Marine nematode deep-sea biodiversity – hyperdiverse or hype?

ABSTRACT

Nematodes have been identified as a potentially hyperdiverse group and the deep sea as a potentially hyperdiverse environment (i.e. > 1 million species). A large-scale data set from the equatorial central Pacific is used to estimate regional diversity with results that challenge this view; regional diversity is higher in some coastal waters despite lower sample diversity in coastal waters than in the deep sea. The data suggests a paradigm where the deep sea has modest regional diversity, despite high local diversity through patch dynamics, because similar patches in a similar habitat are repeated for considerable distances. Disturbance in shallow water dominates over patch-dynamic mechanisms reducing local diversity but regional diversity is high because of the close packing of multiple habitats within a single region.

The Pacific data are also used to demonstrate the pitfalls of extrapolating from local to global diversity. There is no reason to conclude that nematodes are less diverse than other benthic groups, indeed where direct comparison is possible the Nematoda appear to be as diverse as the Polychaeta, the most diverse macrofaunal taxon. This analysis is not consistent with the hypothesis that either marine nematodes or the deep-sea benthos are hyperdiverse raising the question whether any environment or metazoan taxon has more than a million species.

Keywords

INTRODUCTION

Human beings seem to have always made collections of curiosities but in the eighteenth century a new concept was born, the idea of making systematic collections as a tool for understanding the natural world. The national collections of the great museums of the world grew from this starting point. The fundamental questions arose early, among them were: what is the biological diversity on Earth, where is it concentrated geographically and taxonomically, and why are certain taxonomic groups, biogeographical regions or ecological habitats more species rich than others? In recent years, these old questions have taken on a greater urgency as new issues have arisen connected with our understanding that the natural world is not fixed and unchanging. In particular, we want to know whether the diversity of the Earth is falling, whether human activity is partly or wholly responsible and whether there is anything we could or should do about it?

In this editorial, we intend to revisit the fundamental questions of how many species might be expected in various regions and whether species are concentrated in certain places because sensible decisions cannot be made about biodiversity change until basic biodiversity patterns are ascertained. We propose to use the free-living Nematoda as a vehicle for studying benthic biodiversity patterns from a novel perspective. Nematodes are better known to the average biologist as parasites but the phylum has an abundant and diverse free-living fauna with a global distribution in soils and sediments. Many, possibly most, free-living nematodes are marine and we shall focus on this understudied taxocene.

Nematodes have been flagged as a taxon that is diverse and possibly hyperdiverse (which we may define as a species richness in excess of 1 million) and the deep-sea ocean flagged as a potentially hyperdiverse environment. This suggestion is based on speculation from local diversity (Grassle & Maciolek, 1992; Groombridge, 1992; Lambshead, 1993; Boucher & Lambshead, 1995; Heywood, 1995) rather than from large scale data sets. New data from the central Pacific allow us to assess regional biodiversity in the deep sea for the first time and then to reanalyse extant data on other deep-sea and coastal regions in the light of the Pacific results.

Biodiversity definitions are closer to subjective 'value judgement' concepts such as quality of life than an objective measure of an environmental property. The result is that there are a variety of ways to analyse biodiversity, depending on the exact question asked and the scale employed. Because organisms are not geographically or ecologically randomly distributed, the geographical, temporal and taxonomic scales chosen for data collection will have a strong impact on the results of any analysis. For example, a

square metre of European chalk grassland is more botanically diverse than a square metre of lowland Amazonian rain forest; the reverse is true for a square kilometre (Groombridge, 1992). Spatial and temporal scales tend to be inter-related; ecological processes will tend to dominate over short time-scales and local distances while evolutionary processes are more important over large time-scales and regional/global distances.

Nematode abundance in marine and terrestrial domains is surprisingly similar (Lambshead, in press). Impoverished habitats, including the extensive deep-sea abyssal plains, have roughly 10^5 nematodes per square metre while productive habitats contain about 10^6 or, exceptionally, 10^7 possibly with an upper limit of 10^8 animals per square metre. Nematode abundance is closely correlated with food supply and local productivity. This is most clearly seen in marine sediments where abundance declines with depth and distance from the continents (Cook et al., 2000). The highest nematode abundance, therefore, tends to be found in the rich lowlands, marshes and marine mud around the coastline except in some tropical areas where terrestrial export can be toxic for the fauna (Alongi, 1987; Boucher & Clavier, 1990).

The pattern of declining abundance with declining productivity suggests an immediate null hypothesis, that species richness and ecological diversity should mirror the basic abundance pattern.

DEFINITIONS, MEASUREMENT AND SAMPLING

There are essentially two ways to measure diversity, species richness or ecological diversity. Species richness, a count of the total number of recorded species, is the simplest and 'purest' of the measures. But such a species count is only meaningful if it is related to some external measure of sampling size such as number of individuals sampled or area of habitat sampled. Clearly, if one samples a larger area, or collects more animals, one would expect to find more species. In practice, the two ways of measuring species richness can give surprisingly similar results (e.g. Gray, 1994) because the two parameters tend to correlate for the same data.

Measuring species richness can be problematic where the region to be assessed is large, open (i.e. has no biogeographical boundaries) and/or highly species rich. In this situation, the collectors curve may never come to an asymptote but, after a settling down period, each new sample adds to the estimated species richness. No upper limit to the number of species can be determined in practice. Species richness is not a good measure for analysing the effect of localized ecological factors on biodiversity because it does not incorporate quantitative information about the relative abundance of each species. Species richness counts also require a reasonably good knowledge of the taxonomy of the group in question, as it is essential to determine conspecificity in samples taken over a whole region or area. This has severely limited marine nematode biodiversity research, as the taxonomy of the group is immature. Few species have been described and descriptions tend to be clustered in biogeographical regions that have clusters of taxonomists, notably northwest Europe, and to easily sampled habitats such as the littoral (intertidal).

Ecological diversity has traditionally been interested in two properties of samples, the number of species in a sample (species richness) and the proportional abundance of each species (equitability). These two inter-correlated parameters are amalgamated into a single number as an ecological diversity index; it is this amalgamation that is problematical. There are a number of ways of calculating a diversity index and they are not guaranteed to place samples in the same rank order of diversity. Marine nematologists have tended to focus on ecological diversity for pragmatic reasons. Core sampling take precise, quantitative environmental samples from any depth and fauna can be extracted from the sediment with high rates of efficiency. Worms can then be sorted into morphological species with an acceptable level of accuracy even if most of them are new to science as is not unknown in deep-sea samples (Lambshead, 1993). The quantitative data produced is ideally suited for ecological diversity analysis so it is not surprising that marine nematode biodiversity studies have focussed on this aspect.

Ecological diversity, often used to measure the diversity of individual samples, equates to Whittaker's (1970) 'alpha diversity', although Whittaker more properly meant the species richness at a single point. Whittaker divided regional diversity into two concepts. The first is gamma diversity, the species richness of a region (although 'region' is an imprecise term). The second is beta diversity, the rate at which species accumulate with distance in a sampling programme.

LOCAL DIVERSITY

The first impression of a student of marine nematology peering down a microscope at a concentrated mass of nematodes extracted from a core sample is that not only are they abundant but that the species richness in a single core is astonishing (thirty to forty-five species for 100 individuals).

Ecological diversity has been more comprehensively studied for marine nematodes than species richness. Seventeen data sets from a variety of biotopes were compared by Boucher & Lambshead (1995; see their Fig. 2). The main conclusion of this study was that ecological diversity had a nonlinear association with depth, alpha diversity being highest at abyssal and especially bathyal depths, a pattern that has been reported for other benthic organisms (e.g. molluscs, Rex, 1976, and polychaete worms Paterson & Lambshead, 1995; Gage *et al.*, 2000).

The explanation of this depth-diversity pattern has been associated with a non-equilibrium interaction between productivity and disturbance, both of which are correlated with depth (Huston, 1994). This would tend to give a peak ecological diversity at bathyal depths. Grassle & Morse-Porteus (1987; see also Grassle, 1989) postulated the non-equilibrium spatial–temporal mosaic theory. They suggested that the deep sea could support a large local species richness through the patchy distribution of ephemeral resources in the absence of continuous wide-scale disturbance.

This hypothesis is difficult to test in practice because many of the patches that might be important to the organisms might not be obvious to human observation so it is difficult to judge whether the scale of the sampling is appropriate to the scale of the patch-creating mechanism. One of the suggested resources that might cause a spatial mosaic, however, was the seasonal phytodetritus input into parts of the deep sea. Not only is this visible on the bottom but it can form patches on a scale suitable for investigation by the standard deep-sea meiofauna corer (diameter 57 mm). Rice & Lambshead (1994) tested the hypothesis and found that more deep-sea nematode species were aggregated, rather than randomly dispersed, in a phytodetritus influenced region than a non-phytodetritus influenced region and that species aggregations were discordant (i.e. species tend to avoid each other). This is the pattern that would be expected if phytodetritus caused a series of ephemeral patches, temporally out of synch with each other (see Lambshead, 1993). Recent studies in the Atlantic (Lambshead *et al.*, 2000) and the Pacific (Lambshead *et al.*, 2002) have confirmed that nematode local diversity is higher in phytodetritus enriched regions. Also Lambshead *et al.* (2001) demonstrated that a turbidite (a large-scale underwater sediment slide), one of the few large-scale physical disturbances in the deep sea was associated with a lowered local diversity.

These results are consistent with the spatial–temporal mosaic theory and give a plausible link between pattern and process. They show how patchiness of resources in a resource-limited habitat could create high local diversity. In principle, this hypothesis could also explain the high local diversity in rain forests (Grassle, 1989) suggesting that similar processes might be important.

GLOBAL DIVERSITY

The problem is how does one get from an understanding of local diversity to an estimation, let alone comprehension of the factors influencing, regional or global diversity. Lambshead (in press) lists three primary ways to estimate global diversity from local sampling. The first is to estimate by extrapolating from known regions to cover unknown regions (May, 1988). The result for a high diversity group such as insects is about a million species. Although subjective, this method is probably not an unreasonable approach provided one has enough known regions to establish a secure basis for estimation. Unfortunately, this is not the case for marine nematodes. The coastal waters of the British Isles (and north-western Europe generally) are as well known as any marine nematode region in the world but only 450 species have been recorded. Although this is about 10% of the global described fauna, it is probably an underestimate because offshore habitats have been undersampled. Most surveys in European waters still discover that *c.* 30–40% of species are new to science, e.g. Boucher (1980) in sublittoral sands of the Bay of Morlaix, Brittany; Lambshead (1986) in Clyde sandy beaches; Ferrero (unpubl. data) in Dublin Bay.

A second method was attempted by Lambshead (in press) to estimate global nematode species richness by working backwards from total global nematode abundance, which is rather easier to calculate. Unfortunately this method relies on untestable assumptions about the number of individuals per species for nematodes.

A third method that appears to be the most objective is that used by Erwin (1982, 1988) for estimating global insect species richness. Essentially, this involves generating a 'species accumulation with distance' curve along a transect. The curve climbs quickly at first but then in a high diversity, open, environment may settle down into a steady, apparently linear rate of increase in species per distance. This method gives extremely high and similar estimates for global species richness (of around 10^8 species) whether applied to rain forest insects or deep-sea benthic macrofauna (Grassle & Maciolek, 1992), which might imply similar mechanisms at work. This method is, however, also based

on assumptions that are debatable. The assumption of linearity of the species accumulation per distance is fundamental. Because of the enormous extrapolation involved, a change in the type of fitted model from linearity to a flat curve could substantially alter the predicted global species richness. Even assuming linearity, small changes in the gradient of the line can give large differences in predictions. There is also the problem that we have every reason to expect local diversity to be heavily influenced by local ecology. It is likely that the exact location or time that the data is obtained could also substantially alter the predictions.

Recently, a new marine nematode data set was produced by Brown (1998) that covered more than 3000 km of abyssal plain of the north-central equatorial Pacific, the Clipperton-Clarion Fracture Zone (CCFZ). This area has been extensively studied by deep-sea standards as part of JGOFS, the US Joint Global Ocean Flux Study (Smith *et al.*, 1996), and the biodiversity of the nematode fauna investigated (Brown *et al.*, 2001; Lambshead *et al.*, 2002, 2003). These data (21 core samples from five stations) are the first large-scale marine nematode data and the first data for any abyssal infaunal taxon.

The Pacific transect is large enough to test the concept of estimating ocean-scale diversity from a regional data set. Figure 1a shows a species accumulation curve plotted against sample distance in degrees latitude calculated by including the accumulation of new species in samples ordered from north to south down the transect. The graph shows a rapid accumulation of species and then settles down to a linear relationship between species accumulation and distance in degrees (where $y = -79.6 + 12.6x$, respectively, $R^2 = 90.6\%$, with the line fitted to the four southern stations). A degree of latitude is about 111.3 km, so 0.1 new species might be expected per kilometre along a transect in the abyssal plain. Taking this figure as 0.1 new species per square kilometre, the global diversity of marine Nematoda might be calculated to be of the order of roughly 10^7, which is not so dissimilar to the estimates produced by Erwin (1988) and Grassle & Maciolek (1992) for tropical rain forest canopy fauna and bathyal deep-sea macrofauna, respectively. Indeed, Grassle & Maciolek (1992) predicted that abyssal fauna would give an estimate an order or magnitude less than bathyal.

When calculated from south to north (Fig. 1b), the species accumulation per distance data plotted is quite different, giving a concave curve that approaches asymptote. If the terminal section of the curve (northern two stations) is treated as linear ($y = 200 + 0.65x$, $R^2 = 71.2\%$), a figure of 0.006 species
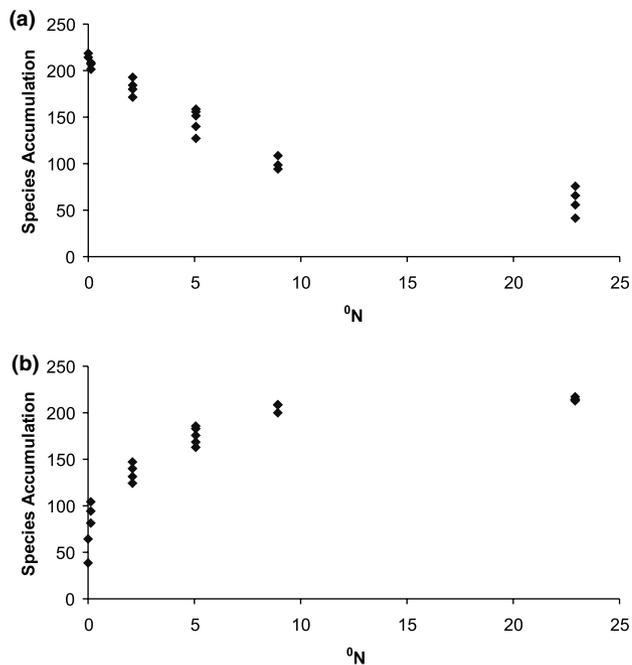

Figure 1 (a) Species accumulation curve plotted against distance in degrees latitude from north to south along a transect in the central equatorial Pacific. (Note that as convention usually decrees that the Equator should be at the origin of the graph, the species accumulation curve runs from right to left.) (b) Species accumulation curve plotted against distance in degrees latitude from south to north along a transect in the central equatorial Pacific.
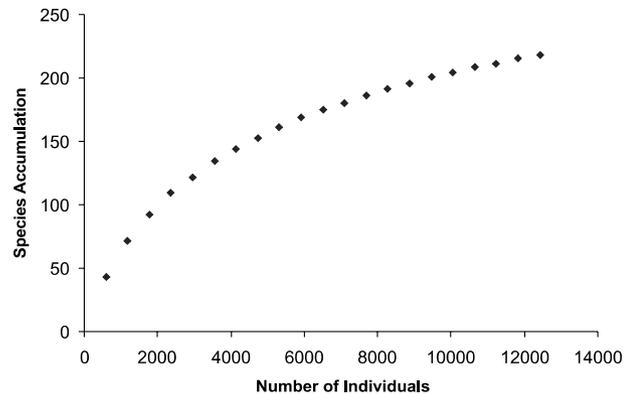
Figure 2 Randomized (fifty times) species accumulation curve for a 3000-km transect in the central equatorial Pacific.

per kilometre may be calculated giving a global diversity of 10^5, a difference of two orders of magnitude from the earlier estimate achieved merely by reordering the way the data are calculated.

The explanation is straightforward; there was a gradient of organic flux to the seabed, declining from the equator northwards. Deep-sea nematode abundance and species richness tend to be positively associated with organic flux (Lambshead *et al.*, 2000) and this is also the case in the central equatorial Pacific (Lambshead *et al.*, 2002) hence the asymmetric species accumulation curves. The area can be divided into two subregions based on diversity (Lambshead *et al.*, 2003). Nevertheless in terms of species present, the area is a single region. Fully 71% of the species in the two northern stations were also collected from the more speciose southern stations. Given the limited number of samples taken from such a large transect this suggests a high degree of conspecifity and hence a single biogeographical region despite the ecological gradient.

This example illustrates the problem of extrapolating from the local to the global. A local ecological influence, in this case quantity and type of organic flux, can seriously influence the extrapolation.

DEEP-SEA REGIONAL DIVERSITY

Regional diversity has been estimated from inadequate sampling (and sampling is always inadequate in large, open, speciose environments) in three main ways (Chazdon *et al.*, 1998). The first is to fit a parametric distribution such as the lognormal or log series. These have proved problematical in benthic biodiversity studies (Lambshead & Platt, 1985) and the lognormal in particular is difficult to fit so this approach is not followed here.

The second, and oldest, method is to extrapolate a species accumulation curve. Sample-based data can be used to generate a randomized species accumulation curve. Gotelli & Colwell (2001) advise that where possible such a curve should be sample-based to account for patchiness in the data, and there is good evidence that deep-sea nematodes are patchily distributed (Rice & Lambshead, 1994). Gotelli & Colwell (2001) also note that species accumulation should be plotted as a function of the accumulated number of individuals rather than samples because of inevitable differences in the mean number of individuals per sample.

The curve generated by this approach (using Colwell's *EstimateS* program, http://viceroy.eeb.uconn.edu/EstimateS, with fifty randomized runs used to generate the curve) is shown in Fig. 2. The curve is convex, which suggests that an asymptote exists, although sampling was inadequate. Hyams (http://www.ebicom.net/ dhyams/cvxpt.htm) *Curve Expert* was utilized to fit a model to the data. A sigmoidal growth model [$y = (ab + cx^d)/(b + x^d)$ where $a = -12.14$, $b = 154.42$, $c = 385.86$ and $d = 0.66$] fitted the data closely ($R^2 = 0.99998$). Extrapolating this model give an estimated regional diversity of 386 for this region of the Pacific abyssal plain.

A third type of species richness estimation involves nonparametric estimators. Of the various methods, the incidence-based coverage estimator (ICE) statistical estimator is probably best suited to this type of data because it is robust to sample size and the effects of patchiness (Chazdon *et al.*, 1998). ICE is a relatively recent example of estimators based on 'sample coverage', which utilizes the distribution of rarer species (those with ten or fewer individuals) to estimate true species richness (Lee

Table I Estimation of marine nematode species richness for various locations, N, number of samples/individuals identified to species; S, number of species recorded; D, maximum distance between samples (km); Dp, Depth (m); CFE, curve-fit estimation (R^2); ICE, incidence-based coverage nonparametric estimator prediction. (1) Boucher (unpubl. data), (2) Boucher (1997), (3) Ferrero, Mitchell & Lambshead (unpubl. data), (4) Boucher & Gourbault (1990), (5) Brown (1998), (6) Thistle & Sherman (1985), (7) Ferrero (unpubl. data), (8) Lambshead *et al.* (2000), (9) Ferrero, Mitchell & Lambshead (unpubl. data), (10) Kotta & Boucher (2001), (11) Lambshead (1986), (12) Lambshead *et al.* (2000), (13) Lambshead *et al.* (1994), (14) Ragot (1999), (15) Kotta & Boucher (2001), (16) Rzeznik *et al.* (unpublished)

	Location	N	S	D	Dp	CFE	ICE
1	English Channel	12/1200	320	465	10–40	2103 (0.9987)	922
2	New Caledonia Lagoon	30/3000	333	10	6–16	1734 (0.9999)	702
3	Mersey Estuary	77/68426	323	22	Littoral	384 (0.9987)	327
4	Guadeloupe	10/997	140	85	0.5–5	871 (0.9972)	303
5	Central Equatorial Pacific Abyssal Plain	21/1877	218	3195	4301–4994	360 (0.9999)	281
6	HEBBLE North West Atlantic Abyssal Plain	18/2432	174	1	4626	623 (0.9999)	238
7	Irish Sea	15/9113	158	10	39–56	287 (0.9997)	221
8	Porcupine North East Atlantic Abyssal Plain	6/1211	119	1	4850	306 (0.9999)	160
9	Thames Estuary	40/6769	152	76	Littoral	230 (0.9999)	152
10	Fiji, Ono Reef	7/700	95	4	30	244 (0.9997)	138
11	Clyde Inland Sea Sandy Beach	16/8896	113	50	Low water spring	129 (0.9988)	133
12	Madeira North East Atlantic Abyssal Plain	6/576	71	1	4950	287 (0.9999)	106
13	San Diego Trough, Bathyal East Pacific	6/1381	98	0.5	1050	102 (0.9989)	100
14	Mangrove Swamp, Guyana	30/2997	65	2	Intertidal	131 (0.9992)	76
15	Moorea, Polynesia	7/700	42	0.1	1.6–3.1	56 (0.9998)	56
16	Mudflat, La Rochelle, France	36/3600	43	4	Intertidal	65 (0.9986)	49

& Chao, 1994). ICE predicted a similar regional species richness, 281 species (Table 1), to the curve extrapolation. Ellingsen & Gray (2002) have evidence that nonparametric estimators may underestimate by up to *c.* 100% so the true figure for the regional nematode species richness of the CCFZ may be closer to 600.

It is possible that the predicted numbers of species are underestimates because of inadequate sampling which is also clustered into stations rather than random, nevertheless they are surprisingly modest for such a large transect. Another potential source of error is that the identification of conspecificity between samples is based on morphology as determined using light microscopy. Given the immature state of marine nematode taxonomy, it is possible that detailed morphological or molecular determination of species might alter the estimation, for example by the detection of cryptic species.

Nevertheless, the data suggest a hypothesis that, although small-scale diversity is high in the deep sea through a spatial–temporal mosaic (Grassle & Morse-Porteus, 1992), the similar patches with similar species are duplicated over large areas resulting in a more modest regional diversity. In Whittaker's (1970) terms, alpha diversity is high but beta, and hence gamma, diversity is more modest.

This can be tested to some degree by carrying out an analysis of the smaller, less well-sampled, roughly 1 km diameter stations from the North Atlantic abyssal basins. Unlike the central Pacific, the deep North Atlantic tends to be divided into distinct basins separated into two groups, east and west, by the mid-Atlantic Ridge. The data available include the HEBBLE site off Newfoundland, the Porcupine Abyssal Plain (southwest of the British Isles) and the Madeira Abyssal Plain (Lambshead *et al.*, 2000).

The HEBBLE site (eighteen cores from two stations *c.* 1 km apart) gave similar species richness estimations to the central equatorial Pacific, with a higher estimation from the curve fit and a lower from the nonparametric estimator. This result reinforces the model of modest beta diversity, despite the high alpha diversity.

Because of the time demands of deep-sea sampling only six cores were taken for the eastern North Atlantic stations; six was considered at the time to be adequate for ecological analysis, which is why the samples were collected. Unfortunately six is an inadequate number for estimating regional species richness but curiosity led us to perform the calculations anyway (better deep-sea data not being available). Astonishingly, the predicted regional diversity is not much lower than from the better sampled regions suggesting that patchiness is so pronounced in the deep sea that a significant

proportion of the species occur over a surprisingly small area. Again, this is consistent with Grassle & Morse-Porteus' (1992) spatial–temporal mosaic hypothesis, which appears to be a plausible explanatory mechanism for the structure of deep-sea nematode assemblages. The Madeira Abyssal Plain site data result is the lowest predicted regional species richness for the abyssal sites. This site was located in the area of a turbidite disturbance so the estimated regional species richness, like alpha diversity, appears to be reduced by the impact of this physical disturbance (Lambshead *et al.*, 2001).

The only suitable bathyal data set we have available for analysis of regional diversity is from the San Diego Trough (Lambshead *et al.*, 1994). These data produced the lowest estimated regional species richness for all the deep-sea data despite having the highest alpha diversity (Boucher & Lambshead, 1995). This region is anomalous in other ways, for example having unusually low nematode abundance, so it may be untypical for reasons that are not clear.

The primary point here is that an estimated modest regional diversity for large areas of the deep sea raises a number of important issues, not least severe doubts about the higher estimates for global nematode species richness.

COASTAL REGIONAL DIVERSITY

Comparison of different biotopes suggested that nematode local ecological diversity peaked at abyssal and especially bathyal depths, coastal offshore diversity being significantly lower especially in intertidal estuarine stations (Boucher & Lambshead, 1995). We propose to investigate whether regional species richness follows a similar pattern.

The samples used to investigate deep-sea regional species richness above were chosen from single habitat sites; this is even true of the large central equatorial Pacific data. The Irish Sea coastal offshore data were also probably from a single habitat site (T. J. Ferrero, unpubl. data; Table 1). The regional species richness estimates for the Irish site (221) is similar to those obtained for the abyssal sites (100–281).

The Clyde Inland Sea sandy beach data (Table 1) were also from a single habitat (fine sand, low water spring mark) so the nematode assemblages were exposed to wave action but not the kind of desiccation/salinity/temperature gradients associated with intertidal fauna. The estimated species richness for this habitat was lower than most offshore sites but still high (133). The lowest estimated species richness (forty-nine and seventy-six, respectively) were obtained for the intertidal mud site transect at La Rochelle (Rzeznik *et al.*, unpublished) and an intertidal mangrove site in Guyana (Ragot, 1999).

Thus far, with the exception of the San Diego Trough, the pattern follows the alpha diversity pattern reported by Boucher & Lambshead (1995). Lower sample diversity for intertidal and low-water spring sites is also not inconsistent with Grassle & Morse-Porteus' (1992) spatial–temporal mosaic hypothesis. The increased disturbance through wave action, and temperature, desiccation and salinity changes in the intertidal will tend to ecologically dominate, reducing the importance of small-scale patchiness and hence local and regional species richness. Lambshead (in press) speculates that the fragmentation of intertidal habitats might also be instrumental in low habitat species richness.

However, compared with the abyssal deep sea where a single habitat may extend for thousands of kilometres, intertidal and coastal habitats usually have boundaries restricting their scale from kilometres to tens of metres, or even less. Such habitats are too small to be considered regions so a coastal region contains a number of different types of habitats governed by such factors as hydrodynamics, sediment type, productivity gradients, oxygen gradients, desiccation gradients, temperature range gradients and salinity gradients. Close packing of dissimilar habitats may cause high *regional* species richness because sampling at a regional scale crosses a number of such habitats, each with a different suite of species. The highest regional species richness estimates therefore are obtained from shallow water regions that include a variety of habitats. A transect from Dover down the English Channel to Brittany (G. Boucher, unpubl. data) has a high estimated species richness (922) because it includes a number of nematode habitats (including sublittoral sediments typical of the English channel such as muddy sand in the bay of Plymouth, coarse sand off North Brittany and in the Bay de Seine, and pebbles in the Dover Straight). The southwest New Caledonia lagoon data (Boucher, 1997), where three different sediment types could be identified (Chardy *et al.*, 1988), also showed a high species richness (702). British estuarine intertidal data (T.J. Ferrero, N.J. Mitchell & P.J.D. Lambshead, unpubl. data), also showed high estimated regional species richness (150–327) because of strong close-packed ecological gradient despite the extremely low alpha diversity of the samples from individual estuarine habitats (Boucher & Lambshead, 1995). Nematode alpha and

gamma diversity therefore do not show the same patterns; Ellsingen & Gray (2002) have reported similar results for coastal macrofauna.

One interesting point is that there is no evidence for a latitudinal influence on estimated coastal nematode regional species richness replicating the alpha diversity analysis of Boucher & Lambshead (1995). Species richness in Ono Reef lagoon in Fiji (138) or Moorea in Polynesia (fifty-six) was similar or lower than that estimated for temperate coastal habitats. Ellsingen & Gray (2002) similarly report no sign of a latitudinal gradient in the regional diversity of Norwegian shelf macrofauna supporting the conclusions from the alpha diversity macrofauna analysis of Kendall & Aschan (1993).

A model for the biodiversity of coastal regions therefore is for lower alpha diversity than the deep sea because disturbance tends to predominate over the effects of patchiness, especially in the intertidal and estuaries, but a high beta and gamma diversity because of the variety of closely packed, ecologically different, habitats. This explanation is supported by Ellsingen & Gray's (2002) analysis of the biodiversity of Norwegian continental shelf macrofauna. These authors found that beta and gamma diversity was positively associated with environmental variability. Note that in both the Norwegian and current study it is not spatial scale that is important in creating a high regional diversity but the degree of habitat variability in the region. To quote Ellsingen & Gray (2002), 'Change in environmental variables (has) a stronger effect on beta diversity than spatial distance between sites.'

COMPARISON OF NEMATODE SPECIES RICHNESS WITH OTHER BENTHIC TAXA

The estimated nematode species richness for the central Equatorial pacific region suggests a lower global benthic diversity than that indicated by Grassle & Maciolek (1992). There are a number of possible explanations for this. Grassle & Maciolek's data were from bathyal samples from the New Jersey continental slope where alpha diversity is thought to be high and, indeed, these samples may straddle a depth zonation increasing regional diversity. Unfortunately, we lack suitable nematode bathyal data to test whether the apparent anomaly between the nematode and macrofauna data is a product of the different depths or of the sampling locations.

The New Jersey data were analysed for the macrofauna size class and include some fourteen phyla. This may artificially increase species richness extrapolations, not just because of the number of phyla, but because the different taxa may respond to different ecological factors and gradients in different locations along the transect.

Finally, it is possible that macrofauna are more regionally species-rich than nematodes but this hypothesis is not well-supported either by theoretical principles or by extant data. The most abundant and diverse taxon in macrofauna data is the polychaete worms that generally make up 40% or more of a macrofauna sample. Blake & Grassle (1994) report an intensive survey of a bathyal area off the Carolinas to the south of the New Jersey study and report 1202 macrofauna species but the most diverse single taxon is the polychaete worms at 542 species; the rest of the macrofaunal taxa have 100 or fewer species. This is a diverse community but one would hesitate to use these figures alone as evidence for hyperdiversity.

The Carolinas deep-sea macrofaunal species richness is large but not orders of magnitude greater than macrofaunal data from coastal regions. For example, Ellsingen & Gray (2002) recently reported finding 809 species (344 of them polychaetes) from the Norwegian continental shelf (out of a historical database of 2500 species).

The highest diversity for a single macrofauna taxon was discovered for coastal macrofauna species off New Caledonia. Bouchet et al. (2002) made an intensive study of a 295 km site along the west coast and reported cataloguing 2738 species of Mollusca. This compares with the 180 species of Mollusca found by Blake & Grassle (1994) in the deep sea off the Carolinas.

Data do exist for the polychaete fauna of the CCFZ in the central equatorial Pacific (Glover et al., 2002). A total of 177 polychaete species were recorded from the same five stations as the 218 nematode species. Another similarity between the abyssal Pacific nematode and polychaete data is that those species that were common enough to be reasonably well-sampled proved to have wide distributions, for the polychaetes '70–90% of individuals (belonged) to widespread or ubiquitous species' (Glover et al., 2002). Ellingsen & Gray (2002) report that 'No species spanned the entire sampling area' in their coastal macrofauna data for the Norwegian continental shelf so it seems likely that deep-sea species may have higher dispersal ranges than shallow-water species, which is counter-intuitive but is probably linked to the greater habitat heterogeneity in coastal waters.

Certainly, at the alpha level of diversity in the deep sea nematodes are more diverse per core than polychaetes because of higher abundance but when rarefaction is used to compare expected number of species per set sample size the diversity of the two taxa is similar (Lambshead, 1993).

Microbial eukaryotes appear to show an extreme version of the pattern of high local and low regional (and apparently global) species richness because the dispersal of microbial species is rarely, possibly never, restricted by geographical barriers (Finlay, 2002). Fenchel *et al.* (1997) reported that 75% of all ciliated protozoa ever recorded from lake and coastal marine sediments, respectively, were found at single investigated sites suggesting that for microorganisms 'everything is everywhere' and that their global species diversity is relatively limited.

A widespread dispersion of individual metazoan species over a large area of the deep sea also argues for a more modest deep-sea diversity than the higher estimations obtained from extrapolation of 'species accumulation per distance' curves. There is no *a priori* reason to expect nematodes to have a higher dispersal capability than other benthic taxa. Indeed, nematologists have always assumed that deep-sea nematodes have limited dispersal ability as they are non-swimming, infaunal organisms with rheotropic behaviour and limited mobility that lack an obvious dispersal phase, such as the pelagic larvae found in many macrofauna including many polychaete species (Castillo-Fernandez & Lambshead, 1990; Lambshead, 1993). This raises interesting issues concerning deep-sea nematode dispersal; the evidence here suggests that these organisms may have unsuspected capabilities and this may be a ripe area for future research.

CONCLUSION

The argument presented here is not that the deep sea is not highly diverse – it clearly is, not least because of its enormous size (*c.* 50% of the Earth's surface) – but that it is not hyperdiverse. Indeed, the close-packed coastal habitats may well contain a higher fraction of global nematode species than earlier reports might suggest. This point has already been made with respect to macrofauna (Gray, 1994). Similarly, these data offer no support for the hypothesis that nematodes are hyperdiverse, which leads us to question whether any Metazoa are hyperdiverse given the ubiquity, high abundance and conservative life history of nematodes.

Grassle (1989) makes the intriguing suggestion that the deep sea and rain forests might have similar patch-dynamic mechanisms supporting their high diversity. If rain forests are hyperdiverse then the data presented here would cause this hypothesis to fall but, alternatively, this also raises the question of how well-established is rain forest hyperdiversity?

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