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ECOLOGICAL MODELS FOR IMPACT EVALUATION OF DREDGING

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Abstract

Models based on academic ecological theory specifically aimed at impact evaluation of dredging on populations and communities in their environment do not exist for the moment. Nevertheless, the very rapid development in theoretical ecological modeling over the last two decades has generated an extremely diverse ensemble of theories on populations and communities. It has become increasingly recognized that perturbations are frequent and natural phenomena that allow persistence of populations on larger spatial and temporal scales. In this view, equilibria do not exist, at least not on the small scale, in patches. Many models point out that extinction on this scale is both natural and frequent. Current efforts to model local, transient dynamics, in patches may well prove to be more realistic than the large ecological models trying to describe the functioning of the whole system. Models of local dynamics will also have to incorporate local history and natural selection.

In the absence of theoretical models the impact of dredging on populations and communities is often assessed using empirical or statistical methods. These may serve as descriptions and may generate hypotheses but are usually unable to determine causal relationships and must be supplemented by field or mesocosm experimentation. Often fundamental errors are made in which the basic assumptions to apply statistical procedures for true hypothesis testing are violated. Many monitoring programmes contain fundamental procedural flaws. A summary is given of the more classical procedures used, based on changes in abundance, species-abundance relationships, diversity indices, classification and ordination.

Introduction

Dredging, from an ecological point of view, may be considered as an environmental perturbation causing stress in ecosystems. It creates an important physico-chemical change on a very short temporal and a relatively large spatial scale. The biota will be severely affected and mortality, even heavy mortality, of organisms is involved. Dredging may thus exert a strong selective pressure.

Biological models to evaluate the impact of dredging may be constructed at different levels of biological organisation and may be derived from biochemistry, physiology, ethology, population biology and community and systems ecology since stress effects may be found at all levels of organisation, from cell organelles to ecosystems. However, effects on any level of organisation will usually be buffered by the homeostatic mechanisms existing at that level and are not necessarily transmitted to the next (Bayne *et al.*, 1985). It may therefore be argued that only when effects become visible at the population level (e.g. increased mortality or reduced fecundity) there is need for concern since this involves large spatial and temporal scales. One should realise as well that a response at the population or ecosystem level will only be visible in a later stage of the response-cascade and so-called early warning signals may sometimes have to be found at lower stages of organisation, e.g. for particularly toxic and persistent toxicants.

The term stress has been used in different ways; in this paper as usually in ecology stress is defined as a factor or a group of factors from the environment that have either physical or physiological effects on organisms or both. Stresses are part of all types of changes in the environment that may be termed perturbations. The effect of environmental stress is a disturbance. It must be noted that stress is also used in the sense of the effect itself, which is the more usual physiological definition.

On the organismal level it is obvious to determine stress as any environmental influence that reduces darwinian fitness, i.e. the ability to contribute to the next generation. Fitness incorporates survival probability, development rate and fecundity and links responses at the individual level to variables that influence the density of populations and their future contribution to the gene pool (Calow, 1989). The link with evolutionary processes is important: it requires a distinction between short-term (proximate) and long-term (ultimate) effects.

To determine proximal effects individual organisms are often modelled as a system that acquires resources and then allocates them between catabolic and anabolic processes (Koehn & Bayne, 1989). The catabolic processes break

down resources to yield energy for physical and chemical work. The anabolic processes are concerned with growth and reproduction. The allocation between catabolism and anabolism can be translated in effects on survival, growth and reproductive investment so that, at least in principle, the molecular, cellular and physiological traits associated with stress resistance can be related to general metabolic properties of organisms that can be linked in turn to demographic variables that influence population dynamics (Calow, 1989).

The ultimate effect of stress may be the selection of resistant genotypes. For this reason it may be argued that the long-term effects of stress are properly evaluated only at the population level. In the literature on marine pollution in general this aspect is largely ignored. It may for instance be argued that many benthic populations living in shallow waters are adapted to the mechanical stress that is caused by dredging, e.g. due to the frequent occurrence of storms.

This paper will from now on only deal with effects on populations, communities (assemblages) and ecosystems. Except for functional attributes of ecosystems such as primary production or respiration, these effects are nearly always deduced from observations on individual organisms and therefore reflect some average effect on individuals. An implicit link with physiology and genetics thus exists but population abundances are also determined by ecological interactions such as competition and predation that may be influenced by perturbations themselves and may result in evolution as well. The theories on the interactions between populations that result in changes of their relative abundance are at the moment insufficiently accurate to be used in actual problems. A pragmatic empirical approach to problems of detecting stress in natural ecosystems has therefore been advocated that only makes use of the observed changes in abundance without trying to explain them. There thus still exists a large gap between theoretical ecology and its applicability in environmental problems.

Models from theoretical ecology

Introduction

Conceptually the anthropogenic impact of activities such as dredging is often related to implicit and usually vague ideas about stability, equilibrium, carrying capacities of ecosystems and the like. The intuitive idea that a balance of nature exists has a long tradition in Western thought. It was central in many natural history studies over the last several centuries, it is often used in political discussions on environmental problems and has permeated efforts to model ecological systems mathematically as well. Many models have been structured on the basis of a community of species in an ecosystem having an equilibrium state (steady state or dynamic equilibrium). Species can deviate from equilibrium and the equilibrium state can be unstable giving rise to population fluctuations around it, but the equilibrium state exists. The classical example of this equilibrium view in mathematical ecology are the Lotka-Volterra equations. In the last decade or so the equilibrium view of ecological systems has been challenged by an increasing number of ecologists to the point on whether it is valid to define the existence of an equilibrium state at all, stable or unstable.

The concepts of equilibrium and stability are not sharply defined when applied to real species or systems. Often one refers to ideas that have been developed in the engineering sciences in which equilibrium points or states are referred to as unstable, neutrally stable, locally stable depending on whether the system returns to them after perturbation. The terminology is still confusing. In this paper we define the attributes of stability that allow or not populations or communities to recover from perturbations as inertia and resilience. Inertia is the lack of response to perturbation, i.e. no change in numbers. Resilience is the ability to return to equilibrium. Persistence is the ability of the system to remain within certain boundaries over a certain time.

Equilibrium and stability

DeAngelis and Waterhouse (1987) give a lucid review of the different approaches to this problem that will be summarized here. In general one may picture communities, assemblages of biological populations, as existing along a spectrum from stable equilibrium systems with strong biotic interactions and few stochastic effects to nonequilibrium systems where biotic interactions are weak or non-existing and the stochastic effects are large (Wiens, 1984). The former systems are structure primarily by biotic forces, the latter are controlled more by environmental variations. Strong biotic interactions may also destabilize ecological communities and it is useful to consider a category of unstably interacting communities in this spectrum (DeAngelis & Waterhouse, 1987)

Instability caused by biotic interactions

Communities may become unstable through biotic interactions and through stochastic effects. Biotic interactions do not necessarily increase stability. When the strength of predation and competitive interactions between species increases, the simple two-species models predict instabilities. Instabilities also occur for discrete-time systems even those involving only one species (May & Oster, 1976). This type of behaviour is called chaotic : it is deterministic but mimics a random process. Chaotic behaviour can also occur for sets of ordinary nonlinear differential equations.

Despite recognition that instability is a common feature of ecological models it was assumed by many ecologists that if these models were made much more complex by including a larger number of species these systems would be stable. May (1972) showed that for randomly assembled linear ecosystem models this assumption is false : an increase in system size or in strength of interactions actually increases the probability of instability. These results clearly indicated that there are real difficulties with the idea of the ecosystem as a balance of interacting species. Mathematical models seem to reveal a potential biotic feedback instability inherent in complex natural systems.

Instability caused by stochasticity

Two general types of stochasticity may be distinguished (May, 1973 ; Nisbet & Gurney, 1982). The first is demographic stochasticity which refers to population fluctuations that arise because real populations consist of a finite number of discrete individuals. Individual reproductive and mortality events are stochastic, even though averages over a whole population over sufficiently long time intervals display regularities. A birth and death model is stochastically dominated when the rates are density independent. In such a case there is no possible equilibrium state.

Environmental stochasticity is probably more important for ecological communities. This type of stochasticity has been added to population models in at least three general ways : a) the addition of white noise or pink noise where low frequencies dominate to population values in deterministic equilibrium models ; b) the addition of discrete perturbations separated by intervals of random length to deterministic population models ; c) the replacement of deterministic population parameters by random variables in the model.

The first method was used by May & McArthur (1972) who introduced white noise into competition communities described by deterministic equations. One can picture this model as a struggle between random forces pushing the system away from equilibrium and homeostatic forces pulling it back. Hanson & Tuckwell (1978) assumed that the deterministic logistic model describes the unperturbed population and that discrete perturbances occurring at intervals described by a Poisson process continually reduce the population. Pimm & Lawton (1977) hypothesized that the lengths of food chains are limited by the resilience, defined as $1/T_c$ where T_c is the characteristic return time to equilibrium after perturbation. The third type of environmental stochasticity, the stochastic fluctuation of deterministic population parameters, was first proposed by Lewontin & Cohen (1969). They considered the growth rate r of the deterministic discrete-time model to be totally governed by a stochastic environment rather than by current population size. They showed that even under circumstances in which the mean expected value of N_t increases towards infinity with t , a population will always become extinct. These results were extended to age-structured populations (Leslie-matrices) in which Markovian fluctuations in the different matrix elements can occur at each time step. Again the unpredictable fluctuations drive the population toward extinction.

Stability and persistence

In the previous two paragraphs it was shown that highly interactive ecological communities may become unstable due to biotic feedback and that weakly interactive ecological communities are sensitive to stochastic extinctions. What then enables a community of species to persist in an ecosystem over the course of time ? According to DeAngelis & Waterhouse (1987) models addressing this question are of two kinds : a) they incorporate stabilizing mechanisms into basic classical models that could preserve the stability of the equilibrium state b) they abandon the stable equilibrium state as a fundamental property at the local scale and examine mechanisms ensuring long-term persistence of communities.

The stability of the equilibrium state

In general one can distinguish between three types of mechanisms that can preserve the stability of the equilibrium state :

- a) intrinsic population dynamical mechanisms
- b) disturbances in feedback dominated systems
- c) biotic compensatory mechanisms in stochastic environments

The recognition that simple deterministic predator-prey systems can exhibit instabilities led to a search for functional relationships involving prey refuges, predator searching time, predator interference, predator switching behaviour and other processes that could stabilize such systems. It was also argued that constraints on structure and parameter values would have evolved through natural selection so that May's (1972) assumptions of randomly assembled linear models may not hold. A similar search for mechanisms of stabilization in competitive communities led to the investigation of phenomena as predation, nontransitive competitive loops, intraspecific competitive interference and greater model realism in reducing the likelihood of competitive exclusion. This research suggests that some ecological food webs and competitive systems may have inherent biases and mechanisms that stabilize the system even on small spatial scales. However, laboratory experiments have shown that stability is not possible if the spatial scale is too small (Huffaker, 1958).

One of the stabilizing mechanisms which has been increasingly recognized as playing a major role in persistence are disturbances. The idea that disturbances may be vital in promoting coexistence of competing species dates back to Hutchinson (1953) who was puzzled by the high diversity of phytoplankton competing for the same basic resources of nutrients and light and surmised that disturbances would interrupt the process of competitive displacement. Huston (1979), who considered a large number of competing species and the effect of disturbances that decreased all the species by similar fractions, showed that too low a disturbance rate resulted in competitive displacement by the dominant species, while too high a rate prevented the slow-growing dominants from becoming established. A medium level disturbance rate led to the highest diversity of species. This intermediate disturbance idea is relevant to observations of diversity in a variety of systems.

Communities dominated by stochastic environmental fluctuations may persist through biotic compensatory mechanisms such as a higher probability of survival of individuals in populations that reach low densities. Another possibility is that when a species is rare, deleterious effects of interspecific competition are reduced. Populations can also respond to drastic reductions in size by greatly increasing their reproductive effort following the disturbance. When this density dependence of population parameters is weak or indiscernable at medium ranges of population density but strong at upper and lower levels it can create a situation called density-vague regulation where populations wander over a broad range of densities in response to environmental variations and disturbances but seldom go to extraordinarily high values or to extinction (Strong, 1984).

Local dynamics without equilibrium

A real population generally occupies a large enough space so that the dynamics within any particular small unit of area or patch may not be too important for the species as a whole. The extinction of local subpopulations may be a natural and tolerable situation in terms of the total population. The concept of spreading of risk introduced by Den Boer (1968) is that whatever temporal variations there are in environmental factors they will probably vary from place to place so that populations may increase in some and decrease in other areas. If there is migration between patches spreading of risk may be a very strong factor in stabilizing a population.

Extinctions through competitive displacement or prey overexploitation can occur in individual patches but these local extinctions will be continually compensated for by invasions from other patches. Models of competition of this type were developed in the early seventies. All of these models contain extinction rates for each species and migration rates from one habitat to another. They are deterministic and the possibility of stable equilibrium on the regional scale exists. Another class of models designed for computer simulation of competitive or predator-prey systems over large spatial domains chooses migration transfers by random number generation. The possibility of stable equilibrium over large spatial domains is not obvious and these studies focus on persistence at the large scale. The general conclusion from the above models is that spatial dispersal can have a significant effect in permitting the persistence of unstably interacting species in situations where extinction would otherwise occur.

Another fundamentally differing model type is that which includes spatial heterogeneity. This type of model stems from the recognition that any environment generally contains a variety of habitat types where some may favor one species and others may favor another species. The modeling of populations and communities on spatially heterogeneous regions has a voluminous literature. They reflect a wealth of empirical observations that indicate that in a variety of cases coexistence is better explained by heterogeneity in space and time than by the equilibrium theory of resource partitioning. Again the reader is referred to DeAngelis & Waterhouse (1987) for more details.

Patch dynamics and dredging

Ecological models trying to predict equilibrium in natural communities have now nearly been abandoned by theoretical ecologists. All natural communities are dynamic and spatially heterogeneous. Recruitment, growth, repro-

duction and survival are influenced by local environmental conditions and biotic interactions and therefore all vary spatially. Equilibrium and climax may only exist on a large spatial and temporal scale. The structure of most if not all natural communities reflects local events and history so that present day patterns can only be interpreted if the organisms themselves yield clues as to the identity and timing of historical events or if the assemblage has been monitored continuously over a long time.

It is clear that models to be practical will have to mimic local situations and will have to deal with the non-existence of local equilibria and with temporal and spatial variability, which are essential features of population and community dynamics. In the absence of such variability many species would cease to exist. Disturbance is both a major source of temporal and spatial heterogeneity in the structure and dynamics of natural communities and an agent of natural selection in the evolution of life histories. Physical disturbance is one of the major mechanisms that breaks the inhibition of new settlements and generate conditions favorable for recruitment, growth and reproduction. Disturbances reduce resident organisms and lessen competition for resources that are present and in some cases even replenish nutrients.

The mechanical effects of dredging events must be placed in such a framework. If local extinction is a common and natural phenomenon, attention should be focused to the life-history of species, their distribution and recruitment mechanisms. In a patchy environment where coupling between patches exists, dredging may be expected to have long-term effects only in exceptional cases. A rational management of the operations in time and in space based on ecological knowledge and local conditions must be possible although the possible physiological effects of dredging due to the release of toxics or nutrients can probably not be treated in the same way.

If frequent extinctions in patches is a fundamental feature of population dynamics, models of ecosystems have to take this into account. Several theoretical models have been based on this. Trends are now the modeling of transient patches, small units of area for which no presumption of the existence of an equilibrium state is made. Levin & Paine (1974) model for the spatial and temporal patterns of the rocky intertidal shore may serve as an example. The model has two components, a submodel for transient dynamics of vacant patches (shrinkage through time due to growth in from the sides) and a rate of creation of patches by wave disturbances. The models of Botkin *et al.* (1972) explicitly embody the view that small landscape units are unstable with respect to vegetation cover. These models start with gaps created through the deaths of canopy trees. The gaps are the sites of regeneration and growth. All trees growing in the gap are individually modeled. Such organism-by-organism models have also been used to simulate coral communities (Maguire & Porter, 1979). Another general class of models for the transient dynamics of a patch was used by Roughgarden *et al.* (1985) to model barnacle settlement of empty space. This models resembles the Leslie matrix type, dividing the barnacles into age classes; the recruitment of the O-age class barnacles is limited because of space being occupied by older individuals.

Stability and trophic structure

The transition from local models to global, land(sea)scape-type models dealing with large geographical areas is an interesting and important ecological problem. Although theory and increasingly also observations confirm that chaos and unpredictable population dynamics on the local scale are typical for ecosystems, many ecologists argue that the current diversity of life and the persistence of highly specialized species in many ecosystems indicate that interactions between populations on successive trophic levels are quite likely to result in a stable equilibrium on larger scales. Hairston *et al.* (1960) explained how order can arise from darwinian struggle for existence: carnivores severely exploit their resources and have guilds structured by competition. The herbivores, being regulated by predators, are unable to have much impact on the vegetation which therefore is structured by competition. The emergent properties of ecosystems can thus arise by chance from unregulated darwinian struggles between individual organisms and from interactions between populations deriving from such struggles. The world is green because of predation.

This model has a long history and its validity for terrestrial systems has been intensely discussed (Oksanen, 1988). The model has been adapted by Menge & Sutherland (1987) who include disturbance and recruitment as the basic mechanisms to determine community composition. It is assumed that mobile organisms are more strongly affected by stress than sessile organisms and that food web complexity decreases by stress. Under conditions of high recruitment, consumers have no effects in stressful environments but competition for space becomes important in benign environments. A reduction in recruitment intensity reduces the importance of competition for a given level of stress.

When competition for space leads to exclusion and recruitment is high the relationships between diversity and predation or disturbance according to this model are distinct. Diversity is low in harsh environments because only opportunistic and resistant species survive. When the environment is more moderate, diversity increases because

of the intermediate disturbance effect, decreases because of competitive exclusion, increases because of moderate predation on competitors and decreases again because of too strong predation. With high recruitment a bimodal diversity curve is expected along an axis of environmental stress. If competition permits coexistence or recruitment is low the diversity curve is expected to be unimodal.

Evolution, ecosystems and ecological modeling

The applicability of models of the Menge & Sutherland (1987) type, which are based on logics, in practical problems is unclear, but the implication that structure in ecosystems may arise from interactions between populations in a purely darwinistic way is important since this indicates that populations should be the focus for understanding effects of perturbations.

Instead of studying populations or the structure of communities, general functional characteristics of ecosystems that may change response to stress have been proposed. Some of these effects have been reviewed by Rapport *et al.* (1985) and Schindler (1987). They list changes in primary production, decomposition rates, nutrient cycling, frequency of disease, changed amplitude of fluctuations, reduced diversity, retrogression to opportunist species and reduction in size as possible ecosystem stress symptoms. Schindler (1987) argued that, because of feed-back, monitoring ecosystems functions would be a poor approach to detecting early signs of impending ecosystem damage.

For benthic communities, reductions in diversity, retrogression to dominance by opportunistic species and reduction in size are all extensively discussed by Gray (1989) who shows that there are many examples where these changes have been observed. In some particular cases such as organic pollution by a point source a predictable set of events has been described (Pearson & Rosenberg, 1978).

Whether ecosystems are an appropriate level to study the effects of stress depends on views of how these effects may be translated at the system level. At the one extreme are population biologists who see the physical environment as just a constraint to the darwinian struggle for existence, which is the sole organizing principle in nature; at the other extreme is the (survival of the cybernetic), the necessity of cybernetic organisation postulated necessary for the persistence of ecosystems (Patten & Odum, 1981). In any case, evolutionary theory is rarely an integral part of systems ecology or ecological modeling. Many systems ecologists believe that evolution will provide mutual adaptation of species to form organized, functionally integrated ecosystems. System-level constraints and causal feedback loops are often treated as higher-order phenomena and studied and modeled without considering the evolution of individual species (Loehle & Pechmann, 1988).

Population ecologists, as evolutionary biologists, focus primarily on adaptation and selection at the level of individual organisms. It is generally assumed that selection above the individual level rarely occurs. If ecosystems are not real entities but just a collection of species in a particular environment then the question is whether ecosystems can be understood and modeled by theories that address only current relationships and phenomena.

Several system ecologists have proposed that ecosystems evolve to maximize some quantities such as stability. To test whether such attributes may evolve one can check whether they are formulated in terms of extensive or intensive variables. Slobodkin (1972) pointed out that natural selection operates at the level of individuals that are governed by intensive variables such as food availability, temperature etc, rather than extensive variables such as carrying capacity, diversity etc. because information on extensive variables is available to humans but is generally not available to organisms in the system. Natural selection is incapable of responding to extensive variables (Loehle & Pechmann, 1988)

A second question is whether properties are emergent or collective. For example, total biomass is a collective property. A true system or emergent property is one that results from interactions in the system and is not predictable from studies of the system components. If these properties are important it becomes necessary to ask how evolution may affect them and how ecosystem dynamics affects natural selection of individual species.

The question whether individual organisms are the appropriate level of study is also relevant for ecological modeling. When models are constructed it is necessary to aggregate components in e.g. trophic levels. It has been argued (Rowe, 1961) that there are no intermediate subsystems between individual organisms and ecosystems and that populations and communities cannot be considered subsystems because they are not objects that can be physically separated from other subsystems. Webster (1979) stated that populations and communities do not necessarily have stronger internal than external interactions and thus violate criteria for hierarchical systems as established by Simon (1962). Trophic levels, functional groups and guilds cannot be considered subsystems for the same reason, but distinct physical subdivisions such as the sediments can perhaps be viewed as subsystems. Loehle & Pechmann

(1988) propose to use evolutionary criteria for determining groups of species with stronger internal than external interactions and hence for defining hierarchies; groups of highly interactive, coevolved species that form mutualistic, commensal, competitive, predator-prey or parasitic associations should therefore be examined as possible hierarchical subsystems within ecosystems.

The long, old discussions on whether benthic communities may be considered as subsystems may regain some interest in this perspective. Many multivariate analyses support the idea that assemblages of species represent discontinuous entities with a coherent geographical distribution. Whether these species coevolved, whether there has been group selection operating or whether benthic communities must be considered as weakly interacting are open questions. To check the effects of dredging against this background is impossible at the moment since it requires much additional information on the natural history of the species.

Monitoring, empirical models and statistics

Introduction

It has been argued above that the ecological consequences of dredging operations should be studied in the local context and rely on the natural history of the species involved. Models should be based on the dynamics of patches, local populations of species. For the moment models of this kind applicable to dredging (or mechanical perturbation in general) do not exist. It may be argued that the general ecological models which are now being developed and which try to mimic the functioning of whole ecosystems are not compatible with this view unless they will be capable of incorporating species populations and local conditions and unless they are based on darwinian processes which are the ultimate basis of adaptation.

To study the impact of dredging empirical studies are still needed. Dredging operations will cause physiological stress and mortality of organisms but the long-term effects of such stress or mortality are hard to predict. It has been shown in many experiments that resistance to burial, survival etc. are species dependent. One can therefore expect changes in the relative abundance of species to occur. As extensively discussed, such changes can also be caused by the natural fluctuations in populations due to e.g. stochastic changes in recruitment or long-term climatological factors. Only when changes due to dredging fall outside the natural variability of the system can some causality be inferred. This requires careful set-up of monitoring programmes.

Monitoring changes in density

Stress may be determined by a change in abundance of a population following a perturbation, abundance being measured as density, the numbers per sampling unit. A good summary of the problems with monitoring changes in abundance of populations has been given by Underwood (1989). Since natural systems are characterized by high variance in space and time, anthropogenic stress is part of a set of perturbations. Detection of whether a particular perturbation has caused a response would be possible if it were already established that the population were at some known equilibrium abundance and that the perturbation caused the abundance to be different from that equilibrium. Even if an equilibrium exists this seems hardly possible in the field. Many natural populations have considerable temporal and spatial variance in abundances so that the detection of stress requires that the observed change in abundance is larger than can normally be expected given the processes that are already stressing the population.

Besides the great conceptual difficulties in defining equilibria discussed above several more down to earth problems exist as well. They have been extensively discussed by Underwood (1989) and may be summarized as sampling problems (frequency, replication etc.) and problems of methodology (before-after contrasts, comparison of perturbed and unperturbed populations, correlations and spatial comparisons).

Sampling

Both the timing and precision of sampling have inherent difficulties. For very long-lived organisms no change will be observed unless there is a large stress or unless the observations are over a period longer than the natural life-expectancy of the individuals. For resilient populations of very short-lived organisms the sampling scheme may miss the important events altogether. If recruitment depends on adult density, as is often the case for benthic species, the destruction of an adult population by a dredging operation may promote the settlement of larvae. Another problem, on which a huge statistical literature exists, is the imprecision of sampling (e.g. Frontier, 1983). Abun-

dances are estimated by some regime of sampling leading to probabilistic estimates of mean and variance. The size of this variance is a function of the intrinsic variability and the number of replicate samples examined. To ensure that the difference between sampling dates are not larger than would be expected from the errors in estimation the procedure of analysis of variance requires that sampling at different times is sufficiently independent.

Independence of sampling is in fact a prerequisite for most statistical procedures and is often violated in benthic research. Sampling on fixed stations, as in permanent quadrats, at successive times may introduce severe bias for several reasons. Random subsampling of (but not too) large areas is the only solution if one wants to apply the classical hypothesis testing statistics (Underwood, 1989).

Comparisons before and after perturbation

A popular procedure in monitoring to detect effects of perturbation is to determine whether the trajectory of mean abundance of a population has altered as a result of perturbation. This comparison may be in time, in space or in both. If it is known when the perturbation will occur, the population can be monitored before and after the event. Detection of change is then based on comparison of the abundances before and after. Detection of stress is inferred from the observation that mean abundance after the perturbation has become larger or smaller than the fluctuations recorded before.

This procedure is seriously flawed unless considerable spatial replication is involved (Underwood, 1989). If monitoring is done at a single site before and after the perturbation there is no method for determining whether any change during the perturbation is associated with the particular perturbation. The population may change in the area due to some climatological factor. No single site can be expected to remain constant indefinitely. To expect that the population would remain near an equilibrium value that existed before the perturbation is an inductive conclusion.

Comparison of perturbed and unperturbed populations

The second procedure for detecting stress is to compare the abundances of a population in an area that has been or is being perturbed with that in a similar area that has not been affected. This is often done in an attempt to determine the effects of potential stress once it has been observed, e.g. after an oil spill. The rationale behind such comparisons is that if the observed perturbation is a stress the abundance of the target population in the perturbed area will subsequently differ from that in an area where no similar perturbation has occurred.

A technical problem that has recently been given much discussion is that of pseudoreplication (Hurlbert, 1984). Comparison of populations at two sites does not reveal why they differ. Even if perturbed and control sites are compared before and after the perturbation (Stewart-Oaten *et al.*, 1986) the problem remains since this assumes that any pattern of difference between the populations evident before the perturbation would have continued unchanged through time if the perturbation has no effect. Since populations in two habitats often have different dynamics this is not the rule.

The only solution to the problem of spatial and temporal variance is to compare the populations in several, replicate perturbed and unperturbed habitats or, at worst, to have several control sites even when there is only one perturbed site. The mean abundance of a population and the changes in that population through time when averaged over a number of sites will be the same from one whole sample (perturbed) to another (unperturbed). Any difference in mean abundance of some species between the perturbed and control sites can then be attributed to the presence of stress in one set of sites. Where only one perturbed site exists, the abundance or change in abundance through time should be compared with the average in a set of control sites. Only if the data from the single perturbed site fall outside the range of the control sites is it possible to argue that the perturbation is causing a change in the population (Underwood, 1989).

Correlations and spatial comparisons

Another procedure that is sometimes used to detect stress is to compare populations in a series of sites that have been perturbed to different extents, e.g. due to gradients in concentrations of toxicants. The pattern of abundance is associated with an increase or decrease in amount of perturbation. This procedure also has flaws since it does not unambiguously demonstrate that the pattern of difference among sites is caused by the perturbation, e.g. salinity in an estuary.

On the usefulness of monitoring

The detection of stress acting on a natural population is most likely for stresses caused by planned perturbations such as dredging. In that case a well designed monitoring programme including perturbed and control sites can

be established. The identification and detection of slow, chronic stresses is much more difficult. Monitoring programmes usually have the aims of determining what changes occur in a population or set of populations and of estimating natural rates of change in response to various forms of perturbation so that responses to particular perturbations can quickly and unambiguously be detected. Monitoring is done to describe changes and to explain changes that are due to perturbation. Populations that have little inertia to a range of perturbations will be difficult to monitor because their abundance will change in response to a variety of perturbations and they will have considerable temporal and spatial variance. Monitoring programmes are most likely to be successful for relatively inert and not very resilient populations (Underwood, 1989).

Knowledge of stability properties is required to plan an effective sampling programme. This requires knowledge on recruitment, longevity and fecundity of populations. The effects of stress will only be predictable and explainable when the natural history of the organisms and their interactions with other organisms are well understood. The latter usually requires field experimentation to investigate perturbations at different magnitudes and rates.

The usefulness of monitoring programmes is therefore primarily the estimation of natural rates of change of populations. If designed properly variability in time or space can be estimated at several scales. This provides information against which to detect the existence of a stress but provides no useful information what may happen once a stress occurs. Monitoring programmes are unlikely to detect many sorts of stresses that are short-term or local except, as in the case of dredging, when a deliberate and planned perturbation is studied.

There is also the problem of determining in advance which species to monitor. In order to evaluate changes in the relative abundance of species due to dredging impact usually benthic species are considered. The choice of benthic species in biomonitoring is generally based on their relatively long life-span, their sedentarity as adults, relative ease of collection and determination. The sedimentary subsystem in shallow waters and the benthos often represents a considerable part of the total energy flow through the system. In the case of dredging, which involves large scale destruction of sediment structure, such a choice seems appropriate, but, as argued before, one should realize that benthic species occurring in estuaries or coastal zones have evolved there and have been subjected to stress due to sediment displacements continuously. Within the benthic assemblage, the choice of abundant or rare species is difficult. The most widespread and abundant species may be those that are well adapted to perturbations because they have great and rapid powers of dispersal and recolonization. The rare species may be difficult to sample and taxonomical problems may exist as well.

Models of relative abundance

To evaluate changes in the absolute or relative abundance of species and to correlate these changes with known impacts has been done using different statistical techniques, both univariate and multivariate. The rationale is that one can describe environments and changes in them by the species that occur and their dynamics. Species are descriptors of environments and most techniques are based on their abundance as the variable of interest. From the abundance or density (abundance per sampling unit) the structure of communities can be described using univariate measures (density, diversity) which can be treated with classical statistics or multivariate methods such as classification based on similarity or distance measures and ordination.

The following is a shortened version of a paper by Heip, Herman & Soetaert (1988) which should be consulted for more detail.

Species-abundance distributions.

If one records the abundances of different species in a community, it is invariably found that many species are rare, whereas a few are abundant. This fundamental feature of ecological communities is independent of the taxonomic group or the area investigated. Species-abundance data are often visualised as plots in which the S species are ranked from 1 (most abundant) to S (least abundant) (ranked abundance plots). Density (often transformed to percentage of the total number of individuals N) is plotted against species rank. Both axes may be on logarithmic scales. It is especially interesting to use a log-scale for the Y-axis, since then the same units on the Y-axis may be used to plot percentages and absolute numbers (there is only a vertical translation of the plot). In so-called k -dominance curves (Lambhead *et al.*, 1983) the cumulative percentage (i.e. the percentage of total abundance made up by the k th-most dominant plus all more dominant species) is plotted against rank k , or log rank k .

The collector's curve addresses a different problem. When one increases the sampling effort, and thus the number of animals N caught, new species will appear in the collection. A collector's curve expresses the number of species as a function of the number of specimens caught. Collector's curves tend to flatten out as more specimens are

caught. However, due to the vague boundaries of ecological communities they often do not reach an asymptotic value : as sampling effort (and area) is increased, so is the number of slightly differing patches.

Two kinds of models have been devised to describe the relative abundances of species. Resource apportioning models make assumptions about the division of some limiting resource among species. From these assumptions a ranked abundance list or a species abundance distribution is derived. The resource apportioning models have mainly historical interest. In fact, observed species abundance patterns cannot be used to validate or discard a particular model, as has been extensively argued by Pielou (1975, 1981). Statistical models make assumptions about the probability distributions of the numbers in the several species within the community, and derive species abundance distributions from these.

The niche preemption model (geometric series ranked abundance list) is a resource apportioning model that was originally proposed by Motomura (1932). It assumes that a species preempts a fraction k of a limiting resource, a second species the same fraction k of the remainder, and so on. If the abundances of the species are proportional to their share of the resource, the ranked abundance list is given by a geometric series :

$$k, k(1-k), \dots, k(1-k)^{(S-2)}, k(1-k)^{(S-1)}$$

where S is the number of species in the community.

The negative exponential distribution (broken stick model) is given by the probability density function :

$$P.D (y) = S e^{-Sy}$$

Stated as such, it is a statistical model, an assumption about the probability distribution of the numbers in each species. However, it can be shown (Webb, 1974) that this probability density function can be derived using the broken stick model (MacArthur, 1957). A limiting resource is compared with a stick, broken in S parts at $S-1$ randomly located points. The length of the parts is taken as representative for the size of the S species subdividing the limiting resource. If the S species are ranked according to size, the expected size of species i , $E(y_i)$, is given by :

$$E(y_i) = 1/S \sum 1/x$$

The negative exponential distribution is not often found in nature. It describes a too even distribution of individuals over species to be a good representation of natural communities. According to Frontier (1985) it is mainly appropriate to describe the right-hand side of the rank frequency curve, i.e. the distribution of the rare species. As these are the most poorly sampled, their frequencies depend more on the random elements of the sampling, than on an intrinsic distribution of the frequencies. Pielou (1975, 1981) showed that a fit of the negative exponential distribution to a field sample does not prove that the mechanism modelled by the broken-stick model governs the species-abundance pattern in the community. Moreover, the broken-stick model is not the only mechanism leading to this distribution. The same prediction of relative abundance can be derived by at least three other models besides the niche partitioning one originally used (Cohen 1968, Webb 1974). The observation of this distribution does indicate (May, 1975) that some major factor is being roughly evenly apportioned among the community's constituent species (in contrast to the lognormal distribution, which suggests the interplay of many independent factors).

The log-series distribution was originally proposed by Fisher *et al.* (1943) to describe species abundance distributions in large moth collections. The expected number of species with r individuals, E_r , is given as :

$$E_r = \alpha (x^r)/r$$

($r = 1,2,3,\dots$). α ($\alpha > 0$) is a parameter independent of the sample size (provided a representative sample is taken), for which X ($0 < X < 1$) is the representative parameter.

The parameter α , being independent of sample size, has the attractive property that it may be used as a diversity statistic. Kempton & Taylor (1974) give a detailed derivation of the log-series distribution. It was fitted to data from a large variety of communities (e.g. Williams, 1964 ; Kempton & Taylor, 1974). It seems, however, to be in general less flexible than the log-normal distribution. In particular, it cannot account for a mode in the species - abundance distribution, a feature often found in a collection. According to the log-series model, there are always more species represented by 1 individual than there are with 2. The truncated log-normal distribution can be fitted to samples with or without a mode in the distribution. Caswell (1976) derived the log-series distribution as the result of a neutral model, i.e. a model in which the species abundances are governed entirely by stochastic immigration, emigration, birth and death processes, and not by competition, predation or other specific biotic interactions. He proposes to use this distribution as a yardstick, with which to measure the occurrence and importance

of interspecific interactions in an actual community. Other models have been proposed to generate the log-series distribution (Boswell & Patil, 1971) but they all contain the essentially neutral element as to the biological interactions.

The log-normal distribution was first suggested by Preston (1948) for the description of species - abundance distributions. It was shown by May (1975) that a log-normal distribution may be expected, when a large number of independent environmental factors act multiplicatively on the abundances of the species (see also Pielou, 1975). When the species-abundance distribution is log-normal, the probability density function of y , the abundance of the species, is given by :

$$P.D (y) = \frac{1}{y \sqrt{2\pi V_z}} \exp \frac{-(\ln y - \mu_z)^2}{2 V_z}$$

The mean and variance of y are :

$$\mu_y = \exp(\mu_z + V_z/2) \quad V_y = (\exp(V_z) - 1) \exp(2\mu_z + V_z)$$

where μ_z and V_z are the mean and variance of $z = \ln(y)$. If the species abundances are lognormally distributed, and if the community is so exhaustively sampled that all the species in the community (denoted S^*) are represented in the sample, the graph of the cumulative number of species on a probit scale against log abundance will be a straight line. This is not normally the case. In a limited sampling a certain number of species $S^* - S$ will be unrepresented in the sample (S being the number of species in the sample). The log-normal distribution is said to be truncated. In the terminology of Preston (1948) certain species are hidden behind a "veil line".

The Mandelbrot model was derived in information science to model rank-frequency curves of messages in complicated systems (e.g. words in a natural language). It describes the frequency of a species with rank r as :

$$f_r = f_0 (r + \beta)^{-\gamma}$$

in which $-\gamma$ is the slope of the asymptote towards which the curve approximates ; is related to the deviation at the left-hand side of the curve. This model is extensively discussed in Frontier (1985), where useful references may be found. The model is particularly useful to describe the rank-frequencies of the dominant species in a community. However, for the rare species large deviations may be found.

Indices of diversity and evenness.

Introduction.

It is common practice among ecologists to complete the description of a community by one or two numbers expressing the diversity or evenness of the community. For this purpose a bewildering diversity of diversity indices have been used or proposed. Two different aspects are generally accepted to contribute to the intuitive concept of diversity of a community. These are (following the terminology of Peet, 1974) species richness, a measure somehow related to the total number of species in the community (note that the actual number of species in the community is usually unmeasurable), and equitability, which expresses how evenly the individuals are distributed among the different species. Some indices, called heterogeneity indices by Peet (1974), incorporate both aspects. It has convincingly been shown by May (1975) that no single diversity index can summarize the species - abundance distribution in a community. However, this is seldom a goal in itself in ecology. Usually, one tries to show how some characteristic feature(s) of the ecosystem may change in relation to environmental variables. Depending on the situation, several indices may give a good idea about these relations. Anyway, it is useful to keep in mind that a complete specification of the species-abundance relationship contains more information than a single index.

Indices derived from species-abundance distributions

Historically, the first diversity measure was derived by Fisher, Corbet and Williams (1943) as a result of the derivation of the log-series distribution. As mentioned earlier, the parameter of the log-series distribution is independent of sample size and describes the way in which the individuals are divided among the species, which is a measure of diversity. The same reasoning can be extended to the log-normal distribution where diversity can be expressed as the (calculated) total number of species in the community.

Rarefaction

An obvious index of species richness is the number of species in the sample. However, it is clear that this measure is highly correlated with sample size, an undesirable property. Sanders (1968) proposed a method to reduce samples

of different sizes to a standard size, so as to make them comparable in terms of the number of species. The formula used by Sanders (1968) was corrected by Hurlbert (1971), who showed that the expected number of species in a sample of size n is given by :

$$E(S) = \sum_{i=1}^S \left(1 - \left(\frac{N-N_i}{N} \right)^n \right)$$

where N_i is the number of individuals in the i -th species in the full sample, which had sample size N and contained S species. Alternatively, random samples can be drawn by computer from the original sample (Simberloff, 1972).

Hill's diversity numbers

Hill (1973) provided a generalized notation that includes, as a special case, two often used heterogeneity indices. Hill defined a set of diversity numbers of different order. The diversity number of order a is defined as :

$$N_a = \left(\sum p_i^a \right)^{1/(1-a)}$$

where p_i is the proportional abundance of species i in the sample.

N_0 can be seen to equal S , the number of species in the sample.

N_1 can be shown to equal

$$N_1 = \lim_{a \rightarrow 1} (N_a) = \exp H'$$

where H' is the well known Shannon-Wiener diversity index :

$$H' = - \sum p_i \log p_i$$

Note that in the usual definition of the Shannon - Wiener diversity index logarithms to the base 2 are used. Diversity then has the peculiar units "bits/ind". The diversity number is expressed in much more natural units. It gives an equivalent number of species, i.e. the number of species S (that yields if all species contain the same number of individuals, and thus if all $1/S$).

An additional advantage of N_1 over H' is that it is approximately normally distributed.

The next diversity number, N_2 , is the reciprocal of Simpson's dominance index, which is given by :

$$SI = \sum p_i^2$$

for large, sampled communities. If one samples at random and without replacement two individuals from the community, Simpson's index expresses the probability that they belong to the same species. Obviously, the less diverse the community is, the higher is this probability. In small, fully censused communities, the correct expression for Simpson's index is :

$$SI = \sum \frac{N_i (N_i - 1)}{N(N-1)}$$

The diversity number of order $+\infty$, N_{∞} , is equal to the reciprocal of the proportional abundance of the commonest species. It is the dominance index. May (1975) showed that it characterizes the species - abundance distribution as good as any, and better than most single diversity indices.

Hill (1973) showed that the diversity numbers of different orders probe different aspects of the community. The number of order $+\infty$ only takes into account the commonest species. At the other extremum, $N_{-\infty}$ is the reciprocal of the proportional abundance of the rarest species, ignoring the more common ones. The numbers N_0 , N_1 and N_2 are in between in this spectrum. N_2 gives more weight to the abundance of common species (and is, thus, less influenced by the addition or deletion of some rare species) than N_1 . This, in turn, gives less weight to the rare species than N_0 , which, in fact, weighs all species equally, independent of their abundance. It is good practice to give diversity numbers of different order when characterising a community. Moreover, these numbers are useful in calculating equitability (see below).

Equitability.

Several equations have been proposed to calculate equitability (evenness) from heterogeneity measures. The most frequently used measures, which converge for large samples (Peet, 1974) are :

$$E = \frac{D - D_{\min}}{D_{\max} - D_{\min}}$$

and

$$E = D/D_{\max}$$

where D is a heterogeneity index, and D_{\min} and D_{\max} are the lowest and highest values of this index for the given species number and the sample size. To this class belongs Pielou's $J = H'/H'_{\max} = H'/\log S$. As discussed by Peet (1974) these measures depend on a correct estimation of S^* , the number of species in the community. It is quasi impossible to estimate this parameter. Substituting S , the number of species in the sample, makes the equitability index highly dependent on sample size. It also becomes very sensitive to the chance inclusion - exclusion of rare species in the sample. Hill (1973) proposed to use ratios of the form :

$$E_{a,b} = N_a/N_b$$

as equitability indices (where N_a and N_b are diversity numbers of order a and b respectively). Note that $H' - H'_{\max} = \ln(N_1/N_0)$ belongs to this class, but that $J' = H'/H'_{\max}$ does not. These ratios are shown to possess superior characteristics, compared with J' . Hill (1973) also showed that in an idealized community, where the hypothesized number of species is infinite and the sampling is perfectly random, $E_{1,0}$ is always dependent on sample size. $E_{2,1}$ stabilizes, with increasing sample size, to a true community value. However, in practice all measures depend on sample size. Heip (1974) proposed to change the index $E_{1,0}$ to $(e^H - 1)/(S - 1)$. In this way the index tends to 0 as the equitability decreases in species-poor communities. Due to a generally observed correlation between equitability and number of species in a sample, $E_{1,0}$ tends to 1 as both $e^H \rightarrow 1$ and $S \rightarrow 1$. In general, one cannot attach too much importance to equitability indices. Species - abundance distributions show more information about the equitability than any single index.

The choice of an index.

Lambshead *et al.* (1983) have noted that, whenever two k -dominance curves do not intersect all diversity indices will yield a higher diversity for the sample represented by the lower curve. Equivocal results arise as soon as the k -dominance curves intersect. Different measures of diversity are more sensitive to either the commonest or the rarest species (see Hill's diversity numbers). An elegant approach to the analysis of this sensitivity is provided by the response curves of Peet (1974). In order to summarize the diversity characteristics of a sampled community, it is advisable to provide the diversity numbers N_0, N_1, N_2 , possibly also N , the dominance index. If permitted by the sampling scheme, one can use these indices in a study of hierarchical and or spatio-temporal components of diversity. Equitability indices should be regarded with caution. Hill's (1973) ratios seem preferable if an index is desired. However, one should rather use species-abundance plots to study equitability. In any case, it should be remembered that the indices depend on sample size, sample strategy (e.g. location of the samples in space and time), spatio-temporal structure of the community, and sampling error.

Classification and Ordination

When dealing with a large number of species or stations the simple application of uni- or bivariate statistical methods not only is cumbersome but may be misleading as well. Multivariate methods have become indispensable tools in ecology since the general availability of large computers made their use practical. They have two basic roles : to discover structure in the data and to summarize the data objectively. In contrast with classical statistics, which are concerned with hypotheses testing, ordination tries to elicit some internal structure from which hypotheses can be generated (Williams & Gillard, 1971).

Classification or clustering aims at grouping objects that are sufficiently similar and the usual product of the operation is a graph called a dendrogram. Similarity (or distance) may be measured by many different methods and the classification procedure also requires some choice on sorting strategy. In benthic ecology very often a procedure called group-sorting average based on the Bray-Curtis similarity index is used (Heip *et al.*, 1988)

Ordination is simply an operation by which objects are placed along axes that correspond to relationships of order, or on graphs formed by two or more of these axes. The relationships may be metric or not. Ordination tries to reduce the number of dimensions in which the dispersion of stations or species is represented so that the great tendencies of variability in the sample for the ensemble of all descriptors are distinguished. The dispersion of stations is first represented in a multidimensional graph with as many axes as species. One then looks at the projections in planes of this multi-dimensional graphs which are of most interest. These planes are defined by new axes that permit to represent the variability in the data in an optimal way in a space with reduced dimensions. The end product of an ordination is therefore a graph, usually two-dimensional, in which similar species or samples (or both) are near each other and dissimilar ones are far apart.

The most powerful of ordination techniques is Principal Component Analysis (PCA). PCA starts with an association matrix A of similarities between stations based on correlation coefficients or covariances/variances and can only validly be used on cross-product similarity coefficients. Relationships between stations may be more validly expressed by distance measurements as is done in principal coordinate analysis (Gower, 1966) which permits the analysis of every association matrix Q based on a metric distance coefficient.

If an environmental gradient exists there often is a non-linearity between similarity measures and the between-station distance along the underlying gradient. This phenomenon is at the basis of most of the unsatisfactory features of PCA. Ordination based on ranking of similarity seems attractive and has been developed by Kruskal (1964) in a technique called nonmetric multidimensional scaling.

Two other popular techniques are Reciprocal Averaging and Detrended Correspondance Analysis. Reciprocal Averaging (Hill, 1974) is a form of PCA in which the species ordination scores are averages of the station ordination scores and vice versa. The modified version of reciprocal averaging, detrended correspondance analysis (DCA) (Hill, 1979a) is now one of the most widely used ordination methods in benthic ecology.

The mathematical methods used imply particular models concerning the shape of species response curves. PCA specifically assumes a linear model of relationships measured in terms of covariance or correlation coefficients. If the species response curves are bell-shaped the linear model is inapplicable and a one-dimensional gradient becomes distorted into a horse-shoe. The newer techniques of detrended correspondance analysis and multidimensional scaling are more robust. RA and DCA are currently the most popular ordination methods but have been criticized. In RA the ecological model is unclear and mathematically a polynomial relationship exists between higher dimensions (axes) and the first. When there are more than one major ecological axis the spurious polynomial axes interact with the ecological axes. In DCA the expected arch is removed by detrending but the adjustment makes no allowance for interaction between a two- or threedimensional set of gradients and the mathematical distortion.

Twinspan is a method which consists of carrying out a one-dimensional Reciprocal Averaging ordination and breaking the axis at the centroid so as to divide the data points into two classes. Each of the two classes is then itself split in the same way, after a RA ordination, etc. (Hill, 1979b).

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