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A Source-Sink Hypothesis for Abyssal Biodiversity

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ABSTRACT: Bathymetric gradients of biodiversity in the deep-sea benthos constitute a major class of large-scale biogeographic phenomena. They are typically portrayed and interpreted as variation in α diversity (the number of species recovered in individual samples) along depth transects. Here, we examine the depth ranges of deep-sea gastropods and bivalves in the eastern and western North Atlantic. This approach shows that the abyssal molluscan fauna largely represents deeper range extensions for a subset of bathyal species. Most abyssal species have larval dispersal, and adults live at densities that appear to be too low for successful reproduction. These patterns suggest a new explanation for abyssal biodiversity. For many species, bathyal and abyssal populations may form a source-sink system in which abyssal populations are regulated by a balance between chronic extinction arising from vulnerabilities to Allee effects and immigration from bathyal sources. An increased significance of source-sink dynamics with depth may be driven by the exponential decrease in

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organic carbon flux to the benthos with increasing depth and distance from productive coastal systems. The abyss, which is the largest marine benthic environment, may afford more limited ecological and evolutionary opportunity than the bathyal zone.

Keywords: deep sea, benthos, bathymetric gradients of species diversity, source-sink dynamics, Allee effects.

Bathymetric gradients of species diversity are the most well-documented biogeographic patterns in the deep-sea soft-sediment ecosystem. They have been attributed to a wide range of ecological influences that vary with depth, including environmental stability (Sanders 1968), food availability and biotic interactions (Rex 1981), sediment grain-size heterogeneity (Etter and Grassle 1992), metapopulation dynamics and dispersal (Etter and Caswell 1994), boundary constraints (Pineda and Caswell 1998), topography (Vetter and Dayton 1998), hydrodynamics (Gage 1997), bottom-water oxygen concentration (Levin and Gage 1998), and gravity-driven sediment failure (Levin et al. 1994). While diversity-depth trends remain incompletely understood, it seems likely that they are shaped by a complex of interacting factors that operate at different scales of time and space (Levin et al. 2001; Stuart et al. 2003).

Knowledge of bathymetric gradients of diversity is largely based on studies of α diversity conducted in the bathyal zone, which descends from the shelf-slope break ($\sim$200 m) to $\sim$4,000 m and extends as a narrow ribbon along continental margins. Seaward of the continental margins ($>$4,000 m) lie the great abyssal plains that form the floor of the world ocean. The abyss, covering 53% of the seabed globally (Menard and Smith 1966), is the largest and most recently explored marine benthic habitat. The transition from the bathyal to the abyssal environment is a very gradual slope with no obvious barriers or abrupt habitat shifts. However, it parallels the strongest biological gradient in the deep sea, the exponential decrease of standing stock as depth and distance from land increase. This decline in standing stock is caused by the decrease in organic carbon flux to the benthos from overhead produc-

tion, terrestrial runoff, and offshore transport (Rowe and Pariente 1992).

Standing stock of the macrofaunal community decreases two to three orders of magnitude from the upper bathyal region, where density reaches tens of thousands of individuals per square meter and biomass is tens of grams per square meter, to extremely low levels of tens to hundreds of individuals per square meter and <1 g m^{-2} in the abyss (Rowe 1983). The trend of decreasing standing stock with depth and distance from productive coastal systems appears to be quite general, with predictable regional variation associated with the level of surface production, current patterns, bottom topography, and oxygen minimum zones (Levin et al. 2001). The pronounced gradient of nutrient input and standing stock has vital implications for the development of biodiversity in the deep-sea benthos, particularly at tremendous depths where populations of individual species are very sparsely distributed (Rex 1981; Etter and Rex 1990; McClain et al. 2004). In the North Atlantic, where depth-correlated patterns of diversity are especially well documented, α diversity of the macrofauna decreases from the bathyal zone to the abyss (Rex 1981; Cosson-Sarradin et al. 1998). Abyssal communities also appear to have truncated trophic structures characterized by an increased dominance of deposit feeders and fewer predators compared with bathyal communities (Rex 1976, 1981). The simplest explanation for depressed abyssal diversity is that severe energy constraints at these depths prevent many species from attaining the critical densities required to sustain reproductively viable populations (Rex 1973). In other words, for many species, the abyss may be a marginal environment where they experience chronic extinction arising from vulnerabilities to Allee effects (Courchamp et al. 1999).

In this article, we present the largest database ever compiled on depth ranges of gastropod and bivalved mollusks across bathyal and abyssal zones of the eastern and western North Atlantic. Assessing diversity as the number of coexisting ranges confirms that abyssal diversity is depressed on regional as well as local scales. The depth distributions, along with information on abundance and larval development, also reveal something surprising. The abyssal fauna mainly represents sparsely occupied range extensions for a subset of bathyal species with high dispersal ability. This pattern suggests a modified explanation for abyssal biodiversity. We hypothesize that the continental margin and abyss constitute a source-sink system (Holt 1985; Pulliam 1988) in which many abyssal populations are maintained by immigration from the bathyal zone. We do not propose that the bathyal zone and abyss are distinct environments or that source-sink dynamics account entirely for abyssal biodiversity. However, the evidence presented here suggests that a balance between local extinction

from inverse density dependence at low density and immigration from bathyal populations becomes progressively more important in regulating abyssal diversity with increased depth and distance to land. We also describe how the source-sink hypothesis can be tested further with existing archived collections of deep-sea organisms by documenting biogeographic ranges, gradients of standing stock, reproductive patterns, and genetic population structure. If source-sink dynamics do play a major role in community assembly on such enormous spatial scales, this would fundamentally change our understanding of deep-sea biodiversity.

Population Density

We assume that the primary force driving an increase in the significance of source-sink dynamics in the abyss is the decrease in organic carbon flux to the benthos with increased depth and distance from productive coastal systems. This decline in nutrient input causes the well-known exponential decrease in macrofaunal standing stock (Gage and Tyler 1991). The deep-sea macrofaunal community as a whole in the western North Atlantic shows a decrease in abundance with both depth (fig. 1A) and distance from land (fig. 1B). Abundance in the abyss is two to three orders of magnitude lower than on the continental margin. Standing stock is typically plotted against depth in deep-sea studies. The relationship of abundance to distance from land (fig. 1B) shows the dramatic difference between the continental margin and the abyssal plain and is more relevant to our discussion of dispersal potential presented later. While the fauna of the eastern North Atlantic has not been sampled as intensively, the existing data suggest a very similar pattern (Flach and Heip 1996). As mentioned above, the 4,000 m isobath indicated in figure 1, while traditionally used to demarcate the foot of the more steeply descending continental margin and the beginning of the abyssal plain, is neither a biogeographic boundary nor ecotone. It is a conservative estimate of where the exponentially decreasing standing stock of the bathyal zone reaches low levels and begins to decline much more slowly across the abyssal plain. For convenience, throughout the article, we use the terms "bathyal" and "abyssal" as source and sink habitats, respectively. We are referring to the gradual transition occurring at around 4,000 m in depth and 300 km from land, where standing stock becomes consistently low (fig. 1). Abundance continues to decrease significantly seaward across the abyssal plain ($r^2 = 0.313$, $P < .05$) and reaches very low levels (38–149 individuals m^{-2}) beyond 600 km from land.

Population densities for abyssal mollusks are extremely low. In the western North Atlantic, where detailed data for each taxon are available, abyssal gastropod and bivalve
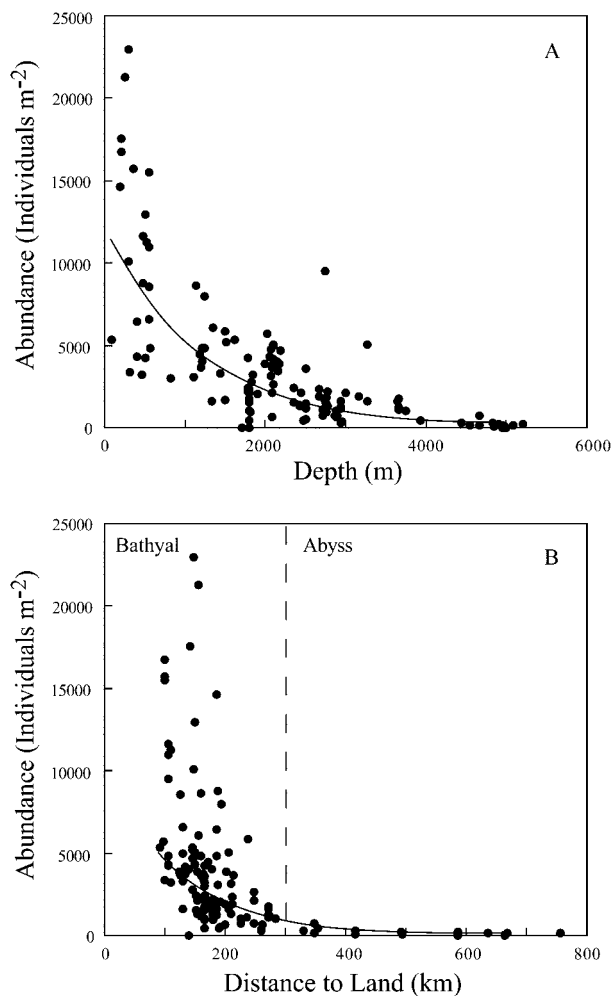
Figure 1: Relationships of macrofaunal abundance to depth (*A*) and distance from land (*B*) in the western North Atlantic. Bathyal and abyssal environments are distinguished by the vertical dashed line in the plot of abundance versus distance from land. Abundance data are from Sanders et al. (1965), Rowe et al. (1974, 1982), Smith (1978), and Maciolek et al. (1987*a*, 1987*b*). Regression equations are $Y = 10{,}373e^{-0.0081X}$, $R^2 = 0.27$, and $Y = 12{,}296e^{-0.00084X}$, $R^2 = 0.62$, respectively.

abundances are 0.73 individuals m^{-2} and 5.0 individuals m^{-2}, respectively (Sanders et al. 1965). Estimates from the abyssal central North Pacific are similar: 0.4 and 8.0 individuals m^{-2}, respectively (Hessler and Jumars 1974). Bathyal densities are one to three orders of magnitude higher (Sanders et al. 1965). We estimated species' densities by comparing the relative abundances of species in large abyssal samples collected with qualitative epibenthic sleds (Rex and Warén 1982; Allen and Sanders 1996) with quantitative density estimates for gastropods and bivalves as whole taxonomic classes (Sanders et al. 1965). This indirect approach is necessary because smaller quantitative samples

taken at abyssal depths do not yield a sufficient number of specimens to ascertain relative abundances. Abyssal assemblages of both taxa are heavily dominated by a single species. *Ledella ultima* comprises 60% of bivalve individuals and *Benthonella tenella* 66% of gastropods. Most other abyssal species are rare. Bathyal relative abundance distributions are much more equitable (Rex 1973, 1981). For bivalves, the 11 largest epibenthic sled samples ($N > 100$) taken at abyssal depths yielded 17 species and 6,502 individuals. Relative abundance estimates indicate that three species live at average densities of 1–3 individuals m^{-2}, one species at 1 individual 10 m^{-2}, 10 species at 1–5 individuals 100 m^{-2}, and three species at 2 individuals 1,000 m^{-2}. For gastropods (20 species among 833 individuals from six abyssal samples of $N > 100$; Rex and Warén 1982), the density estimates are even lower: one species at 1 individual m^{-2}, two at 1 individual 10 m^{-2}, six at 1–2 individuals 100 m^{-2}, and 11 at 1–5 individuals 1,000 m^{-2}. With few exceptions (the bivalve *Microgloma*), sexes are separate in these deep-sea mollusks. Populations tend to show low fecundity, continuous reproduction, and low recruitment rates (Rex et al. 1979; Zardus 2002). It is possible that low-density populations could be reproductively viable if individuals lived long enough to encounter members of the opposite sex for mating. Longevity of deep-sea gastropods is unknown; protobranchs now appear to live only on the order of a decade (Gage 1994), much less than earlier estimates of a century (Turekian et al. 1975). It is improbable that populations of minute gonochoristic organisms with low gamete production, low adult mobility, and modest life spans could be reproductively self-sustainable at the extremely low densities found in many species.

Bathymetric Ranges

We present data on the bathymetric ranges of two important macrofaunal taxa, gastropod (Caenogastropoda and Vetigastropoda) and protobranch bivalved mollusks, in the eastern and western North Atlantic. This approach allows us to determine changes in both α diversity (the number of coexisting ranges) and species composition (β diversity) along depth gradients. Representing 300 species, this is the largest and most geographically comprehensive database to have been analyzed for depth distributions in deep-sea invertebrates.

It is useful to compare the diversity patterns of gastropods and bivalves because they have different ecological characteristics. Gastropods show high species diversity (Rex 1981) and low abundance (Rex et al. 1990). They constitute a trophically complex group of predators and deposit feeders (Rex 1976). By contrast, protobranch bivalves exhibit relatively low diversity and high abundance

and are exclusively deposit feeders (Allen and Sanders 1996). The taxonomy of both taxa is well established (Bouchet and Warén 1980, 1985; Allen and Sanders 1996).

The distribution of species ranges (figs. 2–5) shows that the abyssal (>4,000 m) molluscan fauna not only exhibits depressed α diversity but also is essentially an attenuation of the lower bathyal fauna. Figure 2 shows depth ranges of gastropods (Rex and Warén 1982) collected along a depth transect south of New England by the Woods Hole Oceanographic Institution's (WHOI) Benthic Sampling Program (Sanders 1977). Of the 22 abyssal species, 16 represent deeper range extensions for bathyal species composed of populations living at very low densities. Data on depth ranges in the eastern North Atlantic (fig. 3) come from a comprehensive systematic revision of deep-sea neogastropods collected over a much larger geographic area, east of the Mid-Atlantic Ridge from the Azores to the Norwegian Sea (Bouchet and Warén 1980, 1985). All but three of the 32 abyssal species are range extensions from the bathyal zone. Protobranch bivalves collected from WHOI Benthic Sampling Program transects south of New England and in the West European Basin show a similar pattern (figs. 4, 5). Of 21 abyssal species in the western North Atlantic, 17 are range extensions of the bathyal fauna, and of 20 abyssal species in the eastern North Atlantic, 15 are range extensions.

In all four cases presented (figs. 2–5), the abyssal zone does contain several unique species not found at bathyal depths. For both protobranch bivalve analyses, and for gastropods in the western North Atlantic, these unique species may not be true abyssal endemics; rather, they could be species encountered by chance only in the abyss along what is essentially a transect of samples taken along a depth gradient. The largest and most geographically inclusive study, of neogastropods in the eastern North Atlantic (fig. 3), shows the smallest proportion of unique abyssal species, 9% compared with 19%–27% in the other cases, suggesting that unique abyssal species in figures 2, 4, and 5 may have bathyal distributions in neighboring regions of the continental margins that are simply not detected in the more geographically restricted transect studies.

The level of apparent abyssal endemism is sensitive to where the bathyal-abyssal boundary is placed. If moved shallower from 4,000 to 3,500 m, there is virtually no difference ($\leq$1%) for the eastern faunas, but the proportion of endemics in western faunas actually doubles. This increase may represent sampling bias to some extent and also probably reflects the higher rate of zonation at bathyal depths (Rex 1977). The extreme lower bathyal samples at ~3,800 m, while only 200 m shallower than 4,000 m, are 200–400 km closer to the coast and nearer highly productive surface waters than abyssal samples in this study.

However, the hypothesis proposed here predicts that source-sink dynamics become more important at deeper rather than shallower depths. If the bathyal-abyssal transition is moved to 4,500 m, there is little change in the proportion of endemics for the three transect studies ($\leq$2% in figs. 2, 4, 5). In the most comprehensive survey, of neogastropods in the eastern North Atlantic (fig. 3), abyssal endemism drops from 9% to 0.

It is interesting that when the number of coexisting ranges is summed for successive 1,000 m depth intervals (figs. 2–5), species diversity in all four groups peaks at bathyal depths and is lower in the abyss—a pattern shown earlier by calculating α diversity for individual samples arrayed along depth gradients (Rex 1981). This unimodal diversity-depth pattern seems very robust in terms of its general shape and is scale invariant with respect to the area of seafloor sampled by different types of gear ranging from small precision 0.25 m^2 box corers (Etter and Grassle 1992) to large trawls towed for kilometers (Rex 1981).

Larval Dispersal

Source-sink dynamics require dispersal, which in most benthic marine invertebrates occurs through pelagic larvae. Protobranch bivalves have a demersal swimming lecithotrophic pericalymma larva (Zardus 2002). Deep-sea gastropod species can have either planktotrophic or nonplanktotrophic development (Bouchet and Warén 1994). Planktotrophic development occurs in some caenogastropods through a swimming feeding larva. Nonplanktotrophic development can take two forms: larvae can develop lecithotrophically in an egg capsule with little or no dispersal phase in caenogastropods or as a lecithotrophic swimming demersal larva in vetigastropods. As a generality, among deep-sea taxa, caenogastropods with planktotrophic development (*Planktotrophic C* in figs. 2, 3) and vetigastropods (*Nonplanktotrophic V* in fig. 2) have greater larval dispersal ability than do caenogastropods with nonplanktotrophic development (*Nonplanktotrophic C* in figs. 2, 3).

In both eastern and western North Atlantic gastropod faunas, the proportions of species with dispersing larvae increase with depth (Potter and Rex 1992), as is readily apparent in figures 2 and 3. In the western North Atlantic, 91% (20 out of 22) of abyssal species have either planktotrophic or lecithotrophic dispersing larvae. In the eastern North Atlantic, 78% (21 out of 27) of abyssal species for which the mode of larval development is known have planktotrophic development. Species with dispersing larvae are more well represented in the abyss than in the bathyal zone ($\chi^2 = 4.307$, $P < .038$ and $\chi^2 = 8.570$, $P < .0034$ for western and eastern North Atlantic faunas, respectively). All protobranch bivalves, including those with
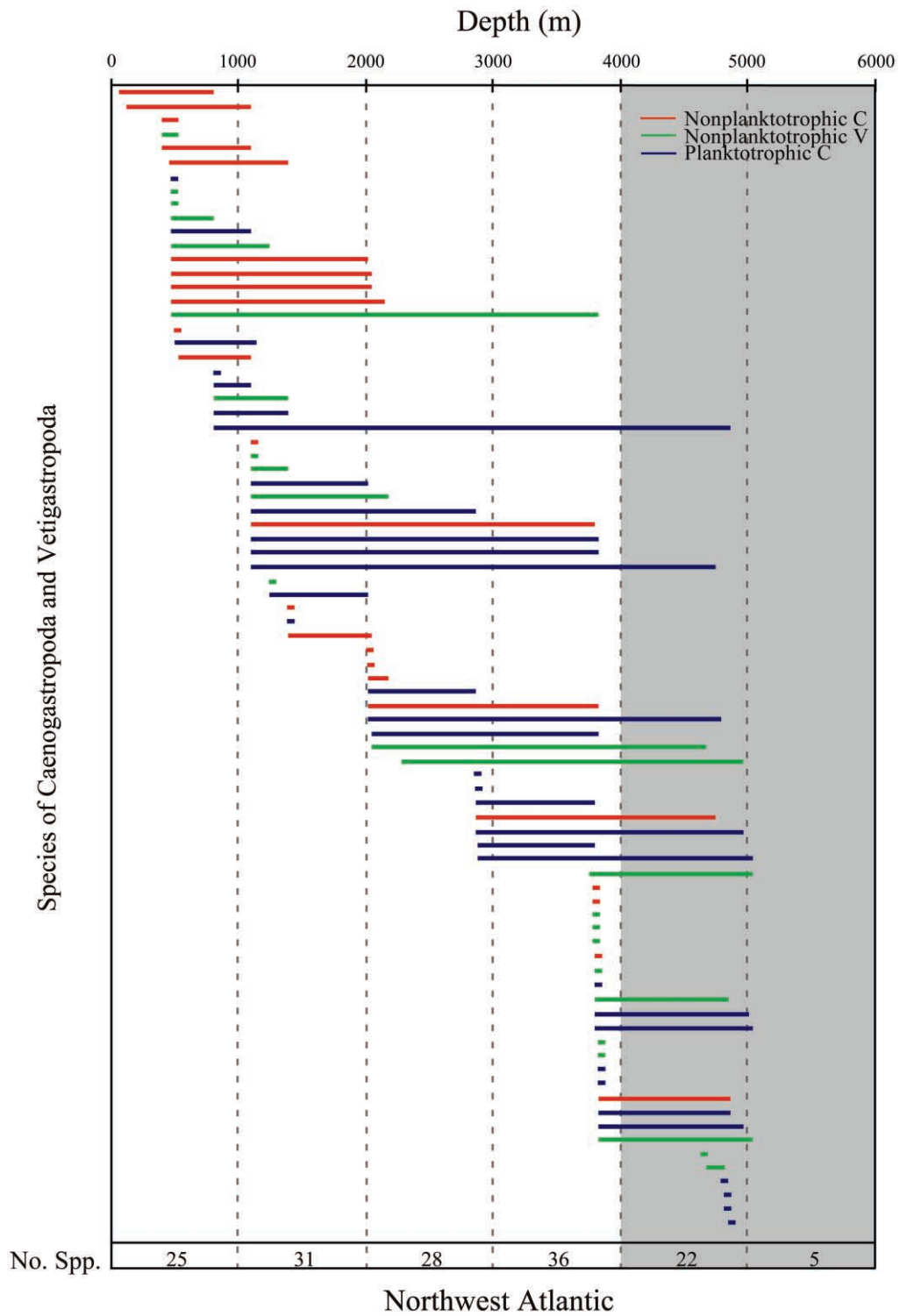
Figure 2: Bathymetric ranges and modes of larval development for deep-sea prosobranch gastropods collected south of New England in the western North Atlantic. The depth region of the abyssal plain is shaded. Data are from Rex and Warén (1982) with updated species names and locality records. Ectoparasitic forms are excluded because of their equivocal phylogenetic status and uncertainty about mode of development (Stuart and Rex 1994). The number of species (*No. Spp.*, bottom) represents the number of coexisting ranges in 1,000 m depth intervals. Species names and depth ranges are provided in the online edition of the *American Naturalist*.

Figure 3: Bathymetric ranges and modes of larval development for deep-sea neogastropods in the eastern North Atlantic. The depth region of the abyssal plain is shaded. Data are from Bouchet and Warén (1980, 1985). The number of species (*No. Spp.*, bottom) represents the number of coexisting ranges in 1,000 m depth intervals. Species names and depth ranges are provided in the online edition of the *American Naturalist*.

168
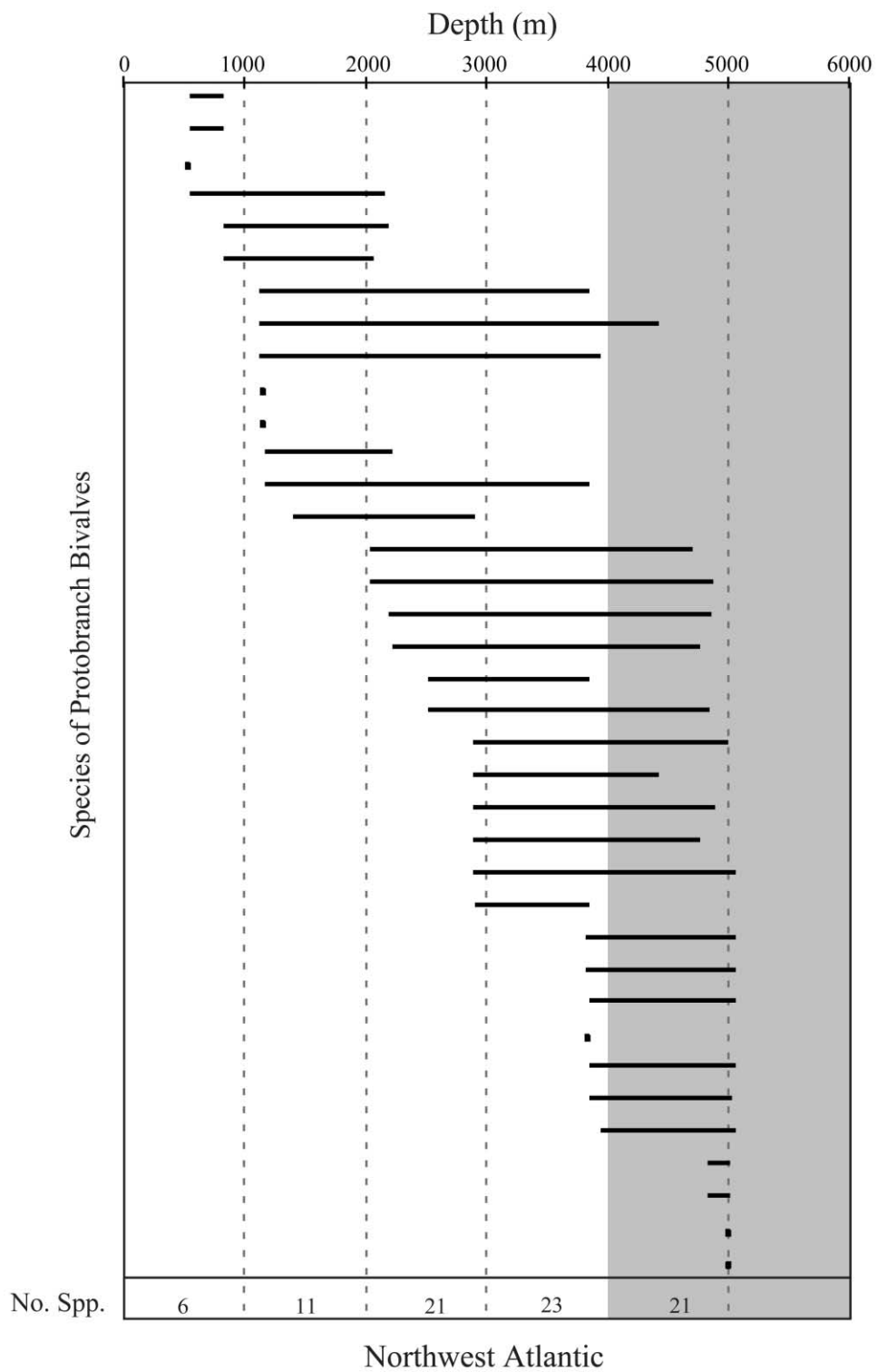
Figure 4: Bathymetric ranges for deep-sea protobranch bivalves collected in the western North Atlantic. The depth region for the abyssal plain is shaded. Data are from Allen and Sanders (1996). The number of species (*No. Spp.*, bottom) represents the number of coexisting ranges in 1,000 m depth intervals. Species and depth ranges are provided in the online edition of the *American Naturalist.*

169

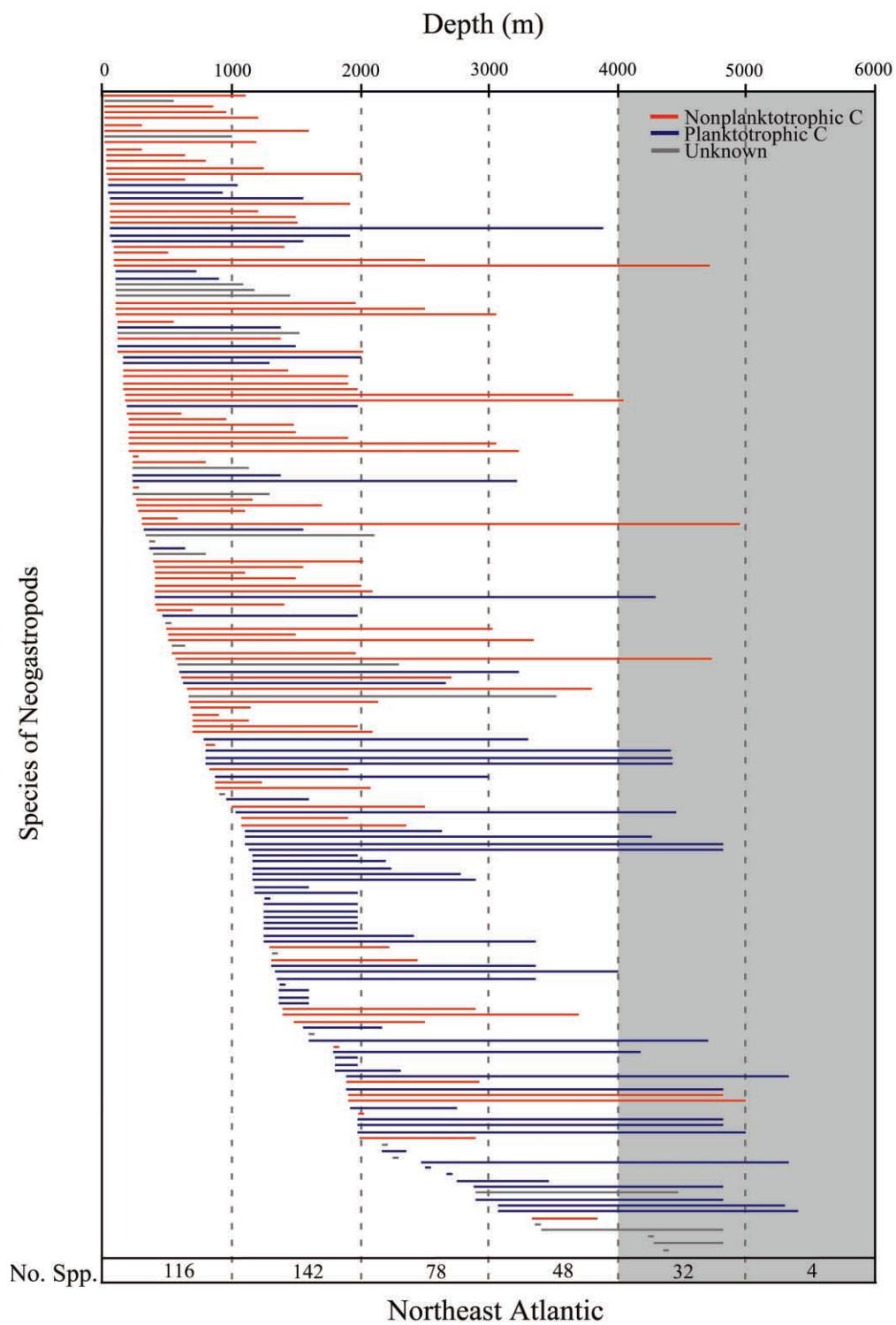**Figure 5:** Bathymetric ranges for deep-sea protobranch bivalves collected in the eastern North Atlantic. The depth region for the abyssal plain is shaded. Data are from Allen and Sanders (1996). The number of species (*No. Spp.*, bottom) represents the number of coexisting ranges in 1,000 m depth intervals. Species names and depth ranges are provided in the online edition of the *American Naturalist*.
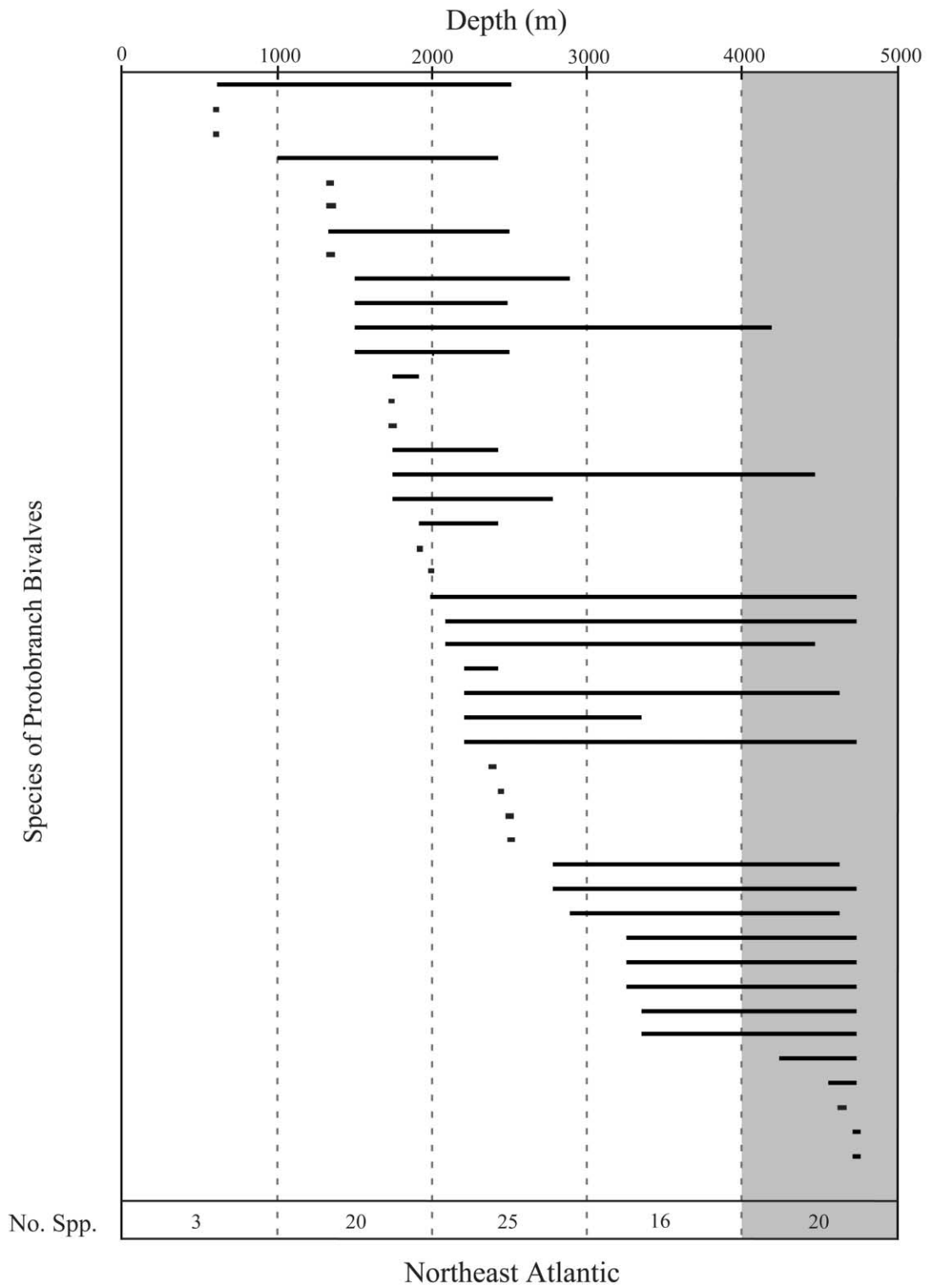
abyssal distributions, have dispersing larvae. The overwhelming majority of abyssal molluscan species in the North Atlantic are capable of maintaining an abyssal presence by larval migration from bathyal sources.

While there is now general agreement that many deep-sea macrofaunal groups, including mollusks, have much greater dispersal ability than earlier supposed (Young 2003), the actual dispersal routes remain virtually unknown. How do larvae of bathyal species reach the abyss? It is impossible to be specific about larval trajectories in the deep sea, but we can at least discuss the plausibility of bathyal to abyssal dispersal.

We assume that the larvae are passive dispersers in ocean currents. For planktotrophic larvae with ontogenetic vertical migration in the water column, such as some caenogastropods (Bouchet and Warén 1994; figs. 2, 3), larvae are dispersed in strong surface currents and could traverse the distance between the continental margin and abyssal plain just as coastal species do (e.g., Scheltema 1989). Less obvious is how the nonplanktotrophic larvae of protobranchs and vetigastropods disperse over these distances in near-bottom currents, which typically are weaker than surface currents. It is also conceivable that planktotrophic larvae might have a demersal phase or even develop demersally while feeding in the benthic boundary layer. If demersal larvae had a dispersal period of 2 weeks, which seems reasonable for coastal snails with nonplanktotrophic pelagic development (e.g., Moran, 1997), and if we assume a steady near-bottom flow of 5–10 cm s^{-1} (e.g., Richardson et al. 1981), larvae could be transported ∼60–120 km. Clearly, this is not far enough. To reach even the most distant abyssal site in figure 1, larvae must travel 500–600 km, and far reaches of the abyssal plains lie thousands of kilometers from continental margins. The source-sink hypothesis explored here does not permit stepping-stone colonization across the abyss because rare abyssal populations are assumed to be nonreproductive.

However, demersal larvae may be able to disperse much farther in the deep ocean for two reasons. First, the near-freezing temperatures of the deep sea may prolong development. Experimental studies of Antarctic echinoderms show that larvae can survive for 6 months at −1° C without feeding and probably much longer if even very low concentrations of dissolved organic material are available for absorption (Hoegh-Guldberg et al. 1991; Shilling and Manahan 1991; Welborn and Manahan 1991). If deep-sea mollusks have evolved similar low metabolic rates at low temperatures, then dispersal potential may be greatly increased. Nonplanktotrophic molluscan larvae are known to take up dissolved nutrients (Jaeckle and Manahan 1989). Second, dispersal is not limited by sluggish deep-sea currents. In the deep western North Atlantic, bottom currents are complex and intermittently quite strong. The

Western Boundary Undercurrent flows along the seafloor southwesterly between 1,500 and >5,000 m and has a high-velocity core between 4,400 and 5,200 m (Bulfinch et al. 1982). On its eastern margin, it collides with the north-flowing western margin of the anticyclonic Deep Gulf Stream Gyre (Worthington 1976; Gardner and Sullivan 1981). Throughout this region, which includes the lower bathyal and abyssal sampling sites analyzed here, near-bottom flows can reach speeds of 20–30 cm s^{-1} for periods of weeks (the highest recorded speed is 73 cm s^{-1}; Richardson et al. 1981). The currents vary in direction (Richardson et al. 1981) and are strong enough to resuspend bottom sediments. The resulting "benthic storms" appear to be caused by the high kinetic energy of the Gulf Stream and its eddies (Hollister and McCave 1984) and by atmospheric storms (Gardner and Sullivan 1981). The deep western North Atlantic is likely to be a region where mesoscale eddies are generated by the intersection of bottom currents and by Gulf Stream eddies impacting the seafloor. Mullineaux (1994) predicted that mesoscale flow features accumulate and retain larvae in the deep sea and advect them to distant habitats.

Periodic strong near-bottom currents and mesoscale flow dynamics make large-scale dispersal linking bathyal to abyssal populations much more plausible. If larvae could survive 6 months at frigid bottom temperatures, they could travel up to 1,500 km at 10 cm s^{-1}. If they were entrained in a mesoscale flow at 40 cm s^{-1} for just 2 weeks of this period, the distance would approach 2,000 km. If they absorb dissolved organic material and delay metamorphosis like some coastal gastropods (Scheltema 1989), the distances could be much farther. Current patterns in the deep eastern North Atlantic are less well known (Bower et al. 2002), but it is also a region of high kinetic energy with deep-reaching eddies and current speeds attaining 27–39 cm s^{-1} (Gage 1997). In more quiescent parts of the abyss, current speeds may be more like 2–4 cm s^{-1} (Gage 1997). Under these circumstances, larvae could potentially disperse 500 km in 6 months even without the aid of mesoscale flows or delayed metamorphosis.

A Source-Sink Hypothesis

Many theories have been advanced to explain patterns of α diversity in the deep-sea benthos. These include deterministic and stochastic models that invoke habitat heterogeneity, productivity, biological interactions, succession, and disturbance (reviewed by Etter and Mullineaux 2001; Levin et al. 2001; Snelgrove and Smith 2002; Stuart et al. 2003). While there is little direct evidence for any of these mechanisms, all may operate at different scales of time and space to structure bathyal communities where population growth and densities are high enough to permit

biological interactions to occur. However, it is difficult to imagine how such mechanisms might be effective at the extraordinarily low densities found at abyssal depths.

We propose that the bathyal-abyssal transition parallels a gradual change in how the deep-sea ecosystem functions. Abyssal molluscan faunas of the North Atlantic are composed mainly of range extensions for a subset of bathyal species. Populations forming these abyssal range extensions exist at very low abundance—levels that would seem to preclude successful reproduction. The vast majority of bathyal species that are represented in the abyss have larval dispersal. This combination of circumstances suggests the hypothesis that bathyal and abyssal zones of the deep sea constitute a source-sink system (Holt 1985; Pulliam 1988).

In relative terms, the bathyal component is characterized by higher species diversity and higher animal abundance. It displays consistent regular patterns of α and β diversity (Rex et al. 1997), and there is ample evidence of successful reproduction and recruitment in bathyal species (Gage and Tyler 1991; Young and Eckelbarger 1994). Bathyal communities are probably structured by the same set of environmental variables that regulate other marine communities (Levin et al. 2001). By contrast, the abyss may be an unfavorable environment where energy constraints severely limit population growth and reproductive potential in many species. Abyssal populations may experience chronic extinction from inverse density dependence at low density. Much of the abyssal fauna may represent a mass effect (Shmida and Wilson 1985) from bathyal sources, that is, a sink where reproductively unsustainable populations are maintained by immigration.

The concept of mass effects in the deep-sea fauna is not entirely new. Lemche (1948) suggested that bathyal populations of the coastal opisthobranch gastropod *Diaphana minuta* were nonreproducing and maintained by larval migration. Mileikovsky (1968) offered a similar explanation for bathyal populations of the continental shelf polychaete *Euphrosyne borealis*. Larvae of the upper bathyal ophiuroid *Ophiocten gracilis* settle at lower bathyal depths but have much lower survivorship and growth rates there (Gage and Tyler 1982). Juvenile echinoderms of the eastern North Atlantic often exhibit broader depth ranges than adults (Gage et al. 1983, 1985). Snelgrove and Smith (2002) suggested that source-sink dynamics might augment local diversity in the deep sea and even suggested that it could be particularly important in explaining downslope patterns of diversity. Bouchet and Taviani (1992) proposed that the impoverished molluscan fauna of the deep Mediterranean Sea might be composed of nonreproducing "pseudopopulations" maintained by larval immigration from the Atlantic over the Gibraltar Sill. Here we expand the concept and apply it on a larger scale as a potential explanation for abyssal biodiversity.

Qualifications and Tests of the Hypothesis

It is important to stress that while there is reasonably convincing evidence from mollusks in the North Atlantic, we advance the source-sink explanation of abyssal biodiversity as a hypothesis to be tested further. As we caution below, the biogeographic and life-history data on which the hypothesis is based—all of it originally collected for different purposes—are incomplete and contain numerous uncertainties. Nonetheless, the hypothesis seems plausible and is testable. If borne out, it has considerable explanatory power and could play an important role in directing future ecological research in the deep sea.

The most obvious potential problem with the supporting data for the source-sink hypothesis concerns the possibility of sampling error in estimating abyssal diversity and endemism. Abyssal populations live at very low density, and species diversity is sample-size dependent. Does the abyssal fauna appear to have lower diversity and endemism than the bathyal fauna simply because the abyss is undersampled? Several indirect lines of evidence suggest not. Comparisons of numerous individual bathyal and abyssal samples that are normalized to a common sample size show a clear decline in abyssal diversity (Rex 1981). A recent analysis that combines groups of lower bathyal and abyssal samples to make regional-scale comparisons at comparable large sample sizes also shows the abyssal fauna to be a much reduced subset of the bathyal assemblage (McClain et al. 2004). The depth ranges of gastropods in figure 2 are based on more abyssal samples (9) collected over a much larger area than for any other 1,000 m depth interval (2–4). Collections based on large qualitative samples suggest that the abyssal molluscan fauna shows high faunal similarity over large spatial scales (Rex 1977; Allen and Sanders 1996). To clearly determine whether there are fewer abyssal endemics and whether the faunas of bathyal and abyssal zones are adequately characterized, it would be necessary to quantitatively sample multiple sites in both habitats and establish that their species accumulation curves are asymptotic. Intensive quantitative sampling has been carried out at upper- to mid-bathyal depths in the western North Atlantic (Maciolek et al. 1987*a*, 1987*b*), but no comparable study has been conducted at lower bathyal and abyssal depths. If more extensive abyssal sampling reveals additional species, these species are apt be even rarer than those discovered so far. The critical question still remains: How could populations living at such extraordinarily low densities be reproductively viable?

It should be recognized in testing the hypothesis that the abyssal and bathyal zones are not discrete biogeographical entities. They represent a spatial continuum. The crucial underlying environmental gradient producing the

source-sink system is presumed to be the rate of nutrient input that decreases with depth and distance from land. However, the relationship between seafloor physiographic features and food availability can vary geographically with spatial and temporal variation in overhead production, carbon flux to the benthos, lateral advection, and down-slope transport. Tests of the source-sink hypothesis should focus on resource availability and biogeography rather than just topography alone. Also, source-sink phenomena are completely relative to particular species, adaptive properties, and habitat suitability. Not all species inhabiting both bathyal and abyssal zones experience these environments as a source-sink system. For example, the two most abundant mollusks in the abyssal western North Atlantic, the caenogastropod *Benthonella tenella* and the proto-branch *Ledella ultima*, are both known to produce mature gametes and to recruit (Rex et al. 1979; Allen and Hannah 1989). In *B. tenella*, the presence of sperm in the seminal receptacles of abyssal females clearly indicates that mating occurs. But these species are unusually abundant and ubiquitous, making up ≥60% of abyssal assemblages. They may form part of an established core of the abyssal fauna that does not rely on source-sink dynamics for its existence. For abyssal mollusks of the western North Atlantic, 76% of bivalve species and 75% of gastropod species are represented by 1% or less of individuals collected. We suggest that many of these rare abyssal species exist largely as a mass effect from bathyal sources. (By contrast, at lower bathyal sites, the relative abundances of the commonest species for protobranchs and gastropods are 27% and 23%, respectively; 64% and 58% of species had abundances of 1% or less, though densities of rare species are presumably higher; fig. 1.) Glover et al. (2001) found that abyssal polychaete assemblages of the northeastern Atlantic were also characterized by a core group of abundant widespread species and a large number of rare species that were unique to each site.

Even populations of rare abyssal species may not function exclusively as sinks. Periodic increases in food availability may allow population growth and permit temporary bidirectional dispersal between source and sink (Gonzalez and Holt 2002). If such environmental variation is auto-correlated, it can inflate population sizes in sinks promoting long-term persistence. This phenomenon may help explain the existence of an abyssal macrofauna in areas of the Pacific that are quite remote from continental margins (Hessler and Jumars 1974). The abyssal fauna of the Pacific experiences decadal-scale cycles of abundance related to long-term climate change (Smith and Kaufmann 1999) and shows elevated abundance >3,000 km from continental land masses under a narrow area of upwelling associated with the equatorial current (Smith et al. 1997; Glover et al. 2002). Similarly, several species of abyssal

eastern North Atlantic megafaunal holothurians appear to undergo decadal-scale fluctuations in abundance related to food supply and can reach high densities (Billett et al. 2001; Wigham et al. 2003). Abyssal sites where high-energy currents cause cycles of erosion and deposition can show elevated abundance but depressed species richness and evenness (Gage 1997), suggesting that they might act as sources for some species.

It is theoretically possible that periodic high immigration rates can lead to rapid adaptive evolution in sink populations through acquiring novel combinations of genes from source populations that confer higher fitness in a previously inimical environment (Holt et al. 2002). This form of selection might be one mechanism responsible for the origin of true abyssal endemics—that is, reproductively self-sustaining populations that have adapted to life in the abyss and do not require continued immigration for persistence.

A related scenario is that abyssal macrofaunal populations that are rare at some sampling sites may exist as part of a large-scale metapopulation if other abyssal sites support dense populations and dispersal among sites is sufficient for persistence. This would mean that abyssal populations were less reliant on bathyal sources or even independent of them. However, it is unclear what mechanism might create a patchwork of distinctive habitats that vary in their potential for population growth of macrofaunal elements. One possibility already mentioned is where high-energy currents introduce reactive organic material. Other as yet little-investigated possibilities include topographic focusing of sedimentation and localized enhanced surface production associated with islands and seamounts. In general, studies of dispersion patterns in the deep-sea macrofauna at spatial scales of 10 cm to 100 km do not suggest a strong environmental mosaic reflected in the distribution and abundance of populations (Jumars 1976). Nonequilibrial patch dynamics have been proposed as a cause of species coexistence in the deep sea (Grassle and Maciolek 1992). However, a recent review of potential sources of patchiness, including biogenic structures occurring in quantitative samples and experimental manipulations of nutrient enhancement or disturbance, reported only little or no change in diversity compared with background levels and shifts in abundance for only a small minority of macrofaunal species (Snelgrove and Smith 2002). Of course, it is quite possible that more intense sampling or sampling at different spatial and temporal scales might detect the kind of environmental heterogeneity that could foster persistence as a metapopulation for macrofaunal species living in the abyss (Jumars and Eckman 1983). Source-sink dynamics and an abyssal metapopulation structure are not mutually exclusive explanations for abyssal biodiversity. Common abyssal species may

persist as a metapopulation that includes bathyal and abyssal populations, and populations of rare abyssal species may represent a mass effect from bathyal sources.

The source-sink hypothesis can be tested further by using existing biogeographic databases and archived collections of deep-sea organisms. It is obviously important to establish the generality of the relationships between species diversity, abundance, geographic distribution, and larval dispersal described here by extending the analysis to other taxa, functional groups, deep-sea basins, and nutrient regimes. Mollusks, the third most diverse deep-sea taxonomic group after polychaete worms and peracarid crustaceans, make up 16% of deep-sea macrofaunal species (Gage and Tyler 1991). It is possible that their basic body plans are not particularly adaptable to abyssal conditions. Taxa probably vary in the extent to which source-sink systems operate to shape distributions. Some macrofaunal peracarid crustaceans, for example, do show a higher level of abyssal endemism (e.g., about half of abyssal desmosomatid isopods in the western North Atlantic; Hessler 1970). Abyssal faunas of deep-sea demersal fishes, a component of the megafauna, appear to mainly represent range extensions (Pearcy et al. 1982; Haedrich and Merrett 1988). Some eastern North Atlantic megafaunal echinoderms are relatively more abundant in the abyss than at bathyal depths (Billett 1991; Howell et al. 2002), suggesting that they are true abyssal endemics.

If the continental margin and abyssal plain represent a source-sink system that is driven ultimately by the proximity to high coastal production, then abyssal communities should show a progressive decline in abundance and diversity as habitat quality deteriorates further with increased distance from the continental shelf. There is some evidence for this. The macrofauna does decrease in density seaward in the abyssal plain of the western North Atlantic (Sanders et al. 1965; Smith 1978; this study) and elsewhere in the Atlantic (Sibuet et al. 1984). Gastropods in the abyssal North Atlantic also show a significant decline in species diversity with increased distance from the continental shelf (Rex 1973). Other taxa could be examined for these predicted effects.

The operation of a source-sink system also should be manifested in the reproductive status of individuals in conspecific bathyal and abyssal populations. The differences in reproductive maturity and mating success should be most pronounced in species that are relatively common at bathyal depths and rare in the abyss. Histological studies of reproductive organs in deep-sea invertebrates have been very useful in detecting reproductive maturity, pattern of gamete production, and incidence of mating (Gage and Tyler 1991; Young and Eckelbarger 1994). The source-sink hypothesis predicts that rare abyssal species will show less evidence of gamete production, and particularly mating, than their bathyal counterparts.

Genetic population structure can provide another test. DNA can now be sequenced from preserved deep-sea organisms (France and Kocher 1996; Chase et al. 1998b; Etter et al. 1999), and several new analytical techniques based on maximum likelihood methods and coalescent theory have been developed that can be used to critically test for the genetic imprints of source-sink dynamics (Templeton 1998; Beerli and Felsenstein 2001; Wares et al. 2001). For example, Beerli and Felsenstein's (2001) maximum likelihood approach for estimating migration rates can detect asymmetries in migration among populations, which would be indicative of source-sink dynamics. Nested Clade Analysis (Templeton 1998) is another powerful technique that can be used to test the source-sink hypothesis. It combines evolutionary relationships derived from haplotype trees with traditional statistics of geographical association to discriminate among restricted gene flow, range expansion, and population fragmentation.

We can formulate several predictions about the genetic composition of sink populations. According to the source-sink hypothesis, individuals in rare abyssal populations should bear no unique haplotypes because they are assumed to originate exclusively from bathyal populations. Since rare abyssal populations are inferred to be nonreproductive, there is no way for occasional mutant genes to be perpetuated by selective or nonselective processes. It would require extensive sampling to collect enough individuals of rare species to test this prediction. As with animal abundance, there should also be an attenuation of the bathyal haplotype diversity seaward across the abyssal plain. Haplotypes present at abyssal depths should be the most abundant and older haplotypes from bathyal depths because these will have the greatest opportunity to contribute colonists to sink populations. Also, abyssal haplotypes/clades should always be nested within bathyal clades because they will be derived from bathyal populations.

Significance of the Hypothesis

If confirmed by studies of other taxa and deep-sea basins, the source-sink hypothesis has several significant ramifications. First, the structure and function of the deep-sea soft-sediment community may change in fundamental ways along the depth gradient from the continental margin to the abyss as source-sink dynamics become progressively more important in maintaining biodiversity. If correct, this greatly simplifies our understanding of deep-sea ecology. It resolves the long-standing paradox of how abyssal communities could possibly be structured by biological interactions or ecological heterogeneity when populations exist

at such extremely low density. The source-sink hypothesis does not require that abyssal communities be ecologically structured. They may be primarily a passive consequence of larval dispersal. It proposes that many abyssal populations are composed of isolated immigrants. This does not mean that the abyssal assemblage is a completely random subset of the bathyal fauna. The bathyal-abyssal transition may act as a selective biogeographic filter at the species level. The environment of the abyss appears to favor deposit feeders and species with larval dispersal, as expected in a low-energy environment where persistence depends on continued immigration. Elsewhere, we show that the abyssal gastropod assemblage is dominated by species with energetically efficient shell architectures (McClain et al. 2004).

Another consequence is that the abyssal ecosystem, despite its disproportionately huge area, may not contribute appreciably to global marine biodiversity. This means that estimates of total deep-sea macrofaunal diversity as high as 10^7–10^8 species, based on extrapolations of midbathyal diversity to the entire seafloor (Grassle and Maciolek 1992), might have to be revised substantially downward.

An impoverished abyss also constrains evolutionary potential for diversification. If many abyssal populations cannot respond to selective gradients and if the abyssal environment lacks sufficient ecological opportunity to support coexistence among the products of speciation, then adaptive radiation within the deep sea may be limited mostly to bathyal regions. Studies of phenotypic and genetic population divergence in deep-sea mollusks suggest that most differentiation occurs in the bathyal zone (Etter and Rex 1990; Chase et al. 1998a). Both evolutionary historical and ecological processes driving deep-sea biodiversity may be largely bathyal phenomena.

Finally, the source-sink hypothesis proposed here has potentially serious implications for conservation and sustainable development. In addition to supporting rich biodiversity of unrealized value, the deep-sea environment contains enormous mineral wealth. As human population size continues to grow and terrestrial and coastal resources dwindle, the deep sea will come under increasing development pressure. Large-scale petroleum exploration and production already extend to midbathyal depths, and seven claim areas (of 75,000 km^2 each) have been licensed in the abyssal Pacific for prospecting and test mining of polymetallic nodules (Glover and Smith 2003; Thiel 2003). Methane hydrate extraction, CO_2 sequestration, and ocean waste disposal are being actively considered. All of these activities could adversely affect the deep-sea benthos, but the severity and scale of their impacts are currently hard to gauge. Most of the deep sea remains unexplored. The most crucial information for assessing extinction potential, the geographic ranges of individual species, is very poorly known. Conservation protocols for the deep-sea benthos have not been formulated, and an international regulatory structure to safeguard the environment is only beginning to take shape. Remediation in this remote environment may not be possible.

One interpretation of the source-sink hypothesis by development interests might be that exploitation of abyssal resources would not result in significant extinction because conspecific source populations would still exist on the continental margins. This would be a premature conclusion. As discussed earlier, there does appear to be an endemic component to the abyssal macrofauna, the size and distribution of which remain to be determined. The source-sink hypothesis presented here is based on the bathymetric ranges, abundances, and life-history traits of species in one taxon (Mollusca) in two regions of the North Atlantic. We feel that it is a promising theory with considerable potential to focus and integrate deep-sea research and to improve our understanding of ecosystem function. However, its validity and generality require much more investigation, and it should not be used as a scientific basis for environmental policy until thoroughly tested.

Acknowledgments

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Associate Editor: Kaustuv Roy