The measurement of marine species diversity, with an application to the benthic fauna of the Norwegian continental shelf

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Abstract

Species diversity includes two aspects, the number of species (species richness) and the proportional abundances of the species (heterogeneity diversity). Species richness and heterogeneity diversity can be measured over different scales; a single point, samples, large scales, biogeographical provinces and in assemblages and habitats. In the literature, the terminology of these scales is confused. Here, scales are given a uniform notation. Scales of species richness and heterogeneity diversity are distinguished from turnover (beta) diversity, which is the degree of change in species composition along a gradient. Methods of measurement of the scales of species richness, heterogeneity diversity, turnover diversity and for estimating total species richness are reviewed. Two methods for measuring heterogeneity diversity are recommended Exp \( H' \) (where \( H' \) is the Shannon-Wiener index) and 1/Simpson’s index, together with an equitability index \( J' \). The reviewed methods are then applied to a data set from the Norwegian continental shelf to illustrate the advantages of the recommended methods. Finally, the application of the methods to assessment of effects of disturbance, to studies of gradients of species richness and to conservation issues are discussed. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

The Convention on Biological Diversity (CBD) requires that its signatory nations undertake to make inventories of their biodiversity, monitor changes in biodiversity and
make plans as to how biodiversity can be conserved. This is highly laudable, but makes the assumption that we know how to measure and monitor biodiversity. In the marine domain, this assumption is far from correct.

Biodiversity encompasses a range of different levels of organisation from the genetic variation between individuals and populations, to species diversity, assemblages, habitats, landscapes and biogeographical provinces. I have earlier given a general review of marine biodiversity (Gray, 1997a) but here will consider the methodological problems in measurement of the number of species and individuals in a given area.

Most studies of biodiversity are confined to the number of species in a given area, the species richness. But the number of species alone does not describe the structure of the assemblage of species in a given area because the number of individuals per species varies. A variety of indices have been derived taking into account the proportional abundance of species (see Magurran, 1984 for a full account). These indices consider both species richness and how evenly the individuals are distributed among species (evenness or equitability). Following Peet (1974), I call this heterogeneity diversity.

Whittaker (1960) suggested that there was a range in scales of species richness. He called the number of species found in a sample alpha (or within habitat) diversity, and felt that this was the basic unit of diversity. Whittaker (1960) also suggested there was beta (or between habitat) diversity, and species diversity measured at the largest scale he called gamma diversity. In contrast, Rosenzweig (1995) felt that the term gamma diversity was redundant since it was simply the total number of species in a biological province. Whilst Whittaker’s scheme appears to have a logic in practical terms, there are difficulties in defining and interpreting these scales. Thus, there is a need to consider these terms in detail to arrive at acceptable definitions and agreed ways to measure the different scales of species richness and heterogeneity diversity.

There are also problems when trying to compare diversity from different areas. For example when trying to publish recent papers comparing coastal with deep-sea diversities (Gray, 1994; Gray et al., 1997), the referees stated that it was not valid simply to compare coastal and deep-sea species richness. The reason given was that the deep-sea samples were always from a single uniform habitat (within habitat diversity) whereas the coastal samples were from many habitats, which the reviewers called between habitat diversity. Such an argument is wrong on two counts. First, it is quite justifiable to ask the question: are there more species in a comparable area of coastal compared with deep-sea sediments, irrespective of possible variations in the habitat? After all, it is valid to compare species richness of a tropical rain forest with that in a boreal oak-forest, even though these are different habitats. But, perhaps more importantly, the referees had not understood what between habitat (beta) diversity really is. Whittaker (1960) defined beta diversity as the extent of species replacement or biotic change along environmental gradients. Beta diversity is not a measure of the number of species in different habitats in an area.

Most studies of diversity and the terminology accompanying them relate to terrestrial systems. Yet marine systems differ from terrestrial in a number of ways. Subtidally, one is usually sampling blind because the extent of a habitat or assemblage often cannot be determined and boundaries are less distinct than on land. Marine systems are open with many species dispersing over large areas by means of larvae. Steele (1985) suggested
that in the sea scales of differences in time and space are different from those on land. Studies of marine diversity have developed their own methods and terminology that have been ignored by terrestrial ecologists. For example, Sanders (1968) rarefaction technique for comparing samples of differing size was reinvented by Coleman (1981) and gives almost identical results (Brewer and Williamson, 1994). This review analyses the above issues, proposes a uniform notation for species richness and uses some Norwegian data to illustrate approaches that can be taken.

2. Alpha, beta, gamma and epsilon diversity

Although Whittaker (1960) suggested that the most basic level of species richness was the number of species in a sample, which he called alpha diversity, he later (Whittaker, 1972) suggested that diversity could be measured at four different scales: point diversity (a single sample), alpha diversity (samples within a habitat), gamma diversity (the diversity of a larger unit, such as an island or landscape) and finally epsilon or regional diversity (the total diversity of a group of areas of gamma diversity). Magurran (1988) related these scales to sample, habitat, landscape and biogeographical province. Rosenzweig (1995) however, called alpha diversity ‘point’ diversity! On the other hand, Pielou (1976) stated ‘alpha diversity pertains to a small area and is a property of a particular community; even though recognition of such an entity is nearly always subjective the risk of being seriously mistaken is negligible.’

Underwood (1986) using Pielou as his source, stated ‘alpha diversity is defined as that within an identified natural community (in whatever way that is to be identified).’ Thus, Pielou and Underwood regarded alpha diversity as a property of a community, begging the question, as Underwood pointed out, of how a community should be defined. Pielou (1976) acknowledged this problem and talking of community (p 288) stated, ‘It should be noted that to define all the species-populations that occur together in one place as the ‘entity’ to be studied is not to assert that they constitute a ‘natural’ entity. The ‘community’ that an ecologist delimits for research purposes may prove to be clearly separated from surrounding communities by abrupt boundaries; or it may merge into them gradually and imperceptibly; or it may be clearly distinct from some but not others of its neighbours.’ Her definition of a community is ‘several or many species-populations that occur together and interact with one another in a small region of space.’ The debate then is whether alpha diversity is a property of a community or is, as envisaged by Whittaker, the property of a sample.

If alpha diversity is a community property, then one has to assess it at the scale of a community, implying a mapping of the community first. Underwood (1986) made the same point emphatically, ‘What sets the angels tap dancing on the head of their pin is that beta diversity refers to spatial variability in the composition of species within a single community. There seems no way to define objectively the appropriate scale for measuring alpha diversity; there is obviously no method for distinguishing between gamma diversity (at some larger spatial scale) and alpha diversity of a community with great beta diversity.’

Similarly in the Global Biodiversity Assessment, a key recent document to biodiver-
sity research, Hengeveld et al. (1997) stated that “alpha diversity is the number of species occurring within an area of a given size”. This is too broad a definition since it does not have any scale and may range from samples within a site to a biogeographical province. The latter is clearly not what is meant by alpha diversity. In a similar vein, Harrison et al. (1992) used the term alpha diversity to apply to a study of species richness within 50 × 50 km square across UK. I believe that confusion could be avoided if alpha diversity were applied only to samples.

Statistically, there are parallels with definitions of sampling units and samples. In order to produce consistent terminology, I follow Whittaker (1965) in calling the sampling units point species richness. More sampling units taken within a broader area comprise the sample (Underwood, 1997) giving sample species richness. Sample species richness is equivalent to Whittaker’s alpha diversity. This is entirely consistent with Whittaker (1972) who stated “alpha diversity measurements are those applied to samples from particular communities”.

2.1. Beta or turnover diversity

Although there are a number of studies of alpha diversity in a marine context, beta diversity has been almost totally neglected. Whittaker’s pioneering research (1960) compared the species richness across an altitudinal gradient in a terrestrial forest in North America. All his studies are concerned with line transects along one or more environmental gradients. Thus, his definitions and methods for measuring species richness relate to line transects and gradients. If the transect is sufficiently long, it will traverse different habitats and thus will become a between-habitat study. More usually, his transects were within one habitat. Whittaker (1975) defined beta (between habitat) diversity as: “the degree of change in species composition of communities along a gradient.” Whittaker stated that beta diversity “should be measured as the extent of change in, or degree of difference in composition among, the samples of a set.” Yet, Rosenzweig (1995), p. 33, using the framework of the equilibrium theory of island biogeography (Macarthur and Wilson, 1967) called beta diversity “the slope of the mainland species–area curve”. This is certainly not what Whittaker had in mind since beta diversity pertains to species identities and how they change across a gradient and not with how species accumulate over areas of mainland and Rosenzweig is incorrect to suggest this as a measure of beta diversity.

From Whittaker’s definition, it is clear that beta diversity relates to the types of species contained and not to the numbers of species within two or more habitats. Magurran (1988) called beta diversity ‘differentiation diversity’ and regarded this as measuring ‘how species numbers and identities differ between communities or along gradients.’ Thus, beta diversity is not simply a measure of species richness at a larger scale than alpha diversity, but a different measure altogether. Since beta diversity is not a scale of diversity it is better to use the term turnover diversity, (Clarke and Lidgard, 1999), which is clearer.

2.2. Gamma diversity

Whittaker (1972) defined gamma diversity as (alpha) samples combined from several
communities, or lists of species for geographic units, or non-areal samples (such as those of light traps) drawing species from a number of communities. Pielou (1976) followed this latter idea in defining gamma diversity as pertaining to a large and almost heterogeneous collection of organisms. Likewise, Hengeveld et al. (1997) in the Global Biodiversity Assessment, defined gamma diversity as the overall diversity within a region. But how large is 'a large collection' and what is meant by, 'a region'? Rosenzweig (1995), who has a strong evolutionary background, defined gamma diversity as pertaining to a biogeographical province, making an important distinction between simply a large area and a functional evolutionary unit. The problem with such a definition is that gamma diversity applies both to a large area of unspecified size and to an evolutionary unit. I believe that it is important to separate these terms since a large area should not be confused with a biogeographical province. Terrestrial ecologists use the term landscape to cover a variety of habitats and assemblages within a given area. Whilst a term such as landscape species richness or landscape species diversity is applicable on land, it is not so easy to apply such a term to the marine environment. I suggest two scales of species richness and diversity larger than the sample scale, large area and biogeographical province.

Spatial scaling studies are not confined to diversity issues. In terrestrial ecology, a new branch of ecology, landscape ecology, has emerged which studies scaling issues. In a marine context Thrush et al. (1999) reviewed scaling problems for soft bottom communities and have adopted the terminology of landscape ecology developed in terrestrial environments. The issues that Thrush et al. (1999) discussed are more general than species diversity and, thus, the terminology used applies more generally. Thrush et al. (1999), based on geostatistical literature, defined grain as "the area of an individual sampler, lag, the intersample distance and extent, the total area from which samples were collected." Such studies usually relate to the scales of distribution of individual species and are thus at a different level to the diversity issues discussed here. As an illustration in his book on terrestrial landscape ecology, Forman (1995) used terms such as grain. "Grain refers to the coarseness in texture or granularity of spatial elements composing an area . . . A fine-grained landscape has primarily small patches and a coarse-grained landscape is mainly composed of large patches. This scale refers to the spatial proportion of a mapped area, and grain refers to the coarseness of elements within the area." Forman (1995; p. 13) defined a region as "a broad geographical area with a common macroclimate and sphere of human activity and interest. A landscape, in contrast is a mosaic where the mix of local ecosystems or land uses is repeated in similar form over a kilometers-wide area." There are, of course, parallels to scales of diversity in that grain in a landscape sense covers patches of habitat within a landscape and a 'broad geographical region' is equivalent to large area diversity. A biogeographical province is, however, an evolutionary unit and is not found in landscape ecology definitions.

From the above analysis I believe that the confusion between terminology can be resolved if a logical series is erected. I suggest that a uniform notation can be achieved by recognising four scales of species richness: point species richness, sample species richness, large area species richness and biogeographical province species richness. The remaining types of species richness, habitat species richness and assemblage species richness are not scales and thus are separate measures referring to habitat or assemblage. Table 1 shows the scheme.
Table 1

Proposed unifying terminology for scales of diversity

<table>
<thead>
<tr>
<th>Scale of species richness</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Point species richness: SR_p</strong></td>
<td>The species richness of a single sampling unit</td>
</tr>
<tr>
<td><strong>Sample species richness: SR_s</strong></td>
<td>The species richness of a number of sampling units from a site of defined area</td>
</tr>
<tr>
<td><strong>Large area species richness: SR_L</strong></td>
<td>The species richness of a large area which includes a variety of habitats and assemblages</td>
</tr>
<tr>
<td><strong>Biogeographical province species richness: SR_B</strong></td>
<td>The species richness of a biogeographical province</td>
</tr>
<tr>
<td><strong>Type of species richness</strong></td>
<td>Definition</td>
</tr>
<tr>
<td><strong>Habitat species richness: SR_H</strong></td>
<td>The species richness of a defined habitat</td>
</tr>
<tr>
<td><strong>Assemblage species richness: SR_A</strong></td>
<td>The species richness of a defined assemblage of species</td>
</tr>
</tbody>
</table>

3. Measuring species richness

At the most elementary level, species richness is the total number of species in a given area. This begs the question: number of species of what? Whilst in the ideal case one would like an assessment of all species from bacteria to large flora and fauna this is impractical. Species richness more often than not refers to a single taxon, since taxonomic expertise is usually limited to specialisation in a single taxon. Ecologists working with marine sediments usually refer to the species richness of the fauna retained on a 0.5, or 1 mm sieve as macrofauna and those passing through this sieve but retained on a 0.62 μm sieve as meiofauna. Here, a size separation rather than a taxonomic division is practised in diversity studies.

Point species richness (SR_p), is the number of species in a single sampling unit from a given area. Following Whittaker (1975), sample species richness can be measured as the total number of species, SR_s and the mean number of species, SR̄_S based on a given number of sampling units.

Whittaker (1975) suggested that the number of species in different-sized sites can be compared by: \( d = \frac{SR_p}{\log A} \) or \( \frac{SR_s}{\log N} \) where \( SR_p \) is the total number of species in the sample, \( A \) is sample area and \( N \) is total number of individuals.

In a similar vein, Pielou (1976; p. 303) wrote: “if a comparison was to be made between the Atlantic and Pacific coasts of North America as to the diversities of the infauna of sandy beaches (in a given latitude belt), many large communities would have to be compared; censusing them would be impracticable and it would be necessary to estimate their diversities from samples.”

Sample species richness almost certainly will be measured within a single habitat and/or assemblage, but it does not necessarily give a reliable estimate of the species richness of that habitat or assemblage. That can only be done if the extent of the habitat and/or assemblage is measured and an adequate number of samples taken to estimate species richness within that habitat or assemblage. (I prefer to use the term assemblage to community, as the former does not imply any associations between species implicit in the latter term). The total number of species in a defined habitat is therefore SR_H and the total number of species in an assemblage SR_A.
Just as with habitat and assemblage species richness, large area (SR_{L}) and biogeographical province species richness (SR_{P}) estimates are made in identical ways. The area covered or province boundaries have to be clearly defined and sampling design be appropriate to the scales of the features sampled.

Often there is interest in the true total number of species (SR_{Max}) for a given habitat, assemblage, large area or province. SR_{Max} can be estimated from species accumulation curves. Traditionally this has been done by taking the cumulative number of species on pooling samples from sample 1 to sample n, the number of samples. Yet whether or not this produces a smooth curve often depends on choice of starting sample. How should one designate the order of the samples? Whilst many simply pick a sample at random and then add the next picked at random, this does not necessarily result in a smooth curve. Today there are a number of ways of randomising samples so that one obtains a mean cumulative number of species and confidence intervals. Grassle and Maciolek (1992) used one method and we (Gray et al., 1997) randomised all samples of size one then size two and so on until the largest size is encountered. This is sampling with replacement. Colwell (1997) described a technique based on randomising without replacement. (The EstimateS programme can be obtained free at the web address: http://viceroy.eeb.uconn.edu/EstimateS)

Karakassis (1995) has produced a new method to estimate the total number of species in a sample. The method is based on plotting the number of species in k samples against the number in k+1 samples. The intercept of the two lines gives an estimate of the total number of species in the area sampled. However, our analyses of data sets using this method showed that it grossly underestimates the true number of species (Ugland and Gray, unpubl.).

Chao (1984, 1987) has derived a rather different method for estimating total species richness for a site. The method is a non-parametric one based on the number of species with one and two individuals per species. Paterson et al. (1998) have recently applied the method to benthos from a deep sea site. Few applications of this promising method exist.

Another measure of total species richness can be obtained from Macarthur and Wilson (1963, 1967) well-known relationship between the total number of species (S) against area (A):

\[ S = CA^z \]

where C and z are estimable parameters with C representing the biotic richness of the area and z the slope of the curve. (There are many recent reviews of species:area curves and I will not treat this topic in detail. The reader is referred to Connor and McCoy, 1979; Sugihara, 1981; Connor et al., 1983; Williamson, 1988; Lomolino, 1989; Rosenzweig, 1995; Williams, 1996; Whittaker, 1999).

Many use Arrhenius plots, species–area curves where

\[ \log S = z\log A + \log C \]

Yet, there is some dispute as to whether the relationship is a log–log relationship or S vs. log A. On theoretical grounds, S vs. log A should give a straight line where the logarithmic series distribution of individuals among species holds, whereas the log–log
relationship holds for a lognormal distribution (Whittaker, 1999). Both Williamson (1988) and Rosenzweig (1995) concluded from analyses of many empirical studies that the log–normal distribution is more general and therefore the log–log plot is the more usual fit. C can be used as a descriptor of the species–area relationship.

4. Measuring heterogeneity diversity

Heterogeneity diversity encompasses not only the number of species but also the proportional distribution of the individuals among the species. Indices based on the distribution of individuals among species contain additional information to that of species richness. There are many reviews of indices of species diversity and three in particular are recommended, Whittaker (1972), Hill (1973) and Magurran (1988). Following Whittaker (1965, 1972), Hill (1973) showed that, of the commonly used diversity indices, total species richness and Simpson’s index between them characterise the partitioning of abundance between species; Shannon’s version of Rényi’s (1961) entropy analogy is intermediate. These three indices are those recommended for characterising species diversity.

Whittaker (1972) proposed as the first index of species diversity an index, which I call HD_1,

$$HD_1 = \exp(H'),$$

where

$$H' = -\sum_{i=1}^{S} p_i \log_2 p_i,$$

H' is the commonly used index the Shannon-Wiener:

$S$ total number of species, and $p_i = n_i/N$ where $n_i$ = number of individuals of the $i$th species and $N$= total number of individuals.

Whittaker (1972) also first suggested using the reciprocal of Simpson’s index (which I call HD_2)

$$HD_2 = 1/(p_1^2 + p_2^2 + \ldots + p_n^2),$$

where $p_1$ is the proportional abundance of the first species compared to the total number of individuals in the $n$ samples. Hill (1973) also used this notation. Whittaker (1972) argued that the Simpson index is primarily a measure of dominance, especially of the first 2–3 species whereas the Shannon index is more strongly affected by species in the middle of the rank sequence of species. Thus, the two indices measure different aspects of species diversity.

Hill (1973) made an important point concerning the measurement of diversity in suggesting that it is easy to define indices of diversity for samples, but such indices very often have no meaning when applied to the whole community. The reason being that, as pointed out by Underwood (1986), the community is often difficult to define. As Hill (1973) stated: “if we wish to use indices of diversity to characterise some features of a hypothetically infinite community, then we must allow for an arbitrarily large number of species.” This point is widely ignored.
An additional aspect is how the abundances are partitioned among the species. This aspect has been called evenness. The most commonly used form is that of Pielou (1976):

\[ J = H' / H_{\text{max}} \]

where \( H' \) is the Shannon-Wiener diversity index and \( H_{\text{max}} \) is maximal diversity i.e. \( \log(H) \). Whittaker (1972) argued convincingly that \( J \) is not, in fact, a good measure of evenness since \( \log S \) is greatly influenced by sample size, whereas \( H' \) is not. Hill (1973) suggested a new index to overcome this problem:

\[ J' = H' - H_{\text{max}} \text{ or } \ln(\text{HD} / \text{SR}S) \]

Marine biologists have often used a version of the Pielou index as \((1 - J)\) to indicate dominance (e.g. Gray, 1982). Recently, another method for measuring dominance has been used by Levin and Gage (1998) referred to as \( D \) and called Rank 1 dominance. It was defined as the percentage of the total fauna represented by the single most abundant species. This has been described before and is, in fact, the Berger-Parker index:

\[ dN_{\text{max}} / N \]

where \( N_{\text{max}} \) is the number of individuals in the most abundant species (Berger and Parker, 1970).

5. Turnover (beta) diversity

As mentioned earlier, turnover diversity is a different property from that of the scales of diversity. It relates to the species composition and the extent of change in, or the degree of difference in composition among, the samples along a gradient.

The simplest measure of turnover diversity is that of Whittaker (1960)

\[ \beta = \gamma / (\alpha) \]

where \( \gamma \) is the number of species resulting from merging a number of individual samples and \( \alpha \) is the number of species in a sample. For a single sample, \( \beta = 1 \) (Whittaker, 1975) and for 2 samples that have no species in common, \( \beta = 2 \). For three samples sharing no species, or a larger set of samples with the same total number and mean number of species as those three, \( \beta = 3 \), implying that the extent of difference in composition among the samples of the larger set is equivalent to that in three samples with no species in common.

Two authors who have reviewed beta diversity (Magurran, 1984; Harrison et al., 1992) stated wrongly that Whittaker (1960) defined beta as:

\[ \beta = S / (\alpha - 1) \]

where \( S \) is the total number of species in a large area and \( \alpha \) is the number of species in a sample. Wilson and Shmida (1984) claimed that Whittaker used this version:

\[ \beta = S / (\alpha - 1) \]
where $\alpha$ is the average number of species found within samples. It is quite remarkable that no-one seems to have read the original paper!

Beta diversity measures the degree of change in composition of samples along a gradient, or the extent of the difference in samples from the opposite ends of a gradient. Since there are usually more than one measurement of point diversity, it is sensible to use the mean point diversity as suggested by Wilson and Shmida (1984). In the terms used here, this gives:

$$\beta_s = \frac{S_{R_s}}{(S_{R_p})}$$

where $S_{R_s}$ = total number of species found in a sample and $S_{R_p}$ is the mean number of species found within the point samples. It is, however, also possible to compare the species richness of the largest area studied with that of sample species richness:

$$\beta_l = \frac{S_{R_L}}{(S_{R_S})}$$

In a comprehensive review, Wilson and Shmida (1984) evaluated six different measures of beta diversity and concluded that the two best were Whittaker’s $\beta_s = \frac{S_{R_s}}{(S_{R_p})}$ and a new index:

$$\beta_T = \frac{\left[ g(H) + l(H) \right]}{2(S_{R_S})}$$

where $g$ = number of species gained along the gradient and $l$ = number of species lost along the gradient.

The two measures give very similar results. Wilson and Shmida (1984) stated that $\beta_s$ is the most widely used and does not assume a gradient structure, whereas $\beta_T$ standardises by average sample richness. These two measures are currently the best measures of turnover diversity.

Harrison et al. (1992) modified Whittaker’s formula to allow comparisons of two transects of unequal size:

$$\beta - 1 = \frac{\left[ S/S_{R_s} - 1 \right]}{(N - 1)} \times 100$$

where $S$ is the total number of species in the transects, $N$ is the number of sites, and $\beta - 1$ ranges from 0, complete similarity to 100, complete dissimilarity.

Harrison et al. (1992) also introduced a new measure for species turnover which takes account of situations where species drop out along the gradient but are not replaced by new species.

They called this index $\beta - 2$:

$$\beta - 2 = \frac{S}{S_{R_{S\text{ max}}}} - 1/(N - 1) \times 100$$

where $S_{R_{S\text{ max}}}$ is the maximal value of sample diversity in the collection of $N$ sites. $\beta - 2$ measures the amount by which large area diversity exceeds the maximum sample diversity. These new indices have not been widely tested.

There is another way of assessing beta diversity, that is how the species similarity changes along a gradient. Pielou (1976) suggested two measures, coefficient of community $CC$ and the percentage similarity, $PS$, but these have been little used. Many other indices of similarity between samples are in use (Magurran, 1988). Multivariate
statistical analyses are now in wide use in benthic ecology. Of the packages available, the Plymouth Routines in Marine Environmental Research (PRIMER; Clarke and Warwick, 1994; Carr, 1996) is widely used as is the British Natural History Museum’s BiodiversityPro (McAleece, 1997). Both calculate Bray-Curtis and other similarity indices that can be used to assess similarities between sites. Other commonly used marine programmes include NESS (Grassle and Smith, 1976; Gallagher, 1996) which has recently been used by Paterson et al. (1998) to assess similarities of fauna (beta diversity) over a depth gradient. The PRIMER package has another useful routine, SIMPER, which extracts the species that are instrumental in distinguishing between sites along a gradient. This can again be used in the context of assessing turnover diversity.

6. Comparing diversities over different scales

Most, if not all, indices of species diversity are sample-size dependent (Hill, 1973). Thus, in order to compare species diversities, methods are needed to reduce samples to a common size. Two methods are widely used, the rarefaction method (Sanders, 1968, corrected and modified by Hurlbert, 1971) and Coleman’s method (Coleman, 1981; Coleman et al., 1982). Both of these assume that: (a) samples are homogeneous, with similar distributions of individuals among species and (b) species are distributed randomly and are not aggregated (Brewer and Williamson, 1994). As early as 1972, Fager (1972) showed that the rarefaction method of Sanders overestimates the number of species (see also Simberloff, 1979). Surprisingly these papers have been ignored in the marine literature, although Gage and May (1993) in a paper in *Nature* plotted a figure (almost identical to that of Fager), showing the effect of non-homogeneity between samples.

Fig. 1 illustrates the likely sources of error in using these techniques when patterns of dominance vary. Gray et al., 1997 has shown that dominance is greater in small than in large sample sizes. This leads to the rarefaction method overestimating species richness especially at small samples. The degree of overestimation depends on the degree of dominance.

Although Fager (1972) showed the problems with the rarefaction method, it is still widely applied (e.g. Sanders, 1968; Jumars and Hessler, 1976; Rex et al., 1993; Grassle and Maciolek, 1992; Gage and May, 1993; Levin and Gage, 1998; Paterson et al., 1998; Flach and de Bruin, 1999). In many of these papers, the estimated number of species for *n* individuals (ESₙ) was calculated for extremely small samples (e.g. only 20 or 50 individuals). The effects of changing degrees of dominance (Fig. 1) on rarefaction estimates show that the true number of species for ESₙ of 50 in the example given lies anywhere between 4 and 40 depending on the degree of dominance. Fager (1972) also illustrated the effects of aggregation on rarefaction. For a field sample, he showed that the rarefaction method estimated 89 species for a sample of 1000 individuals, but with clump sizes of mean size 8 the estimate is reduced to 51 and with mean clump sizes of 16 reduced to 39 species. Few acknowledge these failings of the method. An exception is the study of Vetter and Dayton (1998) who, although using the rarefaction method of Hurlbert (1971), cautioned that the rarefaction method “may overestimate the number of
species present when species distributions deviate strongly from random”. The problem is that nearly all species distributions depart from random. Most species have aggregated distributions and random distributions are, in fact, extremely rare in nature (Preston, 1962; Williams, 1964). Thus, rarefaction severely overestimates the species richness of small samples by making wrong assumptions concerning dominance and by assuming random rather than aggregated distributions of individuals.

It is very surprising that the rarefaction method should have taken such a large hold given these problems. An alternative, which to me seems far more logical, is to calculate species accumulation curves for randomised samples (e.g. the EstimateS programme of Colwell, 1997). This gives a mean and confidence intervals (C.I.) of numbers of species up to that of the whole sample. Plots of a series of samples of different sizes can be shown and then estimates can be given of species richness at the size of the smallest sample. If this is done then there will be a mean and 95% C.I. for each sample size smaller than the whole.

7. Taxonomic distinctiveness

Warwick and Clarke (1998a,b) have suggested a new method for measurement of biodiversity based on the taxonomical relatedness of the species found. They have proposed two new indices: taxonomic diversity and taxonomic distinctness. The former measures the average path length along Linnean taxonomic classification of individuals of different species. In fact, the term is a generalisation of the Simpson diversity index
which measures whether any two organisms selected at random from the full set of individuals are from the same species. Taxonomic distinctness is the expected path length of any two randomly chosen individuals from the sample, provided that they belong to different species. As yet, the method is rather new and has been applied to data sets to illustrate the value of the indices in assessment of environmental impacts rather than in diversity studies per se. Until the indices have been more widely applied, it is premature to recommend their use.

8. Applying species diversity measures to a data set

The data used to illustrate various measures of diversity are from a transect along the Norwegian continental shelf used by Gray (1994). The transect covers 1,100 km, with a total of 625 species and 40,000 individuals. The data were collected as part of the routine monitoring of the effects of the oil and gas industry. At each of the areas studied, the same sampling design was used. Sampling was at logarithmically increasing distances (250 m, 500 m, 1000 m, 2000 m and 4000 m) from the central facility, on four lines at right angles to each other. At each of the sampling points five 0.1 m² grab-samples were taken; the fauna remaining on a 1 mm sieve were retained and identified to species where possible. As one single grab cannot possibly be used to estimate even local species richness, the data from five grabs were pooled and such pooled data constitute the sampling unit. There were varying numbers of samples within each area. Quality control is high at all stages of the study. A species-abundance per site matrix was generated and multivariate statistics applied to measure effects of the oilrig operations on the benthic fauna (see Olsgard and Gray, 1995 for a review). In this study, only the data from samples in undisturbed sites were used. Thus, each area covered 50 kin², but the number of undisturbed samples within each field varied. In the Snorre area, a baseline survey was conducted before oil extraction began and, thus, this sample has the largest number of samples.

The methods described above are used to illustrate the measurement of the different scales of diversity. Biogeographical province species richness, SR₄, was not measured since it was unclear where the boundaries for biogeographical provinces occur along the Norwegian continental shelf and this study was not designed to cover the biogeographical province scale. All the calculations were done using the BiodiversityPro programme (McAleece, 1997).

Table 2 shows the basic data (taken from Gray, 1994). The depth varied from 70 m to 305 m and sediments from mud (Snorre) to medium coarse sand. Compared with the other areas, Gullfaks has a high number of individuals and species for the area sampled. Table 3 shows the species richness and heterogeneity diversity measures. Mean point diversity is highest at Gullfaks (91.46), but drops below Snorre, Heidrun and Tommeliten when heterogeneity diversity is considered. Gullfaks has a relatively large number of rare species but a relatively even distribution of individuals giving lower heterogeneity diversity. Using 1/Simpson, Gullfaks is lowest (11.28), again reflecting the influence of the distribution of individuals among species because Simpson’s index
Table 2
Location of the areas along the Norwegian continental shelf and the basic data. Samples were taken with a 0.1 m² Van Veen grab with five sampling units taken at each site giving an area of 0.5 m². The number of samples per area is thus the area divided by 0.5.

<table>
<thead>
<tr>
<th>Area</th>
<th>Lat. Long.</th>
<th>Depth</th>
<th>Type of sediment</th>
<th>Area sampled</th>
<th>Total no. of species</th>
<th>Total no. of individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Heidrum</td>
<td>65°20’N, 07°18’E</td>
<td>305</td>
<td>Fine sand</td>
<td>12.5</td>
<td>163</td>
<td>5746</td>
</tr>
<tr>
<td>Snorre</td>
<td>61°27’N, 02°08’E</td>
<td>300</td>
<td>Mud</td>
<td>20.0</td>
<td>330</td>
<td>15 053</td>
</tr>
<tr>
<td>Gullfaks</td>
<td>61°14’N, 02°14’E</td>
<td>210</td>
<td>Med. coarse</td>
<td>7.0</td>
<td>292</td>
<td>10 917</td>
</tr>
<tr>
<td>Ekofisk</td>
<td>56°32’N, 03°15’E</td>
<td>72</td>
<td>Fine-med. Sand</td>
<td>4.5</td>
<td>144</td>
<td>2236</td>
</tr>
<tr>
<td>Tommeliten</td>
<td>56°29’N, 02°58’E</td>
<td>70</td>
<td>Fine sand</td>
<td>5.5</td>
<td>620</td>
<td>39 582</td>
</tr>
</tbody>
</table>

is sensitive to the abundance of only the common species (Hill, 1973). Thus, the indices illustrate different facets of diversity.

At the sample level, Snorre has the greatest heterogeneity diversity, as measured by $H^*$, but drops below Heidrun using 1/Simpson. Values are greater at the sample level since more species are encompassed in the analyses. In order to illustrate these results more clearly, plots are shown of the data beginning with species richness of the individual sampling units (Fig. 2).

Point species richness increases from Heidrun and Snorre to Gullfaks area and decreases thereafter to Ekofisk (lowest) and Tommeliten (Fig. 2). At Snorre, which has the largest number of samples (40) there is a gradual increase in species richness.

Fig. 3 shows plots of heterogeneity diversity. The most frequently used index of

![Fig. 2. Plot of point species richness (SRp) for the transect, arranged in a N–S direction, as in Table 1. Key: open triangles, Heidrun; diamonds, Snorre; solid triangles, Gullfaks; squares, Ekofisk; circles, Tommeliten.](image-url)
<table>
<thead>
<tr>
<th>Area</th>
<th>Mean point species richness SR_p</th>
<th>Point heterogeneity diversity: HD_{p} (Exp H')</th>
<th>Point heterogeneity diversity: HD_{p} (1/Simpson)</th>
<th>Sample species richness: SR_A</th>
<th>Sample heterogeneity diversity: HD_{sA} (Exp H')</th>
<th>Sample heterogeneity diversity: HD_{sA} (1/Simpson)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Heidrum</td>
<td>52.08±2.82</td>
<td>31.16±2.51</td>
<td>23.43±2.85</td>
<td>163</td>
<td>48.84</td>
<td>32.25</td>
</tr>
<tr>
<td>Snorre</td>
<td>83.57±4.03</td>
<td>40.29±2.04</td>
<td>23.66±1.82</td>
<td>330</td>
<td>71.06</td>
<td>28.32</td>
</tr>
<tr>
<td>Gullfaks</td>
<td>91.46±6.89</td>
<td>26.71±4.77</td>
<td>11.28±3.57</td>
<td>292</td>
<td>39.59</td>
<td>12.04</td>
</tr>
<tr>
<td>Ekofisk</td>
<td>52.00±11.46</td>
<td>22.24±3.74</td>
<td>13.16±1.34</td>
<td>144</td>
<td>36.91</td>
<td>17.29</td>
</tr>
<tr>
<td>Tommeliten</td>
<td>72.83±8.63</td>
<td>32.27±4.28</td>
<td>19.23±2.73</td>
<td>163</td>
<td>44.94</td>
<td>23.02</td>
</tr>
</tbody>
</table>
species diversity, the Shannon-Wiener index (Fig. 3a), has little variability and there are no obvious trends along the transect, except that Gullfaks and Ekofisk have slightly smaller values. The recommended heterogeneity indices are shown in Fig. 3b (Exp \( H' \)) and 3c (1/Simpson’s Index). Exp \( H' \) and the 1/Simpson’s Index both show much more
variability and are clearly giving more information than the Shannon-Wiener index. This confirms Magurran’s (1988) view that the Shannon-Wiener is ‘less informative’ than the other indices. In these data, Gullfaks has especially small values of Exp $H^\prime$ and of $(1/\text{Simpson})$, whereas Ekofisk has small Exp $H^\prime$ but greater $(1/\text{Simpson})$ than Gullfaks. Snorre has the largest values of Exp $H^\prime$.

Fig. 4 shows two dominance indices, the Berger-Parker, $d$ (Berger and Parker, 1970) and Equitability ($J = H - H_{\text{max}}$). Both plots show very similar patterns with the greater dominance at Gullfaks (and an anomalous point at Heidrun). The equitability measure seems, however, to have more information, with a wider range of values. These data explain further why it is that, although Gullfaks has a large mean point species richness, it has small values of heterogeneity diversity because dominance is high throughout.

As mentioned in the introduction, there are almost no published studies of differentiation ($\beta$) diversity from marine data. Table 4 shows the two scales, small ($\text{SR}_a/(\text{SR}_p)$) and large ($\text{SR}_l/(\text{SR}_s)$). From Table 2 the rank of sample size is Snorre > Heidrun > Gullfaks > Tommeliten > Ekofisk. This pattern is in general matched in $\beta_S$ (Table 4), where there is an increase from small to larger scale, save that Tommeliten has a smaller value than Ekofisk and Heidrun a smaller value than Gullfaks. $\beta_L$ shows an interesting contrast in that Snorre has a small value and Ekofisk a large value. $\beta_L$ clearly shows an inverse correlation with area as can be expected since Snorre has a greater proportion of the total number of species present and Ekofisk the smallest. These results show clearly that $\beta_L$ can only be meaningfully applied to data from comparable areas. The important data are therefore, from $\beta_S$. 

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**Fig. 3. (continued)**
Fig. 4. a) Berger Parker dominance index (d); and b) Equitability $J' = (H' - H_{max})$ for Norwegian continental shelf data. Symbols as in Fig. 2.
Table 4
Turnover (beta) diversity calculated for sample against point species richness and large area against sample species richness and Harrison et al. (1992) $\beta -$ 2

<table>
<thead>
<tr>
<th>Area</th>
<th>$\beta_1 = \text{SR}_P / \text{SR}_S$</th>
<th>$\beta_2 = \text{SR}_P / \text{SR}_S$</th>
<th>$\beta - 2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Heidrun</td>
<td>3.12</td>
<td>3.80</td>
<td>2.36</td>
</tr>
<tr>
<td>Snorre</td>
<td>3.94</td>
<td>1.88</td>
<td>2.92</td>
</tr>
<tr>
<td>Gullfaks</td>
<td>3.19</td>
<td>2.12</td>
<td>2.63</td>
</tr>
<tr>
<td>Ekofisk</td>
<td>2.77</td>
<td>4.30</td>
<td>2.71</td>
</tr>
<tr>
<td>Tommeliten</td>
<td>2.23</td>
<td>3.80</td>
<td>1.86</td>
</tr>
</tbody>
</table>

In a recent paper, Parry et al. (1999) made the remarkable statement that “There is no adequate measure of species turnover...” and then proceeded to use species-area curves as a direct measure of turnover diversity. Both the statement and the application are incorrect. The study was of the sediment-living fauna of four sites off the South coast of UK. Parry et al. (1999) recorded data for mean point species richness and sample species richness and it is possible to calculate turnover diversity $\beta$. The values are Jennycliff Bay, 1.47; Cawsand Bay, 1.76; Eddystone, 2.18 and Queens Ground, 2.24. These values are smaller than the range found on the Norwegian shelf, where $\beta$ ranged from 2.23 to 3.94, Table 2.

The only other marine data on turnover diversity are from Clarke and Lidgard (1999) who calculate values of $\beta - 2$ of 1.76 to 3.29 for a latitudinal gradient of marine bryozoans. The largest values in their study were at depths between 10 and 74 m, with
Fig. 6. a) Estimated cumulative species richness ($S_{\text{est}}$) using EstimateS programme, (Colwell, 1997), with 50 randomisations and no replacement. Bars = 1 s.d.; b) Estimated cumulative number of species ($S_{\text{Chao}}$) using the Chao 2 estimates (Chao, 1987) in the BiodiversityPro programme (McAleece, 1997).
smaller values at shallower and deeper areas down to 200 m. On the Norwegian continental shelf, $\beta - 2$ values range from 1.86 to 2.92.

The mean similarity of the fauna within fields is 60.02% and decreases rapidly with increasing distance (Fig. 5). The similarity of the benthic fauna of the Norwegian continental shelf is halved over a distance of approximately 150 km and reduced to a quarter over approximately 400 km. For Bryozoa of the N. Atlantic, Clarke and Lidgard (1999) reported a turnover of half of the species over 450 km and 75% turnover by 5000 km latitudinally. Turnover rates are much greater for the fauna on the Norwegian continental shelf.

Finally, how does the number of species vary with area and what is the predicted total number of species along this transect? Fig. 6a shows plots using randomised cumulative species numbers against area, suggesting an asymptote at ca. 600 species. The Chao 2 estimate gives ca. 800 species (Fig. 6b). Yet it is only within the last few species that there is a tendency to reach an asymptote. The data are not unlike Grassle and Maciolek's (1992) species accumulation curves for the fauna at 2100 m off the East coast of the US, which showed an almost linear increase in the rate of addition of species. These data do, however, represent estimates of the total number of species to be found and Grassle and Maciolek did no similar analysis. It is unlikely that 800 is a reasonable estimate. The Norwegian continental shelf has been monitored since the late 1970s and, over the years, a large data base has been built up which covers the whole continental shelf (see Gray et al. (1999) for an account). In the database, there are some 2500 species of macrofauna from the soft-sediment monitoring programme. This suggests that much larger sample sizes are needed before Chao 2 would give a reliable estimate of the total number of species. As yet there are few published studies that have used this method. Paterson et al. (1998) showed, using Chao 2, for the Domes A site in the North Pacific at 4842–5283 m depth, that the estimated total species number is around 140 species although the species accumulation curve gave ca. 100 species. They reported that at two other sites Chao 2 did not reach an asymptote.

9. Discussion

Species richness and heterogeneity diversity measures have most commonly been used to assess the impact of disturbances on the marine environment. In this context, surprisingly, much importance has been given to values of the Shannon-Wiener index. For example, in Norway the index has been incorporated into environmental legislation (Molvær, 1997). In this legislation, sediments are classified as: very good quality: $H' > 4$; good quality: 4–3; moderately impacted: 3–2; poor quality: 2–1; and very poor quality < 1. Fig. 3 shows that the Shannon-Wiener index is insensitive, showing little variation along the transect when compared with the other two measures (Exp $H'$) and (1/Simpson's index). In addition it has been demonstrated that use of multivariate statistics gives a much more precise way of detecting changes in benthic assemblages in space and time than use of diversity indices, (e.g. Gray et al., 1990).

The other component of heterogeneity diversity that should be measured is equitability. For the Norwegian shelf data, one of the key trends observed was the decline in
equitability along the transect, with particularly small values occurring at the Ekofisk field (Fig. 4). From these data it is clear that in order to understand the biology underlying changes in species richness and heterogeneity diversity, a suite of measures are needed. In addition, it is important, in relation to the question being posed, to consider the scale over which species richness and heterogeneity diversity are measured. Too often only Point species richness, \( (SR_p) \) or Sample species richness, \( (SR_s) \) are calculated, whereas the study was of an assemblage or habitat, where \( SR_A \) or \( SR_H \) are the appropriate measures. It is hoped that the review and analyses presented here may lead to a reappraisal of the appropriateness of using diversity indices alone to detect environmental change.

In the context of ecological and evolutionary theory there is great interest in patterns of species richness. Two patterns have dominated the marine literature, the latitudinal gradient and the gradient from shallow-water to deep-sea. Although the scales of these gradients are extremely large, surprisingly, most marine studies cover only a few square metres (e.g. Sanders, 1968; Rex et al., 1993; Kendall and Aschan, 1993). But what does a sample of species richness over a few square metres mean ecologically? It is well-known that species richness varies with increasing area sampled. This may be due to the fact that there are more species with increasing area, and/or there are more individuals and hence more species with a larger sample and/or that a larger area encompasses more assemblages and habitats (Rosenzweig, 1995). Yet it is valid to ask: do comparable small areas of a similar habitat in polar, temperate and tropical regions (or coasts and deep sea) have similar \( SR_s \) (Gray, 1997b)? For example, Kendall and Aschan (1993) took samples off the coast of Svalbard, in Arctic Norway, off the temperate coast of Britain and in tropical Java. They found, using rarefaction, expected numbers of species \( (E_{ss}) \) for 200 individuals of 32.9±1.4 (95% c.i.) species at Svalbard, 34.6 (no c.i.) in UK and 33.2±1.9 (95% c.i.) in Java. Since there was no difference in sample species richness between areas, they concluded that there was no evidence of a latitudinal gradient of species diversity. Yet what they sampled was \( SR_s \) and their study shows that sample species richness does not vary with latitude.

Although Rex et al. (1993) claimed to show a latitudinal gradient in species richness of deep-sea organisms, in fact they showed that \( SR_s \) of two samples from the tropics was greater than that of samples from temperate and polar areas. The variance between samples at any one latitude was, however, extremely large, except in the tropical area, where the two samples, by chance, had small variance. Since there is great variance between samples, this study does not give support to the idea that sample species richness varies with latitude. Recently, Levin and Gage (1998) have compared a range of \( SR_s \) from a variety of sites over varying latitudes and depth from the Atlantic and Pacific Oceans. As one might expect, \( SR_s \) again showed great variance between latitudes. The shallowest site at 10° S >500 m had an \( E_{ss} \) 100 of just 5 and 9 species; at other latitudes, sample species richness varied from below 10 to over 60 species. Again, no conclusions can be drawn as to whether or not sample species richness varies with latitude.

All the above results confirm MacArthur’s observation, quoted in Whittaker (1975; p. 119) “alpha and beta diversity will be recognised as the consequences of niche diversification and habitat diversification of species, respectively. MacArthur found that
alpha diversity for birds, which is closely related to vegetation structure, was not much higher in tropical than in temperate communities of similar structure, but beta diversity increased towards the tropics. Evolution in the tropics acts not to increase alpha diversity but to fit additional species along environmental gradients by habitat differentiation and narrowed habitat distributions.” An alternative focus for marine diversity research then should be on turnover diversity rather than sample species richness. Studies of turnover diversity are potentially far more interesting ecologically than studies of sample species richness or estimates of total species richness of an area. Yet there are few marine data, a fact that Gaston and Williams (1996) lamented.

In a terrestrial study in Britain, Harrison et al. (1992) calculated turnover diversity ($\beta - 2$) for a range of taxa along a N–S and E–W transect across the British Isles. They found values in the N–S transect ranging from 0.5 in moths to 3.8 in woodlice with a mean value of 1.54. For the E–W transect values ranged from 0.7 (native trees) to 6.3 (woodlice), with a mean of 3.19. Harrison et al. concluded that turnover diversity was not very great in Britain over the scales measured. The same is true for the 1000 km transect of the Norwegian coast (Fig. 5), with values equivalent to those reported for Britain. Harrison et al. (1992) report that tropical areas have turnover diversity almost an order of magnitude greater than in UK terrestrial systems. Whether or not this is true for the marine domain remains to be studied.

Recently, Clarke and Lidgard (1999) have analysed diversity of bryozoan species in the North Atlantic and found turnover diversity did not correlate significantly with latitude. There was a greater turnover at low latitudes within biogeographical provinces if one excluded data from the Mediterranean Sea. It is important to analyse how turnover diversity varies between marine taxa (as done in Harrison et al.’s (1992) study) and whether or not there are variations with size (meiofauna compared with macrofauna) and whether or not tropical areas show turnover diversity of similarly large values to those in terrestrial systems.

Likewise, there have been few studies of the species richness ($\text{SR}_n$) of large areas in the marine environment. The data from the Norwegian shelf transect (Fig. 6) showed a large underestimate of the actual number of species. The predicted total number of species was 800 compared with 2500 found on the continental shelf over time (Jensen, unpublished). These data suggest that more studies are needed on species:area relationships over varying spatial scales, particularly in relation to the sizes of areas needed for sustainable conservation of marine fauna and flora.

Two studies have examined species richness at the scale of biogeographical province ($\text{SR}_p$). Roy et al. (1996) compared latitudinal clines in species richness using a database of over 2,500 species of prosobranch molluscs. Crame (1999) has done the same in the Northern Hemisphere but, for prosobranchs, the greatest species richness was between 20° and 30° N rather than in the tropics. Crame’s study reviewed the fossil record and recent fauna and showed clear clines in both hemispheres, with much greater species richness occurring south or north of latitude 400. He further suggested that rates of speciation were not necessarily slower in polar regions and that the age of the fauna was the likely cause of the latitudinal gradient. These two studies are at the appropriate spatial scales to answer evolutionary questions related to patterns of species richness. More are needed.
Finally, in the Convention on Biodiversity there is a major focus on conservation of marine biodiversity. Two of the key issues relating to conservation are whether one should conserve areas of high species richness and/or areas containing many rare species. In this context Schlacher et al. (1998) have applied many of the techniques discussed in the foregoing to the conservation of the soft-sediment fauna of a coral lagoon. Their pioneering study examined two strategies for conservation, one based on hotspots of high diversity and one based on the conservation of ‘rare’ species. Of a total of 189 species of macrofauna, 63 were restricted to a single site (‘rare’ species) and 7 species occurred at 2 sites only. As a measure of turnover diversity, they used the number of species common to two sites for all pairwise permutations of sites and found a weak correlation with intersite distance. A single measure of turnover diversity rather than plotting each single sample point would, however, be more likely to give the pattern found in Fig. 5, with a clear relationship with distance.

In an interesting comparison, they distinguished between species restricted to a single site (‘uniques’ or spot endemics) and species represented by a single individual (‘singletons’) following the terminology of Colwell and Coddington (1994). Whereas the cumulative number of spot endemics showed a rapid approach to an asymptote, total species richness did not. This led them to the conclusions that species with small local densities dominate, distribution ranges are highly compressed (spot endemics), boundaries of assemblages overlap, there is a large turnover and a positive interspecific abundance–range size relationship. For conservation purposes, they concluded that a strategy based on total species richness would lead to missing a significant fraction of rare species. Thus, strategies based on spot endemism were the recommended approach for conserving macrofauna inhabiting sediments in this coral lagoon. Studies of other lagoons are needed to test the generality of the conclusions. The study has many useful lessons that need to be tested elsewhere.

In conclusion, it is hoped that this review will provide the stimulus for a broader approach to studies of species diversity rather than simply calculating diversity indices. Studies at all scales are urgently needed, especially in tropical regions. We do not know whether or not sample, assemblage and habitat species richness are greater in tropical than temperate or polar regions. There are few studies at larger scales than sample species richness and thus whether or not rates of species turnover are similar to terrestrial systems remains unknown. Schlacher et al.’s (1998) study showed how some of these ideas can be applied to conservation issues. Their study was, however, concerned with conservation of a part of a single lagoon. Studies that encompass larger areas, such as several lagoons within a biogeographical province, over large areas of more continuous sediment on continental shelves and on a wider range of habitats and assemblages are required if we are to use knowledge on species, assemblage and habitat richness to conserve coastal biodiversity.

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References


