

CHAPTER THREE

PATTERNS IN DEEP-SEA MACROECOLOGY

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Introduction

In *Macroecology*, Brown (1995, 10) defined this emerging field as “a way of studying relationships between organisms and their environment that involves characterizing and explaining statistical patterns of abundance, distribution, and diversity.” It is a relatively new and fundamentally different approach to ecology that centers on large-scale phenomena. Macroecology grew partly out of the recognition that the results of short-term, small-scale experiments could not be extrapolated readily to larger scales (see Roughgarden, Gaines, and Possingham 1988, and Wares and Cunningham 2001 for examples in the marine realm). It also explores the intriguing and often puzzling relationships between community structure and the ecogeographic properties of species that had simply never been seriously examined. Established as both an unabashedly empirical and inductive discipline, the scaling relationships that emerged in macroecology have contributed significantly to the development of a synthetic metabolic theory of ecology, a conceptual framework that has the potential to unify ecology across multiple levels of organization (Brown et al. 2004).

Most macroecological analyses have focused on terrestrial systems because large databases on geographic ranges of species, body size, abundance,

diversity, and relevant environmental variables were already available for regional and often global spatial scales. Much less is known about marine macroecology, a shortcoming that this volume is intended to remedy. Least well known is the deep sea. Ecological investigation in the deep sea began only forty years ago (Sanders, Hessler, and Hampson 1965). Its vast size and extreme environment make exploration technically difficult and expensive. Macroecology would seem to provide a useful and practical perspective for understanding the structure and function of deep-sea ecosystems. Small-scale manipulative experiments conducted on annual time scales in the deep sea have provided important insights into the causes of local species coexistence (Snelgrove and Smith 2002). However, it is now clear that community structure varies on local, regional, and global spatial scales, and on temporal scales ranging from annual to cycles of orbital forcing (Stuart, Rex, and Etter 2003). Local diversity is affected by oceanographic processes that operate on very large scales in both surface and benthic environments (Levin et al. 2001). With present technology, it seems unlikely that experiments could be deployed on geographic and temporal scales sufficiently large to capture the full range of factors that regulate deep-sea benthic diversity. A comparative approach like macroecology seems promising both to integrate our present understanding and to shape an agenda for future research. Ultimately, experiments will be necessary to test inferences from macroecological studies, but large-scale comparative studies will help identify and limit the range of hypotheses that need to be tested experimentally (Brown 1995, Menge et al. 2003).

In this chapter, we present the basic macroecological features of the deep-sea fauna, including geographic variation in standing stock, species diversity, species ranges, and body size. We also explore the relationships among body size, diversity, and abundance, and between body size and metabolic rate. Whenever possible, we compare these trends to those found in other ecosystems. We concentrate on the deep North Atlantic Ocean, which is by far the most intensively sampled region of the World Ocean. We emphasize communities that inhabit the soft-sediment habitats covering most of the seafloor. An excellent summary of biogeographic patterns in deep-sea chemosynthetic habitats is provided by Van Dover (2000). Many of our case studies involve mollusks, because their taxonomy and biogeography are relatively well known, owing to the extensive published work of Philippe Bouchet, Anders Warén, John Allen, Howard Sanders, and their colleagues. While the data are limited and geographically restricted, they begin to provide a macroecological context for studying deep-sea assemblages.

Standing Stock

The pattern of standing stock with depth is the most well-established feature of community structure in the deep-sea benthos. The biomass and abundance of the macrofauna in the western North Atlantic are shown in figure 3.1. Both decrease exponentially by two to three orders of magnitude from the continental shelf to the abyssal plain. Abyssal macrobenthic standing stock is extremely low (10s–100s individuals m^{-2} and $<1 g m^{-2}$). Bathymetric decreases in standing stock also occur in bacteria (Deming and Yager 1992; Aller, Aller, and Green 2002), the meiofauna (Soltwedel 2000), invertebrate megafauna (Lampitt, Billett, and Rice 1986) and demersal fishes (Haedrich and Rowe 1977).

The primary source of food for the benthos is sinking phytodetritus augmented by the sporadic occurrence of sinking plant and animal remains. Food availability decreases with increasing distance from productive coastal waters and terrestrial runoff, and because of remineralization during descent through a progressively deeper water column. Thus, the decline in standing stock is driven by the decrease in the rate of organic carbon input with increasing depth and distance from land. The entire process of surface-benthic coupling is complicated and incompletely understood. It involves the biotic and abiotic factors affecting surface production, the export of organic material to the deep ocean, horizontal dispersal by currents in the water column, transformation during sinking, and redistribution within the benthic community. Despite this complexity, deep-sea macrobenthic standing stock can be accurately predicted by estimates of organic carbon flux at depths determined from satellite imagery of overhead surface production and empirical models of downward flux (Johnson et al. 2005).

Rowe (1983) first showed that the exponential decrease in standing stock is a global phenomenon. Subsequently, it has become clearer that the pattern is modulated in a predictable way by unusual circumstances of food availability at depth. For example, elevated standing stock is caused by organic carbon loading associated with proximity to oxygen minimum zones (Levin and Gage 1998), lateral advection and deposition (Blake and Hilbig 1994), upwelling systems (Sanders 1969), exposure of reactive sediments or deposition of sediments by strong bottom currents (Aller 1997), or where topography concentrates food in canyons (Vetter and Dayton 1998) or trenches (Gambi, Vanreusel, and Danovaro 2003). By contrast, depressed standing stock is found in oligotrophic ocean basins such as the Arctic Sea (Kröncke et al. 2000) and the Mediterranean Sea (Tselepidis et al. 2000). Overall, how-

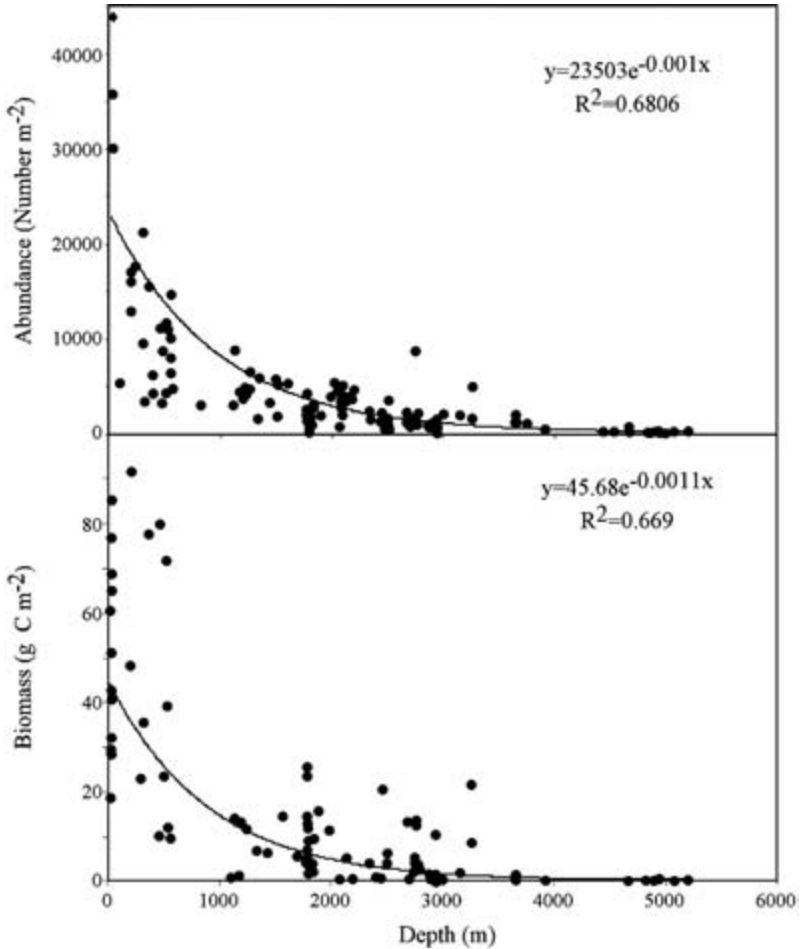


FIGURE 3.1 Standing stock of macrobenthos with depth in the deep western North Atlantic. Data are from Sanders, Hessler, and Hampson (1965); Rowe, Polloni, and Horner (1974); Smith (1978); Rowe, Polloni, and Haedrich (1982); Maciolek et al. (1987b).

ever, as we show in our discussion of body size with a new global analysis of abundance in the macrofauna and meiofauna, there is a strong and clear tendency for standing stock to decrease with depth and distance from land when geography is statistically controlled. Benthic standing stock appears to be the best available correlate of food availability in the deep sea (Smith et al. 1997), and arguably represents the single most significant environmental gradient affecting geographic patterns of biodiversity and evolutionary potential of the deep-sea benthos.

Patterns of Species Diversity

The quantitative study of community structure in the deep-sea benthos began with Hessler and Sanders' (1967) momentous discovery that species diversity is surprisingly high. It had been assumed for a century before that the deep-sea fauna was depauperate, and prior to then that the great depths were essentially sterile. Sanders (1968), in his influential comparative study of marine benthic diversity, showed that bathyal diversity exceeded coastal diversity in the temperate zone and approached shallow-water tropical diversity. The development and deployment of more effective sampling gear (Hessler and Jumars 1974) has indicated that diversity is probably even higher than Sanders estimated (Grassle and Maciolek 1992). Given the brief period of exploration, the enormous size of the environment, and the difficulty of sampling, it is not surprising that our knowledge of ecology and biogeography in the deep sea remains far behind that for terrestrial and coastal systems. All the same, Hessler and Sanders' discovery has inspired remarkably rapid progress, and a picture of diversity in time and space is beginning to take shape. In this section we summarize patterns of diversity on local, regional, and global scales.

On relatively small scales, the number of species coexisting in the deep sea is surprisingly high, exceeding 300 macrofaunal species m^{-2} at bathyal depths in the western North Atlantic (Etter and Mullineaux 2001; Levin et al. 2001). Despite recent controversy (Gray 1994, 2002, Gray et al. 1997), diversity is considerably higher than in nearby shallow-water communities. While true that some deep-sea communities (e.g., western North Atlantic) are less diverse than some shallow-water communities elsewhere in the world (e.g., Australia), it is not clear what this means or how it will help us to identify the ecological and evolutionary forces that regulate diversity. When comparisons are controlled for spatial scale, geography, taxonomy, sampling methods, and habitat, the number of species coexisting at small scales in the deep sea is considerably higher than in shallow-water communities (Etter and Mullineaux 2001, Levin et al. 2001).

The greater diversity in what appears to be a more homogeneous environment has long perplexed marine ecologists (Sanders 1968; Gage 1996; Gray 2002) and remains a major theoretical challenge. Numerous hypotheses have been proposed, including competition, facilitation, predation, disturbance, productivity, environmental heterogeneity, and patch dynamics (reviewed in Etter and Mullineaux 2001, Levin et al. 2001, and Snelgrove and Smith 2002). Existing experimental and comparative evidence suggest that no single factor is responsible. Diversity within local deep-sea assemblages is

apt to reflect a complex dynamical process that integrates a number of interdependent forces operating at different space and time scales and changing in relative importance along various environmental gradients.

Much of our understanding of the patterns and potential causes of deep-sea biodiversity comes from regional-scale sampling studies, particularly along bathymetric gradients (Levin et al. 2001). Sanders (1968) showed that local species diversity of bivalve mollusks and polychaete worms increased from the continental shelf to lower bathyal depths in the western North Atlantic. When the analysis was extended to abyssal depths and more taxa, the overall diversity-depth trend appeared to be unimodal; diversity increased to a peak in the mid- to lower-bathyal zone, and then decreased in the abyss (Rex 1973, 1981, 1983). These early studies relied on estimating diversity from qualitative samples by normalizing the number of species to a common number of individuals with rarefaction, a numerical method to resample the relative abundance distribution devised by Sanders (1968) and formalized statistically by Hurlbert (1971). Recent intensive quantitative sampling with precision box corers confirmed Sanders' finding that diversity increases with depth below the continental shelf (Etter and Mullineaux 2001; Levin et al. 2001), and suggest that peak diversity of the whole macrofaunal assemblage occurred at around 1,000–1,500 m on the continental slope (Etter and Grassle 1992). The depth of maximum diversity may depend on the taxa considered, species' ranges and dispersion patterns, and the spatial scales covered by different sampling gears (Stuart, Rex, and Etter 2003). However, the general unimodal shape of diversity-depth patterns seems to be typical in the western North Atlantic. No other region of the World Ocean has been sampled so intensively. Polychaetes, the most abundant and diverse macrofaunal taxon, show unimodal diversity-depth patterns in the eastern North Atlantic (Paterson and Lamshead 1995) and in the eastern equatorial Atlantic (Cosson-Sarradin et al. 1998). But limited data on other taxa and geographic regions suggest that unimodal patterns may not be universal; and moreover, that the causes of known unimodal patterns may vary geographically (Rex, Etter, and Stuart 1997; Flach and deBruin 1999; Gage et al. 2000; Stuart, Rex, and Etter 2003).

Studies of bathymetric diversity trends have centered on variation in alpha (sample) diversity within basins. Here, we present a different approach, based on species ranges, and extend the analysis to much larger spatial scales that include eastern and western corridors of the North Atlantic. Figure 3.2 shows depth ranges of all protobranch bivalve mollusks collected by the Woods Hole Oceanographic Institution's Benthic Sampling Program (Sanders 1977) from sampling transects in the North American and West European Basins

(Allen and Sanders 1996). All of the material was collected with epibenthic sleds (Hessler and Sanders 1967). The depth distribution of samples in both basins is indicated at the top of figure 3.2. While sampling is not perfectly equable between the eastern and western North Atlantic, both transects extend from upper bathyal to abyssal depths, represent all major seafloor physiographic features, and include a similar number of samples (thirty-five west, twenty-eight east). Species accumulation curves suggest that the faunas are reasonably well characterized, and that the eastern fauna is somewhat more diverse over much of the depth range (Allen and Sanders 1996).

The unimodal diversity-depth pattern discussed previously for alpha diversity of individual samples is also apparent when the number of coexisting species ranges is summed over 1,000 m depth intervals (fig. 3.2, bottom panel). Diversity peaks in the 2,000–3,000 m region and is depressed at upper bathyal and abyssal depths. Eastern and western faunas show similar diversity-depth patterns.

Figure 3.2 reveals a high rate of faunal turnover, or β -diversity, along the depth gradient. High rates of zonation are also common in the megafauna (Haedrich, Rowe, and Polloni 1980; Hecker 1990; Howell, Billett and Tyler 2002), macrofauna as a whole (Rowe, Polloni, and Haedrich 1982; Blake and Grassle 1994; Gage et al. 2000) and meiofauna (Coull 1972). A surprisingly high proportion of protobranch species (twenty-four out of fifty-six, or 43 percent) are shared between the eastern and western North Atlantic (fig. 3.2). Even more remarkable, twenty-one of the shared species (88 percent) have depth ranges that overlap between basins. Only three of these species (connected by thin lines, figure 3.2) have disjunct depth ranges, and even so, occur in the same basic physiographic feature and are separated by <1,000 m. As Sanders and Hessler (1969) conjectured, based on fewer data, some basic features of faunal zones within basins appear to extend as bands around the North Atlantic, at least in protobranchs. This large-scale faunal redundancy has important implications for projecting global biodiversity in the deep-sea benthos, and suggests that diversity might be lower than the 10,000,000 species projected by Grassle and Maciolek (1992).

Allen and Sanders (1996) showed that deeper-dwelling protobranch species tend to be more cosmopolitan, as is borne out in figure 3.2 for the North Atlantic. The proportion of species that occur in both eastern and western basins increases from 44 percent at upper bathyal depths (500–2,000 m) to 54 percent at lower bathyal depths (2,000–4,000 m) to 60 percent in the abyss (>4,000 m). Rex et al. (2005) pointed out that within-basin abyssal endemism in mollusks appeared to be low. On a between-basin scale it appears to be even lower. For example, *Ledella aberrata* would appear to be an abyssal en-

demic in the eastern North Atlantic (see Appendix A), but has a lower bathyal distribution in the western North Atlantic. *Malletia polita* is another case of an apparent eastern North Atlantic abyssal endemic that occurs at bathyal and abyssal depths in the western North Atlantic (Allen and Sanders 1973; Allen, Sanders, and Hannah 1995). Two other apparent western North Atlantic abyssal endemics, *Silicula macalisteri* and *Yoldiella similiris* are known from upper bathyal sites in western South Atlantic (Allen and Sanders 1973; Allen, Sanders, and Hannah 1995). Of the other abyssal endemic species that are described, only one *Ledella galathea*, is known exclusively from abyssal depths (the West European Basin and off West Africa; Allen and Hannah 1989). Three undescribed unique species (*Ledella* sp., *Spinula* sp., and *Tindariopsis* sp.) are also potential candidates for true abyssal endemics (J. Allen, personal communication). A conspicuous feature of figure 3.2 is that the vast majority of species with abyssal distributions (79 percent; 86 percent if we exclude *S. macalisteri* and *Y. similiris* as discussed previously) are range extensions of bathyal species. This has important implications for the causes of diversity discussed in the following.

Variation in species diversity and composition also occurs on oceanwide interbasin scales in the Atlantic (Allen and Sanders 1996; Wilson 1998). There is some indication of latitudinal gradients of diversity in the deep-sea fauna, though this is based on much less sampling than in terrestrial and coastal systems (Roy, Jablonski, and Valentine 1994, 1998; Hawkins, Porter, and Diniz-Filho 2003; Hillebrand 2004a, 2004b, Witman, Etter, and Smith 2004). Rex et al. (1993; Rex, Stuart, and Coyne 2000) found poleward decreases in the diversity for gastropods, bivalves, and isopods in the North Atlantic and Norwegian Sea. The South Atlantic is more poorly sampled. It shows strong regional variation in diversity, and a weak latitudinal signal for mollusks, but not isopods (Rex et al. 1993). Gage et al. (2004) found poleward declines in the diversity of deep-sea cumaceans for the entire Atlantic (a significant parabolic regression with a peak at tropical latitudes). The eastern corridor of the North Atlantic showed a significant latitudinal gradient, but the western corridor did not, suggesting strong interbasin differences and mixed evidence for a simple consistent hemisphere-wide latitudinal gradient. Among the meiofauna, deep-sea foraminiferans show latitudinal gradients in the North and South Atlantic (Culver and Buzas 2000). Nematodes do not show a clear monotonic poleward decline (c.f. Lamshead et al. 2000 and Rex, Stuart, and Etter 2001), but may show peak diversity at mid-latitudes in the North Atlantic (Mokievsky and Azovsky 2002).

The causes of geographic patterns of diversity on local, regional, and global scales have been reviewed several times recently (Rex, Etter, and

Stuart 1997; Levin et al. 2001; Etter and Mullineaux 2001; Snelgrove and Smith 2002; Stuart, Rex, and Etter 2003; Rex et al. 2005), and will only be summarized briefly here, since our chapter is concerned primarily with patterns. Unimodal bathymetric gradients of diversity have been attributed to mid-domain effects based on boundary constraints imposed by the coast and seafloor (Pineda 1993), but recent analyses show that diversity trends depart significantly from the predictions of mid-domain models (Pineda and Caswell 1998; McClain and Etter 2005). Just as in other marine environments, a wide variety of biotic and abiotic factors that act on different scales of time and space appear to affect deep-sea diversity. Apart from catastrophic events such as burial by submarine landslides (Rothwell, Thomson, and Kahler 1998) and ash from volcanic eruptions (Hess and Kuhnt 1996) or global anoxic events (Kennett and Stott 1991), much of the variation observed in deep-sea diversity appears to be related, directly or indirectly, to productivity in the form of carbon flux to the benthos from surface production. Within the deep sea, the relationship between diversity and productivity is unimodal as it is frequently, but not universally, in coastal and terrestrial environments (Rosenzweig 1995; Mittelbach et al. 2001). The most accurate indication available of average carbon flux over large spatio-temporal scales is the standing stock of the benthos (Smith et al. 1997). The unimodal diversity-depth pattern evident in figure 3.2 coincides with the monotonic decline in standing stock with depth shown in figure 3.1. Rex (1983) suggested that depressed diversity at upper bathyal depths, where standing stock is high, might be due to accelerated rates of local competitive displacement driven by pulsed carbon loading from high seasonal productivity in coastal waters (Rex 1981). All of the circumstances mentioned earlier where heavy carbon loading associated with upwelling, topographic focusing of sinking organic material, sediment erosion, and deposition result in high standing stock also show depressed diversity irrespective of depth. Even oxygen-minimum zones on continental margins that limit diversity through severe physiological constraints are ultimately caused by unusually high rates of overhead production and downward carbon flux (Levin and Gage 1998).

Rex et al. (2005) recently proposed that continental margins and abyssal plains of the North Atlantic may constitute a source-sink system for many species. As can be seen in figure 3.2, the vast majority of abyssal protobranchs in both eastern and western basins represent range extensions of bathyal species. These abyssal range extensions are very sparsely occupied because of the low density of all abyssal macroinvertebrates (fig. 3.1). Abyssal protobranch densities have been estimated to be on the order of one to

three individuals m^{-2} for the few commonest species, one to five individuals $100 m^{-2}$ for most species, and two individuals $1,000 m^{-2}$ for the rarest species (Rex et al. 2005). Adult protobranchs are minute organisms with low mobility, low gamete production, and separate sexes. Their larvae are lecithotrophic and disperse demersally, potentially over considerable distances in the frigid deep-sea environment. These conditions suggest that abyssal populations of many species are sinks that experience chronic local extinction as an Allee Effect and are maintained by immigration from more abundant bathyal source populations through larval dispersal. In this view of deep-sea community ecology, bathyal diversity may be regulated by essentially the same equilibrational and nonequilibrational mechanisms that govern community structure in coastal and terrestrial systems where population densities are relatively high (Bertness, Gaines, and Hay 2001)—though the relative importance and operation of these mechanisms in the deep-sea remain far from clear. Much of the abyssal macrofauna may exist as a mass effect from bathyal populations. While source-sink dynamics may help explain abyssal molluscan diversity, at least for rarer species, its potential relevance to other elements of the abyssal fauna has not been examined.

At very large interbasin scales, both differences in regional ecology and the evolutionary-historical development of faunas may be important. Depressed diversity at high latitudes in some contemporary taxa may be caused in part by high-pulsed organic carbon loading resulting from high and seasonal surface production (Campbell and Aarup 1992). However, isopods show a gradient of decreasing diversity from the South to the North Atlantic that Wilson (1998) has attributed to a relatively new wave of invasion from shallow water in the Southern Hemisphere that augments the diversity of an earlier deep-sea in situ radiation. Stuart and Rex (1994) demonstrated that local diversity was a function of regional diversity in deep-sea gastropods, suggesting that the size of the species pool, presumably originating from regional-scale adaptive radiation, influences local diversity. The gradual historical formation of latitudinal gradients in deep-sea foraminifera during the Cenozoic can be traced in deep seabed cores (Thomas and Gooday 1996).

Body Size

Body size is related to a variety of life-history, physiological, and ecological traits (Peters 1983; Brown 1995; Gillooly et al. 2001, Brown et al. 2004, Savage et al. 2004), and thus may provide a link between processes at the individual level and higher levels of organization such as species diversity. The most immediate impression when looking at deep-sea samples is the extraordi-

narily small size of most species. As early as 1880, Mosely commented on the pervasive dwarfism of deep-sea animals. More recently, Thiel (1975, 593) referred to the deep sea as a “small organism habitat.” Gage (1977) showed that the mean weight per individual in coastal waters of Loch Creran in Scotland was 0.039 g, compared to 0.002 g in the Rockall Trough (2,875 m), a full order of magnitude difference. Similar methods have been used to show meiofaunal miniaturization in the deep sea (Shirayama 1984; Pfannkuche 1985; Tietjen 1992; Vincx et al. 1994). Paradoxically, some deep-sea arthropods (isopods, amphipods, pycnogonids, ostracods) are much larger than shallow-water representatives (Gage and Tyler 1991).

Examples of the dramatic difference in body size of snails between the continental shelf and deep sea are shown in figures 3.3 and 3.4. Estimates of size in the deep-sea assemblages collected south of New England (McClain, Rex, and Jabbour 2005) are compared to those on Georges Bank, the adjacent continental shelf (Maciolek and Grassle 1987). The deep-sea fauna shows a smaller average size (deep sea: 8.2mm, and Georges Bank: 21mm). Large deep-sea gastropods are known; for example, *Troschelia berniciensis* reaches 10 cm in the bathyal eastern Atlantic (Olabarria and Thurston 2003), and *Guivillea alabastrina*, the largest deep-sea gastropod known, reaches 16.8 cm in the Southern Hemisphere (Knudsen 1973). But such large individuals and species appear to be very rare in the deep sea. In figure 3.4, we compare the sizes of eastern North Pacific continental shelf gastropods belonging to three families (Roy 2002) to those same families in the deep sea. Body size (geometric mean of length and width of the shell) is significantly

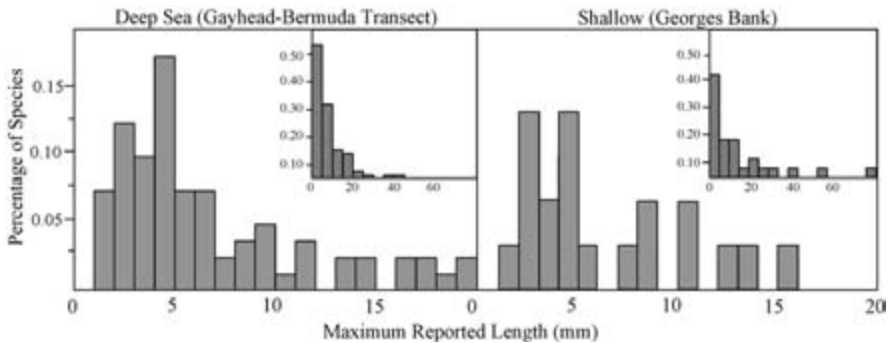


FIGURE 3.3 A comparison of body sizes between coastal and deep-sea benthic gastropods. Deep-sea gastropods were collected south of New England in the western North Atlantic (see McClain, Rex, and Jabbour 2005). Coastal gastropods represent the fauna of Georges Bank (Maciolek and Grassle 1987). Inset histograms reflect the percentage of species in 5mm length bins between 0–80mm. Main histograms reflect the percentage of species in 1mm length bins between 0–20mm.

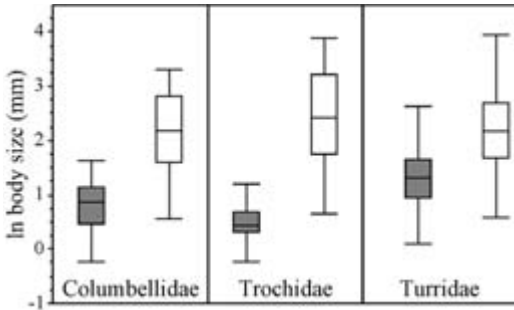


FIGURE 3.4 A comparison of size in deep-sea gastropods (McClain, Rex, and Jabbour 2005) from the western North Atlantic (solid bars) to continental shelf gastropods (open bars) from the Pacific (Roy 2002) for three separate families.

greater on the Pacific shelf (both t -test and Median Test, p -values < 0.0001) in all cases. As a striking example of the size difference between coastal and deep-sea gastropods, a back-of-the-envelope calculation based on data from McClain, Rex, and Jabbour (2005) shows that all of the deep-sea snails collected from the western North Atlantic by the Woods Hole Oceanographic Institution's Benthic Sampling Program (forty-four samples, 20,561 individuals) would fit comfortably into a single large shell of the common New England knobbed whelk *Busycon carica*.

The average size of deep-sea organisms continues to decrease with depth below the shelf-slope transition. Thiel (1979) was the first to demonstrate this trend by regressing abundance of the smaller meiofauna and larger macrofauna against depth. An ANCOVA showed that the meiofaunal regression had a higher intercept and lower slope than did the macrofauna, therefore the meiofauna comprise a larger proportion of the total assemblage as depth increases (average size decreases with depth). The analysis was based on meiofaunal densities off Portugal and East Africa, and macrofaunal densities (from Rowe 1971) off New England, Brazil, the Gulf of Mexico, and Peru. Here we repeat Thiel's analysis using a much larger dataset representing most major ocean basins (sixty-five studies and 705 observations for the meiofauna, sixty-one studies and 912 observations for the macrofauna). To remove regional influences, we regressed the partial residuals of abundance (effects of longitude and latitude removed) against depth (fig. 3.5). The resulting abundance-depth relationships are highly significant, with the meiofauna regression showing a higher elevation, as expected. An ANCOVA (see figure caption) shows that the macrofauna has a significantly steeper slope confirming, on a global basis, Thiel's conclusion that average metazoan size decreases with depth.

A closer look at size-depth patterns within individual taxa reveals a very mixed picture; size can increase, decrease, or show no pattern with depth

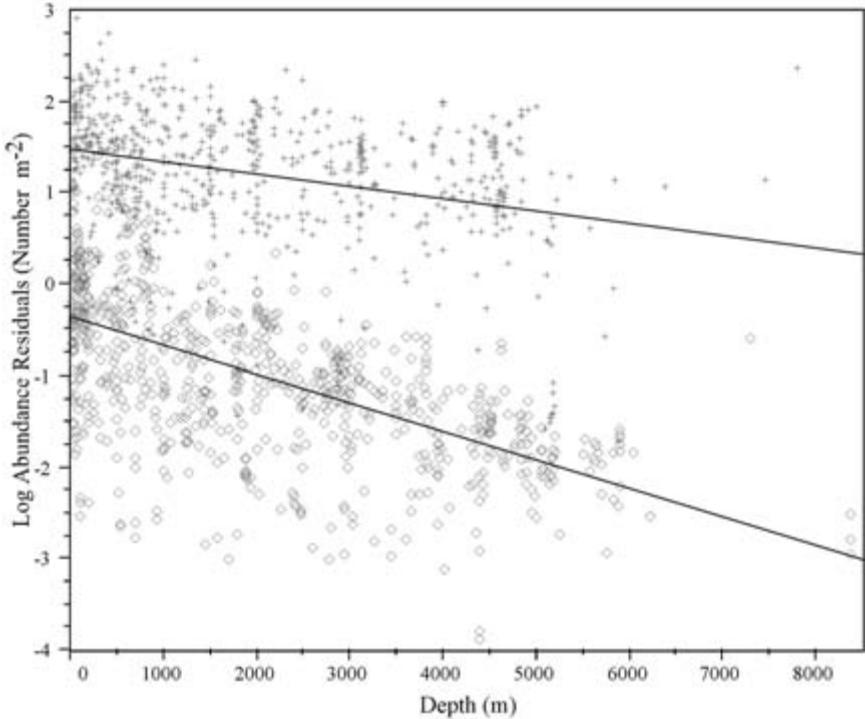


FIGURE 3.5 Regressions of the partial residuals of abundance (with the effects of longitude and latitude removed) against depth for deep-sea meiofauna and macrofauna. Meiofaunal abundance is higher and decreases with depth less rapidly than does macrofaunal abundance. This indicates that the average size of organisms decreases with depth. An ANCOVA shows that the slopes are significantly different ($F = 99.934$, $d.f. = 1,1513$, $P < 0.0001$). Regression equations are: Meiofauna $Y = 5.761 - 0.000135 X$, $R^2 = 0.109$, $N = 705$, $F = 85.931$, $P < 0.001$; Macrofauna $Y = 3.588 - 0.000312X$, $R^2 = 0.452$, $N = 912$, $F = 667.913$, $P < 0.001$. Data references are given in Appendix B.

(reviewed in Rex and Etter 1998, Soetaert, Muthumbi, and Heip 2002). Part of this variation among taxa probably relates to methodological differences in the way size was measured and statistically analyzed, and some of it may reflect differences in the overall biological properties of the taxa and regional ecological differences. It is also important to remember that geographic variation in size might merely be a phenotypic plastic response. The degree to which size-depth trends represent actual adaptations to the environment is best studied at the level of individual species. If adaptive, bathymetric trends at higher taxonomic levels, and within and between functional groups, must result from clinal effects within species or depth-correlated replacement of species that differ in size.

Bergmann's rule states that body size increases toward higher latitudes.

Although the explanations for this trend are contentious, there is some support for increased size toward the poles for homeotherms (Brown and Lee 1969; Brodie 1975; Forsman 1991; Scharples, Fa, and Bell 1996). For ectotherms, Bergmann's rule applies for some insect taxa (e.g., Cushman, Lawton, and Manly 1993; Hawkins and Lawton 1995; Arnett and Gotelli 1999) but not others (Hawkins 1995; Hawkins and Lawton 1995). Few studies have been conducted for marine invertebrates. Roy and Martien (2001) found no relationship between size and latitude for eastern coastal Pacific bivalves. For deep-sea faunas, only two studies have investigated latitudinal-size relationships. Latitude appears to be only a weak predictor of gastropod body size and is often subordinate to depth in multiple regression analyses (McClain and Rex 2001, Olabarria and Thurston 2003).

Many hypotheses have been proposed to explain spatial gradients of size in other systems, including temperature (e.g., Atkinson and Sibly 1997), predation (e.g., Blumeshine, Lodge, and Hodgson 2000), energy input (Blackburn and Gaston 1996), oxygen availability (Chapelle and Peck 1999) and sediment diversity (Schwinghamer 1985). It is unlikely that temperature, relatively invariant throughout much of the deep sea, plays a significant role in determining sizes of deep-sea organisms (McClain and Rex 2001), but this relationship has not been examined statistically. Schwinghamer (1985) proposed that the tendency toward smaller organisms in the deep sea is related to sediment diversity as a reflection of greater habitat diversity. However, the relationship between body size and sediment heterogeneity has not been borne out in coastal and shelf benthic habitats (Duplisea and Drgas 1999; Parry et al. 1999; Leaper et al. 2001). Sediment-organism interactions do appear to be important in the deep sea (Etter and Grassle 1992), but they have not been related to body size. Chapelle and Peck (1999) demonstrated that maximum potential size is limited by oxygen availability in benthic amphipod crustaceans from coastal and freshwater environments. Larger size at more oxygenated sites is also found in deep-sea gastropods (McClain and Rex 2001). Spicer and Gaston (1999) suggested that oxygen content of water should not affect size in aquatic environments, and that these relationships are a spurious consequence of temperature gradients. However, it is clear that body size and oxygen availability are related independent of temperature for both shallow and deep-water organisms (McClain and Rex 2001; Peck and Chapelle 2003). Body size can also be regulated by the effects of oxygen on development, cell size, and cell number (Frazier, Woods, and Harrison 2001; Peck and Chapelle 2003).

Although all of these factors, and others, may account for some of the variation in body size, the most important determinant is likely to be carbon flux to the benthos (Thiel 1975; Rex and Etter 1998). Support comes

from the inference that benthic standing stock decreases exponentially with depth (fig. 3.1), and that standing stock is the best proxy available for carbon flux to the seabed (Rowe 1983; Smith et al. 1997). According to the optimality theory of body size (Sebens 1982, 1987), optimal size should decrease with depth as rates of food intake decrease and the costs of foraging increase (Rex and Etter 1998). In general, this prediction is supported by the decrease in average metazoan size with depth (fig. 3.5). However, as mentioned earlier, size-depth clines within species show considerable variation. This may be because other selective advantages of large size (metabolic efficiency, escape from predation, and the ability to exploit more food resources) displace populations away from optimal size in a taxon-specific way. For gastropods there is a shift from positive to negative size-depth clines within species with increasing depth (McClain, Rex, and Jabbour 2005). There is also an indication of an increase in size across bathyal depths and a decrease in the abyss for gastropod assemblages as a whole and in demersal fishes (fig. 3.6). In the upper- to mid-bathyal zone, where population densities are relatively high, other advantages of larger size may offset selection for optimal size based on maximizing the energy available for reproduction. However, at the extremely low densities found at lower bathyal and abyssal depths, the relative rates of energy intake, and cost may finally enforce smaller size. Alternatively, abyssal snails may be smaller either because severe energy constraints favor small-bodied species as the energy demands become too great for large organisms to maintain reproductively viable population sizes (Thiel 1975), or because individuals of many populations experience retarded growth in an unfavorable sink environment (Rex et al. 2005), or some combination of these phenomena.

Some differences in the shape of size-depth trends also may be due to changes with depth in the fundamental causative agents. Soetaert, Muthumbi, and Heip (2002) showed that the average size of nematodes decreases with depth in the eastern North Atlantic. However, this was a complex response to both food availability and the biogeochemical properties of sediments that limit vertical distribution. Nematodes that occupy the topmost oxygenated layer of sediment scarcely change in size with depth. The overall miniaturization with depth is attributable to larger nematodes being able to utilize deeper more anoxic layers at bathyal depths, but not at abyssal depths.

A major objective of macroecology is to explore how body size relates to the structure of ecological communities (Lawton 1990; Brown 1995; Allen, Brown, and Gilloly 2002; Brown et al. 2004). In particular, this has centered on the relationship between body size, species richness, and abundance in

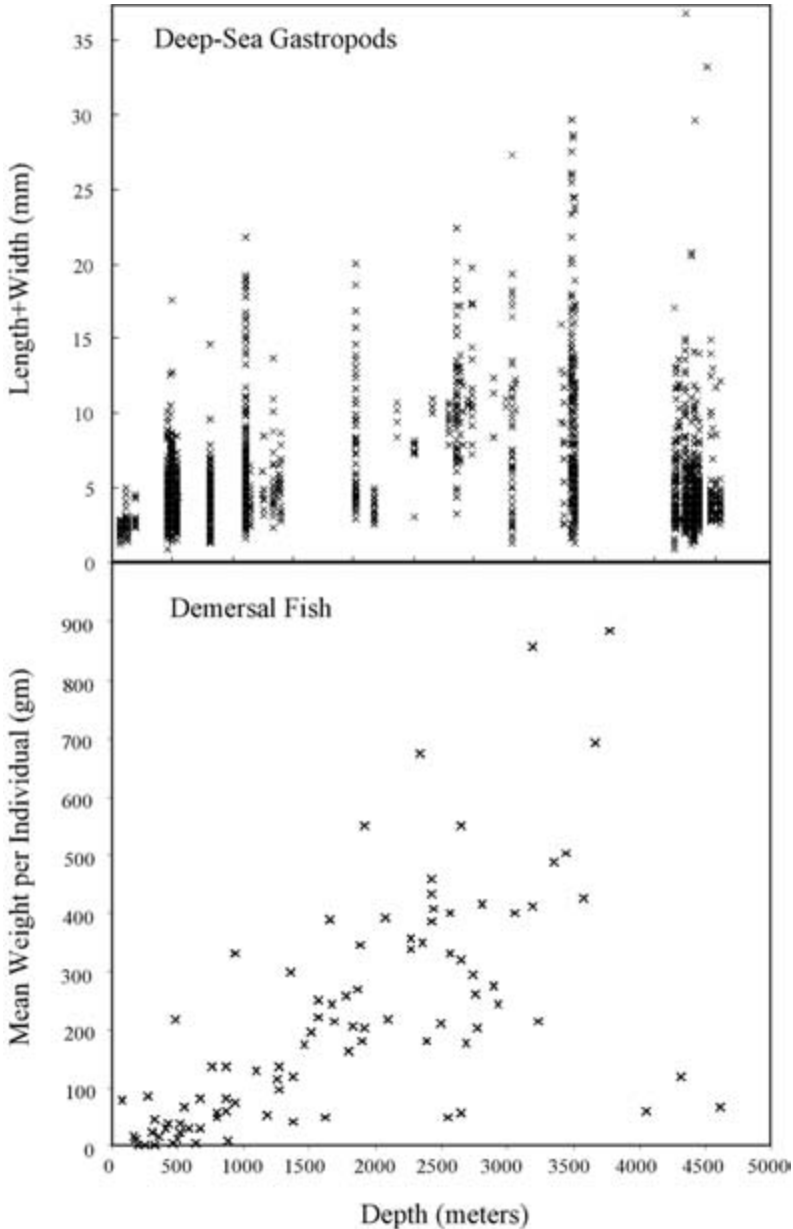


FIGURE 3.6 Maximum Size (length + width) for deep-sea gastropods, each point represents an individual (McClain et al. 2005) and mean weight per individual for demersal fishes (from Polloni et al. 1979) across a depth gradient South of New England, points represent a mean size per trawl.

terrestrial and marine systems, with little research devoted to these trends in the deep sea (but see McClain 2004, and Rex and Etter 1998). The statistical relationships among these variables have important implications for estimating biodiversity and could suggest how resource availability helps determine community structure. Siemann, Tilman, and Haarstad (1996, 1999), using data from a comprehensive sampling study of grassland insects, showed that diversity and abundance had fairly symmetrical unimodal relationships to body size, as had been frequently observed in other studies. When the relationships were reviewed in three dimensions they described a parabola with highest diversity at intermediate abundant size classes. The projection of this parabola on the diversity-abundance plane revealed that the number of species (S) scaled to the number of individuals within size classes (I) according to the expression $S = I^{0.5}$, independent of body size. A study of diversity, size and abundance in rocky intertidal mollusks showed a similar set of relationships (Fa and Fa 2002).

McClain (2004) examined these relationships for deep-sea gastropods (fig. 3.7). Again, the relationships of diversity and abundance to size are unimodal (fig. 3.7, panels A, B), although the diversity-body size relationship is right skewed. This contrasts with the log-normal trends in terrestrial arthropods (Siemann, Tilman, and Haarstad 1996) and coastal mollusks (Roy, Jablonski, and Valentine 2000; Fa & Fa 2002), but agrees with the prevalent right-skewed pattern observed in a variety of other organisms (Brown 1995). The skewed distribution also, of course, affects the shape of the curve in the three dimensional representation (fig. 3.7, panel D), and the distribution of size classes about the diversity abundance regression (fig. 3.7, panel C). Nonetheless, diversity scales to abundance in a way that is similar to terrestrial insects and coastal mollusks. That studies of three such different communities produce such a similar set of relationships suggests a common set of underlying causes. While the causal links remain obscure they are likely linked to scale, energy availability, available niche space, size-biased speciation and extinction, and constraints on minimum size (Brown 1995; Kozlowski and Gawelczyk 2002; McClain 2004).

Metabolic Rates and the Metabolic Theory of Ecology

Metabolism underlies all biological rates because it is the sum of expenditures toward growth, maintenance, and reproduction. The metabolic theory of ecology (MTE) is a potentially unifying framework that seeks to link the factors controlling metabolic rates to higher-order macroecological patterns and processes at population, community, and ecosystem levels (Gillooly

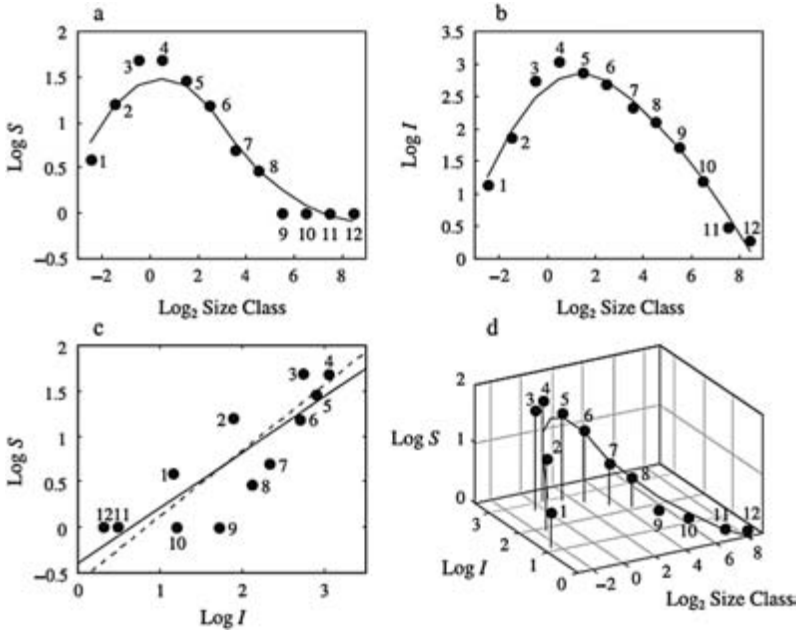


FIGURE 3.7 Panel A: Relationship between log-species richness (S) per \log_2 size class (mm^3). B. Relationship between log abundance (I) per \log_2 size class. C. Relationship between log species richness (S) and log abundance (I) per \log_2 size class. The lines represent fitted regressions (OLS: $S = -0.406I^{0.616}$, $R^2 = 0.719$, $p=0.0005$; RMA: $S = -0.613I^{0.726}$, $R^2 = 0.848$, $p = 0.0500$). D. Relationships between log of species richness (S), log of number of individuals (I), and log₂ size class. All plots are from McClain (2004). Lines represents a kernel smoothing curve fitted to the data and numbers refer to the log₂ size classes.

et al. 2001; Brown et al. 2004). The metabolic theory of ecology has generated substantial interest and criticism (see, e.g., special issue of *Functional Ecology* vol. 18, 2004; and *Ecology*, vol. 85, 2004). It predicts that metabolic rates of all organisms are primarily determined by individual body mass and temperature. Individual mass-specific metabolism is expected to scale with body size at a $-1/4$ power (West, Brown, and Enquist 1997, 1999a, 1999b) and scale exponentially with temperature according to Boltzmann/Van't Hoff-Arrhenius equation, with an activation energy between 0.60–0.70 eV (Gillooly et al. 2001). The value of MTE in deep-sea ecology, if it can be verified, would be to help explain large-scale macroecological patterns in an environment where both experimentation and precision sampling programs are logistically difficult. Because of the recent development of MTE, little research has been conducted to establish its generality, or its applicability to deep-

sea ecology. Metabolic rates of deep-sea organisms are temperature and size dependent, but selective pressures depending on habitat and life styles may lead to some additional variation (Childress et al. 1980; Childress 1995).

Conclusions and a Future Agenda for Research in Deep-Sea Macroecology

The study of macroecological patterns in the deep sea has changed our perception of this remote, enormous, and complex ecosystem and helped to identify many of the ecological and evolutionary processes that might be important in regulating these communities. Several broad-scale patterns have emerged that provide the basic framework for exploring deep-sea ecosystems. Biomass, density, and body size all decrease with depth, presumably reflecting the exponential decline in carbon flux from surface production. Species diversity (or richness) typically peaks at intermediate depths and might also be related to energy flux, but not in a simple monotonic way. The consensus so far is that several interdependent processes that change in magnitude and vary in relative importance across various environmental gradients regulate diversity (Levin et al. 2001). One of the most intriguing hypotheses recently advanced to explain depressed abyssal diversity integrates a number of macroecological, life history, and natural history patterns to suggest that the low diversity at abyssal depths occurs because the abyssal zone acts as a sink habitat (*sensu* Pulliam 1988), relying on more productive bathyal regions as a source of larvae to sustain populations (Rex et al. 2005). If correct, this theory would explain lower diversity on the abyss.

As in other ecosystems, there appears to be a link between abundance, body size, and diversity that changes with spatial scale and energy availability. The relationships appear to be general but remain largely untested. Based on MTE (Brown et al. 2004), metabolic rates, governed by body size and temperature, and energy availability interact to regulate the basic time scales of biological processes, which in turn control population dynamics, rates of biotic interactions and the structure of communities. How applicable MTE is to life in the deep ocean is uncertain.

At global scales, species diversity locally and regionally declines poleward, paralleling similar patterns in shallow-water and terrestrial environments. Because the patterns are manifested at both local and regional scales, the gradient may reflect the evolutionary buildup of the regional species pools and the way in which these pools respond to ecological processes.

Although we have made significant progress, deep-sea macroecology is in its infancy and much remains to be done. The most pressing need is for

more samples, collected over a broader geographic range. Fundamental to any macroecological study is the distribution of individual species, which is poorly documented in the deep sea. New sampling programs should be based on existing knowledge and undertaken in a coordinated fashion at strategic locations to test specific hypotheses (e.g., abyssal source-sink), determine the generality of existing patterns, and expand our knowledge to other taxa, basins, and oceans. Most macroecological studies are based on a limited set of taxa, raising the possibility that observed patterns are not reflective of entire communities. This is especially true for broad-scale studies of species diversity because the patterns for a single taxon (or size category, e.g., macrofauna) may differ from the whole community due to tradeoffs among major taxonomic groups within local assemblages (Wilson 1998).

Most deep-sea research has focused on documenting geographic and bathymetric patterns and inferring mechanisms that might shape these patterns. The next phase of research needs to include an experimental component to test the role of these putative processes in shaping macroecological patterns and establish how those roles vary on large scales. It should also incorporate an evolutionary perspective because macroecological patterns may ultimately reflect evolutionary processes (Brown 1995; Gaston and Blackburn 2000; Brown et al. 2004). For example, recent population genetic (Cardillo 1999; Martin and McKay 2004; Williams and Reid 2004; Xiang et al. 2004) and paleontological (Jablonski 1993; Buzas, Collins, and Culver 2002) evidence suggests that differences in evolutionary rates might be a key factor in generating latitudinal gradients in diversity. Similarly, bathymetric gradients in diversity may reflect differences in the potential for evolution at different depths (Etter and Rex 1990; Rex et al. 2005; Etter et al. 2005). Recent advances in molecular genetics (Chase et al. 1998) make it possible to identify where and how evolution has unfolded in the deep sea, which should allow us to test the role of historical processes. To ultimately understand the origin and maintenance of macroecological patterns, we will need to quantify and critically test the influence of processes operating at a variety of different spatial and temporal scales.

APPENDIX A

Yoldiella frigida (503–808 m, 609 m), *Yoldiella lucida* (503–808 m, 609 m), *Ennucula bushae* (530 m, 1,006–2,430 m), *Ennucula granulosa* (530–2,178 m, 1,336 m), *Ledella pustulosa* (—, 609–4,632 m), *Yoldiella curta* (808–2,178 m, 1,500–4,190 m), *Ennucula similis* (808–2,044 m, —), *Neilonella salicensis* (1,102–3,834 m, 1,500–2,494 m), *Deminucula atacellana* (1,102–3,900 m, 1,500–2,890 m), *Yoldia inconspicua* (1,102–4,400 m, 1,739–4,632 m), *Ledella solidula* (1,144 m, —), *Yoldiella enata* (1,144 m, —), *Phaseolus* sp. (1,144–2,196 m, —), *Malletia johnsoni* (1,144–3,834 m,

1,739–2,777 m), *Ledella similis* (—, 1,336 m), *Ledella acuminata* (—, 1,336–2,503 m), *Nuculana commutata* (—, 1,336 m), *Yoldiella obesa* (1,383–2,886 m, 2,091–4,466 m), *Yoldiella lata* (—, 1,500–2,503 m), *Microgloma turnerae* (—, 1,739–1,922 m), *Tindaria hessleri* (—, 1,739 m), *Bathyspinula filatovae* (—, 1,739 m), *Portlandia lenticulata* (—, 1,739–2,430 m), *Yoldiella insculpta* (—, 1,922–2,430 m), *Bathyspinula subexisa* (—, 1,993 m), *Yoldiella fibula* (2,496–4,825 m, 1,993–4,734 m), *Ledella sublevis* (2,022–4,680 m, 2,209–4,632 m), *Pristogloia nitens* (2,022–4,853 m, 2,209–2,430 m), *Pristogloia alba* (2,178–4,833 m, —), *Brevinucula verrilli* (2,196–4,749 m, 2,890–4,632 m), *Bathyspinula hilleri* (—, 2,209–3,358 m), *Ledella bushae* (—, 2,379 m), *Yoldiella veletta* (—, 2,430 m), *Portlandica minuta* (—, 2,494 m), *Lametia abyssorum* (2,496–3,834 m, —), *Portlandica fora* (—, 2,503 m), *Yoldiella biscayensis* (—, 2,777–4,734 m), *Neilonella whoii* (2,862–4,970 m, 3,250–4,734 m), *Yoldiella jeffreysi* (2,862–4,862 m, 2,091–4,734 m), *Yoldiella ella* (2,862–4,400 m, 3,358–4,734 m), *Malletia cuneata* (2,864–4,749 m, 2,209–4,734 m), *Malletia abyssorum* (2,864–5,042 m, 3,250–4,734 m), *Silicula fragilis* (2,886–3,834 m, 1,922 m), *Ledella ultima* (3,806–5,042 m, 3,358–4,734 m), *Tindaria callistiformis* (3,806–5,042 m, —), *Silicula filatovae* (3,828–5,042 m, —), *Ledella aberrata* (3,834 m, 4,240–4,734 m), *Yoldiella americana* (3,834–5,042 m, —), *Malletia polita* (3,834–5,007 m, 4,550–4,734 m), *Yoldiella subcircularis* (3,900–5,042 m, 3,250–4,734 m), *Ledella* sp. (4,800–5,000 m, —), *Spinula* sp. (4,800–5,000 m, —), *Silicula mcalisteri* (5,000 m, —), *Yoldiella similiris* (5,000 m, —), *Tindariopsis* sp. (—, 4,734 m), *Ledella galathea* (—, 4,734 m).

APPENDIX B

Meiofaunal data from Aller et al. 2002 (NW Atlantic), Alongi and Pichon 1988 (SW Pacific), Alongi 1992 (SW Pacific), Ansari, Paurlekar, and Jagtap 1980 (Arabian Sea), Coull et al. 1977 (NW Atlantic), Danovaro et al. 1995 (Mediterranean), Danovaro et al. 2000 (Mediterranean), Danovaro, Gambi, and Della Croce 2002 (SE Pacific), DeBov e, Guidi, and Soyer 1990 (Mediterranean), Dinet and Vivier 1977 (NE Atlantic), Dinet 1973 (SE Atlantic), Dinet 1974 in Soltwedel 2000 (Norwegian Sea), Dinet 1976 (Mediterranean), Dinet in Vincx et al. 1994 (Tropical E Atlantic), Duineveld et al. 1997 (Tropical W Indian), Escobar et al. 1997 (Gulf of Mexico), Fabiano and Danovaro 1999 (Antarctic), Ferrero in Vincx et al. 1994 (NE Atlantic), Flach, Muthumbi, and Heip 2002 (NE Atlantic), Gage 1977 (NE Atlantic), Gage 1979 (NE Atlantic), Gal eron et al. 2000 (Tropical E Atlantic), Gal eron et al. 2001 (NE Atlantic), Gooday in Vincx et al. 1994 (NE Atlantic), Heip et al. 2001 (NE Atlantic), Herman and Dahms 1992 (Antarctic), Kamenskaya and Galtsova 1996 (NE Atlantic), Khrpounoff, Desbruy eres, and Chardy 1980 (Tropical W Atlantic), Kr oncke et al. 2000 (Arctic), Lamshead and Ferrero in Vincx et al. 1994 (NE Atlantic), Levin and Thomas 1989 (Tropical Central Pacific), Levin, Huggett, and Wishner 1991 (Tropical E Pacific), Parekular et al. 1983 in Soltwedel 2000 (Antarctic), Pequegnat, Gallaway, and Pequegnat 1990 (Gulf of Mexico), Pfannkuche and Thiel 1987 (Arctic), Pfannkuche, Theeg, and Thiel 1983 (NE Atlantic), Pfannkuche et al. 1990 in Vincx et al. 1994 (NE Atlantic), Pfannkuche 1985 (NE Atlantic), Rachor 1975 (NE Atlantic), Relexans et al. 1996 (Tropical E Atlantic), Romano and Dinet 1981 in Soltwedel 2000 (Arabian Sea), Rutgers van der Loeff and Lavaleye 1986 (NE Atlantic), Shirayama and Kojima 1994 (NW Pacific), Shirayama 1983 (Tropical W and NW Pacific), Sibuet et al. 1984 (Tropical W Atlantic), Sibuet et al. 1989 (NE, Tropical, SE Atlantic), Snider, Burnett, and Hessler 1984 (Central N Pacific), Soetaert, Heip, and Vincx 1991 (Mediterranean), Soltwedel and Thiel 1995 (Tropical E Atlantic), Soltwedel, Mokievsky, and Schewe 2000 (Arctic), Soltwedel 1997 (Tropical E Atlantic), Sommer and Pfannkuche 2000 (Arabian Sea), Tahey et al. 1994 (Mediterranean), Thiel 1966, 1975 (Tropical W. Indian), Thiel 1975 (Nor-

wegian Sea, NE Atlantic), Thiel 1979 (Red Sea), Thiel 1982 (NE Atlantic), Thistle, Yingst, and Fauchald 1985 (NW Atlantic), Tietjen 1971 (NW Atlantic), Vanaverbeke et al. 1997 (NE Atlantic), Vanhove et al. 1995 (Antarctic), Vanreusel and Vincx in Vincx et al. 1994 (NE Atlantic), Vanreusel et al. 1992 (NE Atlantic), Vanreusel et al. 1995 (NE Atlantic), Vivier 1978 (Mediterranean), Wigley and McIntyre 1964 (NW Atlantic).

Macrofauna data from Aller, Aller, and Green 2002 (NW Atlantic), Alongi 1992 (SW Pacific), Blake and Grassle 1994 (NW Atlantic), Blake and Hilbig 1994 (NW Atlantic), Carey and Ruff 1974 in Rowe 1983 (Arctic), Carey, Jr. 1981 (NE Pacific), Clough et al. 1997 in Rowe 1983 (Arctic), Cosson, Sibuet, and Galeron 1997 (Tropical E Atlantic), Dahl et al. 1976 (Norwegian Sea), Daule, Herman, and Heip 1998 (North Sea), Desbruyères, Bervas, and Kripounoff 1980 (NE Atlantic), Duineveld et al. 2000 (Mediterranean), Spiess et al. 1987 (Tropical E Pacific), Flach and Heip 1996 (NE Atlantic), Flach, Muthumbi, and Heip 2002 (NE Atlantic), Frankenberg and Menzies 1968 (Tropical E Pacific), Gage 1977 (NE Atlantic), Gage 1979 (NE Atlantic), Galéron et al. 2000 (Tropical E Atlantic), Galéron et al. 2001 (NE Atlantic), Grassle and Morse-Porteous 1987 (NW Atlantic), Grassle 1977 (NW Atlantic), Griggs, Carey, and Kulm 1969 (NE Pacific), Hecker and Paul 1979 (Tropical E Pacific), Hessler and Jumars 1974 (Central N Pacific), Houston and Haedrich 1984 (NW Atlantic), Hyland et al. 1991 (NE Pacific), Jazdzewski et al. 1986 (Antarctic), Jumars and Hessler 1976 (Central N Pacific), Kripounoff, Desbruyères, and Chardy 1980 (Tropical W Atlantic), Kröncke 1998 (Arctic), Kröncke, Türkay, and Fiege 2003 (Mediterranean), Kröncke et al. 2000 (Arctic), Laubier and Sibuet 1979 (NE Atlantic), Levin and Thomas 1989 (Tropical Central Pacific), Levin, Huggett, and Wishner 1991 (Tropical E Pacific), Levin et al. 2000 (Arabian Sea), Maciolek and Grassle 1987 (NW Atlantic), Maciolek et al. 1987a, 1987b (NW Atlantic), Nichols and Rowe 1977 (Tropical E Atlantic), Pfannkuche, Theeg, and Thiel 1983 (NE Atlantic), Rhoads et al. 1985 (NW Pacific), Richardson et al. 1985 (Caribbean), Richardson et al. 1995 (Tropical W Atlantic), Romero-Wetzel and Gerlach 1991 (Norwegian Sea), Rowe and Menzel 1971 (Gulf of Mexico), Rowe 1971 (Tropical E Pacific), Rowe et al. 1982 (NW Atlantic), Rowe et al. 1975 (NW Atlantic), Rowe et al. 1974 (NW Atlantic, Gulf of Mexico), Sanders 1969 (SE Atlantic), Sanders et al. 1965 (NW Atlantic), Schaff et al. 1992 (NW Atlantic), Shirayama 1983 (Tropical W and NW Pacific), Sibuet et al. 1984 (Tropical W Atlantic), Sibuet et al. 1989 (NE, Tropical, SE Atlantic), Smith 1978 (NW Atlantic), Smith 1987 (Central N Pacific), Tselepidis and Eleftheriou 1992 (Mediterranean), Tselepidis et al. 2000 (Mediterranean), Witte 2000 (Arabian Sea).

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