

Relatively little is known of the food web of the high Arctic basin as it is so difficult to work there. The benthos is low in diversity, though it is not clear to what extent this is a function of the relative youth of the system, the heavy input of fresh water and sediment in some areas, or the intense disturbance from bottom-feeding marine mammals. At lower latitudes there are important stocks of shoaling plankton-feeding fish, which have long been exploited by man.

The Southern Ocean Food Web

The Antarctic is in many ways a mirror image of the Arctic. It is a large continental land mass entirely surrounded by a deep ocean. The marine food web is likely to have been in existence for many millions of years, and while the zooplankton community appears to be relatively low in species richness, the benthos exhibits a diversity fully comparable with all but the richest habitats elsewhere.

The summer phytoplankton bloom is formed predominantly of the larger diatoms, and the haptophyte *Phaeocystis* appears not to be as important here as in the Arctic. The zooplankton is dominated by copepods and euphausiids, with *Euphausia*

superba at lower latitudes and *E. crystallarophias* closer to the ice. Midwater planktivorous fish are almost absent, and the fish fauna is dominated by the radiation of two predominantly benthic/demersal groups: notothenioids on the continental shelf and lipariids in the deeper water of the continental slope. As with the Arctic, relatively little is known of the deep sea.

See also

Arctic Basin Circulation. Baleen Whales. Current Systems in the Southern Ocean. Fisheries and Climate. Marine Mammal Overview. Microbial Loops. Seabird Foraging Ecology. Southern Ocean Fisheries. Sperm Whales and Beaked Whales.

Further Reading

- Knox GA (1994) *The Biology of the Southern Ocean*. Cambridge: Cambridge University Press.
 Fogg GE (1998). *The Biology of Polar Habitats*. Oxford: Oxford University Press.
 El-Sayed SZ (ed.) (1994) *Southern Ocean Ecology*. Cambridge: Cambridge University Press.
 Smith WO (ed.) (1990) *Polar Oceanography*, vols 1 and 2. San Diego: Academic Press.

POLICY

See **MARINE MAMMAL OVERVIEW**

POLLUTANTS

See **ATMOSPHERIC INPUT OF POLLUTANTS**

POLLUTION

Effects on Marine Communities

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Introduction

Natural communities of all types of marine organisms all over the world are being affected either directly or indirectly by pollution: directly by discharges of industrial and domestic wastes, offshore oil and gas drilling activities for example, and indirectly as a result of atmospheric pollution and global climate change. Some of these community changes are visually obvious in the field, such as the

effects on reef corals of increased particle sedimentation or abnormally long periods of high water temperatures (causing bleaching). Others require the analysis of samples brought back to the laboratory, such as the assemblages of organisms living in seabed sediments or the plankton. The determination of changes in the structure of these communities, in particular the sediment-dwelling macrobenthos, is widely used in the detection and monitoring of human's impact on the sea for a number of reasons. Attributes of the community level of biological organization reflect integrated environmental conditions over a period of time, whereas methods employing lower levels of organization (biochemical, cellular, physiology of whole organisms) require an experimental approach which reflects the condition of the organisms just at the time of sampling. It is natural communities that are of direct concern, and predicting the consequences for these communities from lower level signals is presently not feasible with any degree of confidence. Monitoring at higher levels of organization, e.g., measuring ecosystem attributes, is often simply not tractable. Community change, especially when measured by multivariate methods (see below) has also been shown to be a very sensitive indicator of environmental conditions. It is not necessary for animals to die for a community response to be elicited, but subtle effects such as shifts in the relative competitive abilities of species or changes in fecundity are detectable.

Aspects of survey and sampling design, that will enable valid inferences to be drawn, and the practi-

cilities of sampling different groups of marine organisms, are beyond the scope of this article (but see Further Reading). Rather, it concerns the analysis and interpretation of community data with a view to detecting and monitoring the impacts of pollution and other Man-induced disturbances, and inferring causality.

Analysis of Community Data

Typically, community data comprise a (usually) large samples by species matrix (Figure 1), in which the cells are filled with species abundances, biomasses, of some other measure of the relative importance of each species, such as percentage cover of colonial organisms. These matrices are likely to have a high proportion of zero entries. The samples may be taken at a number of sites at one time (spatial data) or at the same site at a number of times (temporal data), or a combination of both. When considering environmental problems operating on larger spatial and temporal scales, such as the effects of eutrophication or global warming over large sea areas, the data may be less quantitative, and comprise simple presence/absence information (species lists). There are essentially three classes of methods for analysing such data.

1. Univariate methods. These reduce all the information on the species composition of a sample to a single coefficient, most commonly a diversity index. The occurrence of 'pollution indicator' species also falls into this category.

Species	Sampling stations															
	30	36	37	31	03	35	27	25	26	29	32	38	28	33	34	...Etc.
<i>Abra prismatica</i>	0	0	0	0	23	0	10	2	13	11	13	14	31	17	34	
<i>Acanthocardia echinata</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	
<i>Alcyonium digitatum</i>	0	0	0	2	0	0	0	0	1	0	0	0	2	0	0	
<i>Ampelisca brevicornis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Ampelisca macrocephala</i>	3	1	3	6	5	4	4	5	6	2	0	3	5	5	4	
<i>Ampharete baltica</i>	1	18	0	18	21	18	15	27	18	7	7	34	4	19	17	
<i>Ampharete finmarchica</i>	0	5	0	1	4	7	0	3	0	1	1	8	0	3	4	
<i>Ampharete lindstroemi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Ampharete sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Amphicteis gunneri</i>	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	
<i>Amphictene auricoma</i>	0	0	0	0	0	4	9	4	11	1	5	7	12	20	8	
<i>Amphilocus spencebatei</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Amphitrite cirrata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Amphitritides gracilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Amphiura filiformis</i>	0	1	0	0	4	4	7	3	10	1	7	5	9	2	11	
...Etc.																

Figure 1 Part of a species by stations data matrix for species abundances of the macrobenthos from stations in the vicinity of the Ekofisk oil rig in the North Sea. There are 39 stations and 174 species in the complete matrix.

2. Distributional techniques. Here the relative importance of each species for a single sample is represented by a curve or histogram rather than a single number.

Note that in both these categories comparisons between samples are not based on particular species identities, and that two samples could have exactly the same diversity or distributional structure without having a single species in common. This is in contrast to the third method.

3. Multivariate methods. Here comparisons of samples are based on the extent to which they share species at comparable levels of abundance, biomass etc. These similarity coefficients then facilitate either a classification or clustering of samples into groups that are mutually similar, or an ordination plot in which samples are 'mapped' in such a way that their distance apart reflects their relative dissimilarity in species composition.

Univariate Methods

A variety of different indices can be used as measures of environmental pollution or disturbance, such as the total number of individuals (N), the total number of species (S), the total biomass (B) and also ratios such as B/N (the average 'size' of organisms) and N/S (the average number of individuals per species). These tend to be less informative, however, than measures that describe the way in which the numbers of individuals are divided up among the different species (species diversity indices), or measures of biodiversity based on the degree of taxonomic or phylogenetic relatedness of individuals or species in a sample.

Species diversity indices Indices of species (or higher taxon) diversity are amenable to standard univariate statistical analysis to determine, for example, the significance of differences between replicate sets of samples. A bewildering range of indices have been devised which measure attributes related to the number of species for a fixed number of individuals (species richness), the extent to which abundances are dominated by a small number of species (dominance, evenness and equitability indices), or a combination of these. Some commonly used indices include:

Shanon diversity $H' = -\sum_i p_i \log_e p_i$
(where $p_i = X_i/N$)

Margalef's species richness $d = (S - 1)/\log_e N$

Pielou's evenness $J' = H'/\log_e S$

Brillouin's index $H = (1/N)\log_e(N!/\prod_i X_i!)$

Simpson's index $\Delta^{\circ} = 1 - \sum_i \{X_i(X_i - 1)/N(N - 1)\}$

Note that values for all of these, except Simpson's index, tend to be heavily dependent on sample size (N). This means that it is not valid to compare measured diversity values for samples whose size is not standardized. Also, logs to different bases (e , 2, 10) are used in the literature to calculate these indices, and often the log base used is not stated, which also hampers comparisons.

Increasing levels of environmental stress are generally considered to decrease species diversity, richness and evenness. The 'intermediate disturbance hypothesis', supported by much empirical evidence, suggests however that diversity is maximal at intermediate levels of disturbance, falling off at very low frequencies and intensities of disturbance due to competitive exclusion between species, and decreasing again at high levels as species become eliminated. Thus, the response to increasing levels of pollution or disturbance is not monotonic, and value judgments concerning the effects of pollutants may be difficult to make (Figure 2). With no way of predicting at what level species diversity should be set under pristine environmental conditions, changes due to pollution can only be assessed by comparisons with reference stations (which may often be difficult to find) or with historical data.

Taxonomic relatedness measures A measure of biological diversity ought ideally to say something about how different the inhabitants are from each

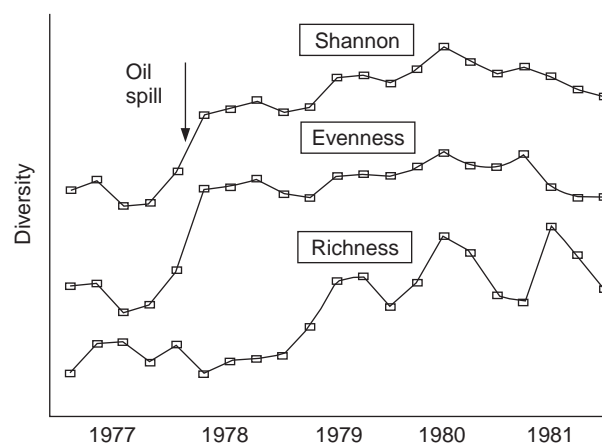


Figure 2 Changes in Shannon diversity and its components of species richness and evenness for the macrofauna at a station in the Bay of Morlaix, France, taken at approximately 3-monthly intervals spanning the period at which the site was affected by oil pollution from the wreck of the *Amoco Cadiz* on the Brittany coast. Note the increase in all three of these indices after the pollution incident.

other. Simply to say whether or not they belong to the same species is clearly insufficient, and recently a variety of different measures have been devised to measure the degree to which species are taxonomically related to each other. Polluted communities usually comprise a limited taxonomic spread of species, whereas under more pristine conditions the species present belong to a wide range of higher taxa. Measures of taxonomic distinctness describe features of this taxonomic spread and they are now beginning to find application in environmental impact assessment. They measure either the average distance apart of all pairs of individuals or species in a sample, traced through a hierarchical taxonomic tree, or the variability in structure across the tree. They overcome many of the problems of species diversity measures noted above, for example, they are independent of sample size, they can utilize simple presence/absence data (species lists), and in the latter case randomization/permutation procedures can test the null-hypothesis that the species present are a random selection from the full spread of taxa in the regional species pool.

'Average taxonomic diversity' (Δ) is simply the average path length through the hierarchical taxonomic tree between every pair of individuals in a sample. 'Average taxonomic distinctness', Δ^* , is Δ divided by its value when the hierarchical classification collapses to the special case of all species belonging to a single genus, and is more nearly a function of pure taxonomic relatedness of individuals (it is equivalent to dividing Δ by the Simpson diversity Δ°). A special case is the use only of presence/absence information for each species, when Δ and Δ^* reduce to the same statistic, namely Δ^+ . Another aspect of the taxonomic structure is the 'evenness' of the distribution of taxa across the hierarchical taxonomic tree. In other words, are some taxa overrepresented and others underrepresented by comparison with what we know of the species pool for the geographical region? Such a difference in structure should be well reflected in variability of the full set of pairwise distinctness weights making up the average, i.e. the variation in taxonomic distinctness, denoted by Λ^+ .

Pollution indicator species Certain taxa of benthic marine invertebrates are known to increase dramatically in abundance when levels of particulate organic enrichment become abnormally high and have become known as 'pollution indicator' species. They tend to be the smaller members of that size category called the macrobenthos, and the larger members of the meiobenthos. Several of these comprise groups of very closely related sibling species, such as the

polychaete worms *Capitella* and *Ophryotrocha*, the benthic copepod genus *Tisbe* and the free-living nematode genus *Pontonema*. No firm protocols have been established with regard to the level at which a community must be dominated by a particular indicator for it to be regarded as polluted, and interpretation of this information remains rather subjective.

Distributional Techniques

Diversity curves may take a number of forms.

1. Rarefaction curves are plots of the number of individuals on the x -axis against the number of species on the y -axis. Sample sizes (N) may differ, but the relevant sections of the curves can still be visually compared.
2. Plots of the number of species in $\times 2$ geometric abundance classes (i.e., number of species represented by 1 individual, 2–3 individuals, 4–7 individuals, 8–15 individuals etc.).
3. Ranked species abundance (dominance) curves in which species (or higher taxa) are ranked in decreasing order of importance in terms of abundance, biomass etc., and their importance, expressed as a percentage of the total for all species, is plotted against the relevant species rank.
4. k -dominance curves are cumulative ranked abundances, biomasses etc. plotted against species rank, or more usually log species rank.

The advantage of dominance curves is that the distribution of species abundances among individuals and the distribution of species biomasses among individuals can be compared on the same terms. Since the two have different units of measurement, this is not possible with diversity indices. This is the basis of the Abundance/Biomass Comparison (ABC) method of assessing disturbance, which has been mainly applied to benthic macrofauna communities. k -dominance curves for abundance and biomass in the same sample are plotted together on the same graph (Figure 3). In undisturbed communities the distribution of numbers of individuals among species is more even than the distribution of numbers of biomass among species, so that the k -dominance curve for biomass lies above that for abundance throughout its length. In grossly polluted communities the reverse is the case, and in moderately polluted ones the two curves are quite coincident and may cross over one or more times. These three conditions are recognizable in single samples and can provide a snapshot of the pollution status

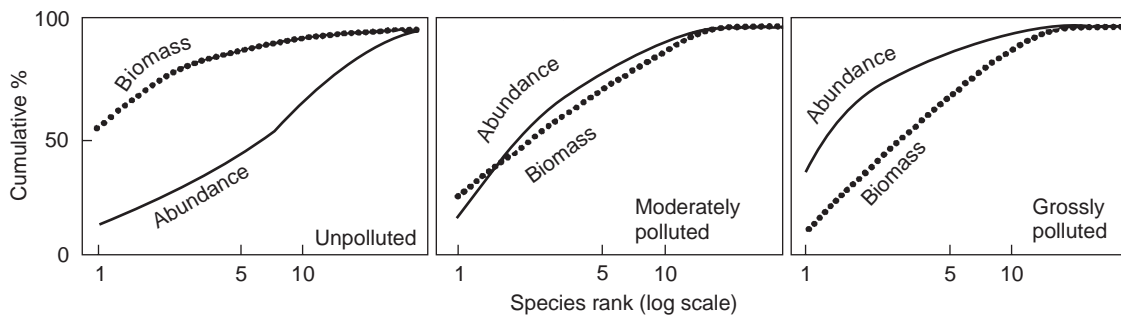


Figure 3 Hypothetical k -dominance curves for species biomass and abundance (ABC plots) showing unpolluted, moderately polluted and grossly polluted conditions.

of a community without reference to spatial or temporal controls, although the latter are of course desirable. Plotting large numbers of ABC curves can be cumbersome, and the information they contain can be summarized by the W statistic, which is the sum of the $B-A$ values for all species across the ranks, standardized to a common scale so that comparisons can be made between samples with differing numbers of species. When samples are replicated, the W statistic, provides a means for testing for significance of observed changes in ABC patterns, using standard univariate procedures.

Multivariate Methods

Multivariate classification, or cluster analysis, aims to find groupings of samples such that those within a group are more similar to each other in biotic composition than samples in different groups. The results of such an analysis are usually represented by a dendrogram (Figure 4A). An ordination, is a map of the samples (Figure 4B), usually in two or three dimensions, in which their distance apart reflects their biological similarity; the samples are not forced into groups, but rather the relationship of each sample with every other is depicted (as far as this is possible in two or three dimensions). There are literally hundreds of clustering methods in existence. Also, several ordination methods have been proposed, each using different forms of the original data and varying in their technique of preserving the true intersample similarities in low-dimensional plots: these include principal components analysis (PCA), principal co-ordinates analysis (PCoA), correspondence analysis and detrended correspondence analysis (DECORANA), and multidimensional scaling (MDS), in particular nonmetric MDS. It is not possible here to give a balanced account of this huge range of techniques, but instead this section focuses on a unified set of protocols based on non-parametric methods which is now gaining worldwide acceptance in the field of environmental

impact assessment, and is implemented by the software package PRIMER, developed at the Plymouth Marine Laboratory, UK.

Compared with univariate or distributional techniques of data analysis, multivariate methods are much more sensitive in detecting differences between communities, and thus evaluating temporal or spatial change. Pivotal to PRIMER's approach is the biologically relevant definition of the similarity between two samples and its utilization in simple rank form, i.e., sample A is more similar to sample B than it is to sample C. Statistical assumptions about the data are thus minimized and the resulting nonparametric techniques are of very general applicability. From the starting point of a ranked triangular similarity matrix (usually using Bray-Curtis similarity) between all pairs of samples, the procedures encompass:

1. the display of community patterns by hierarchical agglomerative clustering and nonmetric MDS;
2. identification of the species principally responsible for determining sample groupings (the SIMPER program);
3. statistical tests for differences in community composition in space and time in one-way and two-way layouts: multivariate analogs of analysis of variance (ANOSIM);
4. linking patterns of community difference to patterns of physical and chemical environmental variables at the same locations or times (BIOENV).

Although causality of community change can really only be established with certainty by means of controlled experiments, inferences can be drawn from the relationships between multivariate patterns in the biological and environmental data, which can be established formally using the BIOENV procedure. In Figure 5, for example, the MDS plot for the

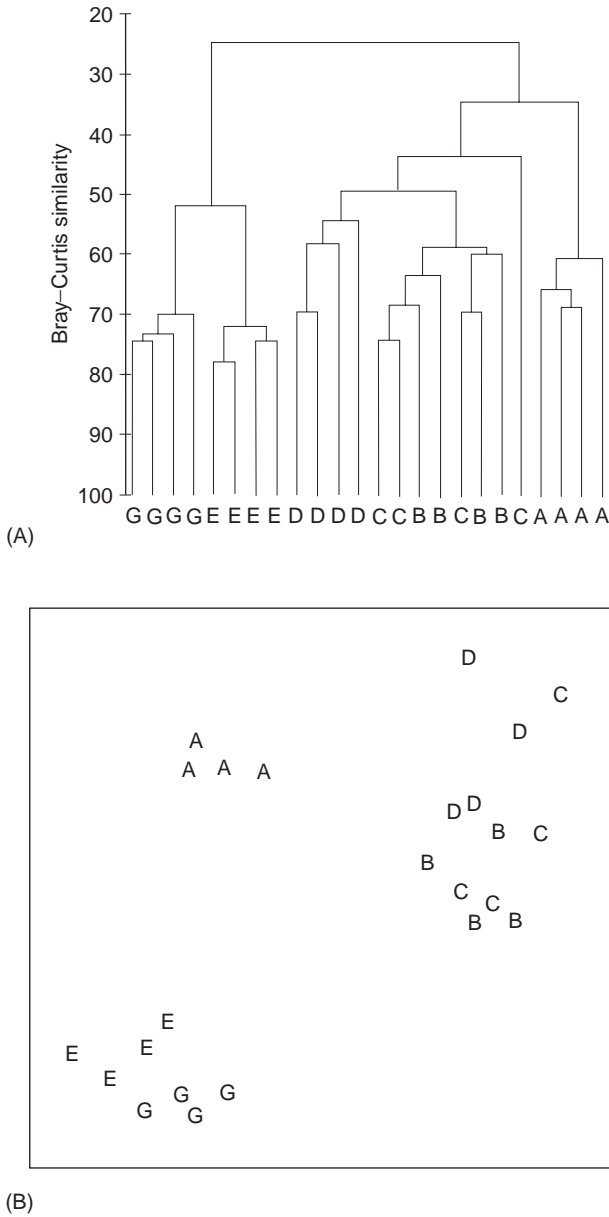


Figure 4 Macrobenthos from four replicate samples at each of six situations (A–E, G) in Frierfiord, Norway. (A) Dendrogram for hierarchical clustering based on $\sqrt{\sqrt{\text{transformed species abundance data and the Bray-Curtis similarity measure. (B) Non-metric MDS ordination based on the same similarity matrix. Note the similarity in the grouping of samples. Stations B, C and D, in the deeper basins of the fiord, suffered from seasonal anoxia.$

macrobenthos in the vicinity of the Ekofisk oil rig in the North Sea closely matches the MDS for those environmental variables that can unequivocally be related to the drilling activity. However, in themselves these multivariate analyses are not intended as measures of biological stress. They do not enable us to put a value judgment (bad, good, neutral) on

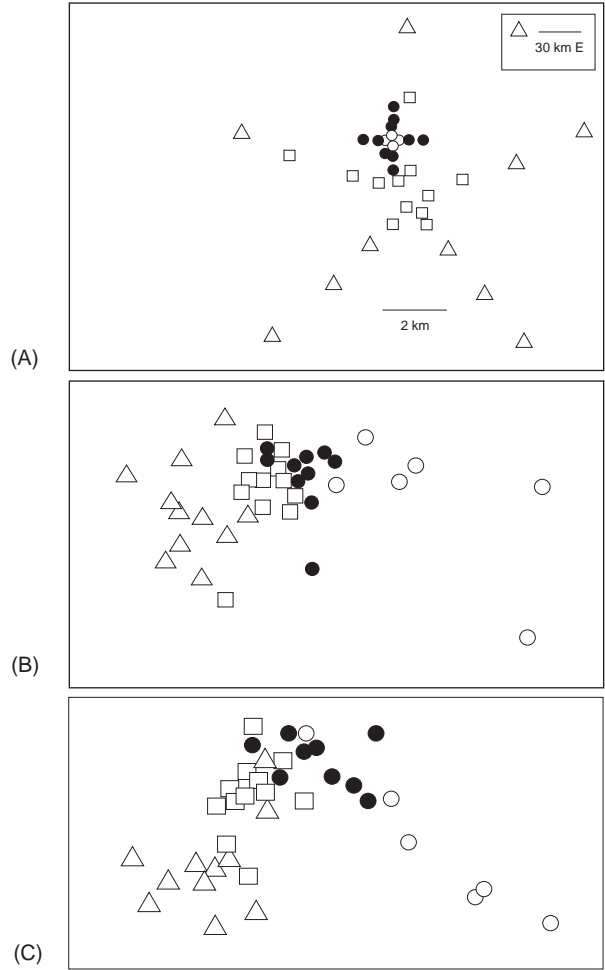


Figure 5 Ekofisk oil rig, North Sea. (A) Map of positions of the 39 sampling stations, coded according to their distance from the active drilling center (Δ , > 3.5 km; \square , 1.0–3.5 km; \bullet , 250–1000 m; \circ , < 250 m). (B) Nonmetric MDS ordination based on $\sqrt{\sqrt{\text{transformed species abundance data and the Bray-Curtis similarity measure, using the same coding. (C) PCA of three environmental variables (% mud, log total hydrocarbons and log barium concentration in the sediment) at the same stations. Note the match between (B) and (C).$

the community change, in the way that univariate or distributional methods can. The three outer distance-zones in the Ekofisk study are indistinguishable in terms of species diversity and k -dominance curves, so do the clear differences in species composition between them revealed by multivariate analysis (Figure 5) really matter?

Ways are now being devised for incorporating the full multivariate information into measures of biological stress. A feature of these analyses is that patterns of community change at the species level, in response to pollution or disturbance, are generally reflected at higher taxonomic levels, even up to the level of phylum (Figure 6), due to the fact that

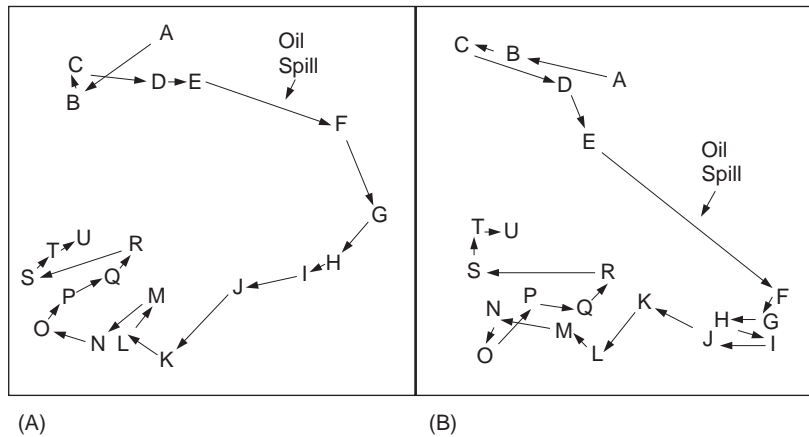


Figure 6 Nonmetric MDS for the macrofauna at a station in the Bay of Morlaix, France, taken at approximately 3-monthly intervals spanning the period at which the site was affected by oil pollution from the wreck of the *Amoco Cadiz* on the Brittany coast (same data as **Figure 2**). (A) Species level data. (B) The same analysis, but with the species data aggregated up into five major groupings: Annelids, Molluscs, Crustaceans, Echinoderms and 'others'. Note, in both cases, the community change after the pollution incident, and the gradual evolution of the community back to a new equilibrium state. The pollution response seems to be even more marked at the higher taxon level than the species level.

related taxa are responding in similar ways. A meta-analysis of a range of well-documented pollution/disturbance incidents on the macrobenthos has shown a commonality of response in terms of phyletic composition in relation to the level of environmental stress. Combining new survey data with these training data, and rerunning the analysis, thus enables the pollution status of the new data to be evaluated on a broadly comparative scale. Multivariate patterns of seriation of community change in response to natural environmental gradients have been shown to break down with increasing environment stress, and the variability between replicate samples in multivariate terms has also been shown to increase. Both these attributes have been developed into stress measures, the Index of Multivariate Seriation (IMS) and the Index of Multivariate Dispersion (IMD), respectively.

Conclusions

The methods described above can be used to detect the biological effects of pollution at a range of spatial and temporal scales ranging from local short-term pollution incidents to basin-wide long-term effects of eutrophication and climate change. For local events, the less mobile components of the biota are perhaps more appropriate for study, such as the macrobenthos and meiobenthos of soft-sediments and the sessile epifauna of hard substrata. Here, with carefully controlled sampling designs, community change can be detected in terms of diversity, distributional curves and multivariate as-

pects of community composition at the species level. For broader scale comparisons, pelagic organisms such as plankton or fish may be more appropriate for study: Because of the methods of collection these community samples tend to integrate ecological conditions over large areas (see, for example, the Continuous Plankton Recorder Survey of the North-East Atlantic). If benthic components of the biota are to be used, biodiversity measures based on taxonomic relatedness may be more useful than species diversity indices since they can utilize species lists rather than strictly quantitative data and are sample-size independent. Also, multivariate analysis at taxonomic levels higher than that of species might be more appropriate, in view of the narrow habitat preferences and restricted geographical distributions of many species.

See also

Beaches, Physical Processes Affecting. Continuous Plankton Recorders. Chlorinated Hydrocarbons. Coral Reefs. Ecosystem Effects of Fishing. Eutrophication. Fiordic Ecosystems. Grabs for Shelf Benthic Sampling. Lagoons. Macrobenthos. Mangroves. Meiobenthos. Metal Pollution. Oil Pollution. Pollution, Solids. Rocky Shores. Salt Marshes and Mud Flats. Zooplankton Sampling with Nets and Trawls.

Further Reading

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18: 117–143.

- Clarke KR and Warwick RM (1994) *Change in Marine Communities: an Approach to Statistical Analysis and Interpretation*. Plymouth: Plymouth Marine Laboratory.
- Holme NA and McIntyre AD (eds) (1984) *Methods for the Study of Marine Benthos*, 2nd edn. Oxford: Blackwell.
- Magurran AE (1991) *Ecological Diversity and its Measurement*. London: Chapman and Hall.
- Sokal RR and Rohlf FJ (1981) *Biometry*. San Francisco: Freeman.
- Underwood AJ (1997) *Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance*. Cambridge: Cambridge University Press.
- Warwick RM (1993) Environmental impact studies on marine communities: pragmatical considerations. *Australian Journal of Ecology* 18: 63–80.
- Warwick RM and Clarke KR (2001) Practical measures of marine biodiversity based on relatedness of species. *Oceanographic Marine Biology Annual Review*.

POLLUTION CONTROL

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Approaches applied to the control of pollution have altered substantially over the last four decades. Historically, emphasis was given to management initiatives to ensure that damage to the marine environment was avoided by limiting the introduction of substances to the sea. This was typified by the attention given to contaminants such as mercury and oil in early agreements for the prevention of marine pollution. Marine environmental protection was achieved through prior scientific evaluations of the transport and effects of substances proposed for disposal at sea and defining allowable amounts that were not thought to result in significant or unacceptable effects. This reflects largely a management and control philosophy. In the closing stages of the twentieth century, however, the philosophy underlying pollution control has undergone substantial revision. Recent policy initiatives rely less on scientific assessments and place greater emphasis on policy and regulatory controls to restrict human activities potentially affecting the marine environment. During this period of change, practical pollution control and avoidance procedures have been adapted to improve their alignment with these new policy perspectives. Simultaneously, it has been widely recognized that pollutants represent only part of the problem. Other human activities such as over-exploitation of fisheries, coastal development, land clearance, and the physical destruction of marine habitat are equally important, and often more serious threats to the marine environment. In recent years, the concept of marine pollution has been

broadened to consider the adverse effects on the marine environment of all human activities rather than merely those associated with the release of substances. This is a most positive development, partly influenced by improved scientific understanding that has led to an improved balance of attention among the sources of environmental damage and threats.

Background

In this article, the term ‘pollution’ implies adverse effects on the environment resulting from human activities. This is consistent with, but broader than, the definition of pollution formulated by the United Nations Joint Group of Experts on Marine Environmental Protection (GESAMP) in 1969 that is restricted to adverse effects associated with the introduction of substances to the marine environment from human activities. The term ‘contamination’ infers augmentation of natural levels of substances in the environment but without any presumption of associated adverse effects. Indeed early approaches to marine pollution prevention reflected the distinction between these terms, while more recent approaches are based on more or less identical interpretations of these expressions with both implying adverse effects.

Early Agreements on Marine Pollution Prevention

The earliest international marine pollution prevention agreements of the modern era were the Oslo and London Conventions of 1972. These conventions were developed at the same time as the heightened awareness of marine pollution issues led to the first major international conference on the topic, the United Nations Conference on the Human Environment, that took place in Stockholm in the