

1-1-2000

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Recommended Citation

Snelgrove, P., Austen, M., Boucher, G., Heip, C., Hutchings, P., King, G., Koike, I., Lambshead, P., & Smith, C. (2000). Linking biodiversity above and below the marine sediment-water interface. *BioScience*, 50 (12), 1076-1088. [https://doi.org/10.1641/0006-3568\(2000\)050\[1076:LBAABT\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2000)050[1076:LBAABT]2.0.CO;2)

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Linking Biodiversity Above and Below the Marine Sediment–Water Interface

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Changes in the marine environment are evident on a global scale (McGowan et al. 1998), and although biodiversity in the oceans is poorly described, abundances and distributions of both commercially exploited (Safina 1998) and nonexploited (Pearson and Rosenberg 1978) species have changed. Not only have major changes occurred but the rate of alteration of marine ecosystems appears to be accelerating (e.g., Cohen and Carlton 1998). Unfortunately, the impact of these changes in biodiversity on the basic functioning of marine ecosystems remains uncertain, as does the oceans' capacity to withstand multiple human disturbances (Snelgrove et al. 1997). The dynamics of many marine ecosystems, as well as of important fisheries, depend on close coupling between benthic (bottom living) and pelagic (water column) organisms (Steele 1974). Our knowledge of the natural history of these systems remains limited, and scientific interest in mapping the diversity of organisms and how they live has been marginalized in recent years. Given the expanding sphere of human influence on the oceans, it is imperative to understand not only patterns of biodiversity and the extent to which changes in biodiversity are occurring but also how changes in the benthic and pelagic realms might affect each other. The oceans provide many important ecosystem services, including production of food, stabilization of shorelines, trapping and removal of excess nutrients and pollutants, and cycling of nutrients and organic matter. How does biodiversity above and below the sediment–water interface influence these services, and will biodiversity loss on one side of the interface impact the services provided by the other?

THE ORGANISMS LIVING ON THE OCEAN FLOOR ARE LINKED TO THOSE LIVING IN THE OCEAN ABOVE, BUT WHETHER OR HOW THE BIODIVERSITY IN THESE TWO REALMS IS LINKED REMAINS LARGELY UNKNOWN

The sediment–water interface (SWI) in marine ecosystems is one of the most clearly defined ecological boundaries on Earth. Many organisms in the water column, such as salps and jellyfish, have flimsy and attenuated morphologies that allow near-neutral buoyancy in their fluid habitat, where horizontal advection, turbulent mixing, and gravitational settling dramatically influence the relative distributions of organisms and transport of materials around them. Physical and chemical gradients in the water column (e.g., from oxic to anoxic waters) occur over scales of meters or more. Surface waters are always well oxygenated, and waters near the bottom are usually well oxygenated except where large amounts of decomposition occur and bacterial respiration drives down oxygen concentration. Below the sediment–water interface, the morphology of organisms and the physical attributes of the environment differ markedly.

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Even the muddiest sediments are more like solids than seawater, with mixing frequently controlled by biological activities such as feeding and burrowing (bioturbation). Infauna, the organisms living within sediments such as polychaete worms or shrimp-like crustaceans, are usually denser than those in the water column because surrounding sediments remove the problem of avoiding sinking. Body forms are more robust to permit the burrowing that can be essential to existence. Physical and chemical gradients are steep; for example, the transition from oxic-to-anoxic sediments often occurs on millimeter scales. In addition, organisms and nutrients are usually orders of magnitude more abundant in sediments than in overlying waters; materials sinking from above accumulate on sediments and fuel bottom-living organisms.

Because of differing ecosystem structure above and below the SWI, the ecologists who study these domains must use different techniques, and often ask different research questions. This specialization can often lead to scientific isolation of the two domains. For example, a recent workshop of hydrozoan specialists emphasized the problem of duplication of species descriptions by those focusing on benthic versus pelagic stages of a given species (Boero and Mills 1999). Despite the dichotomy in research communities, there are numerous strong connections across the SWI. These are seen not only in life cycles (e.g., Marcus and Boero 1998) but also in the dissolved and particulate materials that routinely cross the water-sediment boundary (Figure 1).

Chemical energy for marine benthic systems is often provided by single-celled and chain-forming phytoplankton (algae), which are the dominant primary producers in the ocean. Living cells may sink or be physically mixed to the bottom, or dead cells may sink to the bottom as phytodetritus. In surface waters, crustaceans and other groups of zooplankton feed on phytoplankton and defecate fecal pellets, which may then sink to the bottom and provide undigested phytodetritus and associated bacteria as an important food source for the benthos. Plant material from coastal environments, such as seagrass, mangal (mangrove habitat),

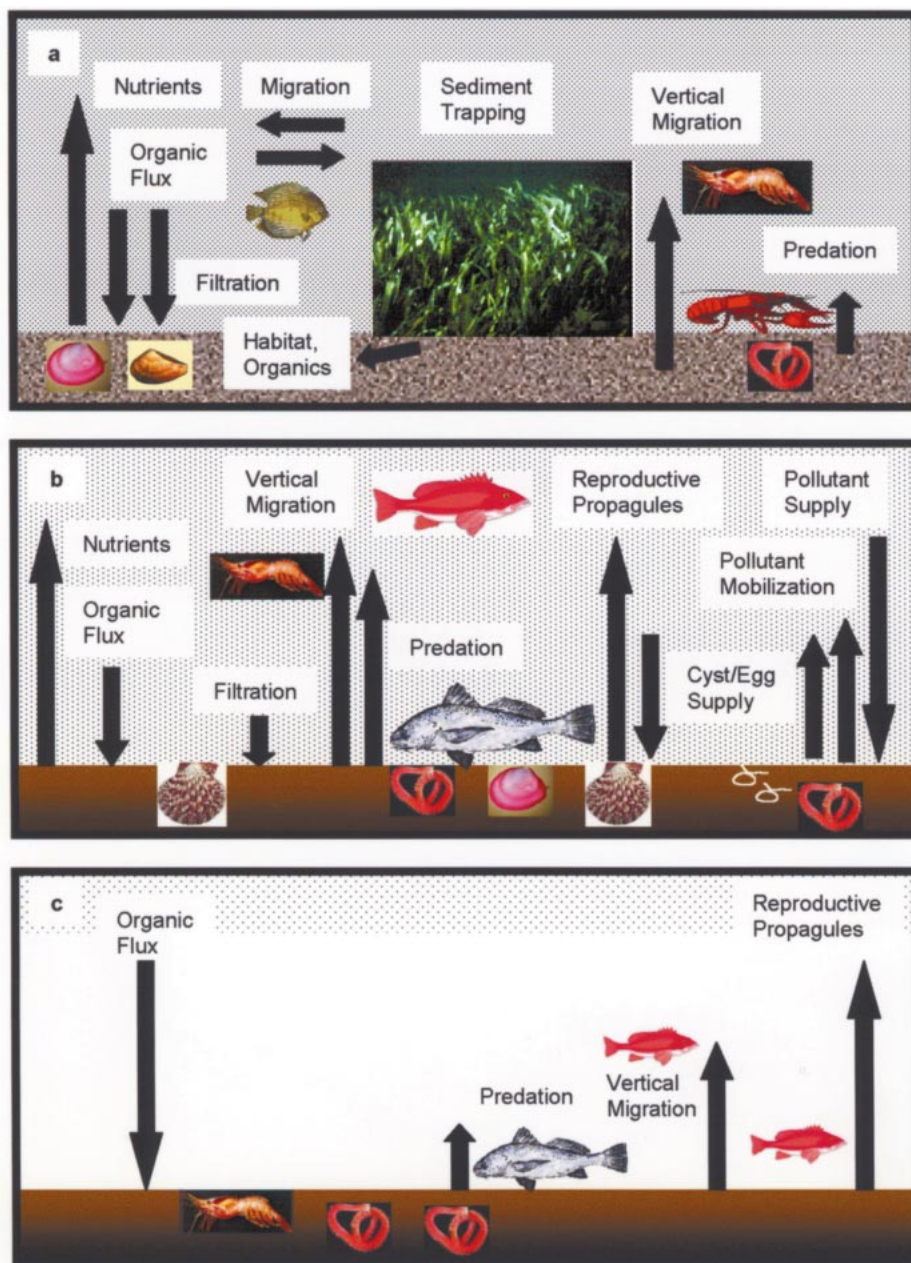


Figure 1. Schematic representation of above-below sediment linkages in shallow habitat with structural vegetation (top), coastal areas without structural vegetation (middle), and open ocean systems (bottom). Stippled area denotes photic zone where photosynthesis is occurring.

and salt marsh plant detritus, may be carried away from the nearshore environment before sinking to the bottom and providing another potential food source. A less predictable but sporadically important food source for the benthos is carcasses of fish, whales, and invertebrates that sink from the water column above (Smith et al. 1998). The benthos, in turn, helps to recycle the nutrients required by the planktonic algae that fuel much of the ocean's benthic and pelagic production (Graf 1992). Clearly, individuals of different species traverse and/or impact other species on more than one side

of this interface, but is biodiversity above and below the SWI interface linked? The goals of this article are to summarize the state of knowledge concerning connections and directionality of effects between organisms living above and below the SWI that may be related to biodiversity, to identify or hypothesize connections that are likely to be important, and to outline approaches that might clarify mechanisms of across-interface biodiversity linkages. Specifically, are there “water column-down” effects in which pelagic diversity affects sedimentary diversity? Are there “sediment-up” effects in which the reverse is true? The potential impact of global change processes on these relationships is reviewed separately (Smith et al. 2000).

For this article, we separate marine ecosystems into three distinct groups based on potential relationships between above- and below-SWI biota. First, shallow sedimentary systems with structural vegetation such as mangals, salt marshes, and seagrass beds support unique faunas and processes; within this grouping, we will also briefly consider green algal and kelp beds, which are primarily hard substrate communities but occasionally contain sediments. Second, we consider nonvegetated shallow-water coastal systems in which wind and turbulence mix the water column to the SWI during part of the annual cycle. These habitats encompass highly dynamic environments, such as sand beds on exposed coastline, and relatively quiescent muddy areas in sheltered regions that are physically disturbed only rarely. Finally, we consider open ocean systems in which mixing and light never penetrate to the SWI. We also divide organisms into those that occur above or below the SWI, and treat organisms that live predominantly on or above the sediment surface (seagrasses and green algae, salt marsh plants, pelagic organisms, hyperbenthos, etc.) as above-SWI. In making this distinction, we acknowledge that many benthic species have a pelagic reproductive dispersal stage, and some above-SWI species have a below-SWI component (e.g., salt marsh grass roots) or life stage (e.g., hydrozoans). In addition, we confine our discussion of linkages to sedimentary benthic systems and largely ignore hard substrate communities, coral reefs, and kelps except where sediments are present. We also acknowledge that the information presented declines as a function of ocean depth; this pattern reflects not only the differences in present knowledge but also our best guess as to the strengths of linkages between above- and below-sediment biodiversity.

The meaning of biodiversity

In keeping with common usage and the Convention on Biological Diversity, we define biodiversity in the broadest sense to encompass the variability of nature in terms of genetics, species, habitats, and even ecosystems. This usage is kept deliberately broad and is not confined to a unit as such. Some of the best examples of above–below linkages that we will summarize are known to directly involve only one or a few species; nevertheless, we feel that they do represent an aspect of biodiversity. In more specific terms, species

richness refers to numbers of species in an area, and composite diversity refers to measures of species diversity that incorporate not only species number but also how individuals are apportioned among those species (evenness). Common measures of composite diversity include the Shannon–Weiner (H) diversity index and Hurlbert rarefaction (expected species, or $E[S_n]$). Where possible, we will use the specific measure of diversity given in a particular study, but the use of different measures in different studies can make comparisons difficult. Moreover, a change (or lack of change) in one measure does not always mean there is no change in another aspect of diversity. We also consider diversity on multiple scales, following the conceptualization of Whittaker (1972). Within this framework, alpha diversity is the diversity within a small, relatively homogeneous area, which for the benthos is operationally the smallest scale sampled (the spatial scales of the smallest core sampler used). Clearly, this scale will vary depending on the organism size-fraction considered, being smaller for bacteria than for urchins. Gamma diversity is the total diversity of a region, obtained by integrating diversity across all patch types.

Whittaker's framework is useful for the many relevant scales (centimeters to hundreds of kilometers) but also reflects a fundamental difference in pelagic and benthic realms. Benthic ecologists, who tend to focus on habitat comparisons and the associated communities, usually sample alpha diversity and sometimes extrapolate from these samples to estimate gamma diversity. The sampling units for most pelagic studies (plankton tows) often cut across multiple patches in the fluid and dynamic water column and thus may sample gamma rather than alpha diversity. Indeed, pelagic biologists are more comfortable stating numbers of species in a given area of the ocean than are benthic ecologists, who recognize that very few bottom areas have been sufficiently sampled for them to be confident that rare species have not been missed.

Structural vegetation and connections with sedimentary biota

There are approximately 50 described mangrove species and 45 species of seagrass, but in both of these systems, a given area typically will contain only a few relatively common species. Kelp beds, which occasionally have associated sedimentary habitat, are also dominated by only a few plant species, although globally there are thousands of macroalgal species. There is evidence from research on seagrass (Edgar 1983), mangal (Gee and Somerfield 1997), and salt marsh ecosystems (Levin and Talley, in press) that different fauna tend to be associated with different vegetation types both above and below the SWI. However, the above SWI diversity of structural plants within a given location in the marine environment is relatively low, with one or only a handful of species represented, and even within these groups there is often zonation of species with tidal and salinity variation.

Teasing out relationships between structural vegetation and sedimentary fauna is therefore difficult because the environmental conditions that regulate distribution of vegetation may be more important in regulating the associated fauna than the vegetation itself. For example, Hutchings et al. (1991) found greater similarity between infauna associated with different seagrass species within one patch than between those associated with the same species of seagrass in different patches. Similarly, Collett et al. (1984) demonstrated that local environmental conditions determine the macroinfaunal composition associated with the seagrass *Posidonia australis* along the Australian coast. As a result of overriding environmental variables, the species pool associated with a patch of a given seagrass is often much smaller than that associated with that seagrass species over a broader scale. Further evidence for an absence of a direct diversity linkage between above-sediment structure and below-sediment biota was found in a Fiji lagoon where above-SWI structural composition is a poor predictor of below-sediment diversity (Schlacher et al. 1998). In summary, there are potential linkages between species associated with structural vegetation and the sediment beneath (Figure 1), but evidence suggests that linkages are coincidental in that both communities are affected by similar environmental variables. One complication in linking above- and below-SWI species numbers and composition is seasonal and annual variability in below-SWI organisms.

Structural vegetation: Water column-down linkages

Although specific biodiversity links are poorly documented, there are numerous examples of above-SWI vegetation structuring the sedimentary environment below. Sediment trapping and water flow baffling by structural vegetation can often alter the grain size of sediments near the vegetation. Given that sediment grain size is a major delimiter of infaunal distribution, there should be a clear linkage of structural vegetation to below-SWI biodiversity and composition. Productivity of vegetated habitats often exceeds that of adjacent areas. Stimulation of microbial growth by root exudates may enhance resources and diversity of nematodes and other below-SWI organisms, particularly in seagrasses (Osenga and Coull 1983). A recent study found little variation in sedimentary species colonizing litter from different mangrove species but some differences depending on which living mangrove species the litter was associated with (Gee and Somerfield 1997). Variability in sedimentary fauna was attributed to the root structure and geochemistry of the mangrove species. Structural vegetation can also depress diversity; large detrital production, combined with the reduced water flow often observed in mangals and salt marshes, can lead to organic loading and reduced sediment oxygen availability (Alongi 1997) with a subsequent depression of below-SWI species richness. Indeed, the geochemistry of structural-vegetation habitats is markedly different from that of non-vegetated areas as a result of increased productivity,

increased sedimentary nutrients, and a greater propensity for anoxia related to the large amounts of detritus produced.

Structural vegetation influences food webs at many levels. Many primary producers, particularly vascular plants, produce "signature" compounds including lipids, polysaccharides, and antiherbivory chemicals that may favor specific bacterial and fungal populations; the effects of these compounds may have ramifications up through the food chain. The tannin-rich detritus produced in mangals, for example, is used by a tannin-tolerant fauna with low composite diversity (Alongi and Christoffersen 1992). But for macrofaunal species able to cope with productive environments such as mangals, competitors are presumably few and organic matter is abundant.

Habitat complexity generally enhances diversity in biological communities, and structural vegetation and root structures provide critical habitat for a diversity of species (Figure 1). An increase in above-SWI macrofaunal richness and composite diversity in seagrass sediment communities has been linked to abundance and numbers of species of seagrass on regional and latitudinal scales (Stoner and Lewis 1985). Species richness of infauna within vegetated areas is elevated in comparison with that of adjacent bare sand habitat. (See Peterson 1979 for macrofauna, defined as organisms retained on a 300- or 500- μ sieve; Boucher 1997 for meiofauna, defined as organisms retained on a 40- μ sieve.) The explanation for this pattern is that predators tend to depress diversity in soft-sediment systems at small scales, and seagrasses may provide a predation refuge (Peterson 1979). The structural complexity of sediments within salt marshes and mangals cannot be used by many species because of the variability in salinity, temperature, exposure, and oxygenation in coastal habitats. In mangals, for example, the below-SWI community is often reduced in diversity relative to adjacent nonvegetated subtidal sediments (Gee and Somerfield 1997). Habitat complexity may also have negative effects on species; the roots of seagrasses and marsh grasses likely exclude some burrowers, tube builders, and infauna (Levin and Talley, in press).

Predators living above the SWI may, in some instances, prey upon infauna. Caging experiments focusing on meiofauna living in mangal sediments suggest that the impact of predation on infauna is modest, and the predator and prey communities operate largely independently (Schrijvers et al. 1995). Salt marsh microcosm experiments with grass shrimp indicated that although the shrimp reduced meiofaunal densities, Shannon-Weiner diversity was largely unaffected (Bell and Coull 1978). It is possible that predation effects in these habitats, like those described below, may prove more important in terms of habitat modification than for predation per se. These findings contrast with the seagrass studies described above, suggesting no simple relationships between predators, vegetative structure, and infaunal diversity.

Structural vegetation: Sediments-up linkages

The effects of below-SWI organisms on above-SWI organisms are likely to be indirect and therefore difficult to document. Microbes living within sediments are critical for mineralization of detritus generated by vegetation; they provide nutrients to roots and above-SWI components of the vegetation (Alongi 1997). Burrowing by macrofauna can improve sediment aeration with positive effects on mangrove growth (Smith et al. 1991), likely through alteration of porewater sulfide and ammonium concentrations. Although one might predict that burrowers would enhance microbial biomass and diversity within sediments, few data suggest an effect on above-sediment diversity. In coastal ecosystems, and particularly coral reefs, organisms that migrate out of sediments at night can be a significant component of the above-SWI fauna (Sorokin 1993), providing a possible opportunity for interaction between above- and below-SWI organisms. Infaunal grazers on seedlings and root structures can also regulate mangrove distributions (see Tomlinson 1986). These examples of bottom-up effects in vegetative systems do not link to biodiversity per se and often involve individual species-species or trophic group interactions. Whether the lack of evidence for bottom-up effects of biodiversity on structural vegetation reflects an absence of interaction or simply inadequate data is difficult to say.

Linkages in coastal areas lacking structural vegetation

Many coastal areas lack obvious physical structures, such as those associated with structural vegetation, although reefs created by polychaete worms and bivalves and other biogenic structures, such as feeding pits and tubes, may fill a similar role. Aside from these structures, potential effects of above-SWI diversity on below-SWI diversity in most areas are likely to be expressed through productivity, predation and associated sediment disturbance (bioturbation), and recruitment processes. In some shallow areas, benthic diatoms and cyanobacteria may form mats on top of sediments that can influence rates of nutrient exchange between sediments and the overlying water column (Sundbäck and Granéli 1988). But for most marine sediments, light is attenuated or lacking at the sediment surface, and primary production occurs only in surface waters. Some of this primary production will sink to the sea floor and fuel the sedimentary system, but the structural complexity of the habitat is not enhanced as it is in systems with structural vegetation. Epifaunal species, such as sponges and anemones, form above-sediment structures, but given that epifaunal organisms do not usually occur over the large spatial scales and high densities typical of many vegetated areas, the scale of impact is probably reduced. Coral and coralline algal reefs are notable exceptions, but these communities include mostly nonsedimentary species. Nonetheless, even non-vegetated sedimentary habitat has a three-dimensional

spatial structure that affects benthic composition, as seen in studies of trawling impacts (Hutchings et al. 1991).

Studies to test specifically the hypothesis that productivity, predation, and recruitment may be related to above-SWI species richness and composite diversity are virtually nonexistent, but some qualitative comparisons can be made, and compelling data suggest the existence of linkages. Long-term pelagic and benthic data sets from the North Sea suggest that changes in biomass and species abundance have occurred in both habitats since the 1970s, but linkages between community structure of habitats are weak (Austen et al. 1991).

Above-SWI productivity may impact sedimentary diversity through three potential routes. Amounts of organic loading, timing, and biochemical composition of products of photosynthesis all can affect sedimentary organisms and their composition. When productivity is extremely high (such as under organic loading), macrofaunal (Pearson and Rosenberg 1978) and meiofaunal (Coull and Chandler 1992) richness and composite diversity are often depressed, but these changes relate to hypoxia resulting from increased productivity rather than to changes in pelagic diversity per se. Increasing areas of ocean bottom are experiencing hypoxic events that can cover thousands of km² of sea floor and eliminate most resident fauna (Malakoff 1998). Toxic algal blooms can have a similar impact.

The anticipated impact of variability in organic loading on sedimentary diversity is even more tenuous. Schratzberger and Warwick (1998) demonstrated in microcosm experiments that continuous inputs at moderate levels promote greater nematode diversity than episodic inputs. By contrast, temporal variability in resource supply, combined with nonlinear responses of different species to resources, is one model to explain high species richness and composite diversity in the deep sea (Grassle and Sanders 1973). Comparison of microbial diversity in shallow and deep tropical and temperate systems with that in deep pelagic systems could provide further insight into the role of variability in resource supply by testing whether microbial diversity is affected by differences in seasonality and the pulsed or episodic nature of organic inputs.

Biochemical diversity of organic inputs from above the SWI could affect diversity of microbial and potentially meiofaunal and macrofaunal taxa (Dauwe et al. 1998). Major groups of primary producers, including various groups of phytoplankton, macroalgae, and vascular plants in shallow systems, produce specific polysaccharides or lipids that can favor specific species of hydrolytic bacteria (Percival and McDowell 1967). For example, the capacity for hydrolysis of agarpectin and carrageenans, compounds produced by red algae, is limited to relatively few bacterial taxa. Thus, inputs of these polymers may affect both the diversity and biogeography of below-SWI bacteria. The nature of polysaccharide inputs, including contributions from terrestrial systems, might also play a role in the diversity and relative importance of fungi, some of which possess unique

hydrolytic capabilities. Because proteins, nucleic acids, and lipids are ubiquitous, they are probably less important than polysaccharides in determining benthic microbial diversity. Distinctive groups of bacteria from species to phylum levels of organization also exhibit substrate preferences for proteins, sugars, lipids, etc., and the relative abundance of polymer classes may therefore affect microbial functional diversity. Abundance of polymer classes varies with planktonic species composition, terrestrial organic loading, and water column depth. Thus, there is good reason to believe that above-SWI diversity will affect below-SWI bacteria and perhaps fungi, but whether this linkage extends to below-SWI meiofauna and macrofauna remains untested. One might predict that higher diversity low in the food chain (i.e., bacteria) could enhance diversity in larger organisms if food diversity enhances feeder diversity. Given the limited data available on diversity of microbial groups, however, we acknowledge the highly speculative nature of these hypotheses and offer them as ideas to motivate research directions.

Evidence suggests that predation and disturbance by above-SWI epifaunal predators (e.g., crabs, shore birds, flatfish) can affect diversity by removing individuals but also through habitat modification. Caging studies suggest that predators reduce macroinfaunal diversity (Peterson 1979), presumably because they often selectively remove slow-growing and vulnerable species. Because these conclusions are drawn from caging studies rather than direct comparisons of above- and below-SWI diversity, they tell us little about changes at scales larger than the cages, but they do suggest that above-SWI diversity can have a direct impact on below-SWI diversity at small scales.

It is likely that the greatest effect of predation on species diversity is through habitat modification; the habitat heterogeneity that predators may introduce can result in enhanced diversity at larger scales. Large and mobile above-SWI bottom feeders, such as rays, tend to cause an initial depression of local diversity as they remove prey and physically disturb the sediment, sometimes followed by transient increases in species richness or evenness, enhancing diversity (VanBlaricom 1982). This sort of biological disturbance opens up habitat and eliminates most species, resulting in a succession through an initial low-diversity stage dominated by a few opportunistic or “weedy” species, an intermediate stage characterized by high diversity because opportunists and background species co-occur, and finally a moderate-diversity, late stage in which opportunists have declined and background species again dominate. A similar sequence occurs when pelagic carcasses fall to the bottom, providing food and a localized disturbance benefiting species that are not abundant otherwise (Smith et al. 1998). Thus, although diversity at the local (sample) scale may often be reduced, species numbers at the landscape scale may be enhanced. Interestingly, most of what we know about predation is from studies of above-sediment species, rather than interactions among infaunal species. This raises the intriguing question of whether there are fundamental differences in the

effects of above-SWI versus infaunal predators on sedimentary biodiversity.

Large sediment diggers above the SWI, such as rays (VanBlaricom 1982), crabs, and shrimp, may also affect sedimentary community diversity through geochemical mechanisms. For example, sediment disturbance, such as from burrowing polychaetes (e.g., Kristensen et al. 1985), can introduce oxygen into anaerobic sediments (Aller 1982), and above-sediment diggers will have a similar effect. Burrows may also help concentrate organic matter through deposition or active sequestration by organisms that live within the burrows. Alternatively, burial of organic detritus can result in increased sediment oxygen demand and production of compounds rich in organic material. Clearly, these activities will influence microbial, meiofaunal, and, most likely, macrofaunal diversity, but studies explicitly addressing geochemical effects on diversity are lacking (although see Soetaert and Heip 1995). As an analog to predator disturbance, animal burrows produce biogeochemically distinct conditions that may be used by specific microbial and meiofaunal populations (Dobbs and Guckert 1988). For example, dehalogenating populations may be enriched in burrows of haloorganic-producing enteropneusts (King 1988). Although it is clear that animal–microbe interactions may be responsible for unique microbial associations with burrows, planktonic diversity could provide an indirect control on microbial diversity in sediments because benthic biogeography is likely related to composition and processes within the plankton.

The co-occurrence of the pelagic stage of some benthic species with holoplanktonic species provides ample opportunity for interaction in the water column. Many benthic species produce planktonic larval stages that may spend anywhere from minutes to months in the water column, potentially interacting with a broad suite of holoplanktonic species through predation or competition for food. The dispersal stages of benthic species usually experience very high levels of mortality, but whether diversity of the plankton plays a role in rates of mortality is untested. For example, greater diversity of predators could increase the likelihood that meroplankton will suffer from predation. Mesocosm experiments offer one approach to test these hypotheses.

Coastal habitats lacking structural vegetation: Sediments-up linkages

Functional groups within sediments can affect above-sediment diversity via selective transfer of matter through the SWI, particle exchange through biological mechanisms (feeding of pelagic species on the benthos and vice versa, migrations from benthic species into the water column including reproductive propagules), and release of dissolved substances after mineralization of organic matter or transformation of pollutants in sediments (Henriksen et al. 1983).

Nutrient regeneration is critical in fueling coastal productivity above the SWI interface, and sedimentary microbes play a key role in the regeneration process (see Snelgrove et al. 1997). In tropical areas, this seasonal effect is less pronounced, and benthic algae may capture most nutrients as they diffuse out of sediments (Alongi 1997). The feeding, movements, and respiration of macrofaunal taxa affect the porewater concentrations and availability of oxygen, nitrate, sulfate, and other electron acceptors in marine sediments, which in turn affects carbon and nitrogen remineralization rates by microbes (Rhoads et al. 1978). The influences of regeneration rates on diversity are undoubtedly complex, but high regeneration can result in blooms of a few dominant phytoplankton species. Rates of regeneration and their temporal variation can affect phytoplankton composition and diversity. Pulsed areas often have a few dominant phytoplankton species at any one time, but less temporally variable areas may be more species rich unless nutrient levels are highly elevated.

Pollutants, much like regenerated nutrients, are affected by microbial diversity and macrofaunal activity that influence the magnitude and timing of release of modified and untransformed pollutants from sediments into the water column. Impacts may be direct, such as when pollutants bound to sediment particles are moved by macrofauna so that they become deeper or shallower in the sediment horizon, or linkages may be less direct. For example, when macrofauna colonize polluted sediments, their reworking typically changes redox conditions and enhances porewater efflux from sediments, triggering release of heavy metals. Degradation of organic pollutants may also depend on the presence of specific microorganisms (e.g., Geiselbrecht et al. 1996), which may in turn depend on macrofaunal activities. Linkages between the nature and magnitude of pollutant release from sediments and pelagic biodiversity are undoubtedly complex, and a descriptive framework does not exist, but species-specific transfers and pollutant effects are known. Demersal fish that feed on the benthic organisms such as shrimp and polychaetes, provide an obvious conduit for sediment contaminants (e.g., heavy metals, PCBs) to the above-SWI domain.

Active vertical migration at night for feeding and reproduction characterizes some adult meiobenthic (Armonies 1988) and macrobenthic species that migrate from below the SWI interface up into the water column (Sorokin 1993). Adults of benthic species will leave sediments at night and make excursions into the water column, but interactions with the above-SWI fauna have not been well studied (Mees and Jones 1997). Often, they are eroded from the sediment by strong bottom currents generated by wind or tides, but mollusks and polychaetes are also known to move after metamorphosis, perhaps in search of better food (Olivier et al. 1996). The effects of these excursions and interactions with the above-SWI fauna have not been quantified, but these benthic migrants lengthen the list of taxa found in the water column.

Meroplankton, the pelagic larvae that are produced by many macrobenthic species in coastal areas, remain in the plankton for hours, weeks, or even months, depending on the taxon. The meroplankton on continental shelves often dominate the holoplankton (wholly planktonic organisms) during a large part of the year, and different species tend to peak at different times of year, particularly in the spring and autumn, when phytoplankton blooms occur. The effects of meroplankton grazing on phytoplankton are expected to be considerable. Meroplankton can also be an important food source for water column species, and meroplankton diversity could impact holoplankton diversity and pattern. An intriguing example is seen in the North Sea, where long-term plankton data indicate that meroplankton have become the dominant taxon in shelf waters in recent years, with corresponding decreases in the formerly abundant copepods (Lindley et al. 1995). This change has been linked to increases in biomass of benthic echinoderms, which in turn may be related to eutrophication or fishing disturbance (Duineveld et al. 1987). Whether increases in meroplankton are responsible for the decline in holoplankton is impossible to determine without experimental data, but the pattern raises interesting questions on above- and below-SWI linkages. How changes in species composition affect the ecosystem will be difficult to determine, given the confounding impacts of fishing disturbance, pollution, and climatic factors that influence the North Sea ecosystem. Fishing impacts on sedimentary fauna remain a difficult question to address in any ecosystem, given that virtually any area that can be fished has been fished, and unimpacted "control" areas either are entirely lacking from a region or represent fundamentally different habitats that also happen to be untrawlable. Smith et al. (2000) discuss fishing impacts in greater detail.

Suspension feeding activity by benthic organisms provides a mechanism of interaction between pelagic and benthic systems (Officer et al. 1982). Suspension feeders often transfer much larger quantities of material to sediments than would be possible by sedimentation alone, and they may deplete the lower water layers of particles and increase transparency (Butman et al. 1994). The intriguing example of the Asian clam, *Potamocorbula amurensis*, and the effects of its introduction into San Francisco Bay, are discussed by Smith et al. (2000). Elmgren and Hill (1997) point out that despite much lower diversity in the Baltic Sea, ecosystem processes such as carbon cycling and trophic transfer occur as they do in the North Sea (Steele 1974), suggesting that total diversity may not be important to these processes. But in one area of the Baltic where suspension feeders are absent, energy flow is markedly different, with reduced phytoplankton flux to the benthos and reduced importance of macrofauna relative to meiofauna. How the absence of suspension feeders affects pelagic processes remains unclear, but primary productivity and fisheries yields are both considerably reduced in this area.

Resting stages in the form of eggs and cysts are produced by a number of pelagic phytoplankton and zooplankton

species, and these stages can be abundant in coastal sediments (Marcus 1996). Among the best known of these are dinoflagellate cysts, which serve as a hardy resting stage and can seed toxic blooms, leading to paralytic shellfish poisoning through ingestion of toxic dinoflagellates by suspension-feeding bivalves. During unfavorable conditions, the sediments provide a refuge for resting stages of various taxa, which may become active when conditions become more favorable or storm events resuspend them (e.g., Marcus and Boero 1998). Emergence from sediments may be suppressed by anoxia, darkness, or physical contact with the sediment and may therefore be affected by the bioturbation activities of below-SWI organisms. Copepod eggs, for example, are extremely hardy and can pass through digestive tracts of macrofauna unharmed, although predation by meiofauna may occur. Resting stages may be relocated by dredging activities or in guts of organisms that are transplanted for aquaculture. Sediments may also provide refugia for other pelagic organisms such as fungi, viruses, and parasites. (See discussion of the predatory dinoflagellate *Pfiesteria piscicida* in Smith et al. 2000). The linkage to above-SWI diversity is very tentative, but removal of key fish predators is likely to affect pelagic food chains.

The benthos can be an important food resource for above-SWI organisms. Changes in size and species composition of infauna, such as after chronic bottom trawling or short-term anoxia events resulting from eutrophication, influence above-SWI species feeding at the sediment-water interface. Bottom-feeding fishes that depend on infauna may then switch to other prey or migrate elsewhere (Feder and Pearson 1988). As described above, a variety of above-SWI species feed on below-SWI organisms, including many that contribute to important commercial fisheries.

Linkages in the open ocean

Within the open ocean, a significant portion of the water column is spatially decoupled from the sediment-water interface, and most organisms living near the ocean's surface have no direct contact with the sediment. Unlike the nearshore environment described above, there is no primary production near the bottom, and the exchange of dissolved materials, including nutrients and dissolved gases, is extremely slow relative to biotic lifetimes. The water column depths involved may be several kilometers, and vertically migrating predators span the full water column only in shallower areas. Thus, linkages between diversity in the above- and below-SWI fauna are likely to be even less direct than in other marine systems, although the potential mechanisms have some similarities. This decoupling presents problems in defining biogeographical provinces (e.g., Angel 1997), which, though well defined in shallow water and open-ocean surface waters, are probably blurred in deeper water, where temperature and light are less variable.

A number of studies have suggested that latitudinal diversity patterns exist in above- and below-SWI communities. Although ocean currents and wind patterns greatly

complicate simple generalizations, it has been suggested that phytoplankton diversity decreases toward higher-productivity areas as a few dominant species take over. Data from McGowan and Walker (1985) suggest a general decrease in pelagic copepod diversity with latitude within the North Pacific, although regional oceanography blurs any simple trend. Angel (1997) suggests a decline in diversity with increasing latitude in the North Atlantic for several pelagic animals, a pattern seen to at least 2000 m depth. In general, this pattern is consistent with macrofaunal shallow-water and deep-sea data, but it contradicts patterns in nematodes (Figure 2a). Although it is tempting to suggest that the diversity of pelagic organisms that provide food for the benthos may be linked to the diversity of below-SWI organisms, the patterns represent a weak correlation.

Another pattern that can be compared between above- and below-SWI communities is the relationship with depth. Rex et al. (1997) reviewed depth-related patterns in the below-SWI fauna and observed highest diversity at intermediate depths of approximately 2000 m. Other studies have also observed peaks at intermediate depths, although peaks are not necessarily at the same depths. Local diversity of phytoplankton tends to increase with depth until light becomes limiting. Zooplankton diversity may also reach a peak at intermediate depths in the North Atlantic (Angel 1997; Figure 2b). Water column diversity has also been compared along a transect running perpendicular to shore (Angel 1997) and suggests a pattern of low diversity across shelf depths, a peak at the shelf break, and a decline over the continental slope (Angel 1997); the sampling transect did not extend to mid-continental slope depths where Rex et al. (1997) observed a diversity peak. There are also intriguing examples of high-diversity shelf habitats (Gray et al. 1997), illustrating the need for better sampling coverage to achieve generalizations.

Although there are some similarities in patterns of above- and below-SWI communities over broad spatial scales (Boucher and Lambshead 1995, Angel 1997), there is little evidence for cause and effect. It is equally plausible that similar processes (e.g., productivity, energy) affect above- and below-SWI biota similarly and that diversity patterns are unrelated. Geological history (e.g., Jablonski 1993), which may have similar consequences for above- and below-SWI organisms, adds further complication.

The open ocean: Water column-down linkages

Productivity is the most likely mechanism by which above-SWI organisms affect the sedimentary infauna living in the highly food-limited deep sea. Materials sinking from surface waters fuel the benthos far below, and it is possible that patterns in the deep-sea benthos may be linked to diversity and temporal variability in food resources. There is ample evidence that food pulses support a somewhat-specialized subset of species in this environment, and there is some evidence that different food resources may support different

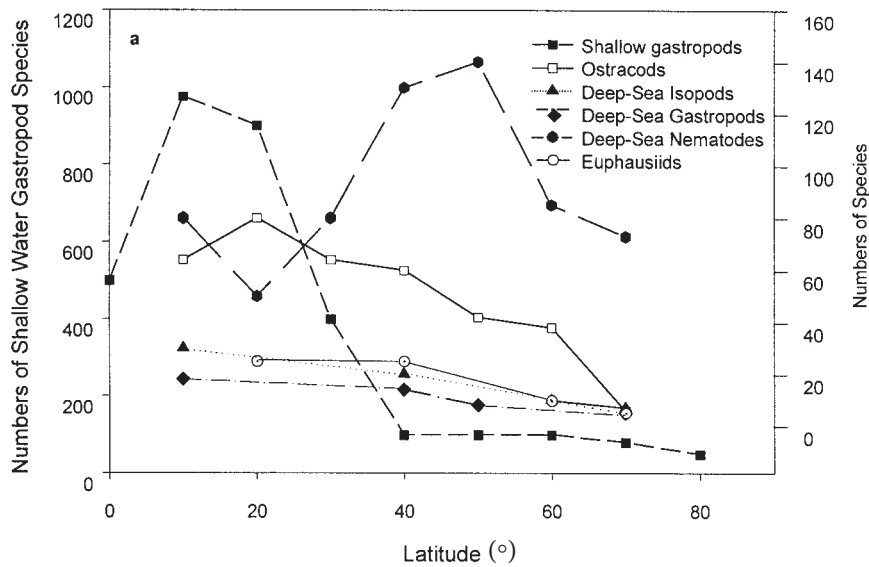


Figure 2a. Patterns of diversity with latitude for a variety of pelagic and benthic taxa. Sources of data are Roy et al. (1998) for shallow gastropods, Angel (1997) for ostracods, Rex et al. (1993) for deep-sea gastropods and isopods, Lambshead et al. (2000) for nematodes, and Pierrot-Bults (1997) for euphausiids. Different sampling intensities and measures were used in different studies so that comparison should be only between patterns in different groups rather than between samples.

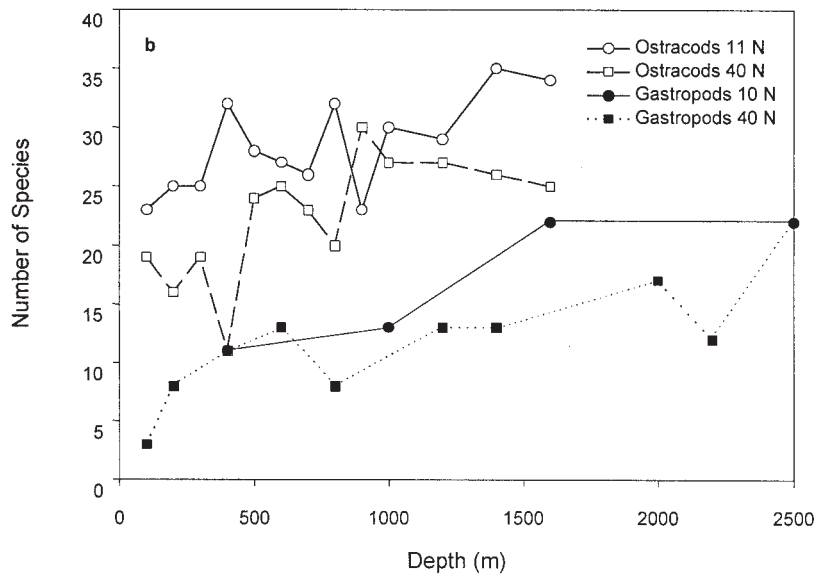


Figure 2b. Changes in diversity with depth for benthic and pelagic taxa. Ostracod data are from Angel (1997), and gastropod data are from Rex et al. (1997). Again, different sampling intensities and measures were used in different studies so that comparison should be only between patterns in different groups rather than between samples.

faunas (Snelgrove et al. 1992). Benthic infaunal species also aggregate, possibly because detritus distribution is not uniform or because different types of detritus might attract different types of species. One current theory is that small-scale patchiness in food supply is critical in promoting deep-sea diversity (Grassle and Sanders 1973). But again, it is unclear whether diversity of food resources (and thus pelagic diversity) makes any real difference. There is some congruence in global-scale patterns of surface productivity and deep-sea biodiversity patterns that suggests ecological coupling through the water column (Rex et al. 1993). The bathymetric diversity pattern has been related to a gradient in productivity that decreases from the coast to the deep ocean. There is sufficient benthic and pelagic biodiversity data to begin testing this idea more thoroughly.

Correlative linkage between broad-scale surface productivity and benthic diversity can be tested with existing data on global export production (Falkowski et al. 1998) and regional studies of infauna. Plotting species counts for different taxa on Falkowski et al.'s estimates for carbon export suggests that there may indeed be a relationship between productivity and diversity for some taxa, with a decline in diversity as productivity increases. (Figure 3; Table 1. See also Watts et al. 1992 for a more detailed analytical approach.) Whether this pattern relates to amounts, or to variability, of carbon export is difficult to judge since sample sizes are small and many highly productive areas are also quite seasonal. Unfortunately, the spatial coverage that has been achieved in the sampling of benthic organisms in the oceans is insufficient to be certain that such relationships exist.

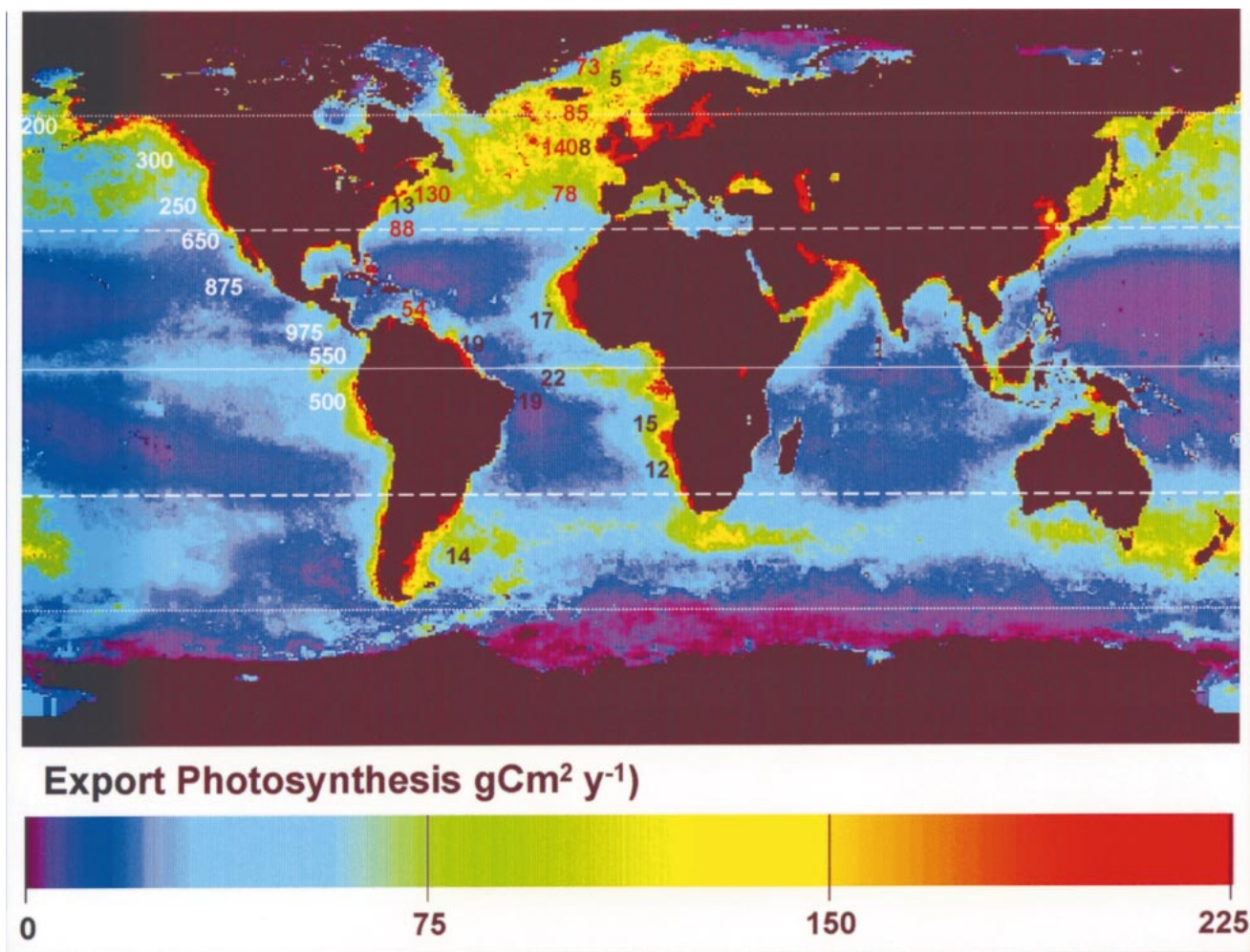


Figure 3. Estimates of deep-sea diversity for various taxa superimposed on an image of global carbon export pattern as estimated by Falkowski et al. (1998). Carbon export image reproduced from Falkowski et al. (1998). Numbers in red are nematode species counts from Lambshead et al. (2000), numbers in white are shallow mollusk species counts from Roy et al. (1998), and numbers in black are expected species in sampling 50 individuals from Rex et al. (1993). Because of different sampling intensities and measures used, comparison should be only between patterns in different groups rather than between samples.

Again, the importance of above-sediment diversity, as opposed to productivity, is unclear.

Predation effects in the deep sea, and particularly effects on diversity, are not well understood. Predation by above-SWI organisms was one of the first processes suggested to be important in structuring deep-sea biodiversity (Dayton and Hessler 1972), although shallow-water data suggest that predators depress diversity at small scales. The role of predators in creating disequilibria that were described for shallow water has a similar potential application here. There is little evidence that pelagic predators feeding on infauna are particularly selective with respect to species composition, but successional mosaics may be created by patchy predation. Recent caging experiments in the San Diego Trough (Eckman et al. 1999) tested the role of predation in maintaining deep-sea diversity. No studies have been designed to test whether the diversity of these predators is significant for

infaunal communities. Another possible effect of predation occurs during the reproductive phase, when some deep-sea species release reproductive propagules into surface waters, where they may be subject to predation or competition with pelagic species. The magnitude of this impact is difficult to evaluate, but given the lesser importance of planktotrophic larvae in the deep ocean than in shallow water and the large spatial decoupling involved, a diversity linkage seems unlikely. One final point regarding deep-sea predators is that many are essentially decoupled from surface waters, where production takes place. Although some species make extensive diel migrations, many deep-sea predators are more tightly coupled to the benthos than they might be in shallow water.

Habitat complexity in the deep sea is considerably less than in shallow water, with bioturbation, predation, and food flux contributing to benthic diversity through creation of

Table 1. Correlational relationships among latitude, productivity export, and diversity.^a

| | | Latitude | Productivity | Diversity |
|------------------------|--------------|----------|--------------|-----------|
| Deep-sea gastropods | Latitude | – | 0.612 | –0.591 |
| | Productivity | 0.180 | – | –0.888 |
| | Diversity | 0.216 | 0.002 | – |
| Shallow-water mollusks | Latitude | – | 0.631 | –0.798 |
| | Productivity | 0.280 | – | –0.840 |
| | Diversity | 0.053 | 0.027 | – |
| Deep-sea nematodes | Latitude | – | 0.534 | 0.225 |
| | Productivity | 0.824 | – | 0.561 |
| | Diversity | 1.00 | 0.741 | |

^aThese analyses are based on different types of diversity estimates as described and from the same sources as in Figure 3, and approximate measures of productivity export as extracted from the color image in Falkowski et al. (1998). As such, this should be treated as an exploratory analysis designed to stimulate more rigorous comparisons. Values above dashes are Pearson correlation coefficients, and those below dashes are Bonferroni-adjusted probability values with significant values shown in bold. It should be noted that more detailed analysis by Lamshead et al. (2000) has indicated a significant positive relationship between productivity and deep-sea nematode species richness.

How can above–below SWI linkages be more effectively tested?

Given the potential relationships outlined above and the current interest in biodiversity, it is critical that we strive for a better understanding of how above- and below-SWI diversity are linked in the oceans before too many of these habitats and their linkages are unwittingly altered by human disturbance. Determining interaction of above- and below-SWI diversity is a great challenge. Analysis of natural patterns with more complete spatial coverage globally, including areas with unusual characteristics, will clarify whether latitude, productivity, and depth influence diversity within the pelagic and benthic domains. Experimental studies will be necessary to determine causality within domains and will be critical for linking above- and below-SWI diversity. An obvious means of testing the importance of diversity in one domain relative to the other is to manipulate diversity in one and monitor response in the other. Unfortunately, manipulation of sedimentary habitats is extraordinarily difficult because removal of specific groups of organisms usually disturbs the sediments and alters basic geochemistry. Baited traps and selective poisoning offer one approach to “removing” certain groups. It is also feasible to build on caging experiments by excluding pelagic species either completely or selectively, allowing effective *in situ* tests of impacts. The importance of organic-matter diversity could

also be tested by manipulating the types of food resources supplied to sediments and below-SWI organisms. Mesocosms, where species composition can be carefully regulated in the above- and below-SWI communities, offer another effective means of studying above–below processes (e.g., Widdicombe and Austen 1998). The trick is to strike a balance between ease of control and maintaining a “natural” ecosystem. In short, the linkages between above- and below-SWI diversity have received little attention, and are an area where many research opportunities exist and many questions remain to be answered.

Acknowledgments

We wish to thank to Diana Wall for her leadership in tackling soil and sediment biodiversity. We also thank the SCOPE Committee on Soil and Sediment Biodiversity and Ecosystem Functioning; an anonymous US foundation; and the Ministries of Agriculture and the Environment, The Netherlands, for providing funds to host the workshop “The Relationship between Above- and Belowsurface Biodiversity and Its Implications for Ecosystem Stability and Global Change” in Lunteren, The Netherlands. The efforts of Gina Adams in orchestrating the workshop that led to this

microhabitat. As mentioned earlier, it is thought that micropatches create habitat heterogeneity that is critical in promoting deep-sea diversity; thus, a greater diversity of predators, bioturbators, and food types should create a greater diversity of patch types and therefore a greater diversity of benthos (e.g., Snelgrove et al. 1992). Sediment diversity has been shown to be a significant predictor of biological diversity in the deep sea (Etter and Grassle 1992), suggesting that habitat is indeed important to deep-sea organisms on many scales. However, linkages of diversity and habitat patchiness have not been broadly established.

The open ocean: Sediments-up linkages

As indicated earlier, there are likely very few bottom-up effects of open-ocean infauna, although their role in global carbon (benthic mineralization) and nitrogen (denitrification) cycles may be underestimated (Heip et al., in press). The huge scales involved suggest that biodiversity likely plays a minor role, except perhaps in terms of functional groups. As in shallow systems, some benthic species produce pelagic larvae. But low faunal densities in the deep sea suggest that reproductive propagules will be few and their impact on above-SWI organisms minimal.

synthesis are also greatly appreciated. Thoughtful reviews by Rebecca Chasan, Paul Dayton, Diana Wall, and three anonymous reviewers improved this manuscript and are much appreciated.

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