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# Diversity in deep-sea benthic macrofauna: the importance of local ecology, the larger scale, history and the Antarctic

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## Abstract

High diversity in macrobenthos in the deep sea still lacks satisfactory explanation, even if this richness may not be exceptional compared to that in coastal soft sediments. Explanations have assumed a highly ecologically interactive, saturated local community with co-existence controlled by either niche heterogeneity, or spatio-temporal heterogeneity embodying disturbance. All have failed to provide convincing support. Local/regional scale biodiversity relationships support the idea of local richness in macrobenthos being predominantly dependent on the larger, rather local scale. Local-scale ecological interactions seem unlikely to have overriding importance in co-existence of species in the deep sea, even for relatively abundant, ‘core’ species with wide distributions.

Variety in observed larger-scale pattern and the strong inter-regional pattern, particularly in the poorly known southern hemisphere, seem to have a pluralistic causation. These include regional-scale barriers and extinctions (e.g., Arctic), and ongoing adaptive zone re-colonisation (e.g., Mediterranean), along with other historical constraints on speciation and migration of species caused by changes in ocean and ocean-basin geometry. At the global scale lack of knowledge of the Antarctic deep sea, for example, blocks coherent understanding of latitudinal species diversity gradients. We need to reconcile emerging understanding of large-scale historical variability in the deep-sea environment—with massive extinctions among microfossil indicators as recently as the Pliocene—to results from cladistic studies indicating ancient lineages, such as asellote isopods, that have evolved entirely within the deep sea.

The degree to which the great age, diversity, and high degree of endemism in Antarctic shelf benthos might have enriched biodiversity in the adjacent deep seas basins remains unclear. Basin confluence with the Atlantic, Indian and Pacific Oceans may have encouraged northwards dispersion of species from and into the deep Antarctic basins so that any regional identity is superficial. Interpretation of the Antarctic deep sea as a diversity pump for global deep-sea biodiversity may simply reflect re-colonisation, via basin confluence, of northern hemisphere areas impoverished by the consequences of rapid environmental change during the Quaternary.

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## 1. Introduction

Terrestrial ecologists searching for general explanations of biodiversity pattern have long appreciated that local ecology is insufficient to provide explanation for the local co-existence of species as observed in samples (e.g., Shmida and Wilson, 1985; Lawton, 1999). In the deep sea a shift in emphasis in biodiversity research on macrobenthos from the local to the larger scale has become urgent in order to address new observations of biodiversity pattern up to the global scale (Rex et al., 1993; Stuart et al., 2003). But this wider view has been impeded by several factors. First, there is the considerable technical difficulty in addressing this remote environment at scales larger than the local scale. This has at best allowed us only to extrapolate from analysis of samples taken at a local scale that is vanishingly small in relation to the global scale of this habitat. Second, the richly diverse fauna requires formidable taxonomic skills to identify in order to provide a consistent and reliable inventory, but which still leaves yawning uncertainty on taxonomic differentiation detectable only in the genotype (Etter et al., 1999). Third, there is a need for studies of deep-sea benthic biodiversity not to overlook the historical source of this diversity (Wilson, 1998) rather than continue in dogged but fruitless search for local-scale explanation. This requires biodiversity studies to assimilate the traditional global approach of zoogeography. Here biodiversity is viewed primarily as a zoogeographic pattern reflecting historical accumulation of species over time influenced by basin age (Dahl, 1972), confluence (Hessler and Wilson, 1983; Allen and Sanders, 1996), deep currents as zoogeographic barriers (Cutler, 1975; Hansen, 1975) or as means of dispersal (Menziez et al., 1973; Hansen, 1975), topographic boundaries (Clarke, 1962), and water-mass structure (e.g. Ekman, 1953; Menziez et al., 1973).

Last, and perhaps least excusable, is the sparseness of data from the southern hemisphere. This seriously limits our understanding of large-scale pattern up to the global scale as well as the zoogeographical origin of deep-sea fauna (Clarke, 2003). Lack of knowledge of the Antarctic deep

sea in particular blocks coherent understanding of global-scale benthic biodiversity pattern. Recognition of this deficiency has inspired recent expeditions to sample the deep-sea basins of the Antarctic (Brandt, 2003).

High deep-sea macrobenthic diversity may not after all be exceptional compared to that of comparable soft-sediment habitats in shallow water (Gray, 1994; Gray et al., 1997; Gray, 2002). However, the unexpected, but nevertheless now well-supported, discovery of large numbers of species coexisting in the food-poor deep-sea soft sediment (Hessler and Sanders, 1967) has prompted a large amount of, mainly theoretical, explanation. This started with Sanders' (1968) Stability-Time Hypothesis, which attempted to link present-day with historical processes in a unifying theoretical framework based on sampling along a depth-related transect off the eastern United States. Diversity is thought to increase along a negative gradient of physiological stress derived from environmental variability at the ecological time scale, which increasingly allows opportunity for niche specialisation over evolutionary time. Later studies, too numerous to cite here, provided a wealth of alternative explanation focused on small scales down to that of the ambit of individual organisms where species might encounter each other. The explanations suggested that co-existence is encouraged by small-scale, mainly biogenic, niche heterogeneity or by spatio-temporal heterogeneity variants of interactive co-existence at the local scale involving disturbance. These studies have been based on small-scale sampling and observations along with seabed recolonisation experiments using sediment trays and manipulative experiments using manned submersibles. Overviews are provided in some recent, wide-ranging reviews on deep-sea benthic biodiversity (Etter and Mullineaux, 2000; Levin et al., 2001; Snelgrove and Smith, 2002). These make clear that explanations remain largely theoretical, with supporting data on the importance of local-scale ecology sparse and tantalisingly unconvincing. However, the reviews agree on the important role of various forms of disturbance in disequilibrium processes in controlling richness at smaller scales, even if no single process emerges to provide

universal explanation. Nevertheless, the strong message, like that of [Stuart et al. \(2003\)](#), is to urge deep-sea biologists also to consider biodiversity pattern at large scales as well as the historical processes that have shaped them.

It is not the purpose of the present contribution to duplicate the content or message of these reviews. Instead the aim is to question some of the assumptions in past studies and to take forward some new ideas on pattern and explanation for high diversity found among deep-sea sediment-dwelling organisms in relation to ecological interaction, spatial scale and history, particularly in relation to the deep Antarctic Ocean. Any re-iteration of material already adequately covered in these comprehensive reviews cited above is done only to set a context for further discussion.

## 2. Is ecological interaction important in maintaining high deep-sea benthic biodiversity?

Perhaps the most important assumption of past studies, and one that underlies major difficulties with the concept of diversity and its causation, follows from the assumed role of species as ecologically interactive elements of an assemblage. In niche heterogeneity models species are presumed to have reached equilibrium in ecological saturation of niche space ([Jumars, 1976](#)). With spatio-temporal heterogeneity models, five ways that [Cornell and Lawton \(1992\)](#) suggest species co-existence might be enhanced include (with some deep-sea examples) the following: disequilibria achieved by similar competitive abilities with unpredictable recruitment, patchy resources ([Grassle and Morse-Porteous, 1987](#); [Rice and Lamshead, 1994](#)) periodic disturbance in concert with relatively slow population growth rates ([Dayton and Hessler, 1972](#); [Huston, 1979](#); [Gage, 1997](#)), combinations of opportunist with competitively superior species ([Sanders, 1979](#)), and spatial variability in predation. Therefore one important question is whether the underlying assumption that the local-scale assemblages are sufficiently interactive to influence biodiversity. If not then niche heterogeneity and/or spatio-temporal het-

erogeneity will not be important factors in allowing large numbers of species to co-exist at the local scale. Furthermore, at the landscape scale, explanation for mid-slope peaks in diversity on the continental margin reflecting intermediate levels of disturbance ([Huston, 1979](#)) or productivity ([Rosenzweig and Abramsky, 1993](#); [Mittelbach et al., 2001](#)) may need re-interpretation ([Srivastava, 1999](#)).

### 2.1. The role of 'core' species

In our search for evidence for ecological interactions it is logical to look first at the most abundant species. In what still constitutes one of the largest coherent data set of deep-sea macrobenthos, the 10 most abundant species on average totalled 42.1% of the total number of individuals in quantitative sampling over a total of 21 m<sup>2</sup> on an isobathic transect along the continental slope off New Jersey ([Grassle and Maciolek, 1992](#)). These common species remained roughly constant members of the assemblage, with the most abundant one, a spionid polychaete, comprising 7–8% of the total. A similar result was obtained by [Glover et al. \(2002\)](#) in the abyssal Pacific where the same 'core' polychaete species dominated over local to regional scale scales (up to 3000 km). [Glover et al.](#) found the 30–40 polychaete species constituting the numerically dominant core species are ubiquitous, representing 70–90% of the total number of individuals. On the Madeira Abyssal Plain in the North Atlantic these polychaete dominants are also typically species with widespread, perhaps even cosmopolitan, distributions ([Glover et al., 2001](#)).

Common species may then constitute constant, repeatable elements of the macrobenthic assemblage over wide areas. It seems reasonable to assume these core species are sufficiently abundant to encounter each other so that populations are reproductively independent, even if supporting evidence is fragmentary. But we may wonder why these species, and not others, are abundant. Perhaps their initial colonisation might have been determined by historical processes creating isolation and extensive open niche space, or adaptive zone, opportunity after regional- or even

global-scale extinction events (Simpson, 1953; Hutchinson, 1959). However, at the local, ecological scale the question is whether their identity and numerical dominance is maintained by superiority in competitive interactions between species.

## 2.2. Does the deep-sea benthic assemblage show species saturation?

If we, for the moment, ignore ‘rare’ species, we can ask whether their identity and relative abundance of assemblage dominants determined by superior adaptive and/or competitive qualities or by chance factors governing their availability? If the former is true rather than the latter, then the persistence and their relative numerical importance of these core species suggests equilibrium involving not only interaction between species, but possibly also a limit to the total species inventory by exclusion of others. These are characteristics of a possibly saturated, interactive assemblage on a conceptual continuum from fully ‘interactive’ to ‘non-interactive’ local ecology of Cornell and Lawton (1992) (Fig. 1).

Whether or not the community is ecologically saturated with species has long interested terrestrial ecologists. This is because saturation will theoretically determine if species from the much larger pool theoretically available from the larger scale are able to invade local-scale habitat (Cornell and Lawton, 1992). Non-interactive species assemblages will always be unsaturated and will show a proportional (linear) relationship in richness at the larger scale (Type I). Conversely, a curvilinear response is indicative of an interactive assemblage and probably, but not always, local saturation (Type II). Study of such relationships on land suggests that local species richness is rarely saturated. Furthermore, many processes can result in the number of species co-existing locally being determined to a great extent by inputs from the wider area (Caley and Schluter, 1997). Therefore the absence of saturation does not imply that local-scale ecology and biotic interactions have no importance on the richness of local assemblages. It is only that such processes do not necessarily limit numbers of locally coexisting species.

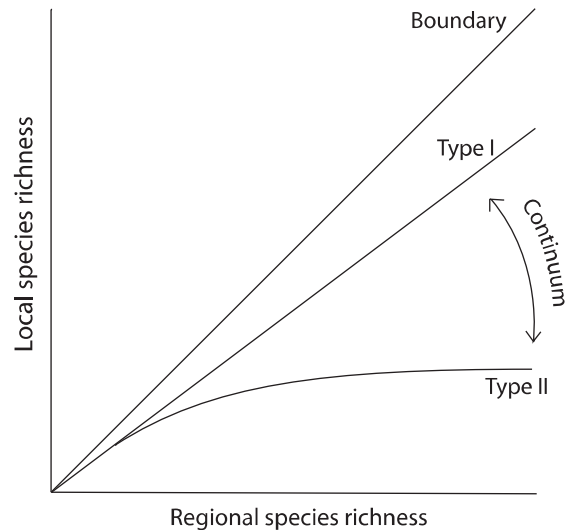


Fig. 1. Local-regional relations: In Type I assemblages local species richness is independent of biological interactions and increases proportionately with regional richness. In Type II assemblages biological interactions limit species richness so that the assemblage is ‘saturated’ and becomes independent of regional richness. Real assemblages probably fall on a continuum between these two extremes with positions dependent on taxon and size class so that a single community might include a range of positions on this continuum (modified after Cornell and Lawton, 1992).

There are few data available to investigate the relationship between local and regional scales of shallow marine species richness, all of which indicate that the regional scale exerts a major effect at the local scale (e.g., Cornell and Karlson, 1996). Furthermore, Gray’s (2002) plotted species–area data from the Norwegian continental shelf suggest a linear relationship, with rare species being incremented regularly as sample size increases. In other words, there is a positive linear relationship, or ‘proportional sampling’, between local and regional species richness of Type I assemblage of Cornell and Lawton (1992) so that local richness is determined not so much by local ecology as by the regional species pool.

No directly comparable studies are yet available for the deep sea because deep-sea biologists are nowhere near assembling a regional inventory of species from which a species–area relationship to a sufficiently large scale can be derived. However, a proportional relationship (indicative of a Type I

relationship between local and regional scale) is suggested from the plotted species–area/individuals data of [Grassle and Maciolek \(1992\)](#). Here the curve shows no sign of approaching an asymptote of species richness along the 176-km long transect, although this distance falls far short of [Rex et al.'s \(2000\)](#) definition of the regional scale as basins. Hence, the very limited amount of comparable data support the idea of local species richness of deep-sea macrobenthos being dependent on the larger rather than the local scale.

Such dependency on the larger scale would not be expected if co-existence were achieved by heterogeneous niche occupancy in the deep sea because this implies the assemblage will always be saturated. This is because co-existence is based on classical Gaussian niche partitioning and competitive exclusion, as embodied in [Sanders' \(1968\)](#) stability-time hypothesis. Alternatively, species saturation might be encouraged by enhanced co-existence resulting from environmental uncertainty, such as might occur through spatio-temporal heterogeneity. The dilemma is that the considerable research effort in shallow water suggests interactions such as predation are rather weak in the benthos of soft sediments ([Woodin, 1983](#); [Wilson, 1991](#)) where direct competition for space and food rarely appears important ([Lenihan and Micheli, 2000](#)). In the deep sea, relevant experimental data to assess the strength of local-scale biotic interaction are sparse. But in any case the low densities of organisms prevailing on the deep sea would, by reducing encounters between individuals, act to further weaken any between-species interactions. Hence, whether any such interaction is sufficient to limit local richness is doubtful if only because of the much smaller (productivity-limited) local population sizes of species in the deep sea compared to coastal areas where interactions are not in any case sufficiently well-developed for ecological interaction to be important ([Gray, 2002](#)). From this it seems likely that it is only when species are abundant (possibly core species) will ecological interaction occur. However, although sufficient to ensure reproductive continuity, it seems unlikely that interaction is sufficiently intense to be an important control of species co-existence in the deep-sea benthos.

### 2.3. *The enigma of 'rare' species*

Consideration of 'rare' species is necessary in order to appreciate the overall importance of any local-scale ecological interaction, and hence whether species saturation occurs, in the deep-sea benthic assemblage. More than 90% of the total of 798 species in the study reported by [Grassle and Maciolek \(1992\)](#) accounted for <2% of the total number of individuals. Because the overwhelming majority occur at very low abundance, these give the distribution of species' abundances a very long right-hand tail. Because total numbers of individuals present in each sub-m<sup>2</sup> area sampled by a box corer are so, low rare species typically are present as singletons. This may explain [Gray's \(2002\)](#) observation that quantitative samples from the deep sea typically show higher species density, the number of species present per unit area, than in coastal samples. The rare species often remain as singletons even when large numbers of replicates from the same local area are summed ([Grassle and Maciolek, 1992](#)). It is possible these rare species also have wide distributions, but their rarity in samples and problems of reliable estimation from such low-density populations means they have been collected at only one place. Questions such as population size at the local scale and distributional range at the regional scale remain unanswered.

Rare species present a challenge to the traditional concept of diversity of macrobenthos in the deep sea. What role do rare species play in ecosystem function compared to that of the 'core' dominants discussed above? Do rare species represent a pool of transient immigrants constantly challenging the local core assemblage, to gain a foothold only when they chance on favourable conditions or opportunity, such as when the wider environment changes in their favour ([Magurran and Henderson, 2003](#))? Even if they do it is unlikely, they represent a self-sustaining component of the community unless occasional breeding populations occur, perhaps in response to chance conditions or at spatially rare habitat at the landscape scale. Because propagule density will be low, recruitment even to suitable habitat may be a matter of chance. If the habitat is marginal but successful reproduction occurs then

population growth, limited by resource quality, will be slow. In other cases population density will be too low to be reproductively viable, and the species will be subject to local extinction. Purely on the basis of their extremely low densities one can conclude it highly unlikely that rare species interact with each other in ecological time.

Experiments undertaken during the 1970s where trays of sediment are laid on the deep seabed in the North Atlantic (Grassle, 1977; Grassle and Morse-Porteous, 1987; Desbruyères et al., 1980) provide some support for the interpretation of rare species constituting a pool of transient potential immigrants. Frozen, native sediment was used in most experiments, but others were enriched with various sorts of particulate organic material, although all would have been enriched to some degree because freezing would have killed any fauna present. The shallow trays were re-colonised by larvae of a greatly varying set of species. Most were polychaetes, and usually were not prominent in samples from the background assemblage, although it was assemblage dominants that re-colonised the trays in similar work in the Pacific (Levin and Smith, 1984). In general many of those present in relatively in large numbers seemed to be generalist, exploitive (often referred to as 'opportunistic') species to varying degree. The importance of this is unclear. Since the re-colonisation process is stochastic the identity of colonists may purely depend on which larvae chance on the trays—whether from 'core' or 'rare' species.

Rare species, then, are able potentially to invade and expand when conditions are favourable, such as chancing on food-enriched sediment (as mimicked by the sediment trays). This also implies local biodiversity is unsaturated with regard to the local assemblage being able to exclude new species unless they happen to be superior competitors. However, the sediment trays by presumably preventing, or restricting, immigration of adjacent fauna would not have reflected any absence of competitive exclusion except between colonists.

Even if the assemblage is 'saturated' in the sense that its diversity is regulated by interactions between the limited inventory of dominant species, the presence of rare species implies it is still possible for local richness to be augmented by

migration or settlement of individuals from adjacent source habitats. Equilibrium might be attained as a balance of stochastic immigration and extinction in patchy local scale habitat, as first suggested by Osman and Whitlatch (1978). This fits in with the concept variously described as 'spatial mass effects', 'source-sink dynamics', or 'spill-over effects' (Shmida and Wilson, 1985; Pulliam, 1988; Cody, 1993) where recipient habitat also will include extreme environments or outlier habitat of populations. Here frequent local extinctions are re-established by re-colonisations from source habitat where the species is persistent. Such process could result in relatively high species densities in the deep sea compared to coastal seas (Gray, 2002), but clearly not as a result of any greater amount of between-species interaction.

#### *2.4. Larval dispersal and the scaling of processes determining species richness*

The discussion above on rare species conveniently skips over the question of the scaling of the processes providing immigrants. Although for core species this may well include the local scale, scales for rare species may be much larger. It is likely this is achieved mostly by larval stages, although later juvenile stages of benthic elapsid holothurians are thought to be transported by currents over vast distances (Hansen, 1975).

The wide dispersal of pelagic, water-borne larvae appears to provide potential for species constantly to expand their range into new habitat within the ecological time frame. That this may be restricted by environmental factors is supported by the observation that post-larval or juvenile stages of echinoderms seem to have a wider spatial and bathymetric range than adults in the Northeast Atlantic (Gage et al., 1983, 1985). Furthermore, near the continental margin the occurrence of some species also may reflect dispersal of planktonic larvae beyond the normal range of adult populations (Gage and Tyler, 1981). This implies mass effects or source-sink dynamics operating at the edge of the species range because growth of these individuals may be retarded and survivorship too low to provide viable extension of the population in ecological time. An extreme example

of this is provided by some constituents of the present-day macrofaunal assemblage in the Mediterranean (whose present-day deep-sea environment dates back no further than the Pliocene and whose assemblages are therefore likely to be highly unsaturated). Gastropod species may be maintained as pseudo-populations by immigration of planktotrophic larvae from the Atlantic entering through the Straits of Gibraltar (Bouchet and Taviani, 1992). It is easy to see how over historical time scales this process allows evolutionary differentiation of distinct species in outlier habitat. Many species in the Mediterranean are very close to congeners found in the adjacent deep Atlantic (Fredj and Laubier, 1985), suggesting past, but relatively recent, immigration.

However, the predominating mode of early development in deep-sea macrobenthos is lecithotrophy. This may result in lower larval density, but dispersal range by drifting in currents in the cold, deep ocean is likely to be well beyond the local scale (Young, 2003).

The prevailing view, well reviewed by Etter and Mullineaux (2000) and Snelgrove and Smith (2002), has been that areas of source habitat constitute a network of patches varying in area, degree of isolation and quality within a background of uniformly unsuitable habitat or 'sink' area. But such patchiness has been thought to be small scale and based on patchy input of labile organic matter to the deep seabed (ranging from phytodetritus to clumps of sea grass and macrophytes such as *Sargassum* to pieces of wood and animal carcasses). These inputs are thought to provide spatially divided and ephemeral food resources to deep-sea macrobenthos (Grassle and Morse-Porteous, 1987). Colonisation of such food-enriched patches linked by pelagic larval stages will result in widely separated sub-populations, which, because they lack spatial autocorrelation, allow very large number of species to co-exist as a spatio-temporal mosaic on the deep-sea bed. Sources where the species flourishes owing to presence of suitable habitat operate as net exporters with most area occupied by the assemblage operates as 'sink' because it is a net importer for a large proportion of the species present (the rare species).

The results of the sediment tray experiments discussed above, when comparing the ambient sediment and un-enriched sediment trays with those with added *Sargassum* or sea grass, indicated it was juveniles rather than adults that specialise on specific patch types on the deep-sea bed, thus contributing to high local-scale diversity (Grassle et al., 1992). However, Snelgrove and Smith (2002) note that the importance of such local scale variability has been demonstrated for only a small subset of species, many of which are opportunists. Furthermore, because studies have provided little indication of large numbers of intense patches harbouring characteristic faunas, they doubt there are sufficient densities and range in patch types to support specialised faunas that will enhance regional diversity. Certainly such patches, and their specialised faunal constituents, appear not to have been encountered by sampling programmes. But equally it is possible that even areas the size of the total of 21 m<sup>2</sup> of sediment analysed in Grassle and Maciolek's study are insufficient in relation to the rarity and ephemeral nature of patches to provide a good chance of sampling one. Hence, we have to conclude that the validity of the patch mosaic coupled with patches operating as source and the intervening sediment as sink, remains theoretical and untested.

However, biodiversity pattern occurring at the landscape scale may provide an at least equally plausible rationale for non-interactive co-existence of species. Our knowledge of environmental variability at this scale is still poor, with the topography of vast area of the deep ocean remaining poorly resolved up to the scale of tens or even hundreds of km<sup>2</sup>. However, at a few places on the continental margin landscape mapping tools, such as multi-beam acoustic bathymetry and side-scan sonar, and ground truthing by deeply towed camera systems have revealed a highly heterogeneous landscape. These include sediment reducing environments such as organic falls (Bennett et al., 1994) and cold seeps (Olu et al., 1996), which as sub-systems are often blended with the normal, oxic sediment environment, and provide a possibly important contribution to macrofaunal richness in soft sediments. It is easy to imagine how in a relatively open environment

with water-borne propagules local species enrichment could be enhanced by essentially non-interactive ‘mass effects’ (Shmida and Wilson, 1985). Here sub-populations of species with negative growth rates within each piece of a mosaic landscape would be supplemented by propagules from areas with reproductive surplus.

On the continental slope perhaps the best known biodiversity pattern is that where diversity peaks at mid-slope depths (Rex, 1981; Paterson and Lamshead, 1995; Gage et al., 2000). The variety of environmental patterns associated with the depth gradient, which may help explain the varying causes of such variability in biodiversity at continental margins, particularly depth-related pattern, is well reviewed by Levin et al. (2001). These range from sediment heterogeneity, productivity and food supply, bottom-water oxygen, deep-sea currents to catastrophic disturbance such as slumps and slides. However, many unimodal biodiversity patterns also might be explained as mid-domain effects where randomly shuffled species’ ranges free of environmental gradients will increasingly overlap towards the domain centre to create a richness peak (Colwell and Hurtt, 1994). On the slope this would include geometric boundary constraints (Pineda, 1993) that may not require an environmental gradient. However, tests of models against observed data show that many features of observed pattern require additional, presumably environmental, explanation (Pineda and Caswell, 1998).

Depth-related pattern in environmental conditions also may provide opportunity for non-interactive enhancement of species richness within areas of transition between two adjacent ecological assemblages, or ecotones. Good examples occur where strongly differentiated water masses impinge on sloping bottom. In the Faroe–Shetland Channel in the Northeast Atlantic off Scotland a cold, sub-zero temperature water of polar origin is overlain by considerably warmer water originating from the North Atlantic. This creates strongly structured water mass with a persistent slope current generating unstable mesoscale eddies that influence circulation. The boundary consequently is a zone of highly variable conditions, the seabed

at about 400 m depth being exposed to temperature varying within hours over several degrees within hours. This is reflected as a transition area of overlapping faunal distributions from the upper and lower boundaries of two distinct assemblages (Bett, 2001) where macrofaunal diversity peaks, declining above and below (Narayanaswamy, 2000). This peak, therefore, may represent richness caused not so much by adaptation to local conditions but an excess of immigrants, derived probably from larval rain, over those becoming locally extinct through maladaptation.

Another example may be provided by the higher diversity found at the lower boundary of oxygen minima on the flanks of seamounts (Levin et al., 1991). Both sets of conditions seems analogous to the ecotone between polluted and cleaner sediments in inshore sea lochs (Pearson and Rosenberg, 1978). In the Faroe–Shetland Channel, the shifting conditions in the ecotone encourages recolonisation by a wider range of species than available either above or below, even if the environmental variability experienced therefore may actually be far from optimal for the organism. Hence, as in source-sink dynamics, these spill-over effects do not necessarily represent viable colonisation from above or below. To see whether such mass effects are important elsewhere, the expectation that benthic species diversity should increase near habitat boundaries, especially where habitat differences are moderate, might be tested in a variety of settings and scales.

In an important new study, Rex et al. (in press) argue that source-sink dynamics operates at a much larger scale. Here source habitat is virtually confined to the bathyal zone at the continental margins. The abyssal deep sea then largely operates as sink habitat-supporting populations that are essentially non-viable outliers of a bathymetric range extending from the bathyal. These authors note that relatively abundant and widely distributed abyssal species, such as the protobranch bivalve *Ledella ultima* and the gastropod *Benthonella tenella*, which can produce mature gametes and recruit, form part of a core group, equivalent to the ‘core’ species of Glover et al. (2001, 2002). These species, because of adaptation and consequent reproductive viability, will (unlike



'rare' species) clearly not be dependent on source-sink dynamics for their existence.

Data summarised by Rex et al. on the bathymetric ranges of deep-sea gastropods and bivalves fit this idea remarkably well, with the majority of species occurrences in the abyssal appearing as simply range extensions from the lower bathyal. The difficulty is that the actual dispersal range of larvae of deep-sea organisms, like that for most other marine species, is unknown, but will need to be extremely large. Slowed metabolism in the cool abyssal water mass conceivably may prolong survival in non-feeding, lecithotrophic larvae of protobranch bivalves, perhaps allowing survival over the very many months required for transport by deep currents. Planktotrophic larvae of gastropods may well be capable of sustaining themselves in the course of drifting over large distances in surface currents.

However, the implied openness in marine ecosystems on which Rex et al.'s (in press) idea depends may be difficult to sustain. Past studies suggest an evolutionary perspective where larvae prefer to settle where their parents have been successful through adaptation to some means of habitat recognition (Butman, 1987), although admittedly evidence from the deep sea is non-existent. Also, in coastal theatres larval retention in and around source populations (Swearer et al., 1999) suggests that a more closed system may operate. Cowan et al. (2000) show that when simple advection models, rather than more complex Eulerian and Lagrangian flow models, are used larval exchange rates may be greatly over-estimated. Such findings challenge the generality of openness in marine ecosystems. Overall, it is difficult to be confident about long-range larval dispersal over ecological time scales for most marine invertebrate species, let alone those in the deep sea. Thus, the functional linkages of marine populations over ecological time scales, such as source-sink dynamics, will remain uncertain until more direct measurements of larval dispersal are made, and the possibility of long-range transports, as well as larval retention in local areas better understood. Genetic and other methods to relate source to sink population structure along with metapopulation models coupled to fine-scale

oceanographic models will be necessary to determine sustainability of such functional linkages over ecological time.

Even if it is uncertain how range in larval dispersal relates to the overall scale of such dynamics as reflected in local richness as expressed at the ecological time scale, the longer term result on the zoogeographic range of major taxa is more obvious. Taxa, such as echinoderms and protobranch gastropods, with a high incidence of planktotrophy, have wider depth-related and geographic ranges (Young et al., 1997) and appear less diverse than those taxa with mainly lecithotrophic larvae (e.g., protobranch bivalves and polychaetes), or direct development (e.g. peracarid crustaceans) where there is much more limited potential for dispersal (Sanders, 1979; Stuart and Rex, 1994).

All this implies that the scaling of mass effects, as played out at small to landscape or larger scales, is important to the extent to which local non-interactive pattern relates to the larger-scale species pool. For example, the operating scale for peracarid crustaceans, which brood their young, will be much smaller scale than that of echinoderms or gastropods with planktotrophic larvae that are widely dispersed at the surface of the ocean. Species with lecithotrophic (yolky non-feeding, but pelagic) larvae may occupy an intermediate position. Clearly obtaining material to test such expectations should form an important priority of future research.

### 2.5. *The importance of scale*

We have noted that the very largely theoretical explanations of deep-sea biodiversity have involved ecological processes at the local scale with an assumed, but still largely conjectural, relationship to the larger scale. Rather than seeking explanation by moving our baggage of assumptions from the local to larger scales, it may be more profitable to regard the local community as assembling itself from the large scale through a series of filters, or stages, operating at different, but overlapping, spatial and temporal scales (Lawton, 1999). For example, species need to arrive and establish populations, with distance and

isolation excluding many. Others arrive but find the habitat unsuitable, with perhaps differences in density and spatial arrangement of habitat patches further filtering and moulding the local assemblage.

Ricklefs and Schluter (1993) conceptualised smaller-scale, ecological processes being embedded hierarchically within and operating at faster rates than larger scale processes (Fig. 2). Hence they operate at shorter time scales than those at landscape (10–100s km<sup>2</sup>) or regional (100s–1000 km<sup>2</sup>) scales. This is because the processes involved take longer to express as biodiversity pattern, involving long-term processes of colonisation/extinction of species in response to environ-

mental gradients, dispersal, metapopulation dynamics (Hanski, 1998), and gradients in habitat heterogeneity. In the benthos, such gradients influence local-scale processes of larval dispersal among habitat patches, thus determining potential membership in local-scale assemblages. Such dispersion of propagules may also operate at the regional scale where species may exist as disparate metapopulations whose local-scale dynamics and overall persistence depend on processes such as reproductive synchrony, or as part of a vast source-sink dynamic from the bathyal. The implication of all this is that local diversity is more usefully considered as a consequence of the larger scale rather than the outcome of ecological processes operating at the local scale.

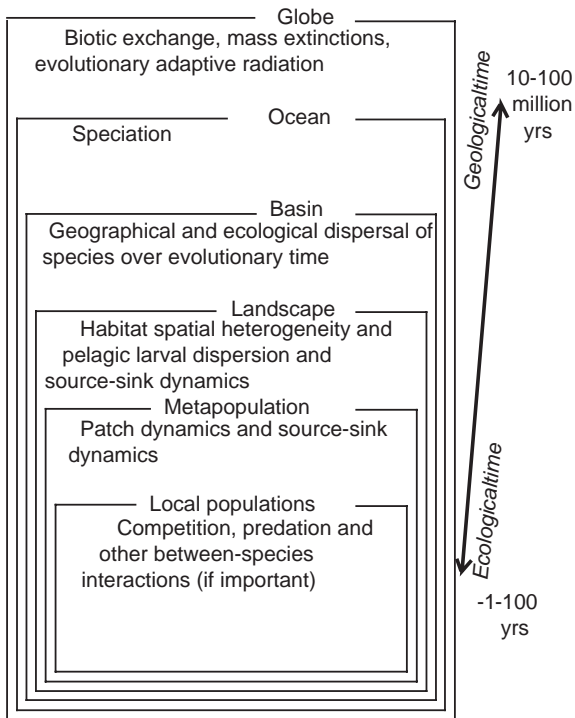


Fig. 2. Processes which have been put forward as influencing deep-sea benthic biodiversity arranged hierarchically according to operational time scale. Smaller scales, which operate at ecological time scales, are shown embedded hierarchically within larger ones which operate at geological time scales. Note that the processes indicated do not exclude stochastic events, such as mass effects and source sink dynamics, which may operate at any level, and which may in reality be much more important than the processes operating at local scales (modified after Ricklefs and Schluter, 1993).

## 2.6. What can species–area relationships tell us?

The little evidence as yet available on species–area relationships from deep-sea benthos reviewed above suggests differing patterns depending on taxon, life-history, dispersal, and rarity. For example, relatively low regional compared to local richness in polychaete dominants (Glover, et al., 2002) also supports the interactive model, at least for the core species. However, by including the long list of rare species recorded at both local and regional (3000 km) scale, a contrasting non-interactive relationship is indicated because their rarity makes interaction between individuals in ecological time virtually impossible. Whether the presence of rare species then reflects mass effects augmenting local richness by migration or settlement of individuals from adjacent (Grassle and Grassle, 1994), or far-off bathyal habitats, as suggested by Rex et al. (in press), is as yet unclear. The success of such, presumably stochastic, local colonisations in any case will be severely restricted by the low levels of food limiting reproduction and population growth rather than by direct competition.

The several other factors listed above, taxon, life-history, dispersal, are interdependent in that differences in dispersal result from differences in life history which, in turn, come from differences in dispersal capability between major taxa. Sanders and Grassle (1971) related differences in

diversity between major taxa to mode of dispersal, contrasting the relatively low richness among brittle stars, many of which have planktotrophic early development, with peracarids, such as isopods, that brood their young with no free-living larval stage. Although exact comparisons of richness are difficult, the exuberant radiation of deep-sea isopods (Hessler et al., 1979), for example, seems unmatched in groups such as ophiuroids (presumably because greater gene flow limits opportunities for allopatric speciation). The consequently larger range of ophiuroids will limit regional compared to local richness compared to isopods, but should not be interpreted as reflecting differences in ecological interaction at the local scale.

Small body size may also act to reduce the regional species pool. For example, the very modest regional diversity compared to high local diversity found in deep-sea meiofaunal nematodes in the Northeast Atlantic or central Pacific abyssal is interpreted by Lamshead and Boucher (2003) as reflecting the importance of local ecology (patch dynamics). However, another explanation for this relationship lies in the finding that species–area relationships are strongly dependent on body size (Hillebrand and Brenckner, 2002). This is simply because such organisms as meiofauna, with unimaginably vast population sizes, are readily transported by currents so that any individual functions as a propagule, will have much wider distributions than larger aquatic organisms (Fenchel, 1993). Ranges may well be cosmopolitan; therefore extinctions are unlikely and allopatric speciation very rare. The consequence is that although many species may be found at the local scale, at the larger to global scales total richness is relatively modest (Finlay et al., 1996).

Useful knowledge to test for the importance of species interactions might be gained from sampling programmes providing estimates of richness at intermediate as well as the local and regional scale. This is in order to test for any trend to curvilinearity in the species area plot that would suggest species saturation of a Type II relationship. However, clearly any such pattern needs careful interpretation in relation to such factors as taxon, mode of dispersal and body size.

### 3. The importance of history

The discussion above on the importance of species interactions to coexistence and saturation of assemblages suggests that in the deep sea local scales may at best be partially interactive, yet unsaturated assemblages, to an extent perhaps depending on taxon and geographic range. This implies that local richness is influenced not only by regional richness, but also by the historical processes determining richness at this larger scale (Stuart et al., 2003). In addition, differences between the northern and southern hemispheres (Poore and Wilson, 1993; Rex et al., 1997) fuel uncertainty whether findings from one area or region can be safely applied to other depths, basins or oceans. This is particularly true when they are of differing size, latitudinal configuration and age, such as the Atlantic versus the Pacific. The validity of comparisons between areas with sharply different environmental histories, such as the North Atlantic versus the deep-sea basins in the Norwegian and Greenland Seas in the Arctic Ocean, is particularly called into question. In addition we need to take into account large-scale geometrical constraints such as mid-domain effects.

We are only just beginning to resolve the imprint of historical processes in present-day pattern in deep-sea biodiversity. However, the processes and rates of evolutionary diversification determine the zoogeographic species pool from which are derived the large numbers of species coexisting at the local scale. These in turn are controlled by processes operating at the ecological time scale. At larger scales, pattern will be increasingly determined historically by pattern in immigration and dispersal from other areas. In the deep sea knowledge of such historical pattern and processes is in its infancy, yet this somewhat punctuated historical progression has largely determined the broad-scale pattern we see today.

For example, in the North Atlantic where microfossil evidence from deep cores obtained by the Ocean Drilling Program (ODP) has been analysed, cyclic shifts in deep-sea benthic ostracod diversity occurred during the Pliocene. These correlate to cycles in surface productivity driven by glacial retreat and advance caused by changes

in solar insolation (Cronin and Raymo, 1997), although any direct causal link is unclear. Furthermore, Glover et al. (2001) suggest that the polychaete dominants represent the opportunists of the Madeira Abyssal Plain habitat in the North Atlantic. This is because they have colonised and now numerically dominate the macrobenthic assemblage still recovering from a series of massive sediment slides, detectable as a wide area turbidite, the most recent just 930 yr ago.

At slightly longer timescales (1.0 and 0.6 myr ago) re-colonisation of the deep-sea sediment may have followed a series of global-scale extinction events caused by geologically sudden shifts in climate during overall cooling through the Tertiary and into the Quaternary. The most recent occurrences in the fossil record of deep-sea benthic Foraminifera in the South Pacific was caused by climatic change as recently as the middle to late Pleistocene (Hayward, 2001). Whether or not these affected the global deep ocean or the regional scale is unclear. But such events would have left a cumulative imprint on community structure and composition with assemblage dominants being drawn from a limited inventory of successful new colonists. It is tempting to suggest this process is going on to-day. Assemblage dominants may represent successful re-colonisation to unsaturated habitat providing a 'core' of species with varying, but probably a generally low degree of biological interaction, while rare species may reflect the dynamic balance between stochastic re-colonisation and extinction of other species as immigrants to marginal habitat from a vast species pool at larger scales.

The paradox is that many apparently successful and highly diverse lineages, such as asellote isopods (Hessler and Wilson, 1983; Wilson and Hessler, 1987) and protobranch bivalves, appear to be much more ancient, with no indication of radiation other than in the deep sea (Wilson, 1998; Allen and Sanders, 1996). This highlights the lack of real convergence of interpretations from phylogeny and cladistics on the likely antiquity of deep-sea faunas, and also on age and rates of evolution to explain the high species richness found to-day. Yet despite the apparently pervasive and recent influence of Quaternary extinctions, the evidence

from cladistic analysis of deep-sea isopod crustacean phylogeny, and the careful morphological examination of large collections of protobranch molluscs, shows a complex but broadly comparable pattern among different major taxa. This indicates possible recent re-colonisation and radiation superimposed on persistence of older families from the Mesozoic to the present despite changing conditions. Clearly reconciling the palaeontological evidence from microfossils with the results of broad-scale zoogeography is necessary before we can arrive at a satisfactory superimposed on a pattern of serial re-colonisation from shallower depths and possibly also from deep-water refugia. This may have occurred in isolated basins that have somehow escaped effects causing extinction elsewhere. In this respect areas with isothermal water columns such as the Antarctic, rather than the almost completely isolated deep water masses and faunal immaturity of the Arctic and Mediterranean deep sea, suggest potential for migration from deep interpretation. This is likely to incorporate a pattern of large-scale extinctions up to and including the Quaternary into shallow water as well as the traditional site for colonisation of the deep sea.

#### 4. The importance of the Antarctic

##### 4.1. What do we know about the Antarctic deep sea?

Unlike the Arctic, the lack of thermal structure in the Antarctic water mass has long been thought to have encouraged colonisation into the deep-sea from the adjacent shelf (Menzies et al., 1973; Hansen, 1975). However, present day benthic assemblages on the isostatically depressed (to 900 m depth in places) Antarctic continental shelf are seen as the product of a substantial and complex historical legacy. The long geological and hydrographic isolation, and persistent cold climate and high, but intensely seasonal, primary production experienced on the shelf may have encouraged development of some of their more unusual features such as extraordinarily high endemism, gigantism and slow rates of individual growth

(Lipps and Hickman, 1982). Clarke (2003) provides a recent review of these earlier data and their interpretation.

But this Antarctic diversity pump on the continental shelf that has generated high rates of in-place speciation and endemism cannot be assumed also to have influenced the contiguous deep sea areas of, for example, the Scotia and Weddell Seas, or to have operated there in a similar way. Unlike the polar basins in the northern hemisphere, the Antarctic deep sea is composed of four contiguous and confluent basins surrounding the Antarctic land mass. The open confluence of the Antarctic deep sea with the three other major oceans (Fig. 3) provides pathways for evolutionary radiation from, and into these basins. One of these Antarctic basins (the Atlantic–Indian Basin) is effectively the most southern part of the South Atlantic Ocean and fully confluent with the Argentine Basin and only separated from the Agulhas Basin to the east by the Atlantic–Indian Ridge. The South Indian Basin runs from Kerguelen to about 150°E and is separated from the main Indian Ocean basin by the Southeast Indian Ridge. There are two Antarctic basins in the southern Pacific, the Southeast Pacific and Southwest Pacific basins separated by the Pacific–Antarctic Ridge.

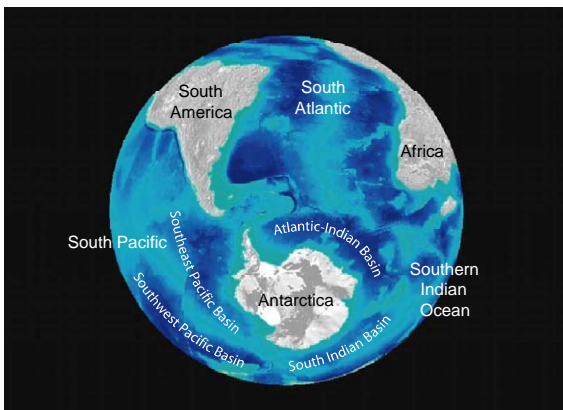


Fig. 3. Antarctica and the major deep-sea basins of the Southern Ocean: The deeper shades of grey (blue in the on-line version) indicate greater depths.

#### 4.2. *The contribution of zoogeographic and taxonomic studies*

Although the deep-sea basins constitute the largest single benthic habitat in the Antarctic, remarkably little is known on the composition and evolutionary history of its fauna, compared particularly to the Atlantic. Pioneering investigations by Russian workers (summarised by [Vinoogradova, 1979](#)) and expeditions to the Atlantic and Pacific basins by American workers during the 1960s ([Menzies et al., 1973](#)) provide virtually the only data on the smaller size classes of the Antarctic deep-sea benthos prior to the sampling undertaken by recent German expeditions. Conclusions from analysis of the latter samples are only just emerging, but suggest many polychaetes and foraminifera species are already known from the North Atlantic and North Pacific ([Cornelius and Gooday, 2004](#); [Hilbig, 2004](#)). These reinforce earlier findings from megafauna of the occurrence of cosmopolitan taxa at abyssal depths ([Clarke, 2003](#)), although a degree of endemism is evident at the generic level among isopods.

The isopods have so far provided by far the bulk of available data to explore what zoogeographic and taxonomic studies and adaptations of deep-sea species can tell us regarding the origin and migratory pathways of the deep-sea fauna, particularly in relation to the Antarctic. The extraordinarily prolific radiation seen among deep-sea asellote isopods ([Hessler and Wilson, 1983](#); [Poore and Wilson, 1993](#)) has attracted the most thorough analyses of evolutionary pathways and origin ([Wilson, 1998](#)). Indeed, the extraordinary richness of this group on the Antarctic continental shelf has fuelled speculation on a possible shallow-water origin of deep sea forms (e.g. [Kussakin, 1973](#)). A contrary view was taken by [Hessler and Thistle \(1975\)](#) based on the distribution of eyes in deep-sea paraselloidean families, which is interpreted as ancient endemism. Many species may have evolved in-place ([Hessler and Thistle, 1975](#); [Hessler et al., 1979](#)). These may be the source of a substantial proportion of the modern-day deep-sea fauna. Equally it is possible that the Antarctic deep sea has absorbed a large number of lineages evolved elsewhere as well. The analysis by [Menzies et al.](#)

(1973) found evidence for complex evolutionary patterns, with some isopod taxa moving into deeper water (evolutionary polar submergence) and other taxa colonising the continental shelf from the deep sea (evolutionary polar emergence). These uncertainties have benefited from detailed studies by Brandt (1992) who has shown that while certain isopod families have migrated into the deep sea from the continental shelves of Gondwana, other families have moved from the deep sea up onto the Antarctic shelf. This complex pattern is echoed in analysis of the evolutionary history in deep-sea fishes (Andriyashev, 1953; Merrett and Haedrich, 1997).

Wilson's (1998) subsequent analysis is pivotal in discussion on the evolution of the global abyssal isopod fauna. He concluded that although many asellote families are endemic to the deep sea, others may not be. In particular, the more recently evolved flabelliferan isopods show a gradient from shallow-to-deep and south-to-north in the Atlantic, with none evolving in the deep sea and reflecting more recent colonisation from shallow habitat in the southern hemisphere, including the Antarctic (Wilson, 1998). Radiation of deep-sea species from the Antarctic into the other ocean basins may have been assisted by the northward spread of deep-water formed in the Antarctic. Deep thermohaline currents systems as carrier mechanism may be of particular importance to northwards radiation in the Atlantic. The resulting zoogeographic patterns will be more obvious because it is more laterally restricted, and likened to a peninsula compared to the Pacific and Indian Oceans deep-sea areas, and has an impoverished end-member in the deep Arctic basins. Rapid environmental changes during the Quaternary, such as warm-cold oscillations and periods of sudden discharge of ice into the North Atlantic called Heinrich events (Bond and Lotti, 1995), also may have decimated the bathyal North Atlantic and perhaps also impacted the adjacent abyssal basins. For example, Allen and Sanders (1996) and Gage et al. (in press) note that the deep north western Atlantic (where Heinrich events were best developed) are more impoverished than the north eastern Atlantic. Comparably brief interstadial events also occurred in the North Pacific (e.g.,

Behl and Kennett, 1996). But whether glacial conditions, although variable, have been significantly more stable in the Antarctic is unclear, with recent analyses indicating major Quaternary changes in glacial history (Berkman et al., 1998) affecting the Antarctic continental margin (Grobe and Mackensen, 1992). Assuming such changes also impacted the adjacent deep sea, any temporal asymmetry might have generated extinctions faster than immigration from the other pole have replaced, perhaps reflected in the differences in biodiversity observed today (Wilson, 1998). Certainly, where investigated at full-ocean scale, endemism among protobranch bivalves is much better developed in the basins of the South than the North Atlantic. However, a simple model of northwards gene flow in protobranchs is confounded by the finding that the protobranch fauna of the Argentine Basin has no similarity with that of the adjacent deep Antarctic, although sources in the Angola Basin, or the little-sampled South Pacific and its adjacent Antarctic basins, cannot be ruled out (Allen and Sanders, 1996).

In conclusion general patterns in origin or radiation of the Antarctic deep-sea fauna remain uncertain, and much remains to be done before a picture, disentangled from the better-understood processes in the deep Northern Hemisphere, emerges.

#### *4.3. Integrating spatial scales of biodiversity and history*

Biodiversity studies now provide abundant evidence that large-scale processes strongly influence both regional, landscape and local diversity at all smaller scales (Ricklefs and Schluter, 1993). The corollary is that the taxonomic components of assemblage organisation can be understood by deep-sea biologists only by placing the local assemblage in its historical and biogeographic context. The hierarchical model, where processes are nested according to both spatial and temporal scale cartooned in Fig. 2, makes clear the differing variables operating at different scales, even if there is some transmission of signal from one scale to the next (Whittaker et al., 2001).

Scaling up from regional and basin scales to the whole ocean in the deep sea is not easy, and interpretations carry high levels of uncertainty. This results from limitations in sampling methodology, lack of statistical replication, severe deficiencies in taxonomic knowledge, and very uneven geographic coverage. However, explanation for pattern at these very large scales, including the grand clines such as latitudinal species diversity gradients (LSDGs), probably can be collapsed to dynamic hypotheses based on climate and/or history (Whittaker et al., 2001). In the deep sea these are likely to reflect global-scale oceanographic processes, as well as factors influencing extinctions and historical opportunity, such as the flooding of the Mediterranean or closure of the Isthmus of Panama, and possible ocean area-related factors influencing habitat variety and immigration (Osman and Whitlatch, 1978; Abele and Walters, 1979) and changes in the geometry of the continents driven by plate tectonics influencing the shape and latitudinal disposition of the deep ocean basins. A particular challenge is to reconcile evidence from microfossil indicators of comparatively recent global-scale extinctions in the deep sea (e.g., Kennett and Stott, 1991; Hayward, 2001) with evidence from detailed cladistic analysis of highly speciose groups such as asellote isopods and protobranch bivalves that have almost certainly radiated in place over a much longer period (Wilson and Hessler, 1987; Allen and Sanders, 1996; Wilson, 1998, in press).

Our theoretical framework of, at best partially ecology-driven, but predominantly non-interactive, local biodiversity, and the influences of regional processes and often punctuated and unique historical events affecting large areas of the deep sea that are rooted in zoogeography are not irreconcilable. They are complementary and necessary to our understanding of biodiversity observed in the deep ocean to-day. For example, study of the macrobenthic biodiversity in the deep-sea basins of the Norwegian and Greenland Seas in the Arctic Ocean shows the fauna is young and community development immature (it is no older than the Pleistocene). The impoverishment in species compared to the adjacent North Atlantic deep-sea basins is striking, with a high degree of

endemism at species level but very low level of endemism at genus and family level (Guryanova, 1970; Dahl, 1972; Svavarsson, 1993; Clarke, 2003). Although the Arctic abyssal fauna contains elements suggesting ancient connection to the faunas of the Pacific and Atlantic, Quaternary glaciation, probably in concert with the massive Storegga slide, must have been the cause of considerable extinction within the deep-sea as well as shelf faunas (Dahl, 1972; Dahl et al., 1976). Because of their isolation and faunal impoverishment, it is unlikely that the Arctic and Nordic Seas basins have contributed in any way to diversification in the remaining global deep ocean.

The reason why the discovery by Rex et al. (1993) of what appear to be LSDGs in certain macrofaunal taxa in the Atlantic bathyal (500–4000 m) was so unexpected and controversial is because of the supposed long and stable history of the deep sea and its remoteness from the solar-driven processes at the surface driving climate. The taxa studied by Rex et al. (1993) were isopod crustaceans, bivalve molluscs and gastropods, and while the pattern indicated a polewards decline in the North Atlantic there was no clear pattern for the South Atlantic. Although Gray (1997) attributed the pattern in the northern Atlantic to very low diversities in the Nordic Seas, a significant, probably productivity-driven, negative relationships between diversity and latitude in isopods and gastropods (Rex et al., 1997) and in cumacean crustaceans (Gage et al. (in press)) remain when data from the Nordic Seas are removed. In the southern hemisphere, bathyal isopods appear to show no such decline, although Antarctic data are sparse (Poore and Wilson, 1993). However, deep-sea Foraminifera show a classical pole-ward decline in both hemispheres (Culver and Buzas, 2000). Establishment of strong seasonal pattern in POC flux to the seabed following cooling of the southern hemisphere and glaciation of the Antarctic 37 myr ago may have contributed to depressed high-latitude diversity of benthic foraminiferans through increase in phytodetrital opportunists (Thomas and Gooday, 1996), this resulting in the bipolar latitudinal gradient peaking at the tropics seen to-day (Culver and Buzas, 2000). Furthermore, the strong inter-regional

variation in diversity in the South Atlantic (Rex et al., 1993; Stuart et al., 2003) also may apply to the North Atlantic where Gage et al. (in press) found significantly lower cumacean diversity in samples from the NW compared to the Northeast Atlantic, a finding previously commented on by Allen and Sanders (1996) for protobranch bivalves. Gage et al.'s results do not support classical latitudinal gradients in Cumacea in the terrestrial sense of a single structuring solar-linked processes.

Overall, a variety of processes exists for different taxa, suggesting a causal balance between history and modern ecology. Also, in the absence of data on geographic range we cannot rule out a mid-domain effect contributing to higher richness at low latitudes. One consistent factor emerging from all these major taxa is the low diversity in the deep Nordic Seas, isolated by submarine sills and water-mass structure from the global deep ocean, and still re-colonising after Quaternary extinction, as a regional phenomenon rather than part of a large-scale latitudinal pattern (Svavarsson, 1997). However, until a sufficient level of knowledge of biodiversity pattern in the deep ocean of the southern hemisphere, and particularly the high latitude end member of the Antarctic deep sea, is attained, our understanding of such latitudinal pattern remains seriously incomplete.

In conclusion, an understanding of the Antarctic deep sea benthic assemblage will best be achieved with a starting point as a 'top-down', global-to-local approach in modelling variation in diversity in the various taxa in which mechanisms are evaluated with explicit reference to scale. Some patterns, such as endemism and radiation, may require a greater input from historical events and geography, such as isolation. Other macroecological patterns such as LSDGs also may benefit from understanding climate-related variables such as productivity. This top-down approach will inform and discipline our approach to understanding how the local community, as revealed by sampling, has assembled itself from the larger pool by passing through the succession of filters working at different spatial and temporal scales, such as evolutionary dispersal, isolation, landscape environment, habitat patchiness and larval dispersal.

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