

Problems of measuring biodiversity in coastal habitats: a summary of issues

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ABSTRACT

Coastal biodiversity is complex due to the large numbers of species interacting in space and time at many different scales. Because little is known of the invertebrates which make up most of this biodiversity, conserving biodiversity is a difficult task. Robust analytical techniques must be developed that can measure natural changes in biodiversity before one will be able to assess whether biodiversity is changing in response to anthropogenic disturbances. Many attempts have been made to reduce the complexity of a species x sample data-matrix, which is the basic measure of biodiversity, into simpler measures, which are more amenable to analysis. These are not generally successful because they capture only part of the variation in assemblages of organisms. This paper introduces the basic components into which measures of biodiversity can be “decomposed” to allow existing methods of analyses and ecological knowledge to understand measures of and changes to biodiversity.

Key words: biodiversity, spatial and temporal variance, multivariate, analyses

Introduction

This contribution summarizes the major points to be developed in any research programme to solve fundamental problems in ecological aspects of biodiversity. Ecological biodiversity is defined here to be the structure of assemblages of species – those that are found in any given location and time. Such a definition includes the types of organisms found (the taxonomic composition of an assemblage) and their relative abundances (i.e. not just presence/absence which captures only taxonomic composition per unit sampled). It eschews the obfuscation associated with concepts of communities (Underwood 1986). It is deficient in that it ignores the functional ecological attributes of biodiversity – be they food-web relationships (Pimm 1982), interactions sustaining biodiversity (Paine 1974; Kastendiek 1982; Steneck 1982) and issues of production, degradation, etc., that are dependent on local diversity (Naeem *et al.* 1995; Tilman 1999).

These functional attributes are not ignored by intention. There are two problems with their inclusion at this stage of understanding. First, the information needed to understand food-webs or other interactions is currently lacking for most assemblages. Where it is known (for coastal habitats, this is best in rocky intertidal habitats), it is still often mensuratively, not experimentally derived. This matters. For a good example, see Dayton's (1984) demonstration of the inadequacy of descriptions of food-webs by simple observation, by measures of functional processes and by measures of actual interactions. Only the lattermost approaches realism – but such analyses are lacking for most coastal habitats.

To proceed in the absence of better ecological understanding requires methods for documenting, analysing and interpreting spatial differences and temporal changes in biodiversity. It does not matter what is the issue for which information about assemblages is needed (conservation, detection of impacts, biographical analysis, restoration of habitat, State of Environment reporting), the same sorts of information are necessary.

What follows is a summary of the main issues that arise in measuring biodiversity in coastal habitats. It is not the intention to give details, which will, of necessity, be presented elsewhere. The main issues are:

1. Measurements are intrinsically complex, because:
 - (i) organisms in assemblages interact in complex, direct and indirect ways;
 - (ii) supply-side ecology and complex disturbances create great variation (Underwood and Keough 2001).
2. Complex multivariate data are intrinsically difficult to analyse, because:
 - (i) they are not easily decomposed into components measuring spatial differences, temporal changes and their interactions;
 - (ii) variations in space or time are simultaneously due to very different and complex differences (in space) and changes (in time) in attributes of assemblages.
3. Simplifying multivariate measures has revolved around indices or indicators but these fail for:
 - (i) reasons to do with lack of information-content in indicators;

- (ii) reliable indicators have not been demonstrated for most (perhaps for any) coastal assemblage.
4. Decomposing multivariate data into simpler characteristics will be better because:
- (i) most of the important features are amenable to more straightforward analytical methods;
 - (ii) this will lead to unconfounded interpretations and precise, directly testable ecological hypotheses.

Intrinsic complexity of data and their analysis

This needs virtually no commentary - except that ignoring it is perilous. As long ago as Darwin (1859), it was recognized that animals and plants live in a web of complex interactions. Many reviews and analyses have shown the vast variety of ways organisms interact ecologically (Andrewartha and Birch 1984). They interact directly by competition, predation, provision of habitat or shelter, etc. In addition, they interact indirectly in definable classes of interactions (Wootton 1977), although direct and indirect interactions can blur and confuse each other (Underwood 1999).

So measurements of assemblages must inevitably be complex because of the intrinsic complexity of the assemblages.

At the same time, abundances and dispersions (spatial variance) alter, sometimes at great frequency. Temporal changes are at numerous scales, as are spatial differences (Morrisey *et al.* 1992 a, b). These two components are also interactive (in the statistical sense of interaction). Differences from place to place at an hierarchy of spatial scales are not the same from time to time. Orthogonally, changes from time to time are not the same for different places (at any scale in an hierarchy).

So, capturing information about assemblages requires complex nested sampling designs (Green 1979), involving hierarchies in space (Underwood 1992) and time (Stewart-Oaten *et al.* 1986; Underwood 1991, 1994).

The results of sampling in this manner are always a matrix of many taxa and numerous sample units (over different spatial scales at different frequencies of sampling).

This complexity has caused major problems of analysis and interpretation. As a result, for example, many assessments of environmental impact on assemblages have no spatial or temporal replication (Green 1979; Fairweather 1991; and references above).

Some of the potentially suitable techniques currently available (e.g. MANOVA) have such restrictive assumptions that they are not generally reliable for ecological data (Johnson and Field 1993).

Although recent technological advances have allowed analysis of the simplest interactions between space and time (npMANOVA; Anderson 2001), there are still numerous logical and philosophical issues to be resolved before there is the same sort of robustness and diversity of analytical procedures as are currently needed for most analyses of univariate data (e.g. Quinn and Keough 2002).

Simplifying by indices or indicators

Indices of multivariate measures of biodiversity have often been proposed. Examples are H, the Shannon-Wiener index or Levins B. These attempt to compound the relative abundances of many species into a single measure (Pielou 1974). The advantages of this are obvious – such an index is then analysable by a vast suite of well-known and robust methods. They must, however, fail to represent all the information in any reliable way. So, similar values occur even though there are quite large differences in abundances of many species from sample to sample. They have failed conspicuously in comparative assessments of environmental impacts (Bayne *et al.* 1988). Attempts to use them in hierarchical analyses (α , β and γ diversity; Pielou 1974) are fraught with logical conundrums (Underwood 1986). Gray (2000) has recently discussed the current state of thinking for marine assemblages. He concluded, after a most careful and thorough consideration, that there is a need for “a broader approach to studies of species diversity rather than simply calculating diversity indices”.

Indicators are supposed to be the solution to problems of complex information. The concept is simple – an indicator is something much simpler, quicker, easier, cheaper to measure than the entire suite of variables, but which contains the same sorts of information about ecological patterns. Indicators are, in practice, of two broad kinds.

First, are physical or chemical measures that represent what the fauna are doing. Thus, numerous classes of illogicality abound in which “water quality” (turbidity, N, P, chlorophyll, contaminants) is measured and used to “indicate” ecological “condition” of different areas. The purpose is usually to indicate what the fauna and flora are doing.

The theory is that water-quality dictates ecology – the patterns of abundance and distribution of fauna and flora. This is intrinsically nonsensical, because it is well-known that these ecological patterns are regulated by a complex mass of interacting biological, ecological, biogeographical, climatic, physical and historical processes. Worse, there is plenty of evidence that abundances of organisms do not respond linearly to chemical variables. They often resist chemicals thought to be toxic (and are therefore unaffected by them) or bio-accumulate chemicals so that responses are not predictable from measurements of chemical variables (Phillips 1978; Raimondi and Reed 1996).

Finally, even if it were appropriate to substitute chemistry for biology, there are no compelling savings in money or time (Bayne *et al.* 1988). This is true even though benthic infauna were sampled, which is known to be very expensive compared with other biota. Certainly, little is to be gained by swapping to a matrix of complex physico-chemical data to avoid a matrix of complex ecological data!

Second are biological indicators or “surrogates” of the whole assemblage. These are very popular in terrestrial studies (e.g. Andersen 1995; Caro and O’Doherty 1999), but have not so far been successful in coastal habitats. The

use of indicators in terrestrial habitats is also problematic (Lawton *et al.* 1998). An example is copepod/nematode ratio (e.g. Coull *et al.* 1981) used in meiofaunal studies. This number has all the problems of interpretability of any complex variable (the top or the bottom can change leading to changes or no changes in the ratio – the ratio is highly right-skewed in distribution, leading to difficulties in reliable sampling).

Trying to identify indicators for marine assemblages is very complex (Jones and Kaly 1996). A useful indicator must, as a minimum, have the following properties:

- (i) there is a characterizable “dose-response” relationship between the indicator and the whole assemblage, so that a change in the indicator is matched by a change in the assemblage;
- (ii) processes causing change or difference in the whole assemblage cause the corresponding change or difference in the indicator (i.e. the assemblage does not change without any indication of change);
- (iii) data about the indicator are simpler to collect, analyse and interpret than data about the whole assemblage.

Determining the first two of these over a wide range of conditions and areas will probably be as difficult, time-consuming and expensive as measuring the whole assemblage. It is essentially the case that the requisite information has never been provided for any proposed indicator.

There is one notable exception, in that many types of change in marine assemblages show the same patterns of difference or change using data from all the taxa and from taxa grouped at less resolved levels (e.g. Families and Orders instead of species). Identifying patterns at lower taxonomic resolution (e.g. Herman and Heip 1988; Gray *et al.* 1990; Chapman 1998) saves time and money and solves problems where taxonomic infrastructure is lacking. When patterns need to be explained, the development of ecological models (theories) often requires detailed knowledge of the species involved. So, often, for interpretation rather than discovery of patterns, detailed identification of important species is needed.

Using reduced taxonomic resolution does, however, fail to solve the problem in (ii) above. Thus, there is still a substantial and complex matrix of multivariate data to interpret.

Decomposition of multivariate data

A much better solution to the problems will be to “decompose” the multivariate data into a useful suite of characteristics or variables. Five characteristics will summarize the assemblage:

- (i) presence/absence of a taxon in set of sample-units;
- (ii) frequency of occurrence of a taxon in a set of sample-units;
- (iii) mean abundances of each taxon in a replicate set of sample-units;
- (iv) variance in abundance of each taxon across replicate units;
- (v) correlations between pairs of taxa in a set of sample-units.

These can be analysed by widely-available, robust procedures. For example, presence/absence data (as in lists of taxa) are analysable by a number of techniques – including new multivariate procedures (Warwick and Clarke 1995). Frequencies of occurrence are analysable by a vast range of procedures (Agresti 1990), as are means and variances of abundance (e.g. Underwood 1997). Correlations between pairs of taxa are slightly more problematic, but new procedures using permutation are available (Potter *et al.* 2001).

These variables are, of course, not completely separable or isolated. Variance and frequency of occurrence must be related for any taxon that is greatly over-dispersed, but has a small mean (variance will be large, but frequency will be small).

Also, there can often be positive relationships between mean abundance and frequency of occurrence and there are very well-known variance:mean relationships for many taxa.

Nevertheless, these variables reach the most important features of structure of assemblages and have ready interpretation to many quantitative and experimental ecologists. There is a long history of being able to interpret patterns in these variables in relation to ecological patterns and processes (Lewis 1964; Connell 1972; Underwood 1979; Paine 1994).

Deriving testable hypotheses about such variables from models about ecological processes has been a successful hallmark of coastal ecology for the last 40 years (Paine 1994; Underwood 1985, 2000).

The next phase for measuring biodiversity in coastal habitats in New South Wales

We need better tools for understanding and interpreting ecological biodiversity. A research programme under way in the Centre for Research on Ecological Impacts of Coastal Cities in the University of Sydney is developing the necessary tools using extensive sets of data from various coastal habitats (rock platforms, kelp-beds, artificial hard structures, mangrove forests, salt-marshes, sand-flats, soft sediments).

In some habitats, such as rocky shores, extensive experimentation all over the world has led to detailed understanding of patterns and processes and the relationships between them. So, large data-sets from all over the coast of New South Wales, collected with good structural design to test hypotheses about temporal changes and spatial differences and collected with the same rigour everywhere, will allow verification of analyses and interpretations. Where analyses identify patterns, their ecological significance (rather than just their statistical importance) will be validly inferable from everything known about the ecologies of the species making up the assemblages. This will provide the underpinning for interpretations of analyses in those habitats where so much less is known. The research is one approach to determining how to analyse the basic components into which measures of biodiversity can be “decomposed” to allow existing methods of analyses and ecological knowledge to understand measures of and changes to biodiversity.

Acknowledgements

The research indicated here is supported by the Australian Research Council through its Special Research Centres Programme. We thank numerous colleagues for discussion in development of the ideas relevant to this programme

of research, anonymous referees for comments, Dan Lunney for a detailed review and Dr P. Hutchings for her forbearance beyond the call of duty in waiting for this through thick, thin and ill-health of AJU.

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