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The Importance of Marine Sediment Biodiversity in Ecosystem Processes

Sedimentary habitats cover most of the ocean bottom and therefore constitute the largest single ecosystem on earth in spatial coverage. Although only a small fraction of the micro-, meio- and macroscopic benthic organisms that reside in and on sediments have been described and few estimates of total species numbers and biogeographic pattern have been attempted, there is sufficient information on a few species to suggest that sedimentary organisms significantly impact major ecological processes. Benthic organisms contribute to regulation of carbon, nitrogen, and sulfur cycling, water column processes, pollutant distribution and fate, secondary production, and transport and stability of sediments. Linkages between groups of organisms and the level of functional redundancy is poorly known, however, there is probably substantial redundancy within groups. There is little evidence that biodiversity *per se* is necessary for benthic systems to contribute to ecosystem services, but because linkages are so poorly known and predictive knowledge confined to a few species, it is not presently possible to predict exactly how species loss will impact these services and ecosystem health. Thus, a precautionary approach of "assume the worst" is advised, and every effort should be made to curtail the species and genetic diversity loss resulting from fishing, pollution, habitat destruction, introduction of non-native (exotic) species, and global warming. Concurrently, scientists must take advantage of exciting, rapidly evolving technology and a rejuvenated interest in biodiversity to provide more concrete and thorough information on benthos and ecosystem processes.

INTRODUCTION

Oceans cover 70% of the Earth, and most ocean bottom is covered in sediments ranging from gravel to fine muds; this makes it the largest habitat on our planet in areal coverage. Some sediments are uniform in grain size, some are mixed, some are biological in origin and others are geological. Much of this habitat (~ 83%) is greater than 1000 m depth (1), so most marine sediments are located in a cold, lightless, high pressure habitat where food is supplied from distant surface waters. Surprisingly, the benthic (bottom) organisms that reside within marine sediments are extremely diverse. For example, of the known 29 nonsymbiotic animal phyla, all but one occurs in marine habitats and 13 are solely marine (2). There are some 10^5 species described from marine sediments and perhaps 10^8 that remain undescribed (Table 1). But is consideration of and inventoring biodiversity little better than stamp collecting as was once suggested by the physicist Ernest Rutherford? Among the many reasons for considering living organisms differently from stamps are their roles in maintaining the Earth's life support system. Indeed, a recent study suggested that oceans account for ~ 2/3 of the value of global ecosystem services (29). They play a major role in climate regulation, provide protein for human consumption, and regulate global water, nutrient and carbon cycling. They absorb and dilute pollutants, provide recreation and employment, and bear ~ 2/3 of human populations on their shores. The purpose of this review is to evaluate how organisms in marine sediments impact the many processes in which oceans are so

important. More specifically, we investigate the importance of sedimentary biodiversity in these processes to evaluate whether species loss will have a major impact on ecosystem health and ecosystem services that oceans provide.

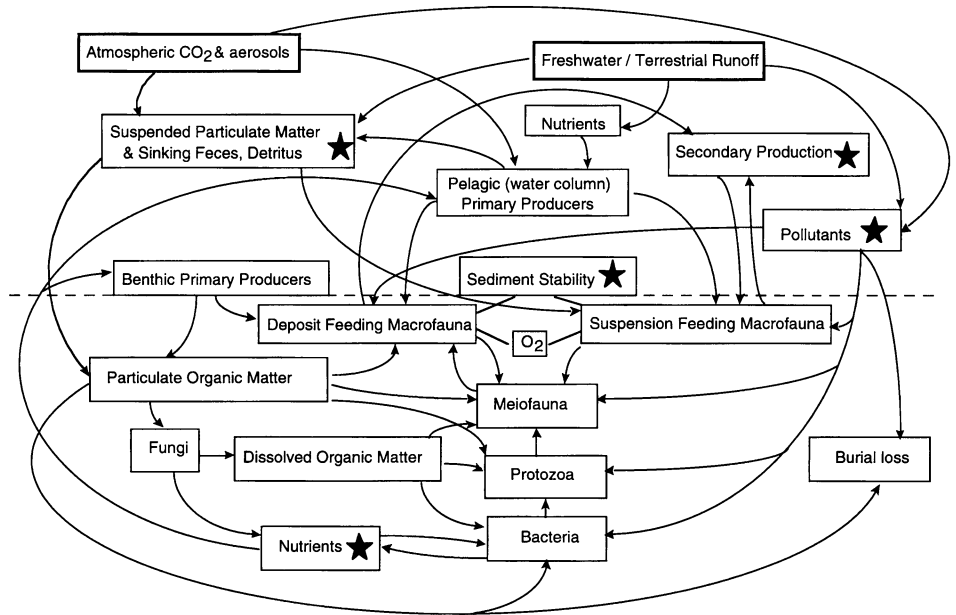
BIODIVERSITY IN MARINE SEDIMENTS

Efforts to evaluate biodiversity on a global scale pale in comparison to the effort that remains. This is largely a problem of logistics. For metazoan taxa there are sampling techniques that scientists agree are sufficiently quantitative (30), and the challenge is in finding resources to sample and process material representative of the 3.6×10^8 km² of ocean bottom. For the phylogenetic domains bacteria, archaea, protozoa, and fungi there is an additional problem defining species. The reproductive biology of these groups does not allow application of a metazoan species concept, and species must therefore be defined on genetic, chemotaxonomic, physiological, and ecological criteria. The task becomes even more daunting because this approach requires culturing microorganisms, and only a small percentage can presently be grown (31). Thus, our discussion of microbial diversity is very preliminary.

There are few syntheses on patterns of global biodiversity, and those that exist include only a subset of all species. Because marine scientists often specialize on one of the size groupings of sedimentary organisms (macrofauna, meiofauna, microbes), biodiversity tends to be treated accordingly. This division is not strictly one of convenience and size because there are major differences between groups. Global biodiversity estimates for any given taxon are also very tenuous, and this is particularly true for benthic marine organisms given the relatively small proportion of habitat and organisms that has been sampled (8). Nonetheless, we have estimated global numbers of described and undescribed benthic species based on existing data (Table 1) for individual phyla. Regional community-level studies have extrapolated species number to a global estimate for several groups. Marine sediments may contain up to 10^8 nematode species (8) and deep-sea macrofauna have been estimated at 10^7 species globally (1). Others argue that macrofaunal estimates of 500 000–5 million (32) are more appropriate. Suggestions that the deep sea is more diverse than shallow habitats (1) have been questioned, indicating that the North Atlantic study (1) may not be globally representative (18, 33). Proposed latitudinal gradients with high tropical and low polar diversity for deep-sea macrofauna (34) have also been debated (9).

Global syntheses of benthic species distributions and composition are generally limited to regional monographs (Table 1), but we can draw generalizations that are common to all groups. Species patterns correlate well with historical disturbance (e.g. glaciation), sediment grain size, organic content, depth and temperature. Global syntheses of species patterns in relation to these factors could be extremely illuminating. Many benthic species, from bacteria (35) to macrofauna (36), are considered cosmopolitan in distribution, but increasing evidence suggests some "species" may in fact be species complexes (36). The large proportion of undescribed species (Table 1) and other taxonomy problems (8) impede estimates of global diversity patterns; science must use all available data and generate new data to improve estimates. For example, changes in distribution and diver-

Figure 1. Schematic simplification of ecological relationships among sedimentary organisms in the oceans. Bold boxes indicate linkages with other (non-marine) domains. Arrows indicate direction of energy/material flow, lines without arrows denote links without transfer of energy/material and dashed line indicates sediment-water interface. Stars indicate ecosystem processes in which sedimentary organisms play a major role. For clarity only the most significant linkages are shown.



sity over geological time could be studied in well-fossilized taxa, e.g. ostracods (37), mollusks (23).

THE BIOLOGY OF SEDIMENTARY ORGANISMS

In terms of ecosystem services, the most important activities of benthic organisms are direct and indirect effects of their efforts to obtain food. Particularly for larger organisms, most activity is in the top 1–2 cm of sediment where O₂ and organic matter are most abundant, but some organisms oxygenate sediments to greater depths and some nematodes, protozoa and bacteria occur in deeper, anoxic sediment.

Fungi and Bacteria

Fungi hydrolyze lignocellulose and chitin, both of which are highly refractory. Bacteria decompose particulate organic carbon, which is composed largely of algal and fecal detritus. Hydrolytic bacteria begin the process and generate dissolved organic carbon (DOC) (Fig. 2, ref. 38). In the presence of O₂, NO₃⁻, Mn⁴⁺, Fe²⁺ or sulfate, DOC is oxidized to CO₂ with the production of corresponding reduced inorganic molecules (H₂O, N₂, Mn²⁺, Fe³⁺ and HS⁻). Alternatively, DOC may be fermented to CO₂ and CH₄. Of these bacteria, the sulfate-reducers are the best characterized in marine sediments. It is presumed the denitrifying bacteria are normal aerobes, respiring NO₃⁻ in an anaerobic environment. Ammonium, which is liberated with carbon oxidation in

addition to the other reduced inorganic solutes (Mn²⁺, Fe²⁺ and HS⁻), may be oxidized by chemolithotrophic bacteria which are also autotrophic. As little energy is gained from these oxidations, there is limited biomass production. However, the oxidations complete the geochemical cycles involving C, N, S, Fe and Mn within sediments and regenerate the oxidants. Whereas the identity of the heterotrophs is largely unknown, the bacteria involved in NH₄⁺ and HS⁻ oxidations have been studied in detail, as have the CH₄ oxidizers. The rates of most of these processes can be measured, even though numbers and identities of the relevant microorganisms are unknown.

Protozoa and Meiofauna

Feeding in protozoa (39) and meiofauna (40) is not well understood, but both groups have representatives that feed on bacteria, fungi, microalgae, and organic detritus. Nematodes and copepods may be roughly divided into different feeding types based on the mechanism and selectivity of how they remove organic particles from sediment grains, though there are predatory species as well.

Macrofauna

Feeding in macrofauna is well-known for a few select species, but for most we must infer feeding behavior from morphology. Although other feeding modes exist, most macrofauna are suspension or deposit feeders. Suspension feeders remove particles passively from overlying water via tentacles (e.g. polychaetes), antennae (e.g. crustaceans) or active pumping through a siphon (e.g. bivalves) or tube (e.g. the polychaete *Chaetopterus*). Deposit feeders obtain nutrition from organic particles associated with sediments. Surface deposit feeders graze on surface sediments (e.g. urchins), and some species cache particles at depth (e.g. sipunculids) (41). Sub-surface deposit feeders burrow beneath the sediment surface and can ingest and defecate sediment very rapidly (42), in some cases subducting surface particles as pits form (e.g. the polychaete *Arenicola*) (43). Somewhat sedentary species (e.g. some maldanid polychaetes) which feed at depth and defecate on the surface are effective “conveyer belts” for sediment particles. There are also mixed-strategy feeders that switch from suspen-

Table 1. Biogeographical diversity of major groups of biota in marine sediments. Figures in parentheses refer to references listed below.

Major groups described	Number of species (/1000) estimated	Number of species (/1000) synthesis	Regional biogeographical synthesis	Global biogeographical
Microbial				
Fungi	~ 0.6 (3)	> 2 (3)	None	None
Bacteria	~ 0.5	10 ⁵ ?	None	None
Ciliates	~ 1.0 (4)	8? (4)	Community	None
Flagellates	~ 1.0 (4)	unknown	Taxonomy	None
Forams	> 0.8	unknown	Comm. + Tax. (5)	None
Meiofauna				
Nematodes	4.0 (6)	10 ³ (7)–10 ⁵ (8)	Comm. + Tax.	(9)
Copepods	2.5 (10)	5 (10)	None	(11)
Turbellarians	~ 0.5	3?	Comm. + Tax. (12)	None
Macrofauna				
Polychaetes	> 10 (13)	25?	Tax. (14–16)	None
Crustaceans	~ 21 (17)	500 (18)	Tax. (19–20)	None
Mollusks	50 (13)	200 (21)	Tax. (21)	(22; 23)
Echinoderms	7.0 (13)		(24; 25)	None
Minor phyla				
Echiura	0.1 (13)	unknown	(26)	None
Sipunculans	0.3 (13)	unknown	(26; 27)	None
Nemertean	1.0 (13)	unknown	(28)	None

**Studies have been based on community structure (Comm.) or on taxonomic considerations (Tax.)

sion to deposit feeding depending on water and food flux (e.g. spionid polychaetes) (44). Macrofaunal tubes and burrows increase the sediment surface area in contact with overlying water and induce currents (45), thereby increasing solute exchange.

FUNCTIONAL ROLES IN ECOSYSTEMS

Production in the oceans begins with pelagic and benthic algae that utilize sunlight and CO₂ to produce ~ 40–50% of global primary production (46). The amount of algal material sinking to the bottom from surface waters is variable but substantial (47), and combined with benthic algae in shallow-water ecosystems, provides fuel for benthic systems. The focus on feeding above is deliberate because feeding is critical in describing how benthos impacts ecosystem functioning (Fig. 1).

Benthos impacts water column processes, and trophic transfer: Plant material and feces may either settle to the sediment or may be removed from the water column by suspension feeders. In some areas, suspension feeders significantly impact water clarity (48), and this is one ecosystem service provided by sedimentary fauna. Deposited material may be directly ingested by deposit feeders or may become part of the particulate organic matter (POM) pool that is eventually ingested by macrofauna, meiofauna or protozoans. Much of this POM may be acted upon by bacteria and/or fungi, particularly if it is initially too refractory for larger organisms to metabolize. Some material will be partially decomposed by bacteria and fungi to enter the dissolved organic matter (DOM) pool, where other bacteria utilize it. Some protozoa and meiofauna also utilize DOM (49). The decomposition of DOM and POM by bacteria and fungi releases nutrients, which are supplemented by meio- and macrofaunal excretion. If POM is buried before organisms decompose it, then POM is lost from the system and the potential for fossil fuel formation begins. Synthesis of cell walls and sorption of dissolved organic carbon to silt particles may create nondegradable products (50) that may be buried and thus lost from the ecosystem.

Benthos impacts global carbon, nitrogen and sulfur cycles, because these cycles are intimately linked to the various chemical transformations described in the previous section on feeding. These cycles are also greatly influenced by transport of solutes and particles (discussed earlier), and macrofaunal organisms are extremely important sediment irrigators; O₂ penetration regulates the cycles described below, and macrofaunal burrows, tubes, and reworking all regulate oxygen penetration (51).

Different groups have roles of different magnitude and function in global carbon cycles. Protozoa and meiofauna have a modest impact on decomposition and carbon cycling, at least in coastal systems (49). It has also been argued that macrofauna have little impact on carbon cycling (52), but microbial breakdown is undoubtedly of major importance. Given the proportion of global production that occurs in oceans and the area of ocean bottom covered by sediments, benthos must impact carbon cycling. Global warming depends on atmospheric CO₂; whether organic matter is recycled as CO₂ or permanently buried in ocean sediments depends on the interplay between microbial breakdown, sedimentation, and deposit feeders mixing/burying particles vertically within sediment.

Nitrogen cycling is also closely linked to benthos. Decomposition and excretion produce ammonia and nitrate that diffuse out of sediments. Both of these nutrients may be utilized by primary producers to begin the cycle anew. Bacterial denitrification within the sediments converts these products to dissolved nitrogen gas, which is unavailable for primary producers other than nitrogen-fixing cyanobacteria. The rates at which these reactions occur is sensitive to O₂ which in turn is impacted by macrofaunal bioturbation (52). Thus, there is evidence that microbes and macrofauna play key roles in nitrogen cycling and therefore in oceanic and global productivity.

Benthos is also important in sulfur cycling. Sulfate reduction

and sulfide oxidation are the two main routes by which sulfur compounds are metabolized in sediments, and bacteria are key players in this process. It has been inferred from the fossil record that benthic organisms have a major effect on sulfur storage in sediments (53), presumably by regulating O₂ and labile carbon penetration. Globally, sulfur is rarely limiting, but it is important in global carbon cycling and cell processes.

Benthos impacts pollutant metabolism, burial and transport. Oceans have some capacity to absorb pollutants by diluting and/or metabolizing them to non-toxic forms, and sedimentary organisms impact this capacity. Some microbes metabolize certain pollutants (54) and thus remove them from the system. Macrofauna can metabolize or concentrate some pollutants, thus reducing concentrations in the water column and sediments but potentially transferring them up the food chain. Macrofauna also impact pollutants through mixing. Some species accelerate removal of material from surface sediments if they feed at the surface and defecate at depth. Alternatively, feeding at depth and surface defecation may impede burial. Diversity of feeding modes and impact on sediment movement has been reviewed elsewhere (43).

A variant on the pollutant theme is the role that coastal transitional systems such as salt marshes, mangroves and seagrasses play. These habitats are a key transition from terrestrial to marine habitats (Fig. 1, Table 1 in ref. 38) and can be important as juvenile habitat for important secondary production described below. But these systems also act as filters for sedimentation, pollutants and elevated nutrients associated with coastal runoff (55). Transitional zones trap sediments and associated pollutants, and they also have a greater capacity to absorb nutrients than coastal oceans because the zones are nutrient-rich themselves. Sedimentation impacts coastal ecology, circulation and geology (e.g. beach erosion,) and elevated nutrients in coastal oceans may lead to algal blooms and associated hypoxia, changes in benthic community makeup, and thus ecosystem service. Thus, removal of these transition zones is likely to accelerate coastal eutrophication and ecosystem health. These zones also reduce coastal erosion.

Benthos impacts sediment stability and transport, which has been reviewed elsewhere (56) and will be described only briefly here. Tubes of animals (e.g. ampeliscid amphipods) and mucous (e.g. motile gastropods) bind particles and stabilize sediments (57). Thus, destabilizing effects of bioturbation (56), stabilizing effects of mucous binding (57), and variable effects of biological sediment redistribution and alteration of bottom roughness, all influence sediment erosion. From a human perspective, sediment mobility is particularly important to coastal geology, e.g. shoreline erosion, deposition, and fate of pollutants.

Benthos provides food for human consumption. Some sedimentary fauna themselves are commercially important (e.g. scallops, lobster) and others are food for adults (58) and juveniles (59) of demersal (near-bottom) species (flatfish, cod) that are an important part of the commercial fisheries of the world. Thus, even lowly polychaete worms are a key part of the marine food chain that ends on kitchen tables around the world.

LINKAGES BETWEEN SIZE GROUPS

None of the processes described above operates completely independently between macro-, meio- and microorganisms (Fig. 1). Bacteria are a major food source for protozoans (4) and meio- (49) and macrofauna (56) feed on bacteria. Macrofauna may prey on meiofauna, and meiofauna can prey on juvenile macrofauna (60). Bacterial grazing by protozoa, meiofauna and macrofauna can increase or decrease bacterial activity (49) and thus remineralization of organic matter (61). There is little evidence that protozoa are a key food source for larger organisms, except in systems such as seagrasses, so they presumably die and are decomposed by bacteria (49). As discussed earlier, macro-

fauna can impact solute flux (including oxygen) as well as vertical transport of organic matter. For example, macrofaunal irrigation results in oxygenation of pore water adjacent to the burrow or tube and this has important repercussions on microbial distribution, activity and processes. However, bioturbation also mixes POM into the lower sediment strata, where sulfate reduction results in HS^- production and O_2 consumption. Clearly, the relationship between groups is complex, and changes in one are likely to have major ramifications for others as well.

DOES FUNCTIONAL REDUNDANCY EXIST IN SEDIMENTARY ORGANISMS?

If genetic and species loss is occurring, a critical question is whether different species have redundant roles in ecosystem services. At present, we feel there is sufficient evidence to conclude that:

- the ecological services provided by macro-, meio- and micro-organisms are quite different; e.g. bacteria cannot compensate for loss of macrofauna. However,
- human disturbances that cause a fundamental change in organism functional type will change the basic ecology of the system along with ecosystem services. For example, complete removal of deposit feeders will decrease O_2 penetration in sediments and alter nitrogen cycle processes as the bacterial community becomes anaerobic. Removal of some macrofauna may leave ecosystem services unaltered if sufficient functional redundancy exists. Thus,
- there probably is redundancy in many systems, and species within each group could be removed without really changing the system. There is no evidence that biodiversity *per se* is needed for healthy ecosystem functioning and habitats often contain, for example, several species of subsurface deposit-feeders or nitrifying bacteria. All are probably not essential for ecosystem functioning. However, there are major caveats to this statement. (i) Some species have disproportionate influence relative to others, and their removal will have major impacts. (ii) A species may have the capacity to “fill in” if another is eliminated, but it may not if other aspects of their ecology differ. (iii) Species linkages are poorly understood, and removal of one could affect services through disruption of others. Thus, we expect that significant functional redundancy exists within groups, but we do not know what caveats apply to each species and which could be lost with least impact.

RESPONSE TO HUMAN DISTURBANCE

Human impacts on marine sedimentary organisms are substantial. They result directly from actions in the marine environment and indirectly from actions in other domains, all of which impact the marine sediments via critical transition zones (38).

Fishing impacts benthos through physical damage to the structural complexity of habitats by trawling (62), redistribution of sediments that damages animals and buries others, injury and death of non-target species (63), disposal of by-catch that creates localized eutrophication-like conditions, and disturbance through removal of major predators that may have a significant impact on benthos. Fishing impacts are best documented for macrofaunal taxa (62) and it is likely that physical disturbance will have little direct impact on meiofauna and microbes, but they are vulnerable given the importance of O_2 and POM in limiting distributions.

Coastal development results in habitat loss through filling and sedimentation.

Pollution and eutrophication are common in coastal areas, and are likely to impact all groups.

Microorganisms are probably less sensitive to toxic pollutants than the other groups, but impacts would be expected. Meiofaunal (64) and macrofaunal (65) species composition and di-

versity are both changed by pollution, which often leads to high abundances of few species. Pollution by heavy metals, oil and heating (power stations) selectively affects species of polychaetes, crustaceans and mollusks (66) through mortality, impacts on fecundity and behavior, and compromised health.

The introduction of exotic species is now becoming recognized as a serious problem. San Francisco Bay ecology has been completely altered by the introduction of nonindigenous species from ballast water or hulls of ships (67).

Global warming could change ocean temperatures, circulation (68) and therefore patterns of surface production. Macrofauna are sensitive to changes in POM input, and to some degree to temperature and salinity. A related example is that global warming is implicated in the northerly shift in California's rocky intertidal fauna (69). Microbes and meiofauna, may be affected indirectly via POM and O_2 changes.

There is little evidence for species extinctions from marine sediments as a result of human activity, though examples of local extinctions abound. Localized extinctions impact genetic diversity (66). Populations often differ in genetic makeup, so population loss may be irreversible if specialized genes are also lost. In addition, biodiversity is so poorly known that global species loss might be occurring without being recorded, and our lack of examples may simply reflect lack of information.

METHODS TO ASSESS FUNCTIONAL BIODIVERSITY

Studying functional diversity is limited by our lack of knowledge of the organisms present, but overcoming this shortcoming is at least now possible for many organisms and improving for microbial groups where methodological problems persist. Molecular methods may be unable to provide answers to some basic questions in microbial ecology, as their main strength is in comparing naturally occurring microbial diversity to well-characterized pure cultures. The detection of mRNA for specific key enzymes may seem to provide an assessment of certain metabolic activities, but there are a number of possible errors. Some enzymes are not constitutively expressed, the mRNA may code for an unrelated protein with a completely different function, degeneracy of the genetic code may prevent detection due to wobble base mutations, and unrelated enzymes may be more important. These problems must be overcome before we can evaluate microbial diversity.

Our ability to assess functional biodiversity is improving rapidly. Many taxonomy problems are now being overcome with molecular and biochemical techniques. Unequivocal taxonomy is important because improved taxonomic capability will facilitate descriptive field work, such as that noted earlier for deep-sea macrofauna, to test hypotheses on biodiversity patterns. Even more exciting are recent advances in observational capability that make it easier to evaluate functional roles, redundancy, and other key questions. The MERL (Marine Ecosystems Research Laboratory) sediment/water mesocosms (University of Rhode Island) are 13 m³ experimental tanks in which miniature, natural ecosystems may be observed and manipulated, in some cases maintaining relatively natural conditions for years (70). Flumes, which are seawater channels that mimic natural flow over sediments, allow direct observations on how feeding groups impact ecosystem processes (71). Fluorescent particles (72), stable isotopes (73) and fine-scale video apparatus (74), allow tracing of processes and observation at scales relevant to the animals themselves and to a degree not previously possible. However, manipulative field experiments are sorely needed for all marine benthic systems. Though they can be difficult, such experiments have even been carried in the deep sea (75), which is the most costly and inaccessible marine habitat. Function can be assessed on the macroscale by net-metabolic rate measurements, and on the microscale by microsensors. In short, rapidly advancing tech-

nologies offer a tremendous array of tools to tackle many exciting questions on how biodiversity and ecosystem services are related.

WHAT NEEDS TO BE DONE?

Assuming that we at least have the capacity to know what is present, which is certainly true for macrofauna and meiofauna, what needs to be done?

Evaluate what and how many species are present in marine sediments from representative habitats around the world. Thus, an international program in marine biodiversity is needed to coordinate efforts of micro-, meio-, and macrofaunal specialists to address the most basic question of what is there, what they are doing there, and what is being lost.

Get quantitative data on exactly how benthos impacts each of the key ecosystem services outlined above. Most of the examples described above are only weakly supported by hard data and are more strongly supported by “gut feelings” of scientists. For example, we know that macrofauna influence sediment O₂ which in turn has a fundamental impact on microbes, but linking species to services such as nutrient cycling is at its infancy. Sufficient information is available for sulfate reducers and ammonia oxidizers to investigate biodiversity roles, e.g. in relation to animal burrows, pollutants, etc. We also know little about the autecology of sedimentary species and much of what we infer about ecosystem services provided by a species is based on data from other species we believe are similar. Thus, besides knowing what’s there, we need quantitative data on what different species are doing there.

Determine exactly where functional redundancy exists both within and across groups. Do different species impact ecological services in ways that are sufficiently similar that loss of a given species will not impact the processes described above? Are there generalities that can be drawn from studies of redundancy, such as whether macrofaunal species have higher or lower functional redundancy than bacteria? How are services provided by one group impacted by perturbations to others? For example, macrofauna may be important contributors to secondary production, so how do changes in meiofauna and microbes impact this service?

CONCLUSIONS

Much is known about bottom-dwelling organisms and flux of materials to and through them, but knowledge of linkages between marine benthic biodiversity and ecosystem processes is based on qualitative data on a few species. These data suggest that some species provide very critical and specific services to marine benthic ecosystems. The next important step is to obtain more quantitative data on individual species, including those that are less abundant or less well known, and recent methodological advances should allow us to evaluate how the loss of these species and functional groups is likely to affect marine systems. A cautionary approach of “assume the worst” is appropriate, but at the same time we feel that it should be feasible to demonstrate quantitative links between marine benthic species and ecosystem functioning in the near future. The present rate of habi-

tat degradation in marine ecosystems is alarming. Although the consequences of this loss are difficult to predict, significant loss of species and natural ecosystem services are likely. There is some solace in knowing that the potential to understand and predict the magnitude of structural and functional loss is within our grasp, and exciting ecological questions are now both socially and economically paramount.

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Research Priorities for Marine Sediments (More detail is provided in the text)

Evaluate species richness and abundance in representative marine habitats, particularly deep ocean sediments. An international collaborative program in marine sediment ecology is recommended for implementation.

Obtain quantitative data on how sediment species impact each ecosystem process, and improve our knowledge at the species level.

Identify ecosystem processes where functional redundancy occurs.

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