MACROBENTHOS

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Introduction

The macrobenthos is a size-based category that is the most taxonomically diverse section of the benthos. Only in shallow water does the macrobenthos include both plants and animals. Here, attached macrophytes (including various algae and green vascular plants) may make up a large part of the benthic biomass in coastal areas. Meadows of sea grass (which root into and stabilize coarser sediments) and forests of macroalgae (usually attached to hard bottoms) provide habitat for smaller plant and animal species. In warm, shallow water, stony corals, which flourish as a consequence of symbiotic algae living in their tissues, overgrow large areas and these reefs provide a biogenic habitat for a wealth of other species, and their broken-down skeletons provide much of the sediment in adjacent areas. But the importance of such areas declines rapidly with declining potential for photosynthesis as light quickly vanishes with increasing depth, and the macrobenthos becomes the exclusive domain of heterotrophic life (fueled by breakdown of complex organic material) in soft sediments. Only at deep-sea hydrothermal vents is there an exception to this. These support lush concentrations of benthic biomass that relies not on photosynthetic production ultimately derived from the surface but on the activity of chemoautotrophic bacteria exploiting the emissions of reduced sulfur-containing inorganic compounds.

The animal macrobenthos may be attached or may be able to move over hard surfaces provided by exposed bedrock, or may use as habitat the much larger and quantitatively important areas covered by soft sediment. Areas of rock, exposed as a consequence of water currents and turbulence (or, in the case of the newly formed sea floor at the spreading centers along the mid-ocean ridges, rock that has not had time to become covered in sediment settling from above) provide habitat for epibenthos, or epifauna. Even if epibenthos, both plant and animal, looks conspicuous between the tides (and is certainly important with respect to fouling of colonizers of submerged hard surfaces made by man, such as ships and jetties), it is only a vanishingly small proportion of the huge area of the benthic habitat covering more than half the globe that is not covered by soft sediment.

The term infauna has been used to categorize the organisms inhabiting soft sediment. But many epifauna, such as sea stars, are motile and can forage over the surface of sediments. The activities of the animals of the so-called infauna are usually focused on the sediment–water interface where their detrital food is concentrated, but this should not be taken to imply that sediment fauna is always burrowed out of sight. None the less, some species, particularly among larger crustacea, are capable of burrowing even a meter or more deep into the sediment. There are also many species closely related to epifaunal groups of hard substrata, such as sponges and Cnidaria (including sea pens, soft and stony corals and sea anemones), that anchor into the sediment for a sedentary life style, catching small particles from the bed flow.

Global Pattern in Macrobenthic Biomass

Extensive Russian sampling after World War II established the precipitous decline in benthic biomass with increasing depth into the abyss. This is caused largely by mid-water consumption of particles escaping from the euphotic zone. Globally, the amount leaving the euphotic zone should be equivalent to the so-called 'new production' of roughly $3.4–4.7 \times 10^9$ tonnes $C\,y^{-1}$, about 10% of total surface primary production. But this is distributed very unevenly. Perhaps 25–60% is exported in shallow seas, while in the deep ocean only 1–10% reaches the bottom; this is also influenced by latitude-related differences in depth of the mixed layer and intensity of seasonality in the upper ocean. **Figure 1** shows how influences such as upwelling and inshore surface productivity will also affect local values of benthic biomass. Overall, these range from highs of more than $500\,g\,m^{-2}$ in shallow, productive waters just tens of meters deep, to less than $0.05\,g\,m^{-2}$ (equivalent to $2\,mg\,C\,m^2$) on the abyssal plains. Trenches are deeper still but, by acting as sumps for material washed in from nearby island arcs and land mass, can support higher than expected biomass.
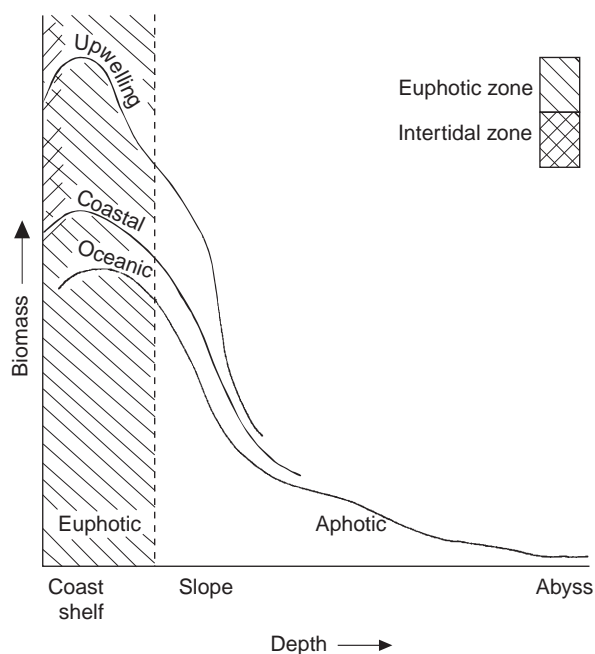
Figure 1 Conceptual model of food availability and benthic biomass in relation to depth. Upwelling areas provide nutrients for enhanced coastal productivity. The 'coastal' curve refers to shelf areas supporting high productivity (usually wider shelves with land inputs, e.g., rivers) compared to the 'oceanic' curve where oceanic effects prevail (usually narrow shelves with little land input). The mismatch in the intertidal between biomass and high food availability is explained by the co-occurrence with the latter of high hydrodynamic disturbance by waves and currents. (Modified from Pearson and Rosenberg (1987).)

History and Size Limits of Macrobenthos

The term macrobenthos dates from the early 1940s when Molly Mare published a study of an area of coastal soft sediment off Plymouth, England. In recognizing that the benthic ecosystem is fueled by a detrital rain of particles derived from photosynthetic production by macrophytes or phytoplankton, she identified the potential importance of the smaller size classes of metazoan and single-celled organism, right down to bacteria, in the decomposition cycle and food chains in the sediment. She differentiated the benthos into several subcategories based on size, or biomass. Before this time a distinct category for macrobenthos was unnecessary because the only part of the benthos generally thought to be worth studying was the animal life large enough to be eaten by fish. We now differentiate these from the very small metazoans and single-celled algae that Mare named meiobenthos. Another category is the hyperbenthos – small metazoan life that can swim off the bottom

and form a distinct community in the benthic boundary layer.

The lower size limit of macrobenthos was determined by Mare as that part retained in a 1 mm sieve, but later became reduced downwards to just 0.5 mm as it was realized not only that small, juvenile sizes were being lost in numbers but also that smaller species of groups already being sampled and taken as part of the macrofauna were not always retained adequately. Mare recognized that the limit might depend on habitat and deep-sea benthic biologists found they had to use even finer-meshed screens to collect the same sorts of animals that characteristically make up the macrobenthos in shallow waters. In the 1970s, Hessler found that he had to use a 297 µm mesh sieve to catch sufficient animal macrobenthos for study in box cores from the abyssal central North Pacific (a very oligotrophic area – nutrient-poor and therefore thin in plankton). Sieves with meshes of just 250 µm are now standard in recent large European studies on the deep-sea macrobenthos.

Sources of Food and Feeding Types

Patterns in feeding of macrobenthos have often been used to distinguish ecological zones. Although exact definition of feeding category for individual organisms has been controversial, the simplest classification is into suspension and deposit feeders, carnivores, and herbivores. More detailed categorization has proved difficult because of overlap and behavioral flexibility. Although most macrobenthos feed on detrital particles settling from the water column, such as feces, molts, and dead bodies of plankton, this passive sinking is augmented by currents that may resuspend particles periodically from the bottom. Macrobenthos may gather these particles either by catching them from bottom flow or by ingesting the sediment itself as deposit feeders, either in bulk or more selectively for the most nutritious particles. Where currents vary periodically, some animals can feed on both suspended and settled particles by simply changing the way they use their feeding appendages. Just as the particles caught by suspension feeders may range from inert floating detritus up to small swimming organisms, deposit feeding shades into predation where the particles encountered include smaller living benthos. Whether macrofauna can utilize dissolved organic matter in the sediment porewaters to any great extent is still unclear.

Wildish has provided the most satisfactory classification of macrofaunal feeding types related to environment. This keeps all three categories but

separates deposit feeders into surface and burrowing deposit feeders. Each of the five groups is subdivided in terms of motility and also in terms of food-gathering technique, such as use of jaws and particle-entangling structures. These may be arranged along an environmental gradient, such as that illustrated in **Figure 2**, to allow insight into the causal basis of previously described composition of macrofaunal communities.

The relation of feeding to small body size in deep-sea macrobenthos may be important. Thiel thought that small body size is a result of a balance between limited food and metabolic rate that makes larger size more efficient than smaller, and of the effects of small population size on reproductive success. Being small allows organisms to maintain higher population densities that increase the chance of encountering the opposite sex and so of reproducing and maintaining the population. The extent

of faunal miniaturization is still debated and, surprisingly, not readily summarized by simply taking the total bulk of the sample and dividing by the number of animals present. The exceptions seem be those organisms that have overcome the reproductive problem by being highly motile scavengers and that need also to be large enough to allow them to forage for the large food falls that occur very sporadically on the deep ocean bed. This scavenger community is quite well developed and includes close relatives of typical macrofaunal organisms in shallow water that in the deep sea grow to a relatively enormous size (**Figure 3**).

Size Spectra

If the sizes of all individuals from an area of sediment are measured and plotted as frequencies along a logarithmic size axis, a pattern of peaks shows up
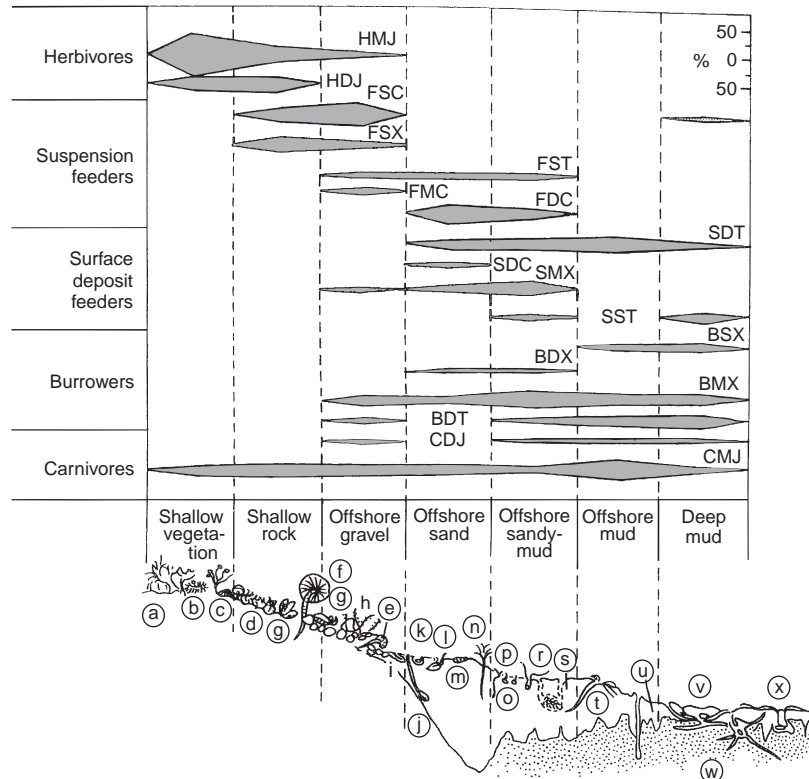

Figure 2 Distribution of functional groups in boreal coastal macrobenthos (compiled from genera listed by N. S. Jones for the Irish Sea) along an environmental gradient of decreasing food availability and water turbulence and increasing depth and sedimentation. Functional groups: H, herbivore; F, suspension feeder; S, surface deposit feeder; B, burrowing deposit feeder; C, carnivore. Motility: M, motile; D, semi-motile; S, sessile. Feeding habit: J, jawed; C, ciliary mechanisms; T, tentaculate; X, other types. In the upper panel, width of line representing each functional group along the gradient indicates proportional composition at that depth. The lower panel gives a diagrammatic representation of typical feeding position of taxa representative of various groups relative to the sediment–water interface along each gradient. Key to taxa: (a) macroalgae; (b) sea urchins, e.g., *Echinus* (HMJ); (c) limpets, e.g., *Patella* (HDL); (d) Barnacles, e.g., *Balanus* (FSX); (e), (f) serpulids, sabellids (FST); (g) epifaunal bivalves, e.g., *Mytilus* (FSC); (h) brittle stars, e.g., *Ophiothrix* (FMC); (i) *Venus* (FSX); (j) *Mya* (FSC); (k) *Cardium* (FDC); (l) *Tellinba* (FDT); (m) *Turritella* (SMX); (n) *Lanice* (SST); (o) *Abra* (SDC); (p) *Spio* (SST); (r) *Amphiura* (FDT); (s) *Echinocardium* (BMX); (t) *Ampharete* (SST); (u) *Maldane* (BSX); (v) *Glycera* (CDJ); (w) Thyasira (BDX); (x) *Amphiura* (SDT). From Pearson and Rosenberg (1987).
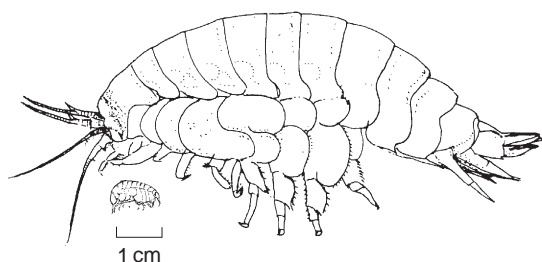
Figure 3 Gigantism in a scavenging amphipod (family Lysianassidae), the cosmopolitan deep-sea species *Eurythenes gryllus*, compared to the size of a typical shallow-water lysiannasid, *Orchomene nana* (bottom left), a northern European shallow-water species. (Redrawn from Gage and Tyler (1991) and Hayward PJ and Ryland JS (1995) *Handbook of the Marine Fauna of North-West Europe*. Oxford: Oxford University Press.)

corresponding to the micro-, meio- and macrobenthic size classes (**Figure 4**). This supports practical intuition but does not explain why such peaks occur (no such peaks occur, for example, in pelagic communities). Schwinghamer thought that these peaks reflect the way the organism perceives its sediment
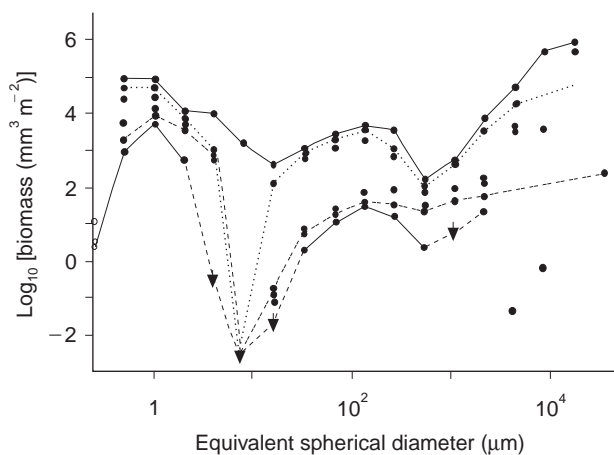

Figure 4 Macrobenthic size spectra measured from an intertidal inlet in Nova Scotia, subtidal Bay of Fundy, and abyssal sediment from the Nares Abyssal Plain south of Bermuda. The median lines (dotted for intertidal and inshore, and double-dashed for abyssal plain) and range (continuous or solid lines) show a coherent pattern with biomass peaks at 1256 and 8192 μm equivalent spherical diameter (ESD). Downward-pointing arrows indicate minimum detectable biomass. Abundance in the bacterial (leftmost) and meiofaunal (middle) peaks averages 5×10^3 mm^3 m^{-2}. The macrofaunal biomass peak is an order of magnitude higher, but shows greater variability. Biomass in the troughs is about 2–3 orders of magnitude less than adjacent peaks. Sediment was a fluid silt-clay. (From Schwinghamer P (1985) Observations on size-structure and pelagic coupling of some shelf and abyssal communities. In: Gibbs PE (ed) Proceedings of the Nineteenth European Marine Biology Symposium, Plymouth, Devon, U.K. 16–21 September 1984, pp. 347–359. Cambridge: Cambridge University Press.)

environment: macrofauna as a continuous medium on, or in, which to move and burrow; meiofauna as a series of interstices between sediment particles; while to microbenthos and bacteria each particle is a little world on which to attach and grow. Warwick provided a complementary explanation that the peaks also reflect size-related adaptation in the way the life history of the organism is optimized to its environment. For example, larvae of macrofauna exploit the trough between macro- and meiofauna to escape from meiofaunal predators, and thereafter quickly grow into the size range of the 'macrofaunal' peak. This is generally lower and less defined than the meiofaunal peak, where organism longevity is just a few weeks at most and there is therefore a narrow range in size, while individual macrofauna might grow over several years so that population size distributions are wider. However, subsequent studies have not found that clear peaks in size spectra occur everywhere. In the deep sea, body size miniaturization does not destroy this pattern, even if the trough at 512–1024 μm between meio- and macrofauna may be less than in coastal sediment (**Figure 4**). It seems more likely that low food supply has become more important than anything else, so that macrofauna, although settling at roughly the same size, simply do not grow anything like as large as similar coastal species, rather than their somehow perceiving the sediment environment differently from typical macrofaunal organisms in shallow water.

We cannot therefore reject the idea that size-based differentiation of the benthos occurs; but is it sensible to stick rigidly to the strict size-based divisions that define the macrofauna as only those organisms within a given range of size, or is it better to compare like with like on the basis of higher taxa determining limits rather than size? With the former definition, the lower limit of the macrobenthos will be determined by size at 1.0 or 0.5 mm, even if this excludes smaller specimens belonging to the same higher taxon, or even much lower-level taxa. This assumes that a size-based functional distinction operates that for the purposes of the study (perhaps environmental impact assessment) will be more important in determining variability than taxonomic affinity. The former function-based definition has been referred to as macrofauna *sensu stricto*, while the latter, taxonomic one as macrofauna *sensu lato*.

Composition and Succession

Macrobenthos characteristically includes a huge range of phyla (the major divisions of the animal

kingdom). In fact, most higher-level taxa are marine and benthic, with most of these part of the macrobenthos. Of the 35 or so known phyla (the major divisions of the animal kingdom), 22 are exclusively marine, with 11 restricted to the benthic environment. Virtually every known phylum is represented in the macrobenthos except for one, the Chaetognatha, or arrow worms (arguably found only in the plankton, although one bottom-living genus is known). This contrasts with the land (including freshwater environments) where only 12 phyla are found (there is only one small, obscure phylum of worm-like animals, the Onychophora, known only on land). This reflects the marine origins of life and the much shorter time of occupation for life on land (barely 400 million years), compared with 800 million years since metazoan organisms first appeared in the ancient ocean. Only five metazoan phyla are normally regarded as part of the next size group down, the meiofauna.

The proportional representation of major taxa is conservative, and seems to vary little worldwide with depth, latitude, or productivity regime. It is only in stressed soft-sediment environments, such as those with high organic loading and depleted oxygen (often occurring together), where major departures to this pattern are found (**Figure 5**). Inshore studies on effects of pollution have contributed to a concept whereby such stress leads to a modified macrobenthos with fewer species, and these characterized by opportunist forms, mainly polychaetes. In tracing recovery after pollution events, it is not clear to what extent a predictable succession occurs. The modern consensus is that there is a random component imposed on a facultative succession in which 'opportunist' species pioneer colonization and bring about amelioration in sediment conditions. This allows a more diverse set of species that are more highly tuned to particular habitats to become established through progressively deeper and more extensive bioturbation (**Figure 6**).

How Many Macrobenthic Species Are There?

Up to a few years ago it was thought that of the 1.4 to 1.8 million or so species recorded on earth there are perhaps only 160 000 or so known marine species, about 10% of the total. A large-scale sampling programme in deep water off the eastern United States has thrown this into doubt. Along a 180 km section of the continental slope at about 2000 m depth, Grassle and Maciolek found 58% of the species – especially among polychaete (bristle) worms and peracarids (small, sandhopper sized crustaceans) – new to science. The curve of the accumulation of species plotted against increasing area sampled showed no sign of tailing off; the steady increment of new (but rare) species encouraging an extrapolation that this will apply over the wider area of the deep ocean.

Depths below the shelf edge cover about 90% of the domain of macrobenthic infauna. But an area of only about 0.5 km^2 out of the almost 335×10^6 km^2 area below 200 m depth has yet been adequately sampled for macrofauna using grabs or corers. Because of this huge unexplored area, the actual number of marine macrobenthic species present today is unknown. It must be vastly greater than earlier estimates based on shallow seas, and according to Grassle and Maciolek is conservatively greater than one million, and more likely to rise to 10 million as more of the deep sea is sampled.

The overwhelming taxonomic challenge of describing these new species, the painstaking work of sorting samples from the sediment, and the difficulty of seabed experimentation have perhaps slowed progress in understanding the deep-water sediment community. In contrast, much more has been achieved in biological knowledge of hydrothermal vents (and to a lesser extent cold seep communities) since their discovery in 1977.

Large-scale Patterns in Macrobenthic Diversity

Large-scale patterns, other than that for biomass, remain controversial. On the basis largely of sampling of the continental shelf, Thorson pointed out that species richness of the epifauna, occupying less than 10% of the total area, and maximally developed intertidally, rises steeply from low levels in the ice-scoured shallows in the Arctic to high values in the tropics. In contrast, the sediment macrofauna he referred to as 'infauna,' usually found deeper and unaffected by ice and meltwater, show much less change. This lack of a latitudinal gradient is supported in some other studies. However, latitudinal comparisons by Sanders in the 1960s found depressed diversity in shallow boreal macrobenthos stressed by wide seasonal temperature change compared to the tropics. Thorson through there were about four times more epibenthic than infaunal species, the microhabitat complexity and consequently high species diversification of the epibenthic habitat being much less obvious in sediments. The sameness of this habitat regardless of latitude led Thorson to his
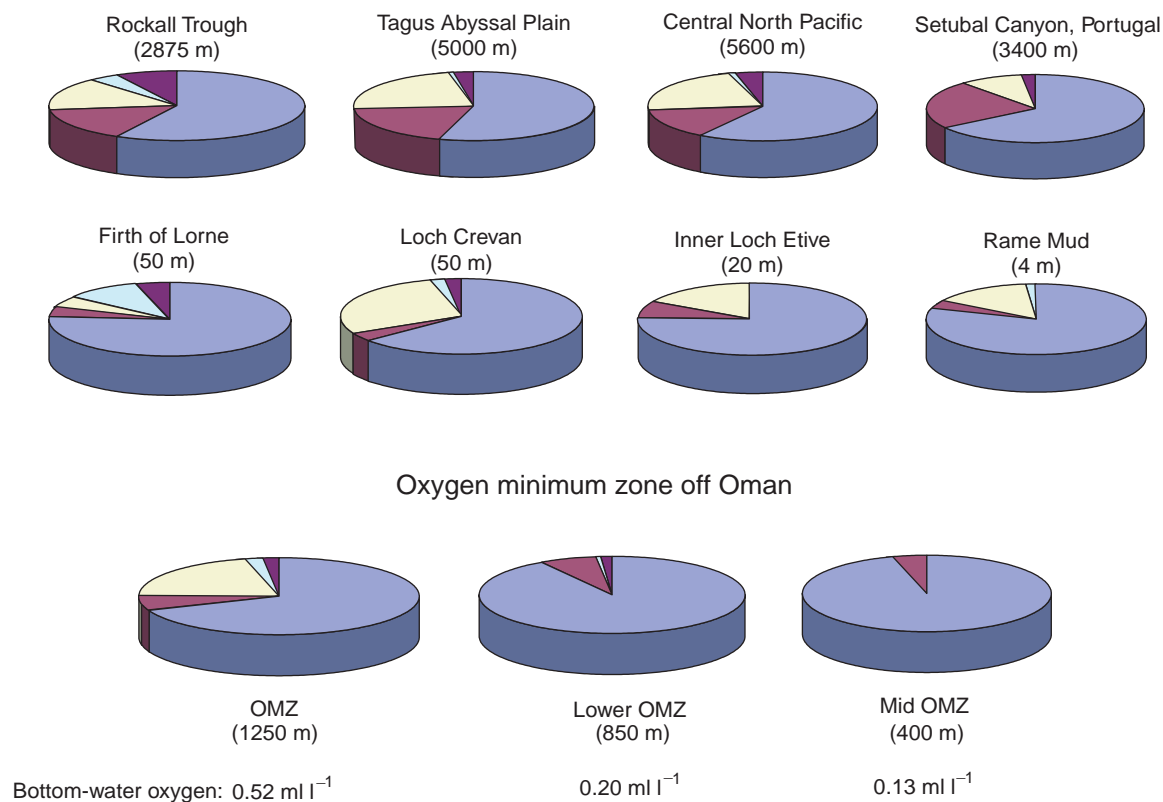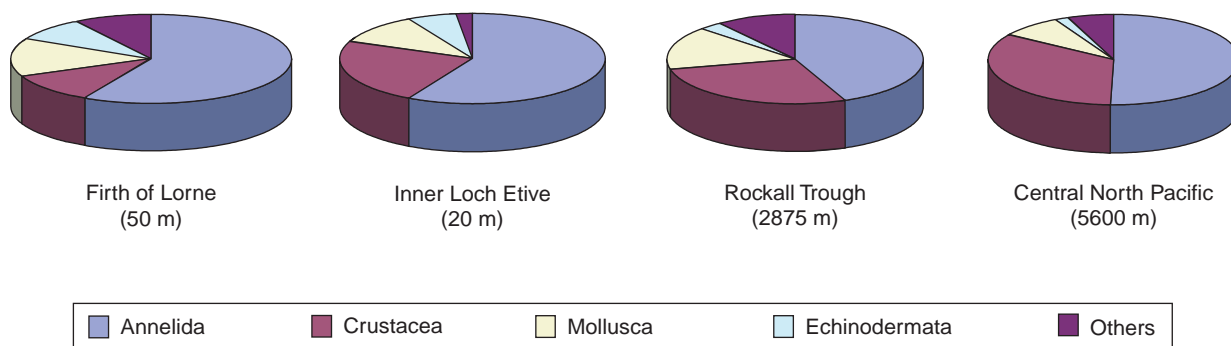
Macrofaunal abundances

Rockall Trough (2875 m)

Tagus Abyssal Plain (5000 m)

Central North Pacific (5600 m)

Setubal Canyon, Portugal (3400 m)

Firth of Lorne (50 m)

Loch Crevan (50 m)

Inner Loch Etive (20 m)

Rame Mud (4 m)

Oxygen minimum zone off Oman

OMZ (1250 m)

Lower OMZ (850 m)

Mid OMZ (400 m)

Bottom-water oxygen: 0.52 ml l^{-1} 0.20 ml l^{-1} 0.13 ml l^{-1}

Macrofaunal species

Firth of Lorne (50 m)

Inner Loch Etive (20 m)

Rockall Trough (2875 m)

Central North Pacific (5600 m)

■ Annelida   ■ Crustacea   □ Mollusca   □ Echinodermata   ■ Others

Figure 5 Proportional representation of the major taxonomic groups of macrofauna in differing soft sediment habitats and depths worldwide. The upper diagrams show this in terms of the relative abundance in these groups; the lower ones in terms of the number of species represented. A broadly similar pattern is shown between both sets although Crustacea are often more abundant in the deep sea rather than shallow-water macrobenthos. Representation of Annelida (mostly polychaete worms) shows most obvious variation in relation to organic carbon loading and oxygen, the three samples from the oxygen minimum zone (OMZ) in the Arabian Sea off Oman showing a pattern of increasing dominance by Annelida, and eventually complete loss of all other groups except Crustacea, with increasing oxygen depletion. (Data from Mare (1942); Gage (1972) Community structure of the benthos in Scottish sea-lochs. I. Introduction and species diversity. *Marine Biology* 14: 281–297, Gage J (1977) Structure of the abyssal macrobenthic community in the Rockall Trough. In: Keegan BF, O'Ceidigh P and Boaden PJS (eds) *Biology of Benthic Organisms* (11th European Marine Biology Symposium), pp. 247–260. Oxford: Pergamon Press; Levin LA, Gage JD, Martin C and Lamont PA (2000) Macrobenthic community structure within and beneath the oxygen minimum zone, NW Arabian Sea. *Deep-Sea Research II* 47: 189–226.)
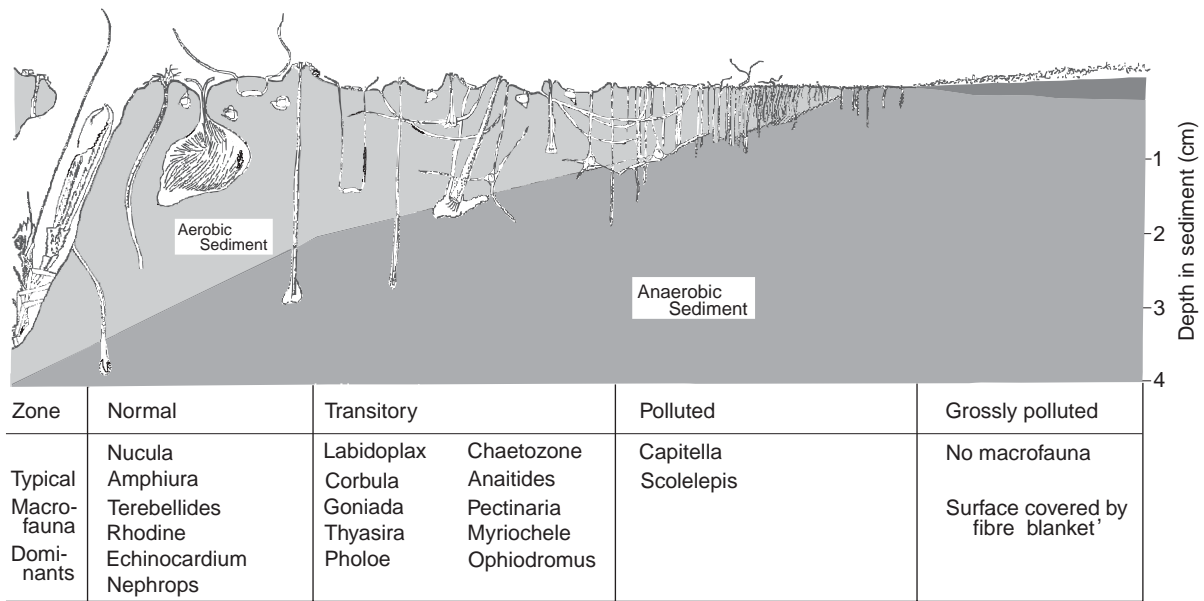
Zone	Normal		Transitory		Polluted	Grossly polluted
Typical Macro-fauna Domi-nants	Nucula Amphiura Terebellides Rhodine Echinocardium Nephrops		Labidoplax Corbula Goniada Thyasira Pholoe	Chaetozone Anaitides Pectinaria Myriochele Ophiodromus	Capitella Scolelepis	No macrofauna Surface covered by fibre blanket'

Figure 6 Changes in macrobenthic fauna along an enrichment–disturbance gradient, such as that associated with pollution. The gradient can be replaced by time in tracing recovery along the *x*-axis to a 'normal' community (left) after a severe pollution event (right). Note the shift in body size (reflecting change from quick-growing and fast-turnover 'pioneer' species to slower-growing, longer-lived population species) from right to left, as well as the increased depth and extent of bioturbation in the sediment. There is also a concomitant increase in macrobenthic diversity. (From Pearson TH and Rosenbeg R (1978).)

concept of parallel level-bottom communities related to sediment type. But several recent studies indicate shallow tropical and deep-sea sediments do not follow this pattern, with much more species-rich communities developing, albeit including lots of 'rare' species, in these habitats.

Depth-related patterns in macrobenthic composition have been studied, particularly for larger benthic invertebrates (technically megabenthos, see discussion earlier) and demersal (bottom-living) fish. Rates of macrofaunal turnover, and clinal variation in individual species, correspond to the rate of change in depth. It is highest in upper bathyal and slowest and most subtle in the abyssal. Many changes in species composition can be related to trophic strategies along a gradient in food and hydrodynamic energy (see **Figure 2**), but changes in the sort and intensity of biological interactions, such as predation, varying with depth, may also be important, as can life-history characteristics (such as the incidence of planktotropic larval development). Recent studies have also established a degree of pressure adaptation during early development that will further limit vertical range. Such ecological processes must be considered in concert with processes at the evolutionary timescale for understanding of zonation patterns. These processes have been summarized using multivariate statistics. While helping in formulating ideas on causal factors, these may obscure the underlying complexity, which is best understood as the sum of the range and adaptation and evolutionary history of individual species.

Rex postulated a mod-slope peak in macrobenthic diversity from studies of sled samples taken throughout the Atlantic by Sanders. However, there is high variability among individual sample values compared and there are conflicting results from other sites worked in the north-eastern Atlantic. That deep-sea macrobenthos has high species diversity seems well founded, but the extent to which this contrasts with shallow water is unclear. In his original study off the north-eastern United States, Sanders showed an impoverished species richness in samples of macrofauna compared to the adjacent slope and rise. Gray has pointed out that on the outer continental shelf off Norway macrofaunal diversity may be comparable to that found in Sanders' deep-sea samples, and it is considerably higher still off south-eastern Australia. This suggests not only that the inshore shelf off New England is rather poor in species richness but that the North Atlantic as a whole may be atypical, with perhaps historical factors operating there to restrict macrobenthic diversity compared to the southern hemisphere.

Such factors may determine the differing response shown in a comparison of deep-sea macrobenthic diversity among sites throughout the Atlantic where the depression at high latitudes is absent south of

the equator. The reduced levels at high latitudes may simply reflect Quaternary glaciation so that the deep Norwegian Sea, isolated by shallow sills from deep water to the south, has a much more recently diverged and quite distinct macrofauna from that in the Atlantic.

Small-scale Pattern

In sampling macrobenthos from a ship it is easy to assume that the animals in this apparently homogeneous habitat are randomly distributed, but sample replicates may not always provide good estimates of the population mean and its sampling error. When samples are mapped over the sediment, or variability is analysed in large numbers of replicates, clumped distributions of some kind are commonplace (**Figure 7**). Nonrandomly even (regular) dispersions have been detected, but only at the centimeter scale, suggesting that they are actively defined by the ambit (such as the area swept by feeding tentacles) of individual animals. To describe rather than just detect such nonrandom spatial pattern has been a challenging task, not least because most macrofauna are not readily visible in seabed photographs and the very analysis of samples by sieving and mud will destroy fine-scale pattern. Spatial pattern is usually envisaged in the horizontal plane because macrobenthic organisms concentrate their activity on the sediment–water interface in feeding, movement, and reproduction. Pattern is
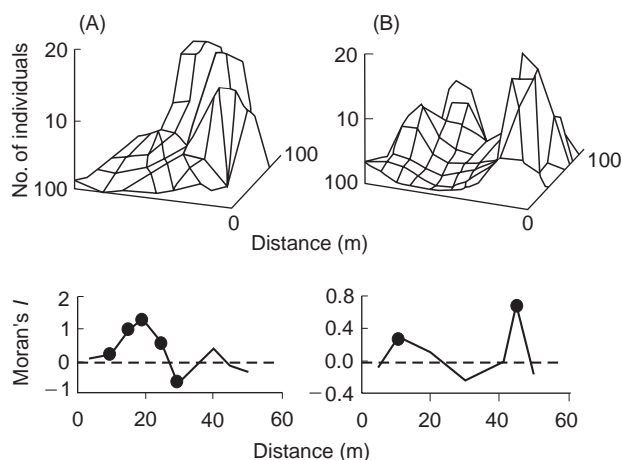
Figure 8 Benthic biological activity and seabed sediment structure. The diagram shows some of the ways macrobenthos, in conjunction with other size classes, influence sediment fabric, physicochemical properties and solute fluxes (see also Table 1). (After Meadows PS (1986) Biological activity and seabed sediment structure. *Nature* 323: 207.)

a dynamic expression of this and consequently may change through time but marine sediments provide a three-dimensional habitat so that vertical as well as horizontal spatial patterns may occur. The latter may be best developed at the small scale where smaller macrofauna (and meiofauna) are concentrated around irrigatory or feeding burrows of larger species (**Figure 8**). The problem is that to analyze this pattern it is difficult not also to disrupt the habitat. Yet in order to understand the basis of such pattern it is vital to analyze and map pattern over a range of scales in conjunction with variability in the sediment habitat. Some of the most revealing studies have examined dispersions of individual species over plots measuring tens of meters square. These may reveal the two aspects of pattern, intensity and form. Intensity can relatively easily be measured by the ratio of variance to mean. This will distinguish distributions that are clumped, regular, or not statistically distinguishable from random. The form of pattern is an aspect that classical statistical tests of nonrandomness do not address. Yet

Figure 7 Upper, three-dimensional plots of abundance showing spatial dispersion patterns of two infaunal bivalve molluscs *Nucula hartivigiana* (A) and *Soletellna siliqua* (B) in a 9000 m² area of mid-tide sandflat with no obvious gradients in physicochemical conditions. Both species show quite different spatial patterns. The lower plots show spatial correlograms with significant autocorrelation coefficients (measured as Moran's *I*) denoted by filled circles (From Hall *et al.* (1984). Thrush *et al.*, (1989).)
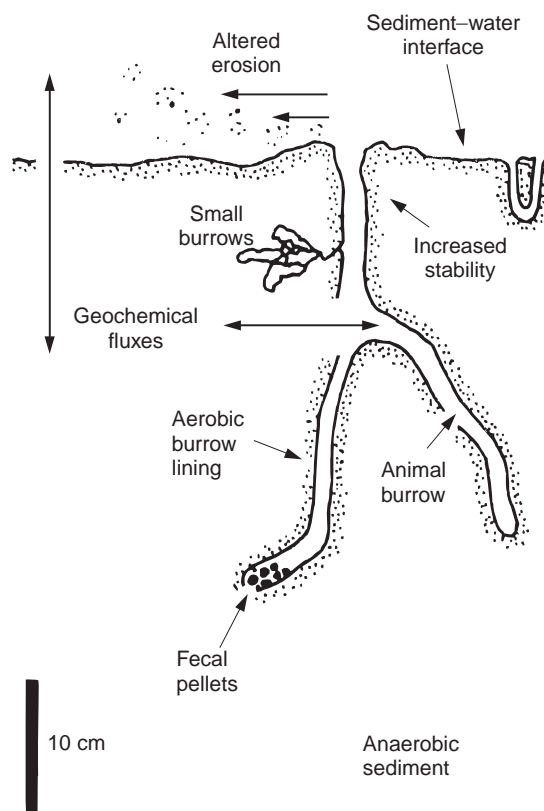
a clumped pattern may be very different in form from that shown by another species that shows similar intensity of aggregation.

Although a nuisance for the easy interpretation of sample statistics, an understanding of the biological basis of patterns will provide important insight into the processes maintaining macrobenthic communities.

Functional Importance of Macrobenthos

Using a grab as a quantitative sampler in the early years of the twentieth century, C. J. J. Petersen hoped to be able to work out from his thousands of samples taken in the North Sea how much food was available to fish such as flounder. Such links were well supported from finds of large numbers of benthic animals in fish guts, even if later work showed that fish are by no means as important predators of macrobenthos as are invertebrates such as sea stars. Petersen also noticed that characteristic and uniform assemblages of macrobenthos were found that could be related to sediment type and that provided him with statistical units that Thorson later used as his descriptive units in his concept of 'parallel level bottom communities.' Ecologists debated whether these existed as anything more than assemblages responding to similar conditions (as originally inferred by Petersen) or reflected functional units or 'biocoenoses' where biological interactions play an important, if unknown, role. However, the importance of biological interactions in the subtidal community is difficult to address experimentally, and most data are available from intertidal mudflats and sandflats where ecological gradients related to tidal exposure pose additional complexity. Manipulative experiments on the effects of predation by caging small areas show that predators like shore crabs can have big effects on prey densities, while other studies show competitive exclusion between worms with different burrowing styles that can be reflected in clumping patterns. This contrasts with the importance of grazers and predators in preventing dominance by fast-growing competitive superior species on rocky shores. Such biological interaction cascades down through the community – so-called 'top-down' control. But, in sediments, effects such as predation are not so marked overall. Perhaps the three-dimensional structure, the uneven distribution of food and irrigatory flows, and the often intense stratification of chemical processes reduce competition. Indirect effects, such an bioturbation, may take the place of competition. By bulk processing large quantities of sediment, large macrofaunal deposit feeders rework the sediment down to the greatest ocean depths and thus exert a major influence on benthic community structure. It has been suggested that this constant process of biogenic disturbance and alteration of the benthic environment by macrofauna (**Figure 8, Table 1**) encourages high species richness among smaller macrobenthos by reducing them to levels where competition is relaxed, so that more species can coexist. It is also argued that the constantly changing micro-landscape created by other, larger species provides a rich niche variety for macrofauna. It is difficult to see this process operating on the vast abyssal plains where faunal densities, and therefore such biogenic effects, are so low but species richness is high. Grassle's spatiotemporal mosaic theory sees the deep-sea bed having patchy and ephemeral food resources that create a relatively small, discrete, and widely separated patch structure promoting coexistence.

Effects of larger-scale disturbances are more difficult to detect let alone manipulate in experiments with the sediment community. Yet the evidence is that physical disturbance such as that caused by storm-driven sediment scour and resuspension may have an important effect on assemblage structure and species richness on the exposed continental shelf and margin. The expectation that, just as on an exposed sandy shore, only a relatively small suite of species will be able to adapt to such conditions is confirmed in the deep sea on the continental rise off Nova Scotia, where benthic storms occur with relatively high frequency. Benthic storms may occasionally occur on the abyssal plains, so it should not be assumed that biogenic structure is simply longer-lasting there because it takes so long to be covered by the very low rate of natural sedimentation.

Perhaps the most important determinant of the macrobenthic assemblage, or community, is the larval stage usually dispersed in the water column. Larvae can test the substratum and swim off until they find conditions suitable for settlement and metamorphosis. On rock this may involve a series of precise cues that can include presence of their own or other species. Less is known about settlement of infaunal species, but it is thought that positive cues such as microtopography may be much less important in sediment dwellers, while negative cues such as the presence of other species or unattractive sediment are more important. Nevertheless, a community will still be very largely constrained by supply of propagules. In a coastal area the access of larvae supply from adjacent breeding populations may be constrained by coastal topography and currents, not to mention barriers formed by features such as

Table 1 Direct and indirect effects of macrofauna on soft sediments and their ecological consequences

Direct effect	Indirect effects and ecological feedback
Bioresuspension: pelletization of superficial sediment as egesta changes sediment granulometry and increases openness of sediment fabric	Bioresuspension and formation of bottom turbidity layers through decrease in threshold where bed-shear stress will mobilize sediment Alteration in benthic community by reducing suspension feeders (trophic group 'amenalism') Reduced numbers of epifauna, and total community diversity Disruption and rapid obliteration of biogenic traces
Biodeposition: increased stickiness of sediment surface, and sediment structure altering hydrodynamic conditions to trap particles in pits, etc.	Biodeposition increases sediment stability and trapping of fine particles utilizable as food Encourages suspension feeders, and hence increases trophic diversity Results in tighter sediment fabric; increased sediment microstructure, and habitat complexity causing greater niche variety, and thereby increasing community diversity Better preservation of biogenic traces
Sediment irrigation	Spatial and temporal variability in exchange of dissolved gases, dissolved or absorbed ions and complex chemical species nutrients across sediment water interface Alteration in vertical gradients in Eh, pH etc. Transfer of reduced compounds from reducing conditions below the interface to aerobic conditions above Enhances recycling of dissolved nutrients Creates chemical heterogeneity from hotspots of elements concentrated by larger organisms in the sediment
Vertical sediment transport by larger deposit feeders	Particle selection may cause vertical shifts, granulometry Alteration of chemical microenvironment and diagenesis of sediment and smearing of stratigraphic signal
Formation of surface traces, by movement, burrowing or defecation	Increases bottom roughness, affecting near-bed flow Increased complexity in microenvironment creates niche mosaic at sediment surface

estuaries. The patch structure in the deep sea is maintained by water-borne dispersal stages with the resulting metapopulations spatially unautocorrelated (presence of an organism not dependent on other occurrences). In deep water the openness of the system may mean that the sediment is exposed to a much larger pool of species, even if they are at very low densities as larvae. In the tropics a similar effect results from the greater incidence of planktotrophy (larvae feeding in the plankton), when the longer larval life will ensure wider dispersal than that of the nonfeeding larvae prevalent in cooler waters. This may help to explain why so many, mostly rare, species can coexist in both environments.

Importance of Macrobenthos in Environmental Assessment

Because the benthic community (unlike fish or plankton) is stationary or at best slow-moving over a small area of bottom, it is useful in monitoring environmental change caused by eutrophication and chemical contamination. Macrobenthos studies have defined the generic effects of such sources of stress by changing representation of major taxa, reduction in diversity, and increasing numerical dominance by small-sized opportunist species causing a downward shift in size structure. This seems to be accompanied by greater patchiness, reflected by increased variability in species abundances in sample replicates. It is also seen as greater variability in local species diversity caused by greater heterogeneity in species identities. This reflects subtle changes in abundance and, particularly in the more species-rich communities, changes in presence/absence of rare species that might be detected earlier at less severe levels of disturbance. It is claimed that in bioassessments comparing species richness using samples of macrobenthos rare species should receive greater attention by taking larger samples because they contribute relatively more to diversity than the abundant community dominants. Other workers argue that very many species, especially rare ones, are interchangeable in the way they characterize samples. This

question requires investigation of the way stressors impact the community, and whether it is the dominant or the rare species that are most sensitive, and therefore most rewarding for study in detecting impacts.

Interpretation of impacts also has to proceed against a background of natural changes in benthic communities caused by little-understood, year-to-year differences in annual recruitment. In establishing a baseline there is a need also to take into account the little-understood effects of bottom trawling on coastal benthos. Such disturbance in parts of the North Sea may date back at least 100 years, and now means that virtually every square meter of bottom is trawled over at least once a year. Such monitoring has in the past entailed costly benthic survey and tedious analysis of samples to species level. Consequently, there has been effort to see whether the effects of stress can be detected at higher taxonomic levels, such as families. Higher taxonomic levels may more closely reflect gradients in contamination than they do abundance of individual species because of the statistical noise generated from natural recruitment variability and from seasonal cycles such as reproduction. This hierarchical structure of macrobenthic response means that, as stress increases, the adaptability of first individual animals, then the species, and then genus, family, and so on, is exceeded so that the stress is manifest at progressively higher taxonomic level.

Such new approaches, along with the nascent awareness of conservation of the rich benthic diversity, and with a need for improved environmental impact assessment on the deep continental margin, should ensure a continued active scientific interest in macrobenthos in the years to come.

See also

Benthic Boundary Layer Effects. Benthic Foraminifera. Benthic Organisms Overview. Coral Reefs. Deep-sea Fauna. Demersal Fishes. Fiordic Ecosystems. Grabs for Shelf Benthic Sampling. Meiobenthos. Microphytobenthos. Phytobenthos. Pollution: Effects on Marine Communities. Rocky Shores. Sandy Beaches, Biology of.

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MAGNETICS

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Introduction

Since World War II it has been possible to measure the variations in the intensity of the Earth's