res.* 33:755–90

Aller JY. 1989. Quantifying sediment disturbances by bottom currents and its effect on benthic communities in a deep-sea western boundary zone. *Deep-Sea Res.* 36:901–34

Aller JY. 1997. Benthic community response to temporal and spatial gradients in physical disturbance within a deep-sea western boundary region. *Deep-Sea Res. Part I - Oceanog. Res.* 44:39

Aller RC. 1982. The effects of macrobenthos on chemical properties of marine sediment and overlying water. *In Animal-Sediment Relations*, ed. PL McCall, MJ Tevesz, pp. 53–102. New York: Plenum

Arntz WE, Tarazona J, Gallardo VA, Flores LA, Salzwedel H. 1991. Benthos communities in oxygen deficient shelf and upper slope areas of the Peruvian and Chilean Pacific coast, and changes caused by El Niño. In *Modern and Ancient Continental Shelf Anoxia*, ed. RV Tyson, TH Pearson, pp. 131–54. Tulsa, OK: Geol. Soc. Spec. Publ. No. 58

Austin MC, Widbom B. 1991. Changes in and slow recovery of a meiobenthic nematode assemblage following a hypoxic period in the Gullmar Fjord basin, Sweden. *Mar. Biol.* 111:139–45

Bachelet G. 1990. The choice of sieving mesh size in quantitative assessment of marine macrobenthos: a necessary compromise between aims and constraints. *Mar. Environ. Res.* 30:21–35

Bagarinao T. 1992. Sulfide as an environmental factor and toxicant: tolerance and adaptations in aquatic organisms. *Aquat. Toxicol.* 24:21–62

Bartel D, Gutt J. 1992. Sponge associations in the eastern Weddell Sea. *Antarct. Sci.* 4:137–50

Berelson WM, Anderson RF, Dymond J, Demaster D, Hammond DE, et al. 1997. Biogenic budgets of particle rain, benthic remineralization and sediment accumulation in the equatorial Pacific. *Deep-Sea Res. II* 44:2251–82

Bernhard JM, Sen Gupta BK, Bourne PF. 1997. Benthic foraminiferal proxy to estimate dysoxic bottom-water oxygen concentrations: Santa Barbara Basin, U.S. Pacific continental margin. *J. Foraminifer. Res.* 27:301–10

Bertness MD, Callaway R. 1994. Positive interactions in communities. *TREE* 9:191–93

Bett BJ, Rice AL. 1992. The influence of hexactinellid sponge (*Pheronema carpenteri*) spicules on the patchy distribution of macrobenthos in the Porcupine Seabight (bathyal NE Atlantic) *Ophelia* 36:217–26

Bianchi TS, Jones CG, Shachak M. 1989. Positive feedback of consumer populations on resource supply *Trends Ecol. Evol.* 4:234–38

Blair NE, Plaia GR, Boehme SE, DeMaster DJ, Levin LA. 1994. The remineralization of organic carbon on the North Carolina continental slope. *Deep-Sea Res.* 41:755–66

Blake JA, Hilbig B. 1994. Dense infaunal assemblages on the continental slope off Cape Hatteras, North Carolina. *Deep-Sea Res.* 41:875–900

Brown JH, Stevens GC, Kaufman DM. 1996. The geographic range: Size, shape, boundaries, and internal structure. *Annu. Rev. Ecol. Syst.* 27:597–623

Brown TN, Kulasiri D. 1996. Validating models of complex, stochastic, biological systems. *Ecol. Model* 86:129–34

Bugge T, Befring S, Belderson RH, Eidvin T, Jansen E, et al. 1987. A giant three-stage submarine slide off Norway. *Geo-Marine Lett.* 7:191–98

Cannariato KG, Kennett JJP, Behl RJ. 1999. Biotic response to late Quaternary rapid climate switches in Santa Barbara Basin: Ecological and evolutionary implications. *Geology* 27:63–66

Caswell H, Cohen JE. 1993. Local and regional regulation of species-area relations: a patch-occupancy model. In *Species Diversity in Ecological Communities.* ed. RE Ricklefs, ED Schluter, pp. 99–107. Chicago: Univ. Chicago Press

Caswell H, Etter R. 1999. Cellular automaton models for competition in patchy environments: Facilitation, inhibition, and tolerance. *Bull. Math. Biol.* 61:625–49

Charles C. 1998. The ends of an era. *Nature* 394:422–23

Cita MB, Podenzani M. 1980. Destructive effects of oxygen starvation and ash falls on benthic life: a pilot study. *Quat. Res.* 13:230–41

Clarke KR, Warwick RM. 1994. Change in marine communities, an approach to statistical analysis and interpretation. *Natl Environ. Res. Counc. UK.* 144 pp.

Cochonat P, Lenat JF, Bachelery P, Boiwin P, Cornaglia B. 1990. Gravity events as a primary process in the construction of a submarine volcano-sedimentary system (Fournaise Volcano, Reunion Island). *C. R. Acad. Sci. Ser. II-* 311:679–86

Colwell RK. 1997. Estimate S: Statistical estimation of species richness and shared species from samples. Version 5. Users Guide and Appl. http://viceroy.eeb.uconn.edu/estimates

Colwell RK, Coddington JA. 1994. Estimating terrestrial biodiversity through extrapolation. *Philos. Trans. R. Soc. London Ser. B* 345:101–18

Colwell RK, Hurtt GC. 1994. Nonbiological gradients in species richness and a spurious Rappoport effect. *Am. Nat.* 144:570–95

Colwell RK, Lees DC. 2000. The mid-domain effect: geometric constraints on the geography of species richness. *Trends Ecol. Evol.* 15:70–76

Connell JH. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302–10

Cook AA, Lambshead PJD, Hawkins LE, Mitchell N, Levin LA. 2000. Nematode abundance at the oxygen minimum zone in the Arabian Sea. *Deep-Sea Res.* 47:75–85

Corliss BH, Emerson S. 1990. Distribution of rose bengal stained deep-sea benthic foraminifera from the Nova Scotian continental margin and Gulf of Maine. *Deep-Sea Res. Part A- Oceanog. Res. Pap.* 37:381–400

Cosson N, Sibuet M, Galeron J. 1997. Community structure and spatial heterogeneity of the deep-sea macrofauna at three contrasting stations in the tropical northeast Atlantic. *Deep-Sea Res.* 44:247–69

Cosson-Sarradin N, Sibuet M, Paterson GLJ, Vangriesheim A. 1998. Polychaete diversity at tropical Atlantic deep-sea sites: environmental effects. *Mar. Ecol. Prog. Ser.* 165:173–85

Cronin TM, Raymo ME. 1997. Orbital forcing of deep-sea benthic species diversity. *Nature* 385:624–27

Culver SJ, Buzas MA. 1998. Patterns of occurrence of benthic foraminifera in time and space. In *The Adequacy of the Fossil Record*, ed. SK Donovan, CRC Paul, pp. 207–26. New York: Wiley

Culver SJ, Buzas MA. 2000. Global latitudinal species diversity gradient in deep-sea benthic foraminifera. *Deep-Sea Res. I* 47:259–75

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

den Dulk M. 2000. Benthic foraminiferal response to Late Quaternary variations in surface water productivity and oxygenation in the northern Arabian Sea. *Geol. Ultraiectina*, No. 188. 205 pp.

den Dulk M, Reichart GJ, Memon GM, Roelofs EMB, Zachariasse WJ, van der Zwaan GJ. 1998. Benthic foraminiferal response to variations in surface water productivity and oxygenation in the northern Arabian Sea. *Mar. Micropaleontol.* 35:43–66

de Rijk S, Troelstra SR, Rohling EJ. 1999. Benthic foraminiferal distribution in the Mediterranean Sea. *J. Foraminifer. Res.* 29:93–103

Deuser W, Muller-Karger F, Evans R, Brown O, Esaias W, Feldman G. 1990. Surface-ocean color and deep-ocean carbon flux: how close a connection? *Deep-Sea Res.* 37:1331–43

Diaz RJ, Rosenberg R. 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanogr. Mar. Biol. Annu. Rev.* 33:245–303

Dickson RR, McCave IN. 1986. Nepheloid layers on the continental slope west of Porcupine Bank. *Deep-Sea Res.* 33:791–818

Douglas RG, Liestman J, Walch C, Blake G, Cotton ML. 1980. The transition from live to sediment assemblage in benthic foraminifera from the Southern California Borderland. In *Quaternary Depositional Environments of the Pacific Coast*, ed. ME Field, AH Bouma, IP Colburn, RG Douglas, JC Dingle, pp. 257–80. Los Angeles: Pac. Coast Paleogeogr. Symp. 4, Pac. Sect., Soc. Econ. Paleontol. Mineral.

Embley RW. 1976. New evidence for occurrence of debris flow deposits in the deep sea. *Geology* 4:371–74

Emerson S. 1985. Organic carbon preservation in marine sediments. In *The Carbon Cycle and Atmospheric* CO_2*: Natural Variations Archean to Present*, ed. I Sundquist, W Broecker, 32:78–87. Washington, DC: Geophys. Monogr., AGU

Emery KO, Uchupi E. 1984. *The Geology of the Atlantic Ocean.* New York/Berlin: Springer-Verlag. Charts I–XI. 2 Vols. 1050 pp.

Etter RJ, Grassle JF. 1992. Patterns of species diversity in the deep sea as a function of sediment particle size diversity. *Nature* 360:576–78

Etter RJ, Mullineaux L. 2000. Deep-Sea communities. In *Marine Community Ecology* ed. MD Bertness, S Gaines, M Hay, pp. 367–93, Chapter 14. Sunderland, MA: Sinauer

Fenchel T, Kofoed LH. 1976. Evidence for exploitative interspecific competition in mud snails (Hydrobiidae). *Oikos* 27:367–76

Fenchel T, Kofoed H, Lappalainen A. 1975. Particle size selection of two deposit feeders: the amphipod *Corophium volutator* and the prosobranch *Hydrobia ulvae. Mar. Biol.* 30:119–28

Flood RD, Shor AN. 1988. Mud waves in the Argentine Basin and their relationship to regional bottom circulation patterns. *Deep-Sea Res.* 35:943–71

Frederiksen RA, Jensen A, Westerberg H. 1992. The distribution of the scleractinian coral *Lophelia pertusa* around the Faroe Islands and the relation to internal mixing. *Sarsia* 77:157–71

Gage JD. 1996. Why are there so many species in deep-sea sediments? *J. Exp. Mar. Biol. Ecol.* 200:257–86

Gage JD. 1997. High benthic species diversity in deep-sea sediments: The importance of hydrodynamics. In *Marine Biodiversity*, ed. RFG Ormond, JD Gage, MV Angel, pp. 148–77. Cambridge, UK:Cambridge Univ. Press

Gage JD, Lamont PA, Tyler PA. 1995. Deep-sea macrobenthic communities at contrasting sites off Portugal, preliminary results: I introduction and diversity comparisons. *Int. Rev. Hydrobiol.* 80:235–50

Gage JD, May RM. 1993. Biodiversity—a dip into the deep seas. *Nature* 365:609–10

Gage JD, Tyler PA. 1991. *Deep-Sea Biology: A Natural History of Organisms at the Deep-Sea Floor*. Cambridge, UK: Cambridge Univ. Press. 504 pp.

Gallardo VA. 1985. Efectos del fenómeno de El Niño sobre el bentos sublitoral frente a Concepción, Chile. In *El Niño y su impacto en la fauna marina*, ed. W Arntz, A Landa, J Tarazona, pp. 79–85. Inst. del Mar del Perú: Lima, Peru: Bol. Extraordin.

Genin A, Lazar B, Brenner S. 1995. Vertical mixing and coral death in the Red Sea following the eruption of Mount Pinatubo. *Nature* 377:507–10

Glover A, Paterson G, Bett B, Gage J, Sibuet M, et al. 2001. Patterns in polychaete abundance and diversity from the Madeira Abyssal Plain, northeast Atlantic. *Deep-Sea Res. I* 48:217–36

Gooday AJ. 1996. Epifaunal and shallow infaunal foraminiferal communities at three abyssal NE Atlantic sites subject to differing phytodetritus regimes. *Deep-Sea Res.* 43:1395–431

Gooday AJ, Bernhard JM, Levin LA, Suhr S. 2000. Foraminifera in the Arabian Sea OMZ and other oxygen deficient settings: taxonomic composition, diversity and relation to metazoan faunas. *Deep-Sea Res.* 47:54–73

Gooday AJ, Hughes JA, Levin LA. 2001. The foraminiferal macrofauna from three North Carolina (U.S.A.) slope sites with contrasting carbon flux: a comparison with the metazoan macrofauna. *Deep-Sea Res. I.* 48:1709–39

Grassle JF, Maciolek NJ. 1992. Deep-sea species richness: regional and local diversity estimates from quantitative bottom samples. *Am. Nat.* 139:313–41

Grassle JF, Morse-Porteous LS. 1987. Macrofaunal colonization of disturbed deep-sea environments and the structure of deep-sea benthic communities. *Deep-Sea Res.* 34:1911–50

Gray JS. 1981. *The Ecology of Marine Sediments*. Cambridge, UK: Cambridge Univ. Press

Gray JS. 1994. Is deep-sea species diversity really so high? Species diversity of the Norwegian continental shelf. *Mar. Ecol. Prog. Ser.* 112:205–9

Gray JS, Poore GCB, Ugland KI, Wilson RS, Olsgard F, Johannessen O. 1997. Coastal and deep-sea benthic diversities compared. *Mar. Ecol. Prog. Ser.* 159:97–103

Gross TF, Williams AJ. 1991. Characterization of deep-sea storms. *Mar. Geol.* 99:281–301

Hall SJ. 1994. Physical disturbance and marine benthic communities: life in unconsolidated sediments. *Oceanog. Mar. Biol.: An Annu. Rev.* 32:179–239

Hall SJ, Raffaelli D, Thrush SF. 1994. Patchiness and disturbance in shallow water benthic assemblages. In *Aquatic Ecology: Scale, Pattern and Process*, ed. PS Giller, AG Hildrew, DG Raffaelli, pp. 333–75. London: Blackwell Sci.

Hanski I. 1998. Metapopulation dynamics. *Nature* 396:41–49

Heezen BC, Hollister CD. 1971. *The Face of the Deep*. New York: Oxford Univ. Press. 659 pp.

Hermelin JOR, Schimmield GB. 1990. The importance of the oxygen minimum zone and sediment geochemistry in the distribution of benthic foraminifera in the Northwestern Indian Ocean. *Mar. Geol.* 91:1–29

Hermelin JOR, Schimmield GB. 1995. Impact of productivity events on benthic foraminiferal faunas in the Arabian Sea over the last 150,000 years. *Paleoceanography* 10:85–116

Hess S, Kuhnt W. 1996. Deep-sea benthic foraminiferal recolonization of the 1991 Mt. Pinatubo ash layer in the South China Sea. *Mar. Micropaleontol.* 28:171–97

Hessler RR, Jumars PA. 1974. Abyssal community analysis from replicate box cores in the central North Pacific. *Deep-Sea Res.* 21:185–209

Hollister CD, Nowell ARM. 1991. HEBBLE epilogue. *Mar. Geol.* 99:445–60

Hollister CD, McCave IN. 1984. Sedimentation under deep-sea storms. *Nature* 309:220–25

Hollister CD, Nowell ARM, Jumars PA. 1984. The dynamic abyss. *Sci. Am.* 250:42–53

Hubbell SP, Foster RB, O'Brien ST, Harms KE, Condit R, et al. 1999. Light-cap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* 283:554–57

Huggett QJ. 1987. Mapping of hemipelagic versus turbidite muds by feeding traces observed in deep-sea photographs. In *Geology and Geochemistry of Abyssal Plains*, ed. PPE Weaver, J Thomson, pp. 105–12. Geol. Soc. Spec. Publ. No. 31

Hurlbert SM. 1971. The non-concept of species diversity, A critique and alternative parameters. *Ecology* 52:577–86

Huston M. 1979. A general hypothesis of species diversity. *Am. Nat.* 113:81–101

Jacobi RD, Hayes DE. 1982. Bathymetry, microphysiography and reflectivity characteristics of the West African margin between Sierra Leone and Mauritania. In *Geology of the Northwest African Margin*, ed. U von Rad, K Hinz, M Sarnthein, E Siebold, pp. 182–212. Heidelberg: Springer-Verlag

Jahnke R. 1996. The global ocean flux of particulate organic carbon, areal distribution and magnitude. *Global Biogeochem. Cycles* 10:71–88

Jensen A, Frederickson R. 1992. The fauna associated with the bank-forming deepwater coral *Lophelia pertusa* (Scleractiniaria) on the Faroe shelf. *Sarsia* 77:53–69

Jorissen FJ. 1999. Benthic foraminiferal successions across Late Quaternary Mediterranean sapropels. *Mar. Geol.* 153:91–101

Jorissen FJ, Buzas M, Culver S, Kuehl S. 1994. Vertical distribution of living benthic foraminifera in submarine canyons off New Jersey. *J. foraminiferal Res.* 24:28–36

Jorissen FJ, Wittling I, Peypouquet JP, Rabouille C, Relexans JC. 1998. Live foraminiferal faunas off Cap Blanc, NW Africa: Community structure and microhabitats. *Deep-Sea Res. I* 45:2157–88

Josefson AB, Widbom B. 1988. Differential response of benthic macrofauna and meiofauna to hypoxia in the Gullmar Fjord basin. *Mar. Biol.* 100:31–40

Jumars PA, Eckman JE. 1983. Spatial structure within deep-sea benthic communities. In *The Sea*, ed. GT Rowe, pp. 399–452. New York: Wiley

Jumars PA, Hessler RR. 1976. Hadal community structure: implications from the Aleutian Trench. *J. Mar. Res.* 34:547–60

Kaminski M. 1985. Evidence for control of abyssal agglutinated foraminiferal community structure by substrate disturbance: results from the HEBBLE area. *Mar. Geol.* 66:113–31

Kamykowski D, Zentara SJ. 1990. Hypoxia in the world ocean as recorded in the historical data set. *Deep-Sea Res.* 37:1861–74

Keller M. 1986. Structure des peuplements méiobenthiques dans la secteur pollué par la rejet en mer de l'égout de Marseille. *Annales Inst. océanog.* 62:13–36

Kidd RB, Hill PR. 1986. Sedimentation on mid-ocean sediment drifts. In *North Atlantic Palaeoceanography,* ed. CP Summerhayes, NJ Shackleton, pp. 87–102. Geol. Soc. Spec. Pub., No. 21

Klein H. 1988. Benthic storms, vortices, and particle dispersion in the deep western European Basin. *Deutsches hydrographishes Zeitung* 40:87–102

Klitgaard AB. 1995. The fauna associated with outer shelf and upper slope sponges (Porifera, Demospongiae) at the Faroe Islands, northeastern Atlantic. *Sarsia* 80:1–22

Kontar EA, Sokov AV. 1994. A benthic storm in the northeastern tropical Pacific over the fields of manganese nodules. *Deep-Sea Res. I* 41:1069–89

Lambshead PJD, Brown CJ, Ferrero TJ, Jensen J, Smith CR, Hawkins LE, Tietjen J. 2001a. Latitudinal diversity patterns for deep sea marine nematodes and organic fluxes—a test from the central equatorial Pacific. *Mar. Ecol. Prog. Ser.* In press

Lambshead PJD, Elce BJ, Thistle D, Eckman JE, Barnett PRO. 1994. A comparison of biodiversity of deep-sea marine nematodes from three stations in the Rockall Trough, northeast Pacific. *Biodiv. Lett.* 2:95–107

Lambshead PJD, Tietjen J, Ferrero T, Jensen J. 2000. Latitudinal diversity gradients in the deep sea with special reference to North Atlantic nematodes. *Mar. Ecol. Prog. Ser.* 194:159–67

Lambshead PJD, Tietjen J, Glover A, Ferrero T, Thistle D, Gooday AJ. 2001. The impact of large-scale natural physical disturbance on the diversity of deep-sea North Atlantic nematodes. *Mar. Ecol. Prog. Ser.* 214:121–26

Lambshead PJ, Tietjen J, Moncrieff C, Ferrero T. 2001b. North Atlantic latitudinal diversity patterns in deep-sea marine nematode data. *Mar. Ecol. Prog. Ser.* In press

Lampitt R, Antia R, 1997. Particle flux in the deep seas: regional characteristics and temporal variability. *Deep-Sea Res. I* 44:1377–73

Lees DC, Kremen C, Andriamampianina L. 1999. A null model for species richness gradients: bounded range overlap of butterflies and other rainforest endemics in Madagascar. *Biol. J. Linnean Soc.* 67:529–84

Levin LA. Blair N, DeMaster DJ, Plaia G, Fornes W, et al. 1997a. Rapid subduction of organic matter by maldanid polychaetes on the North Carolina slope. *J. Mar. Res.* 55: 595–611

Levin L, Blair N, Martin C, DeMaster D, Plaia G, Thomas C. 1999. Macrofaunal processing of phytodetritus at two sites on the Carolina margin: *In situ* experiments using ^{13}C-labeled diatoms. *Mar. Ecol. Progr. Ser.* 182:37–54

Levin LA, DiBacco C. 1995. The influence of sediment transport on short-term recolonization by seamount infauna. *Mar. Ecol. Progr. Ser.* 123:163–75

Levin LA, Gage JD. 1998. Relationships between oxygen, organic matter and the diversity of bathyal macrofauna. *Deep-Sea Res.* 45:129–63

Levin LA, Gage J, Lamont P, Cammidge L, Martin C, et al. 1997b. Infaunal community structure in a low-oxygen, organic rich habitat on the Oman continental slope, NW Arabian Sea. In *Responses of marine organisms to their environments,* ed. L Hawkins, S Hutchinson, pp. 223–30. Proc. 30th Eur. Mar. Biol. Symp., Univ. Southampton

Levin LA, Gage JD, Martin C, Lamont PA. 2000. Macrobenthic community structure within and beneath the oxygen minimum zone, NW Arabian Sea. *Deep-Sea Res.* 47:189–226

Levin LA, Huggett CL, Wishner KF. 1991.

Control of deep-sea benthic community structure by oxygen and organic-matter gradients in the eastern Pacific Ocean. *J. Mar. Res.* 49:763–800

Levin LA, Leithold EL, Gross TF, Huggett CL, DiBacco C. 1994a. Contrasting effects of substrate mobility on infaunal assemblages inhabiting two high-energy settings on Fieberling Guyot. *J. Mar. Res.* 52:489–522

Levin LA, Plaia GR, Huggett CL. 1994b. The influence of natural organic enhancement on life histories and community structure of bathyal polychaetes. In *Reproduction, larval biology, and recruitment of the deep-sea benthos*, ed. CM Young, KJ Eckelbarger, pp. 261–83. Columbia, SC: Columbia Univ. Press

Levin LA, Thomas CL, 1988. The ecology of xenophyophores (Protista) on eastern Pacific seamounts. *Deep-Sea Res.* 35:2003–27

Lipman PW, Normark WR, Moore JG, Wilson JB, Gutmacher CE. 1988. The giant Alika debris slide, Mauna Loa, Hawaii. *J. Geophys. Res.* 93:4279–99

Luth U, Luth CM. 1997. A benthic approach to determine long-term changes in the water column of the Black Sea. In: *The Responses of Marine Organisms to their Environment*. Southampton, UK: Proc. 30th Eur. Mar. Biol. Symp., Sept. 1995. Southampton Oceanogr. Centre. pp. 223–30

MacArthur RH. 1972. *Geographical Ecology. Patterns in the Distribution of Species*, Princeton, NJ: Princeton Univ. Press. 269 pp.

Maciolek-Blake NJ, Grassle JF, Blake JA, Neff JM. 1985. *Georges Bank Infauna Monitoring Program:Final report for the third year of sampling*. Washington, DC: US Dept. Int., Minerals Mgmt. Ser.

Maciolek NJ, Grassle JF, Hecker B, Boehm PD, Brown B et al. 1987a. *Study of biological processes on the U.S. mid-Atlantic slope and rise*. Phase 2. Washington, DC: US Dept. Int., Minerals Mgmt. Ser.

Maciolek NJ, Grassle JF, Hecker B, Brown B, Blake JA et al. 1987b. *Study of biological processes on the U.S. North Atlantic slope and rise*. Washington, DC: US Dept. Int., Minerals Mgmt. Ser.

Magurran A. 1988. *Ecological Diversity and Its Measurement*. Princeton, NJ: Princeton Univ. Press, 179 pp.

Martin JH, Knauer GA, Karl DM, Broenkow WW. 1987. VERTEX: Carbon cycling in the northeast Pacific. *Deep-Sea Res.* 34:267–85

Masson DG. 1996. Catastrophic collapse of the volcanic island of Hierro 15 ka ago and the history of landslides in the Canary Islands. *Geology* 24:231–34

Masson DG, Kidd RB, Gardner JV, Huggett QJ, Weaver PPE. 1994. Saharan continental rise: facies distribution and sediment slides. In *Geological Evolution of Atlantic Continental Rises*, ed. VW Poag, PC Degrocianski, pp. 3–10. New York: Van Nostrand Reinhold

Masson DG, Kenyon NH, Weaver PPE. 1996. Slides, debris flows, and turbidity currents, In *Oceanography: An Illustrated Guide*, ed. CP Summerhayes, SA Thorpe, pp. 136–51. London: Manson

May RM. 1975. Patterns of species abundance and diversity. In *Ecology and Evolution of Communities*. ed. ML Cody, M Diamond.Cambridge, MA: Harvard Univ. Press. pp. 81–120

Menge BA, Sutherland JP. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am Nat.* 130:730–57

Milliman JD. 1994. Organic matter content in U.S. Atlantic continental slope sediments: decoupling the grain size factor. *Deep-Sea Res.* 41:797–808

Moodley L, van der Zwaan GJ, Herman PMJ, Kempers L, van Breugel P. 1997. Differential response of benthic meiofauna to anoxia with special reference to the Foraminifera (Protista: Sarcodina). *Mar. Ecol. Progr. Ser.* 158:151–63

Mullins HT, Thompson JB, McDougall K, Vercoutere TL. 1985. Oxygen-minimum zone edge effects, evidence from the central California coastal upwelling system. *Geology* 13:491–94

Munk W. 1970. The circulation of the oceans. In *Adventures in Earth History*, ed. P Cloud, p. 235–40. San Francisco: Freeman

Murrell MC, Fleeger JW. 1989. Meiofaunal abundances on the Gulf of Mexico continental shelf affected by hypoxia. *Cont. Shelf Res.* 9:1049–62

Neira C, Sellanes J, Levin LA, Arntz WA. 2001. Meiofaunal distributions on the Peru margin: relationship to oxygen and organic matter availability. *Deep-Sea Res.* 48:2453–72

Noble M, Mullineaux LS. 1989. Internal tidal currents over the summit of Cross Seamount. *Deep-Sea Res.* 36:1791–1802

Paterson GLJ, Wilson GDF, Cosson N, Lamont PA. 1998. Hessler and Jumars (1974) revisited: abyssal polychaete assemblages from the Atlantic and Pacific. *Deep-Sea Res. II* 45:225–51

Paterson GLJ, Lambshead PJD. 1995. Bathymetric patterns of polychaete diversity in the Rockall Trough, northeast Atlantic. *Deep-Sea Res. I* 42:1199–1214

Petersen C. 1913. Valuation of the sea. II. The animal communities of the sea bottom and their importance for marine zoogeography. *Rep. Danish Biol. Stn. to Board Ag.* 21:1–44

Petraitis PS, Latham RE, Niesenbaum RA. 1989. The maintenance of species diversity by disturbance. *Quar. Rev. Biol.* 64:393–418

Phleger PB, Soutar A. 1973. Production of benthic foraminifera in three east Pacific oxygen minima. *Micropaleontology* 19:110–15

Pickett STA, White PS. 1984. *Natural Disturbance: An Evolutionary Perspective.* New York: Academic

Pineda J. 1993. Boundary effects on the vertical ranges of deep-sea benthic species. *Deep-Sea Res. I* 40:2179–92

Pineda J, Caswell H. 1998. Bathymetric species-diversity patterns and boundary constraints on vertical range distribution. *Deep-Sea Res. II*, 45:83–101

Pingree RD, New AL. 1989. Downward propagation of internal tidal energy in the Bay of Biscay. *Deep-Sea Res.* 36:735–58

Radziejewska T, Maslowski J. 1997. Macro- and meiobenthos of the Arkona Basin (western Baltic Sea): differential recovery following hypoxic events. In *Responses of Marine Organisms to Their Environments*, ed. L.E. Hawkins, S. Hutchinson, pp. 251–262. Proc. 30th Eur. Mar. Biol. Symp., Univ. Southampton

Reimers CE, Jahnke RA, McCorkle DC. 1992. Carbon fluxes and burial rates over the continental slope and rise off central California with implications for the global carbon cycle. *Global Biogeochemical Cycles* 6:199–224

Reise K. 1985. *Tidal Flat Ecology.* Berlin: Springer-Verlag 191 pp.

Rex MA. 1973. Deep-sea species diversity: decreased gastropod diversity at abyssal depths. *Science* 181:1051–53

Rex MA. 1976. Biological accommodation in the deep-sea benthos: comparative evidence on the importance of predation and productivity. *Deep-Sea Res.* 23:975–87

Rex MA. 1981. Community structure in the deep-sea benthos. *Annu. Rev. Ecol. Syst.* 12:331–53

Rex MA. 1983. Geographic patterns of species diversity in deep-sea benthos. In *The Sea*, ed. GT Rowe, Vol. 8, pp. 453–72. New York: Wiley

Rex MA, Stuart CT, Coyne G. 2000. Latitudinal gradients of species richness in the deep-sea benthos of the North Atlantic. *Proc. Natl. Acad. Sci. USA* 97:4082–85

Rex MA, Stuart CT, Etter R. 1997. Large-scale patterns of species diversity in the deep-sea benthos. In *Marine Biodiversity: Patterns and Processes*, ed. R Ormond, J D Gage, MV Angel, pp. 94–121. Cambridge, UK: Cambridge Univ. Press

Rex MA, Stuart CT, Hessler RR, Allen JA, Sanders HL, Wilson GDF. 1993. Global-scale latitudinal patterns of species diversity in the deep-sea benthos. *Nature* 365:636–39

Rhoads DC. 1974. Organism sediment relations on the muddy sea floor. *Oceanogr. Mar. Biol. Ann. Rev.* 12:263–300

Rice A, Thurston M, New A. 1990. Dense aggregations of a hexactinellid sponge, *Pheronema carpenteri*, in the Porcupine

Seabight (northeast Atlantic Ocean), and possible causes. *Prog. Oceanog.* 24:179–96

Richardson MJ, Weatherly GL, Gardner WD. 1993. Benthic storms in the Argentine Basin. *Deep-Sea Res. II,* 40:975–87

Ricklefs RE. 1987. Community diversity: relative roles of local and regional processes. *Science* 235:167–71

Rogers A. 2000. The role of the oxygen minima in generating biodiversity in the deep sea. *Deep-Sea Res. II* 47:119–48

Rosenzweig ML. 1995. *Species Diversity in Space and Time*. Cambridge: Cambridge Univ. Press. 436 pp.

Rosenzweig ML, Abramsky H. 1993. How are diversity and productivity related? In *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*, ed. RE Ricklefs, D Schluter, pp. 53–65. Chicago: Univ. Chicago Press

Rowe GT, Menzies RJ. 1968. Deep bottom currents off the coast of North Carolina. *Deep-Sea Res.* 15:711–19

Rowe G, Pariente V. 1992. *Deep-Sea Food Chains and the Global Carbon Cycle*, pp. 560. Dordrecht, Netherlands: Kluwer

Rowe GT, Sibuet M, Deming J, Khripounoff A, Tietjen J, et al. 1991. 'Total' sediment biomass and preliminary estimates of organic carbon residence time in deep-sea benthos. *Mar. Ecol. Prog. Ser.* 79:99–114

Sanders HL. 1968. Benthic studies in Buzzards Bay. I: Animal-sediment relationships. *Limnol. Oceanog.* 3:245–58

Sanders HL. 1969. Benthic marine diversity and the time-stability hypothesis. *Brookhaven Symp. Biol.* 22:71–81

Schaff T, Levin L, Blair N, DeMaster D, Pope R, Boehme S. 1992. Spatial heterogeneity of benthos on the Carolina continental slope: large (100-km)-scale variation. *Mar. Ecol. Prog. Ser.* 88:143–60

Self RFL, Jumars PA. 1988. Cross-phyletic patterns of particle selection by deposit feeders. *J. Mar. Res.* 46:119–143

Sen Gupta BK, Machain-Castillo ML. 1993. Benthic foraminifera in oxygen-poor habitats. *Mar. Micropaleontology* 20:183–201

Shepard FP, Marshall NF, McLoughlin PA, Sullivan GG. 1979. Currents in submarine canyons and other seavalleys. Tulsa, OK: AAPG Stud. Geol., Vol. 8

Shmida A, Wilson MV. 1985. Biological determinants of species diversity. *J. Biogeogr.* 12:1–20

Simms RW, Weaver PPE, Kidd RB, Jones EJW. 1991. Late Quaternary mass movement on the lower continental rise and abyssal plain off western Sahara. *Sedimentology* 38:27–40

Smith CR, Berelson W, Demaster DJ, Dobbs FC, Hammond D, et al. 1997. Latitudinal variations in benthic processes in the abyssal equatorial Pacific: control by biogenic particle flux. *Deep-Sea Res.* II:2295–317

Smith CR, Pope RH, DeMaster DJ, Magaard L. 1993. Age-dependent mixing of deep-sea sediments. *Geochim. Cosmochim. Acta* 57:1473–88

Smith KL, Carlucci AF, Jahnke RA, Craven DB. 1987. Organic carbon mineralization in the Santa Catalina Basin: benthic boundary layer metabolism. *Deep-Sea Res.* 34:185–211

Smith KL, Hinga KR. 1983. Sediment community respiration in the deep sea. In *Deep Sea Biology*, ed. GT Rowe, pp. 331–70. New York: Wiley

Snelgrove PV, Butman CA. 1994. Animal-sediment relationships revisited: cause vs. effect. *Oceanogr. Mar. Biol. Ann. Rev.* 32:111–177

Stephens MP, Kadko DC, Smith CR, Latasa M. 1997. Chlorophyll-*a* and pheopigments as tracers of labile organic carbon at the central equatorial Pacific seafloor. *Geochim. et Cosmochim. Acta* 61:4605–19

Stevens GC. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. *Am. Natur.* 133:240–56

Stow DAV, Faugères JCF, eds. 1993. Contourites and Bottom Currents. *Sed. Geol.* 82:310 pp.

Stow DAV, Holbrook JA. 1984. North Atlantic contourites: an overview. In *Fine-Grained*

Sediments: Deep-Water Processes and Facies, ed. DAV Stow, DJW Piper, pp. 245–56. Oxford: Blackwell Sci.

Stuart CT, Rex MA. 1994. The relationship between developmental pattern and species diversity in deep-sea prosobranch snails. In *Reproduction, Larval Biology, and Recruitment of the Deep-sea Benthos*, ed. CM Young, KJ Eckelbarger, pp. 118–36. New York: Columbia Univ. Press

Stuart CT, Rex MA, Etter RJ. 2001. Large scale spatial and temporal patterns of deep-sea benthic species diversity. In *Ecosystems of the World: Ecosystems of Deep Oceans*, ed. PA Tyler. Amsterdam: Elsevier. In press

Suess E. 1980. Particulate organic carbon flux in the oceans—surface productivity and oxygen utilization. *Nature* 288:260–263

Taghon GL. 1982. Optimal foraging by deposit-feeding invertebrates: roles of particle size and organic coating. *Oecologia* 52:295–304

Thistle D. 1998. Harpacticoid copepod diversity at two physically reworked sites in the deep sea. *Deep-Sea Res. II* 45:13–24

Thistle D. 1983. The role of biologically produced habitat heterogeneity in deep-sea diversity maintenance. *Deep-Sea Res.* 30:1235–45

Thistle D, Ertman SC, Fauchald K. 1991. The fauna of the HEBBLE site: patterns in standing stock and sediment-dynamic effects. *Mar. Geol.* 99:413–22

Thistle D, Levin L. 1998. The effect of experimentally increased near-bottom flow on metazoan meiofauna at a deep-sea site, with comparison data on macrofauna. *Deep-Sea Res.* 45:625–38

Thistle D, Yingst UY, Fauchald K. 1985. A deep-sea benthic community exposed to strong near-bottom currents on the Scotian Rise (western Atlantic). *Mar. Geol.* 66:91–112

Thomas E, Gooday AJ. 1996. Cenozoic deep-sea benthic foraminifers: tracers for changes in oceanic productivity? *Geology* 24:355–58

Thunnell R, Tappa E, Varela R, Llano M, Astor Y. 1999. Increased marine sediment suspension and fluxes following an earthquake. *Nature* 398:233–36

Tietjen JH. 1984. Distribution and species diversity of deep-sea nematodes in the Venezuela Basin. *Deep-Sea Res.* 31:119–32

Tietjen JH. 1989. Ecology of deep-sea nematodes from the Puerto Rico Trench area and the Hatteras Abyssal Plain. *Deep-Sea Res.* 36:1579–94

Tilman D. 1982. *Resource Competition and Community Structure.* Princeton, NJ: Princeton Univ. Press

Tillman D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75:2–16

Tyler PA. 1995. Conditions for the existence of life at the deep-sea floor: an update. *Oceanogr. Mar. Biol. Annu. Rev.* 33:221–44

Van Dover C. 2000. *The Ecology of Deep-sea Hydrothermal Vents*, Princeton, NJ: Princeton Univ. Press. 424 pp.

Vetter EW, Dayton PK. 1998. Macrofaunal communities within and adjacent to a detritus-rich submarine canyon system. *Deep-Sea Res.* 45:25–54

Viana AR, Faugères J-C, Stow DAV. 1998. Bottom-current-controlled sand deposits—a review of modern shallow- to deep-water environments. *Sed. Geol.* 115:53–80

Von Rad U, Schulz H, Riech V, den Dulk M, Berner U, Sirocko F. 1999. Multiple monsoon-controlled breakdown of oxygen-minimum conditions during the past 30,000 years documented in laminated sediments off Pakistan. *Palaeogeog., Palaeoclim., Palaeoecol.*, 152:129–61

Waide RB, Willig MR, Steiner CF, Mittelbach G, Gough L. 1999. The relationship between productivity and species richness. *Annu. Rev. Ecol. Syst.* 30:257–300

Warwick RM, Clarke KR. 1996. Relationships between body-size, species abundance and diversity in marine benthic assemblages: facts or artifacts? *J. Exp. Mar. Biol. Ecol.* 202:63–71

Watts MC, Etter RJ, Rex MA. 1992. Effects of spatial and temporal scale on the relationship of surface pigment biomass to community structure in the deep-sea benthos. In *Deep-sea Food Chains and the Global Carbon Cycle,* ed. GT Rowe, V Pariente, pp. 245–54. Dordrecht, The Netherlands: Kluwer

Weatherley GL, Kelley EA. 1985. Storms and flow reversals at the HEBBLE site. *Mar. Geol.* 66:205–18

Wheatcroft RA. 1992. Experimental tests for particle size-dependent bioturbation in the deep ocean. *Limn. Oceanogr.* 37:90–104

Wheatcroft RA, Jumars PA, Smith CR, Nowell ARM. 1990. A mechanistic view of the particulate biodiffusion coefficient-step lengths, rest periods and transport directions *J. Mar. Res.* 48:177–208

Wheatcroft RA, Jumars PA. 1987. Statistical reanalysis for size dependent bioturbation in the deep ocean. *Limnol. and Oceanogr.* 37:90–104

Whitlatch RB. 1980. Patterns of resource utilization and coexistence in marine intertidal deposit-feeding communities. *J. Mar. Res.* 38:743–65

Willig MR, Lyons SK. 1998. An analytical model of latitudinal gradients of species richness with an empirical test for marsupials and bats in the New World. *Oikos* 81:93–98

Wishner K, Levin L, Gowing M, Mullineaux L. 1990. Involvement of the oxygen minimum in benthic zonation on a deep sea mount. *Nature* 346:57–59