

CHAPTER 5

Effects on Community and Ecosystem Structure and Dynamics

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Communities are assemblages of populations structured by biotic interactions and the constraints of their physical and chemical environment. The structure of an ecosystem is defined by the abundance and biomass of all populations and their spatial, taxonomic and trophic organization. The integrated response of the component populations to the presence of toxic pollutants will be reflected in alterations of the structural and dynamic characteristics of the stressed community. It appears that the changes in structural characteristics induced by

toxic pollutants may be similar to those caused by natural forms of stress (Gamble *et al.*, 1977).

Ideally, predictions of structural changes should be based on an understanding of the important biological interactions which cause the restructuring; however, ecological theory has not yet been developed to this point. Moreover, Gray *et al.* (1980) emphasized that populations and their environments co-evolve and, within certain limits, resident communities are the products of the history of their environment. As a result, it is difficult to describe a 'typical' ecosystem on which to base a general theory to interpret interactions. Therefore, the approach to assessment of integrated response to pollutants has been the 'after-the-fact' observation of qualitative and quantitative changes in community structure. Cairns *et al.* (1972) suggested that structural changes may be visualized as an information network reflecting environmental conditions but not demonstrating the external mechanisms or internal interactions which brought about the reorganization.

Marine ecologists have argued that structural indices best meet statistical criteria for the monitoring of community response to toxic substances (Heip, 1980; Gray *et al.*, 1980). These indices do not have the daily periodicity of primary productivity or the short-term variability associated with respiration. Community structure, however, is loosely related to ecosystem function, although aspects of structure (e.g. diversity and dominance patterns) may change significantly under stress with no accompanying disruptions of function (e.g. productivity), or inversely, function may be altered without significant changes in composition and diversity (Matthews *et al.* 1982). The lack of a predictable relationship between structural and functional responses to stress suggests the need for a balanced approach in assessing pollution effects at the ecosystem level.

This chapter focuses on structural responses to toxic pollutants. Figure 5.1 depicts a conceptual scheme, fitting the analysis of changes in community structure into the larger framework of integrated ecotoxicological assessment. The importance of developing a greater understanding of the ecological interactions which determine community organization is highlighted. Listed under the heading of 'community structure and dynamics' are several indices which are useful in assessing pollution effects. Although these indices define a fixed structure, no community is static. Stability and succession as influenced by varying community organization, are susceptible to disruption through pollution-induced changes in that organization, and must be considered in assessing long-term effects.

It is the induced changes in structural properties which are of primary interest in pollution assessment, rather than the specific structure of the community itself although, obviously, this is ecologically important as well. To assess change, an appropriate set of structural references is essential. Baseline data on a community prior to pollution exposure can provide an ideal control for comparisons, however, this situation is seldom realized. A time series of changes

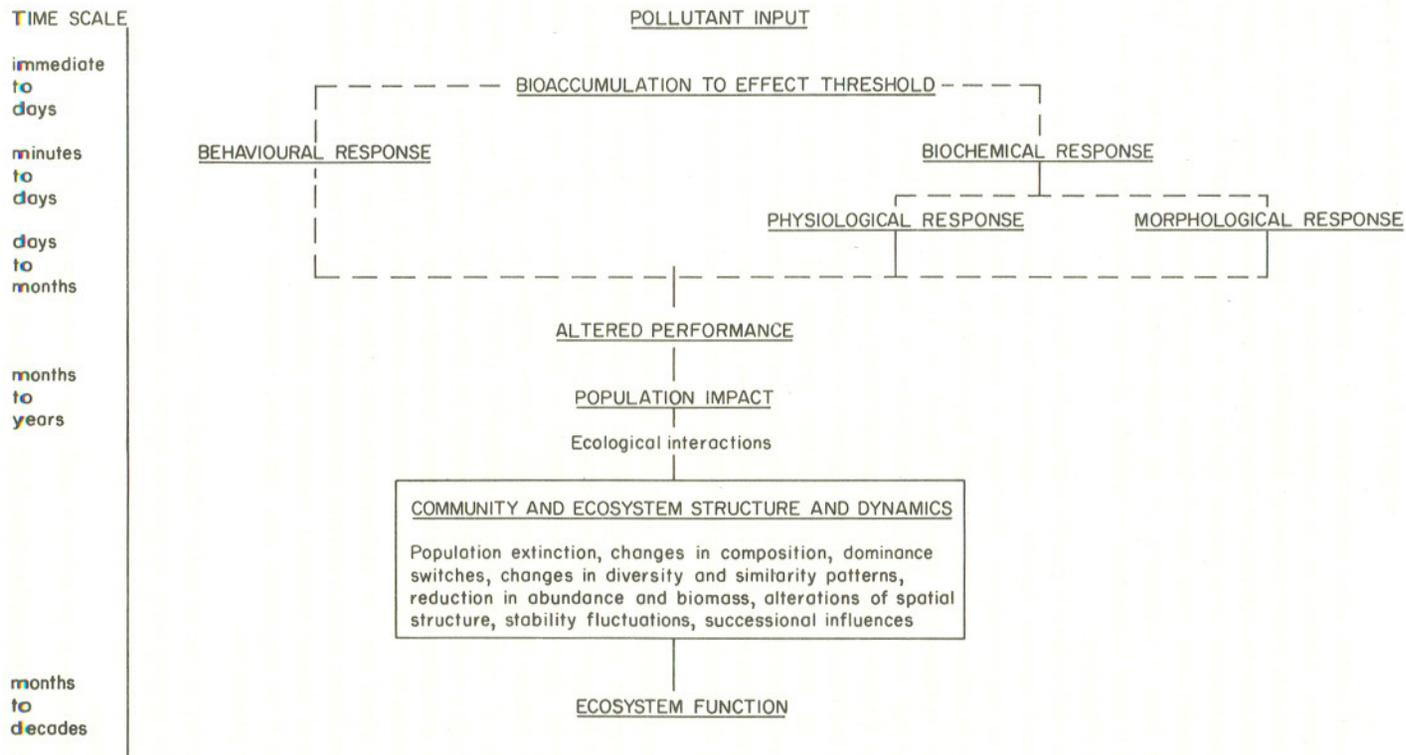


Figure 5.1 A conceptual chronology of induced effects following exposure to toxic pollutants, emphasizing changes in community and ecosystem structure and dynamics

in structural indices after introduction of a pollutant would reflect trends in reorganization. Reductions in numbers, biomass and taxonomic and trophic diversity indicate a disruption in homeostasis. Conversely, increases in these indices with time would infer at least partial recovery of the system. If baseline data are unavailable (as is frequently the case), changes can still be monitored in the community over time but obviously no set of values would be available on which to base a definition of an undisturbed community structure. This approach is used frequently to monitor changes occurring in conjunction with pollution abatement.

In cases where there is insufficient baseline data, structural characteristics can be compared among similar communities to provide a measure of relative response to perturbations. However, it must be realized that the immense variability in natural systems makes it impossible to find duplicate communities. Thus any comparison must be based on a limited number of critical environmental conditions and similarities in the composition of available colonizers. Choice of an appropriate reference community is simplified in cases where the pollutant input is from a point source and sampling sites can be defined in terms of decreasing concentration gradient of pollutant at distances progressively further from the source. The location of the reference community is thus designated as upstream or upwind of the pollution source, or is defined by a site along the gradient at which pollutant concentrations approach background levels.

Structural characteristics and the numerical indices dependent on them provide various types of information which differ in ecological value. For instance, it is more informative to know the taxonomic or trophic composition of a community than merely its biomass or the abundance of organisms. Also, structural indices do not necessarily follow similar patterns of change under conditions of induced stress. Hellawell (1977) described several possible alterations in a community which would be reflected only in biomass, in biomass and relative dominance or in biomass, dominance and composition. Because of the differences in (1) the value of information provided by these indices, (2) the ease with which they are measured or calculated and (3) the sensitivity of their response to stress, certain criteria are essential in order to evaluate the usefulness of structural characteristics in monitoring pollutant effects.

Cook (1976) suggested that the ideal community index would have the following properties:

1. Sensitivity to the stressful effects of pollution on the ecosystem.
2. General applicability to various types of ecosystems.
3. Capability to provide a continuous assessment from unpolluted to polluted conditions.
4. Independence of sample size and ease of measurement or calculation.

Two additional properties should be included in the list:

5. The ability to distinguish the cyclical and natural variability of the system.
6. The index should be ecologically meaningful.

The first four criteria, and the sixth, are rather straight-forward, but the fifth requires additional comment. The overall value of using observed changes in structural characteristics to assess pollutant damage is dependent upon distinguishing natural changes (cyclical, successional, stochastic) from those induced by the pollutant (Hellowell, 1977; Cushing, 1979; Heip, 1980). Miller examines this problem (Chapter 3) in terms of statistical criteria. This task requires careful evaluation, particularly in those very important cases where subtle changes may be induced by chronic low level exposure to toxic pollutants. In order to be of utility, an index must meet criteria of minimal variability in time and space. Since most ecosystems are heterogeneous in both time and space, structural characteristics which can be statistically defined by means of a practical number, frequency, and distribution of samplings, must be chosen. When a large part of its variance is found to be associated frequently with time and/or space, a characteristic must be judged as unfit for the monitoring of pollution effects (Gray *et al.*, 1980).

A recent review by Herricks and Cairns (1982) examined aspects of methodology to assess structural changes in aquatic systems but there is no comparable review for hazard assessment in terrestrial systems. In this chapter the effects of toxic pollution on various indices of community structure will be surveyed, with particular emphasis on the utility and sensitivity of each index in stress assessment.

5.1 ABUNDANCE AND BIOMASS

Abundance and biomass are the most simple indices of community structure. Because of their simplicity, these measures do not provide much information on the general ecological character of the system and, therefore, they are often reported only in conjunction with more informative biological data. Both of these characteristics have been shown to vary seasonally in marine benthic communities (Buchanan *et al.*, 1978). In the same study, biomass was not correlated with habitat type (as defined by sediment composition) whereas taxonomic indices did exhibit such correlation. Seasonal fluctuations in abundance would be expected in those communities dominated by species with large numbers of recruits. There is also a great deal of variability inherent in the estimation of abundance. Edwards *et al.* (1975) reported that a minimum of 10 samples were needed to estimate the total number of invertebrates to within ± 40 per cent, with 95 per cent confidence limits (see Chapter 3)

The choice of numerical density or biomass as an appropriate structural characteristic imparts a certain bias to the researcher's approach. Reporting numbers exaggerates the importance of small abundant species while reporting biomass emphasizes those larger organisms usually present in smaller numbers.

This bias becomes less apparent as the size distribution of the community is narrowed. Such a situation is approximated in the freshwater planktonic community, although there are still size differences between bacteria and the larger zooplankton species.

A reduction in abundance and biomass is generally associated with toxic pollutants although in those cases where organic enrichment accompanies toxic substances both abundance and biomass can be increased. Pearson (1975) observed the latter effect in benthic fauna, associated with their exposure to pulp mill effluents. The number of species was reduced in comparison to pre-pollution levels, however biomass rapidly increased to three times 'normal' and then precipitously declined with depression of dissolved oxygen levels.

The response of aquatic fauna to acidification has been shown to vary with community type. This situation is demonstrated in Figure 5.2 (Crisman *et al.*, 1980) where only the abundance of zooplankton is clearly correlated with lake pH, and the number of benthic invertebrates appears to be totally unrelated to acidification. In contrast, Leivestad *et al.* (1976) found that both biomass and density of benthic invertebrates were reduced in acidified Norwegian lakes. Biomass values showed a greater decline with decreasing pH than did abundance, due to the loss of large predators. Others have reported the

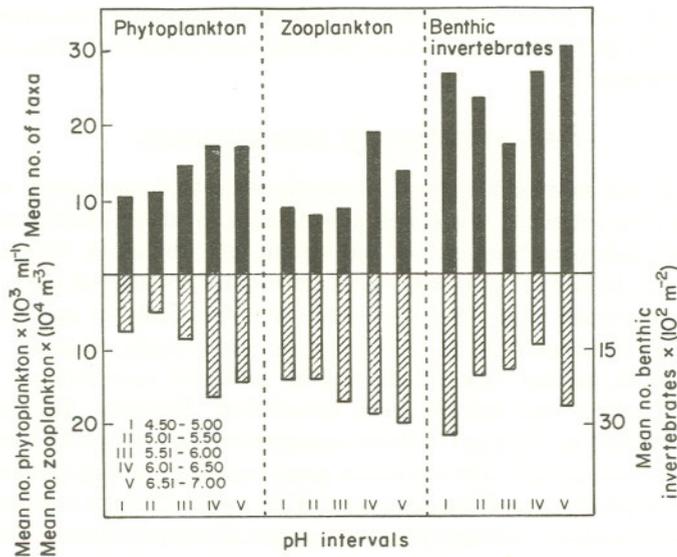


Figure 5.2 Mean annual number of taxa and abundance for phytoplankton, zooplankton and benthic invertebrates from twenty Florida lakes grouped by pH range. (From Crisman *et al.*, 1980. Reproduced by permission of SNSF Project, Box 61, 1432 As-NLH, Norway)

abundance of zooplankton and fish reduced in acidified lakes, but the biomass of periphyton increased (Hendrey *et al.*, 1976). Yan (1979) found that phytoplankton biomass was better correlated with phosphorus concentration than with pH levels in an acid and heavy-metal contaminated lake.

Winner *et al.* (1975) determined that the abundance of benthic macroinvertebrates in a contaminated stream was inversely related to increasing copper concentrations, although the correlation was not as strong for the numbers of individuals as it was for the numbers of species (Figure 5.3). The variation in abundance was high, making it impossible to determine a graded difference in response between the levels of 38 and 120 $\mu\text{g l}^{-1}$ Cu. Reductions in phytoplankton biomass were noted in microcosms after the addition of copper at 50 $\mu\text{g l}^{-1}$; but when exposed to less than 10 $\mu\text{g l}^{-1}$ Cu, algal standing crop increased slightly (Thomas *et al.*, 1977). In a terrestrial ecosystem, mean plant biomass and total number of species present were found to increase with distance

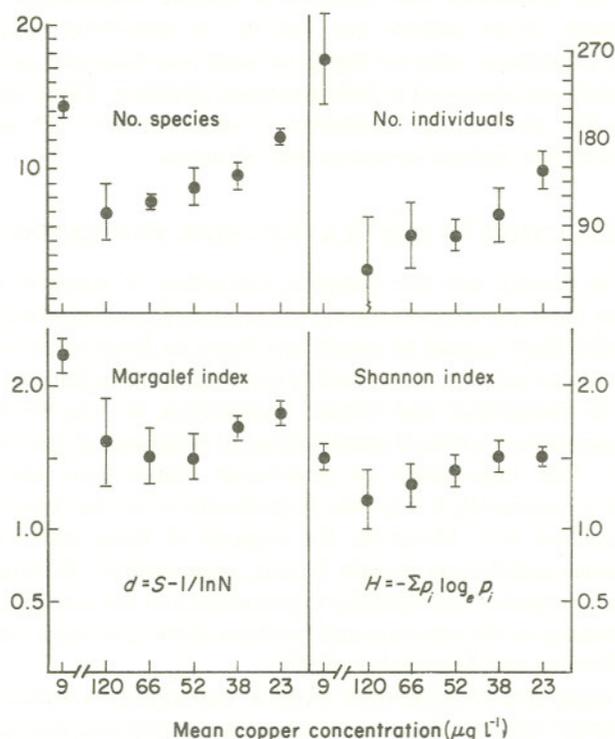


Figure 5.3 Relative changes in four indices of macroinvertebrate community structure at six locations along a copper concentration gradient (from Winner *et al.*, 1975. Reproduced by permission of E. Schweizerbart's che, Verlagsbuchhandlung, Stuttgart)

from a copper smelter but the per cent cover was not correlated with the metal stress (Dawson and Nash, 1980). This situation appears to be explained by the fact that shrubs dominated the vegetation on the sites nearest the smelter. Strojjan (1978b) reported that the average numbers of arthropods in soil cores were inversely related to levels of Zn, Pb, Cd and Cu.

Agricultural insecticides, as expected, reduce the abundance and biomass of arthropods and, consequently, can indirectly contribute to increased plant biomass (Shure, 1971).

Oil spills have been reported to depress the biomass of benthic fauna (Jacobs, 1980), intertidal invertebrates (Thomas, 1978), and zooplankton (Johansson *et al.*, 1980; Lindén *et al.*, 1979). However the biomass of phytoplankton may be increased in response to reduced grazing pressure (Nounou, 1980). Oils decrease the per cent cover and number of colonies in coral reef communities (Loya, 1975).

Although the abundance and biomass of specific communities respond to pollutant stress, these indices are lacking in sensitivity and ecological information; in addition, they are highly variable over time and space. The ease with which they are measured is their strongest attribute. These simple indices certainly do not provide, by themselves, a sufficient basis for assessing the severity of pollutant impact on community structure.

5.2 REDUCTION IN POPULATION SIZE AND EXTINCTION

Reductions in density and the complete extinction of sensitive populations resulting from the stress of pollution are the primary factors altering community structure. Such effects cannot be totally attributed to direct toxic mortality, but may be due also to induced reductions in the abilities of organisms to function successfully in competitive and trophic interactions, or may be the result of increased emigration or reduced immigration, in avoidance of the contaminated environment. The importance of population interactions and avoidance behaviour in a community's response to pollutant stress has been emphasized previously (section 4.4). However, the impacts of these indirect effects on localized species extinctions remain largely unquantified. Ecological factors which influence a species' susceptibility to extinction and the consequent effects of selective extinction on the structure and function of the ecosystem were discussed recently by Fowler and MacMahon (1982).

With the exception of some toxic organic contaminants which provide an important energy resource for certain invertebrates and microbes and actually stimulate population growth (see microbial response to oil: Johansson *et al.*, 1980), most toxic pollutants act to reduce the numbers of individuals in tolerant populations as well as the number of species in the community. Concurrent losses in the numbers of individuals and species in an exposed ecosystem are shown in Figure 5.3 (Winner *et al.*, 1975), where both indicators are inversely correlated

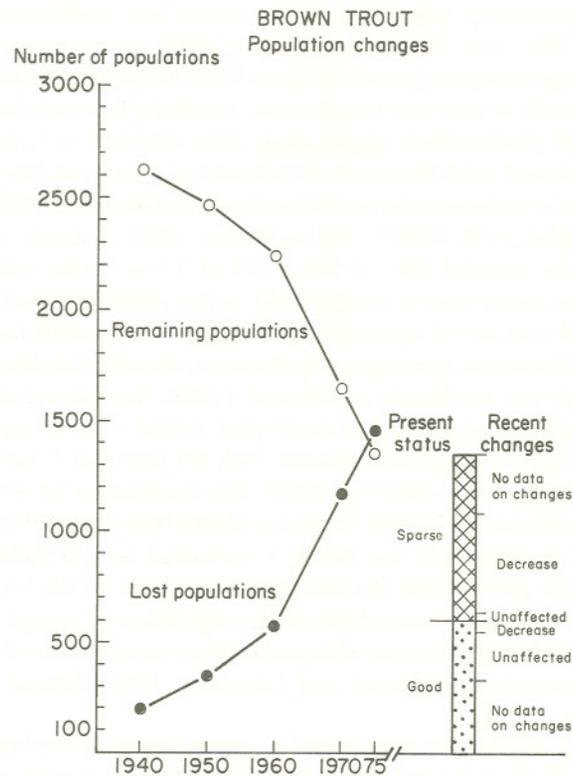


Figure 5.4 Time trend for population losses of brown trout in lakes exposed to acid precipitation in the four southernmost counties in Norway. (From Muniz and Leivestad, 1980. Reproduced by permission of SNSF Project, Box 61, 1432 As-NLH, Norway)

with copper concentrations. It is suggested that the reduced density of stressed populations can accelerate species extinction. Small, severely stressed populations are highly vulnerable to natural forms of biotic stress and environmental fluctuations and, as a result, have a high probability of premature extinction.

One of the better documented time trends in species elimination has been recorded for fish during a period of industrially stimulated acidification of poorly buffered lakes. Data developed from surveys of fisherman and lake owners (Figure 5.4) depicts a decline of nearly 50 per cent in the number of brown trout (*Salmo trutta*) populations in acidified Norwegian lakes during the past forty years. The loss was most exaggerated in lakes with pH < 5.1 (Wright and Snekvik, 1978; Muniz and Leivestad, 1980). Although the use of this type of survey data to

establish a relationship between fisheries status and acidification has been questioned (EPRI, 1979; Brown and Sadler, 1981), there appears to be little doubt that a large number of poorly buffered lakes in southern Scandinavia have lost most, if not all, of their fish populations. Declining fish populations in lakes exposed to acid precipitation inputs have been reported in Canada and the United States as well, and decreased recruitment of young fish has been cited as the primary factor leading to the gradual extinctions (Beamish, 1974; Beamish *et al.*, 1975; Schofield, 1976; NRCC, 1981a; Haines, 1981). A survey of 150 lakes in Ontario, Canada revealed that 70 had a pH of 5.5 or lower, with acid levels having increased more than a hundredfold in the 1960s. Beamish and Harvey (1972) reported that six of seven fish species had disappeared from Lumsden Lake by 1971. The loss of sports fish populations from other acidified lakes in the Sudbury district was confirmed by Beamish (1974). Further reductions in fish species have occurred in this region in the past decade (Harvey and Lee, 1980). More than 100 lakes in the Sudbury area, with pH less than 5, have lost all fish populations (OME, 1979; Harvey, 1980). Documentation of acidification in waters of the northeastern United States has shown that almost 50 per cent of the lakes surveyed, in which pH was below 5, contained no fish (Schofield, 1976).

The loss of fish populations has had profound effects on the lake ecosystems since these top consumers contribute to the regulation of energy and nutrient turnover, and to the maintenance of the community composition of zooplankton and benthic invertebrates (Muniz and Leivestad, 1980; Økland and Økland, 1980; Raddum, 1980).

Although the uniqueness in role and in sensitivity of individual species has been stressed (Resh and Unzicker, 1975), difficulties in species identification, particularly of the larval stages, has led to the use of higher taxonomic categories in pollution assessment. Unfortunately, a comparison of data from different levels suggests that only species and generic numbers provide sufficient sensitivity to monitor changes in pollutant stress. Furthermore, even though these two taxonomic levels follow similar trends (see Hellowell, 1977), there is a significant loss of information when identification is made only to the generic level.

5.2.1. Loss of Species with Unique Functions

Although it is very difficult to evaluate the loss of any one species, it is easier to appreciate the disappearance of those that fulfill unique roles within the community. These can be species that perform unique individual actions (e.g. pollination) or 'key' species which have an important role in controlling ecosystem function and stability (Lewis, 1978).

A reduction in natural pollinator populations through pesticide application can affect fertilization and seed set in natural plant communities. The accidental killing of bees resulting from the use of insecticides has been a problem in the United States for nearly a century. Johansen (1977) concluded that the long-term

loss in yield of insect-pollinated crops was greatest when a crop was dependent upon natural pollinator populations which require several years to recover from severe kills. The reduction in native bee populations following aerial application of fenitrothion in New Brunswick forests has caused a decline in production of wild blueberries (Kevan, 1975; NRCC, 1981b). Plowright and Rodd (1980) reported a significant correlation between seeds per flower in *Clintonia borealis* stands and bee counts, with the mean fecundity of *Clintonia* significantly reduced in fenitrothion-sprayed stands.

In reviewing the problems of long-term ecological surveillance of the rocky intertidal community, Lewis (1976) emphasized the important ecological interactions of the 'key organisms (large algae/barnacles/limpets/mussels/starfish) in controlling community balance and regulating the later stages of succession following disturbance. The sequence of intertidal floral and faunal recovery from the impact of an oil spill illustrated that recruitment of key organisms was an important factor in the reestablishment of biological interactions essential to the regulation of the structure of intertidal communities (Southward and Southward, 1978).

Since pollution studies are rarely exhaustive enough to consider species loss in all taxonomic and functional categories of biota, factors such as personal preference, economics, ease of classification, type of habitat and pollutant dispersal can bias the choice of the community selected for research. There has been a disproportionate effort toward reporting the loss of large, easily classifiable organisms which sometimes may not play a critical role in efficient ecosystem functioning. In aquatic ecosystems, benthic macroinvertebrates, plankton and fish communities have received the greatest attention, while mammals, birds, insects, forests, and agricultural plant species have been the focus of most terrestrial studies. Exceptions to the above generalization concerning both size and functional importance are the detailed reports on phytoplankton and, in particular, diatom community structure (Patrick, 1949, 1968; Patrick *et al.* 1968). Diatoms constitute a major portion of the producer community in many aquatic systems and, thus, perturbation of their community structure could affect primary productivity. Unfortunately, there have been few studies examining the structure of soil and sediment invertebrate and microbial communities associated with the important processes of decomposition and nutrient cycling.

5.2.2 Species Richness

Decreases in the number of species (species richness) in an ecosystem is a useful measure of the severity of pollutant stress. Species richness is quantifiable for all identifiable organisms although the observed values are dependent on the number and size of the samples taken and various life history factors (see Edwards *et al.*, 1975; Rosenberg, 1977; Buchanan *et al.*, 1978). This measure is

sensitive to pollutant concentration, and has obvious significance in relation to the structural integrity of the ecosystem. However, the severity of the impact of population extinctions on ecosystem dynamics is less well defined and will depend on, among other factors, any redundancy in functional roles which might compensate for those losses of individual species.

Many reports have documented significant decreases in species richness in response to long- and short-term exposure to toxic pollutants. Decreases in the numbers of zooplankton, phytoplankton and fish species in acid-rain-polluted lakes have been found to be inversely related to pH of the water (Leivestad *et al.*, 1976; Crisman *et al.*, 1980; Harvey, 1980, respectively). Fewer than four species of fish and zooplankton, and ten species of phytoplankton, were observed at pH < 5 in comparison to nearly double this number at pH 6.5. Jacob (1980) reported a dramatic reduction in the numbers of invertebrate species in an eel grass community shortly after the *Amoco Cadiz* oil spill (Figure 5.5). Although the indices in this study were not correlated with the concentrations of oil or of any particular aromatic fractions, measurements were taken throughout a two-year time span encompassing the spill, and thus presented a relative measure of

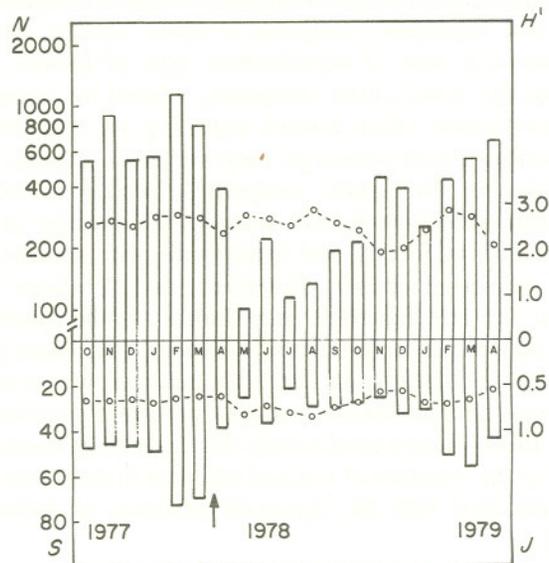


Figure 5.5 Characteristics of the fauna of an eel grass community at Roscoff, October 1977 to April 1979. Total numbers per 400 cm² of individuals (N) and species (S); calculated diversity index (H') and evenness (J) given as broken lines. Arrow: moment of oil arrival at Roscoff. (From Jacobs, 1980. Reproduced by permission of Inter-Research, Box 1121, Halstenbek, West Germany)

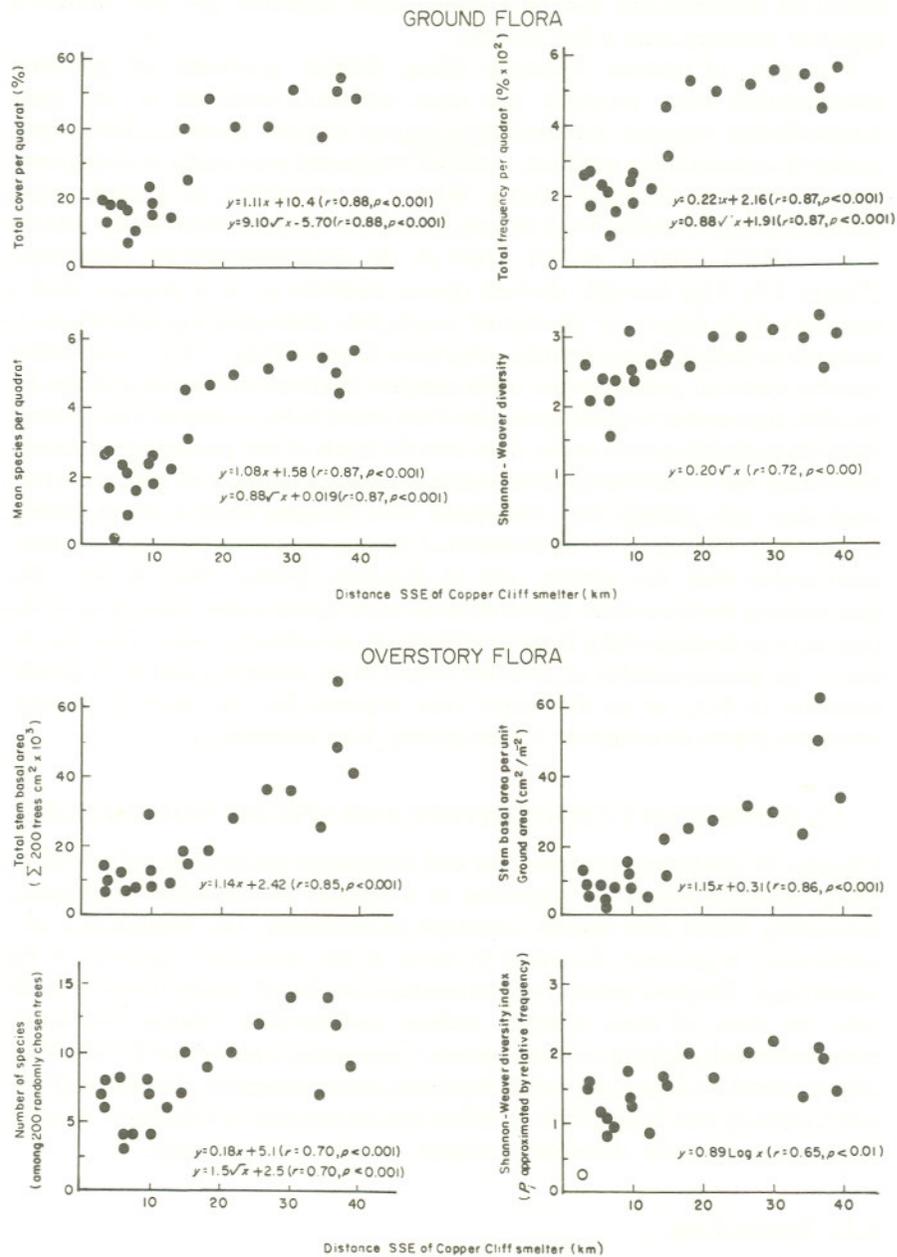


Figure 5.6 Vegetation parameters versus distance from Copper Cliff smelter. (Reproduced by permission from Freedman and Hutchinson, 1980a)

structural simplification due to a single, acute exposure and also indicated apparent recovery after a few months.

Examples of species response along defined gradients of pollutant concentration have provided the most definitive evidence of the basic concentration–response relationship in natural systems. Species richness data, gathered at sites along a gradient, could be interpreted most easily as a long-term natural bioassay (Sheehan, 1980). Winner *et al.* (1975), in a study using controlled copper addition to a stream, found that the number of species was the most sensitive measure of this stress on the macroinvertebrate community (Figure 5.3). This example showed species numbers to be a measure with a relatively high degree of ‘structural’ resolution, distinguishing differences in response to pollutant concentrations between 37 and 120 $\mu\text{g l}^{-1}$ Cu. In terrestrial systems where air pollutants are often complex mixtures and concentrations are variable, the number of plant species has been found to be correlated with distance from the pollution source rather than with the levels of any particular substance. Freedman and Hutchinson (1980a) reported species richness of both overstorey vegetation and ground flora correlated with distance from a metal smelter (Figure 5.6). Variability in the numbers of plant species per quadrat was most accentuated near the smelter and at distances greater than 30 km. The groundstorey measurements appeared to be more conservative than those of the overstorey in distinguishing between disturbed and reference sites. This may be due to the greater number of sensitive species in the overstorey and to its greater exposure to SO_2 , or to the longer time required for the recovery of large overstorey plants as compared to the ground flora community.

5.3 COMMUNITY COMPOSITION AND SPECIES DOMINANCE

Changes in community composition and dominance patterns as influenced by pollutant stress reflect the responses of a number of individual populations interacting within their specific tolerance requirements. The composition of a community is generally described in terms of the taxonomic make-up of the assemblage. The description could be as simple as a list of species found or could take the form of more complex indices incorporating relative abundance measures or subjective importance values. Community composition has also been characterized by functional rather than taxonomic categories. Cummins (1974) and Cummins and Klug (1979) classified stream macroinvertebrates in terms of feeding strategies, i.e. shredders, scrapers, piercers and predators.

5.3.1 Species Lists

Nearly all early biological studies of pollution effects consisted of partial lists of taxa present at different sampling stations. Much of the early information was compiled from freshwater ecosystems receiving organic sewage rather than

generally more toxic chemical substances (Forbes and Richardson, 1913, 1919). These studies indicated that downstream from sewage input qualitative zones of pollution were defined by the differences among species assemblages. The species list approach is still commonly used in environmental impact assessment.

Two other qualitative indices have been developed as offshoots of the species list concept:

1. The species list–relative abundance (common-rare) measure.
2. The use of species or taxonomic groups as ecological indicators.

The addition of relative abundance information to the species list does provide a qualitative measure of importance, in addition to the presence–absence data. However, this combination does not provide an index which is comparable among similar ecosystems and has thus received limited attention.

5.3.2 Indicator Species

The relative susceptibility of individual species to toxic pollutants forms the basis for the indicator species concept. The term ‘tolerant’, with reference to species, is applied to those populations found in the contaminated ecosystem. Conversely, ‘sensitive’ species are those either not found in the contaminated area or found to occur only in low abundance as compared to their normal density in the system prior to pollutant introduction, or their abundance in similar but unpolluted systems. The use of these terms in reporting field data, although often inferring that sensitive species are eliminated due to direct toxic mortality, does not provide substantiation of cause as would a more closely monitored laboratory toxic bioassay.

In its pure form the indicator concept states that the continued presence of a certain species is an indication of the existence of a unique set of acceptable environmental conditions, whereas its absence would indicate the lack of appropriate environmental conditions. There is one obvious problem with the uncritical application of this concept: absence of a species does not necessarily infer an unsuitable environmental condition, but may instead imply a lack of distributional opportunity, seasonal absence due to life stages unsampled or absence due to biotic interactions. Thus, application of the indicator organism concept requires knowledge of not only the ecological tolerance or the nature of adaptation of the species to the toxic compound, but, also, its life history strategy (Gaufin and Gaufin, 1966). For indicator species to be of use, they must be able to detect the subtle as well as the gross effects of pollution. Hellawell (1978) has discussed the advantages and disadvantages of various taxa as indicators of water pollution. Often, it is not a single species but an assemblage which must be described when monitoring effects. It is probable that the satisfactory use of the indicator concept requires information on the species absent as well as those present in a stressed community.

Much of the development of the indicator organism concept has been based on organic domestic waste pollution studies (e.g. Gaufin and Tarzwell, 1952; Gaufin, 1958; Turoboyski, 1973) rather than studies with toxic chemicals. It must be emphasized that the effects of organic waste will be very different from those of toxic materials. Components of sewage generally have a stimulatory effect on certain species by increasing food supplies while at the same time reducing competition and predation pressures. Toxic chemicals, on the other hand, generally have adverse, species-specific effects on all members of the contaminated community.

In terrestrial ecosystems, sensitive epiphytic lichens have been used extensively as indicators of SO₂ pollution. Hawksworth and Rose (1970) and Skye (1979) reported qualitative scales to define sulphur dioxide stress, dependent upon the presence, diversity and relative cover of lichen species. Case (1980) used reduced distributions of epiphytic lichens to document SO₂ emissions from 'sour gas' processing plants. His Index of Atmospheric Purity, based on the cover and vitality of nine indicator species, was better correlated with distance from the SO₂ source than was the total diversity of the lichen community. Sundström and Hålgren (1973) proposed using lichens as physiological indicators of sulphurous pollutants by measuring the effects of polluted air on photosynthetic rate, respiration or nitrogen fixation in lichen species. Changes in the rate of lichen growth have also been used to monitor SO₂ stress (Lulman *et al.*, 1980). Sigal and Nash (1980) found lichens to be effective bioindicators of other forms of air pollution such as photochemical oxidants.

Various plant taxa have been used as indicators of other specific types of pollutant stress. Certain terrestrial plants are associated with the presence of high concentrations of heavy metal. Antonovics *et al.* (1971) presented an extensive list of species associated with particular metals in different localities. Patrick (1954) described the use of diatoms as indicators of organic contamination in rivers.

Numerous faunal species have also come under consideration. Domestic animals have been studied as indicators of environmental quality (Buck, 1979). Bayne (1978) and Krieger *et al.* (1981) strongly advocated the coupling of chemical monitoring with the assessment of biological response using marine mussels. Wiederholm (1980) proposed the use of a benthic quality index based on certain species of chironomids. The use of fish species in water quality monitoring was described by Price (1978, 1979). Phillips (1977, 1980) reviewed the use of indicator organisms to monitor trace metal pollution in aquatic systems and suggested that not only species presence, but the concentration of metals within the tissue of certain species, represented a moving time-averaged value of the relative biological availability of metals at each evaluation site. However, there appears to be relatively high natural variability along with seasonality in the element concentrations in bivalves (Boyden and Phillips, 1981).

5.3.3 Biological Indices

The stream zone index is a slight variation of the indicator species technique which describes the stream in zones, from organically polluted to clean (or recovered), in terms of organism groups (Brinley, 1942; Bartsch, 1948; Patrick, 1949; Fjerdingstad, 1964). A similar type of classification has been developed for plants on metal-contaminated soils by Lambinon and Auquier (as described in Antonovics *et al.*, 1971).

The qualitative nature of the indicator organism concept has prompted a number of researchers to suggest numerical rating of species or species groups to provide semi-quantitative indices. Several biological indices for aquatic pollution are listed in Table 5.1. The effectiveness of these indices has been evaluated most recently by Hellowell (1977) and by Persoone and De Pauw (1979). Most of these measures are restricted to the assessment of effects due to municipal sewage or organic wastes of similar composition, therefore their utility in assessing the impact of toxic chemicals remains largely undemonstrated. Armitage (1980) has reported that a combination of organic enrichment and mine drainage with elevated zinc levels (7.6 mg l^{-1}) lowered the biotic score (Chandler, 1970) to values below 1800, in comparison to scores of 2500–3500 at unpolluted sites. Solbé (1979) reported that the biotic scores for macro-invertebrates in a zinc-polluted stream were extremely low (approximately 500).

In attempting to establish what combination of species typifies a particular community, as defined by a specific set of environmental conditions, it has been observed that common species (those which appear often in collections) generally tend to be successful over a wide range of environmental conditions. In contrast, species with narrow response ranges for specific environmental variables are rarely found in samples from contaminated systems. These factors have led ecologists to question the value of searching for indicator species or assemblages to effectively describe the impacts of pollutant stress.

5.3.4 Dominance Patterns

The concept of dominance is an integral part of defining community composition. A species is considered to be dominant if it is present in the greatest abundance. However, the dominant species may also be the one with the largest individuals, the one which covers the greatest amount of space, or the one which has the greatest impact on community dynamics. Dominance implies a position of advantage in community interactions. It does not, however, necessarily correlate directly with tolerance to pollutant stress. The dominant species must be able to perform all essential functions (growth, development, reproduction) efficiently at the existing pollutant concentration, but need not be the most resistant member of the community. Abundance under pollutant stress often

Table 5.1 Summary of the main properties of several indices of stream pollution (modified from Hellawell, 1977)

Index	Author	Data ¹ type	Equation	Range of values min. max.		Comments
Biological indices						
Species deficit	Kothé (1962)	ql	$I = \frac{S_u - S_d}{S_u} \times 100$	→ - ∞	100%	S_u : no. of species above outfall, S_d : no. of species below outfall. Value of index limited by possibility that there may be more species below outfall than above.
Modified species deficit	Hellawell (1977)	ql	$I = \frac{S_u - S_m}{S_u} \times 100$	0%	100%	S_m : no. of species missing at downstream site. Overcomes problem of unmodified index above.
Pollution index	Beck (1954)	ql	$I = 2C_1 - C_2$	0	→ ∞	C_1 , no. of macroinvertebrate species intolerant, and C_2 , no. tolerant to modest organic pollution. Index rarely exceeds 10.
Saprobic index	Zelinka & Marvan (1966)	semi-qt	$I = \frac{\sum ahg}{\sum hg}$	0	10	a : saprobic valency in each of 5 saprobic classes (sum = 10). g : indicator value (1-5, 5 is high). h : abundance. Maximum score in each class gives quality.
Trent biotic index	Woodiwiss (1964)	ql	Derived from table provided	0	10	Uses general responses of key macroinvertebrate groups; not taxonomic but convenient assemblages.

Biotic score	Chandler (1970)	semi-qt	Sum of scores derived from table provided	0	$\rightarrow \infty$	Uses responses of macroinvertebrate groups and their relative abundance. Score in clean water rarely exceeds 2500–3000.
Biotic value	Chutter (1972)	semi-qt	$\frac{\Sigma(a \times b)}{\text{total number of individuals}}$	0	10	<i>a</i> : no. of individuals in a given category; <i>b</i> : subjective quality value related to occurrence of taxa in polluted water (between 0–10). Values of 7–10 indicating highly polluted waters.
			Dominance indices			
	McNaughton (1968)	qt	$D = \frac{N_1 + N_2}{N}$	0	1.0	<i>N</i> ₁ and <i>N</i> ₂ : no. of individuals in the most and next most abundant species. <i>N</i> : total no. of individuals.
	Berger and Parker (1970)	qt	$D = \frac{N_1}{N}$	0	1.0	<i>N</i> ₁ : no. of individuals in the most abundant species. <i>N</i> : total no. of individuals.

¹qt: qualitative, qt: quantitative

depends on opportunistic life histories (Grassle and Grassle, 1974). Species surviving under severe stress are argued to be generalists in the sense that they have endured a wide range of abnormal conditions. Odum (1969) suggested that such species would be selected for rapid growth and reproduction rather than for competitive success.

Mosser *et al.* (1972) reported that diatom dominance was altered by DDT and PCBs at concentrations as low as 10 and $1 \mu\text{g l}^{-1}$, respectively, although these same concentrations produced no detectable effect on the growth of the dominant species in pure cultures. Heavy metal pollution in streams shifts macroinvertebrate structure towards chironomid dominance (Winner *et al.*, 1975, 1980; Sheehan, 1980). In fact this dominance pattern suggests that the percentage of chironomids in macroinvertebrate samples may be a useful index of the severity of heavy-metal pollution. A shift from nematode towards turbellaria dominance in the microfauna in beach sand has been cited as evidence of the impact of oil pollution (Wormald, 1976; Giere, 1979). Toxic effects of pulp and paper effluent caused a switch in dominance in the fish community in the affected bay (Kelso, 1977). The white sucker (*Catostomus commersoni*) was replaced by the yellow perch (*Percha flavescens*) as the most abundant species, under contaminated conditions. From a survey of acid-stressed lakes, Sprules (1975) reported increased complexity of the zooplankton communities with increasing pH. Above pH 5, communities contained 9–16 species with three or four dominant; in lakes with pH < 5, the communities contained 1–7 species, usually with only one dominant.

The sensitivity of shifts in composition and dominance to small changes in the level of pollutant exposure appears to differ with community type and toxic chemical. During the *Tsesis* oil spill, drastic changes in species biomass occurred within the planktonic community, but no obvious changes in phytoplankton or zooplankton species composition could be detected (Johansson *et al.*, 1980). The impacts of the *Florida* spill on benthic macrofauna were minimal at lightly contaminated sites, but more marked changes occurred in heavily oiled sediments (Sanders, 1978). Moore (1979) found macroinvertebrates to be insensitive to low metal concentrations. To the contrary, the per cent composition of chironomids has been shown to be a sensitive indicator of metal concentration (Winner *et al.*, 1980; Sheehan, 1980), and additions of only $0.5 \mu\text{g l}^{-1}$ mercury elicited changes in species composition of attached algae in a microcosm study (Grollé and Kuiper, 1980). Therefore, no generalization seems to be universally applicable concerning the sensitivity of taxonomic composition to pollutant concentration.

Although community composition is most frequently associated with taxonomic structure, it can also be viewed as related to trophic organization in terms of such characteristics as the abundance of producers relative to that of consumers and the proportional distribution of various feeding types. The trophic structure is in part influenced by the community's successional stage and

stability and is related as well to the predominant pathways of energy movement within the system. Osborne *et al.* (1979) reported that trophic specialists became less abundant, while generalists increased, in a benthic macroinvertebrate community affected by limestone strip mining. These authors concluded that deposition of ferric hydroxides contributed to the switch in trophic dominance by reducing food resources. In an acidified stream, shredder species were proportionately more abundant while scrapers and deposit feeders were significantly reduced in relation to the functional composition of non-acid oligotrophic streams (Friberg *et al.*, 1980). A decrease in the overall ratio of consumers to producers has been found to occur in acidified streams (Hall and Likens, 1980). Predators became proportionately less abundant with increasing copper concentrations along a pollutant gradient in a small stream receiving heavy metal effluent (Sheehan, 1980). Because of the limited number of such reports, sufficient data are not available to draw any general conclusions, but a pattern of simplification in the consumer community is suggested. Generalist feeders appear to have the advantage at the expense of specialized predators.

Numerical indices of dominance have been proposed for ecological use but have not been employed to a significant extent in the assessment of pollution effects (see Table 5.1). In one case, dominance indices for macroinvertebrates in sewage-contaminated streams were not correlated with parameters such as quantity of dissolved oxygen, biochemical oxygen demand, or coliform counts indicative of the level of organic enrichment (Cook, 1976).

Ecologists have often looked for ways in which to refine comparisons of community composition or to more definitively relate composition patterns to those environmental variables controlling structural changes. Statistical methods for comparing communities include ordination, numerical classification and reciprocal averaging (see review by Gray *et al.*, 1980). Ordination techniques encompass principal component analysis, principal coordinate analysis and analysis of correspondents, all of which require quantitative data. Soule and Soule (1979) used discriminant and principal component analyses to describe the rather subtle effects of industrial and domestic waste on bryozoans in a contaminated estuary. Zooplankton assemblages, as influenced by a number of physical and chemical parameters, were grouped using cluster analysis followed by multiple discriminant techniques (Green and Vascotto, 1979). Reciprocal averaging has been used to differentiate plant assemblages along a sulphur gas gradient, with increasing proximity to the source (Scale, 1982). The application of numerical classification methods, with either qualitative or quantitative data, in the investigation of ecological effects of water pollution has been discussed by Boesch (1977). Such techniques are now commonly available as part of standard computer programme packages. However, care must be taken to ensure that the relevant assumptions are applied in the interpretation of results from these analytical techniques.

5.4 SPECIES DIVERSITY AND SIMILARITY INDICES

5.4.1 Diversity

Ecologists have devoted a good deal of effort to the explanation of diversity patterns in ecosystems (reviewed by Whittaker, 1972; Peet, 1974). Despite this fact, there is no commonly accepted definition of diversity. Rather, it would appear that diversity has generally been measured using a variety of indices, and this has not fostered the sort of uniformity which permits the formation of clear hypotheses. In addition, the often cited relationship between diversity and ecosystem stability has been seriously questioned (Goodman, 1975). These considerations suggest that there is little ecological theory on which to base a relationship between diversity and community responses to pollution stress. However, the belief that pollution reduces biotic diversity, and with it community 'well-being', has been widely accepted and does have some empirical support. The extensive use of diversity indices in the assessment of pollutant effects on structure is primarily based on their quantitative nature, comparative value, and the fact that no assumptions need be made regarding the nature of the stress.

The concept of diversity possesses two components:

1. The number of species present (species variety or richness).
2. The distribution of all individuals among these species (evenness or equitability).

The individual diversity indices listed in Table 5.2 place varying degrees of emphasis on the respective components. The basic richness index, the number of species in the community, has been discussed previously (section 5.1). The mathematical expressions formulated by Fisher and Margalef are primarily richness indices and, as such, they weight additions and deletions more than the changes in total numbers of organisms. These expressions are inherently dependent on sample size and number; the larger the sample, the greater the number of species.

The Shannon index increases as both the numbers of species and the equitability of relative abundance increase. Therefore, this measure is relatively insensitive to species number effects which might bias richness-based indices. Edwards *et al.* (1975) demonstrated the size bias as reflected in several of these indices. Although it would be desirable to have a richness index independent of sample size, the richness of a community as estimated from samples of arbitrary but similar size can provide an adequate comparative measure of stress-induced changes. Sanders (1968) proposed a 'rarefaction' technique to scale down all samples of uneven size in a set of data, to match the size of the smallest, for comparative purposes.

The evenness component of diversity is based on the idea that when comparing

communities possessing equal numbers of species, those with the most equitable distribution of individuals among the species are the most diverse. The equitability component is specifically emphasized in the evenness indices included in Table 5.2. The relationship of evenness to stress is unclear. Conflicting composition and evenness data from pollution studies has led some ecotoxicologists to question the value of evenness-based indices (including even Shannon's index) in the assessment and prediction of community response (Gray, 1979). A number of natural factors also affect diversity. There is seasonal variation in both species richness and equitability (Buchanan *et al.* 1978). In addition, a wide range of diversity values have been found for natural communities, although certain assemblages such as stream macroinvertebrates normally have a narrow range (Wilhm, 1970). Archibald (1972) observed that low diversity in communities, arising from severe physical conditions, was often unrelated to water quality as judged by chemical criteria, thereby making the use of diversity indices questionable in these cases.

Numerous field studies have demonstrated that decreases in community diversity have been associated with high levels of organic sewage as well as with toxic chemicals. During the late 1960s, and into the early 1970s, there was a proliferation in the use of diversity indices to detect and quantify the relative effects of pollution (primarily sewage) on stream communities (Wilhm, 1967, 1970, 1972; Cairns and Dickson, 1971). Wilhm and Dorris (1968) proposed a relationship between Shannon's diversity value and the level of pollution stress in a stream: > 3 , clean water; $1-3$, moderately polluted; < 1 , heavily polluted. Both numerical and biomass diversity were found to be depressed by organic contamination (Wilhm, 1968).

Decreased diversity has been used as an indicator of gross environmental deterioration. Pearson (1975) reported a gradual decline in diversity of benthos over a period of years with organic enrichment and accompanying oxygen depletion. Diversity of taxa and biomass of fish, phytoplankton, zooplankton and nekton were inversely correlated with the per cent waste water or the toxicity of the water (phytoplankton bioassays) at sampling stations in Galveston Bay (Bechtel and Copeland, 1970; Copeland and Bechtel, 1971). Those areas receiving the greatest amounts of toxic effluent exhibited the lowest mean annual diversities of plankton. Beckett (1978), in reporting the response of macroinvertebrate communities in a multistressed river system (thermal discharges, municipal and industrial wastewater outfalls), concluded that the diversity (H') and the number of taxa present reflected changes in water quality only during periods of severe stress. When moderately stressed, 'normal' controlling factors were more robust than pollution in structuring the community. A similar conclusion was reached by Read *et al.* (1978), who observed that changes in dominance affected equitability with moderate levels of pollution, thereby hampering the effectiveness of diversity indices in **distinguishing stressed and unstressed communities. Also, diversity and evenness**

Table 5.2 Some indices which have been applied to the assessment of pollution effects (modified from Hellawell, 1977)

Index	Author	Data ¹ type	Equation	Range of values min.	max.	Comments
Williams α index	Fisher <i>et al.</i> (1943)	qt	Diversity indices $S \approx \alpha \ln N/\alpha$	$\rightarrow 0$	∞	S : no. of species, N : no. of individuals, α : index of diversity. Derived from nomogram published by Fisher <i>et al.</i> (1943).
	Margalef (1951)	qt	$D = (S - 1)/\ln N$	0	$\rightarrow \infty$	Symbols as above.
	Simpson (1949)	qt	$SI = \frac{\sum n_i(n_i - 1)}{N(N - 1)}$	0	1.0	n_i : no. of individuals in the i th species. Higher the value, lower the diversity. Also presented as $1 - SI$ and $1/SI$.
Information theory index	Shannon (1948); Shannon and Weaver (1963)	qt	$H' = -\sum p_i \log_2 p_i$	0	$\rightarrow \infty$	$p_i = n_i/N$: proportion of individuals in the i th species. Sometimes referred to as Shannon-Weiner or Shannon-Weaver index.
	McIntosh (1967)	qt	$MI = \sqrt{\left(\sum_{i=1}^S n_i^2\right)}$	1.0	$\rightarrow \infty$	n_i : no. of individuals in each species.
Sequential comparison index (SCI)	Cairns <i>et al.</i> (1968)	qt	$SCI = R/N'$	$\rightarrow 0$	$\rightarrow \infty$	R : no. of number of changes in species per scan. N' : total number scanned. Can only be derived from examination of sample.
Improved comparison index	Keefe and Bergersen (1977)	qt	$TU = 1 - \left(\frac{N'}{N' - 1}\right) \left(\sum_{i=1}^K p_i^2 - \frac{1}{N'}\right)$	$\rightarrow 0$	$\rightarrow \infty$	K : no. of taxa present. $p_i = n_i/N'$, ($i = 1, 2, 3, \dots, K$), corrects error in SCI .
Equitability	Lloyd and Ghelardi (1964)	qt	Evenness indices $\varepsilon = \frac{S}{S'}$	$\rightarrow 0$	1.0	S' : no. of species according to McArthur's broken stick model.
	Pielou (1966)	qt	$J = \frac{H'}{\log_2 S}$	0	1.0	Symbols as above: dependent on Shannon diversity.
	Sheldon (1969)	qt	$E = \frac{e^{H'}}{S}$	0	1.0	Symbols as above: dependent on Shannon diversity; problem with lower limit for non-diverse

	Heip (1974)	qt	$E = \frac{e^H - 1}{S - 1}$	0	1.0	approaches 1/s. Symbols as above; dependent on Shannon diversity.
			Alternative indices based on probability theory			
Potential individual encounters	Hurlbert (1971)	qt	$PIE = \left[\frac{N}{N-1} \right] \left[1 - \sum \left(\frac{n_i}{N} \right)^2 \right]$	0	1.0	The proportion of potential inter-individual encounters which is interspecific as opposed to intraspecific assuming every individual can encounter all other individuals; symbols as above.
Expected no. of species	Hurlbert (1971)	qt	$E(S_n) = \sum \left[1 - \frac{\binom{N-n_i}{n}}{\binom{N}{n}} \right]$			The expected no. of species in a sample of n individuals selected at random from a collection of N individuals, S species, and n_i individuals in the i th species.
			Similarity indices			
Coefficient of similarity	Jaccard (1912)	ql	$I = \frac{c}{a + b - c}$	0	1.0	a : no. of species in community A. b : no. of species in community B. c : no. of species common to both.
Quotient of similarity	Sørensen (1948)	ql	$I = \frac{2c}{a + b}$	0	1.0	As above; same as coefficient of community (CC), Whittaker (1972).
	Raabe (1952)	qt	$I = \sum \min(a, b, c, \dots, n)$	0	100%	a, b , etc. are minimum % values of each species common to both communities; same as Sanders (1960) index of affinity.
Percentage similarity	Whittaker and Fairbanks (1958)	qt	$PS = 100(1 - 0.5\sum p_{ij} - p_{ik})$	0	100	p_{ij} is the average proportional abundance of a given taxon in control samples and p_{ik} is its proportion in any single sample.
Bray-Curtis dissimilarity	Bray and Curtis (1957)	qt	$BC = \frac{\sum n_{1i} - n_{2i} }{\sum (n_{1i} + n_{2i})}$	0	1.0	n_{1i} and n_{2i} : the ln transformed numbers of the i th species at two sites being compared.

¹ ql: qualitative, qt: quantitative

indices can be contradictory. Letterman and Mitsch (1978) reported the total abundance and Shannon diversity were depressed but evenness increased with the input of acid mine drainage. Osborne *et al.* (1979) also found evenness to be unrelated to other indices of community structure for macroinvertebrates affected by strip-mining effluents.

Several studies have shown diversity to be related to concentration of specific toxic chemicals. Winner *et al.* (1975) demonstrated that H' -diversity and species richness reflected a graded response by macroinvertebrates to a copper gradient in an experimentally polluted stream (see Figure 5.3). Neither the Shannon nor the Margalef index was as sensitive as the simple richness index in separating communities along the gradient. Marshall and Mellinger (1980) used modifications of Shannon's and Simpson's indices ($\exp - \sum p_i \ln p_i$, and $1/\sum p_i^2$, respectively) as suggested by Hill (1973), to quantify low level cadmium effects on zooplankton assemblages. They found that zooplankton species diversity, as expressed by either index, was relatively insensitive to cadmium at low concentrations ($5 \mu\text{g l}^{-1}$), although they observed a significant reduction in the number of species at that level. Macroinvertebrate diversity has been correlated with hydrogen ion concentrations in a small stream system receiving acid mine drainage (Dills and Rogers, 1974). In terrestrial ecosystems, tree-species diversity (H') and evenness have been inversely related to high levels of exchangeable Al and H, and to decreasing pH (Cribben and Scacchetti, 1977). Tree, shrub and herb richness and diversity were depressed along gradients from air pollutant sources (McClenahan, 1978). Freedman and Hutchinson (1980a) found that diversity of under- and overstory vegetation increased with distance from a metal smelter (Figure 5.6), however biomass indices were more responsive than the diversity measures. Under similar circumstances, Scale (1982) reported that diversity and equitability values were best fitted by a quadratic curve describing a transitory increase with distance from the source out to approximately 35 km, followed by a decrease at greater distances. Species richness showed a more 'normal' increase to a plateau which was maintained for a considerable distance from the effluent source.

With certain pollutants, diversity appears to be ineffective in describing community response to stress. Thomas (1978) found that the diversity of intertidal flora and fauna was unrelated to oil contamination. Likewise, diversity (H') and evenness (J) of eel grass fauna (Figure 5.5) were not depressed by the *Amoco Cadiz* spill although there were severe reductions in the number of taxa and in abundance (Jacobs, 1980). Diversity in this system was characterized as displaying increased fluctuations indicative of a period of instability due to rapid dominance switches. Eisele and Hartung (1976) observed that the pesticide methoxychlor, at 0.2 mg l^{-1} , selectively reduced certain invertebrate populations but did not influence overall community diversity in the contaminated stream.

A number of authors have seriously questioned the usefulness and effectiveness of diversity indices in quantifying toxic stress. At the simplest level,

the difficulty in identifying species had led to the question of utility versus effort. Edwards *et al.* (1975) suggested that if the goal of sampling were merely to detect stress, reduced taxonomic analysis (identification to the family level) might be acceptable. Cairns *et al.* (1968) introduced the sequential comparison index (SCI) as a simplified method for a nonbiologist to estimate relative differences in biological diversity in stream pollution studies (see Table 5.2). This index was modified by Cairns and Dickson (1971), and a similar index based on the theory of runs (Mood, 1940) was recommended as a replacement for SCI, greatly reducing variability in the results of different workers (Keefe and Bergersen, 1977). These simplified diversity indices definitely have their place in certain gross impact studies, but they ignore life history, functional role, and tolerance information, which are associated with knowledge of specific taxa. Simmons (1972) concluded that even though SCI provided a rapid method of gathering information, it did not exhibit sufficient resolution to distinguish between degrees of community recovery from the effects of acid mine drainage.

Taxonomic problems are overshadowed, however, by some more basic complaints. Godfrey (1978) questioned the accepted assumption that water pollution causes a depression in diversity, citing the inconsistencies between diversity and other biological indices. Moon and Lucostic (1979) noted that stressed communities under a relatively constant degree of pollutant pressure develop fairly diverse compositions, rendering any interpretation (using H') of the magnitude of response difficult. The lack of a theoretical basis for the application of diversity indices has also raised questions (Gray and Mirza, 1979). Without a theoretical base and a knowledge of the influences of natural factors on the structure within the polluted system, interpretation of pollutant-induced changes using the value of the index cannot be made with confidence (Rosenberg, 1976). Furthermore, Gray (1979) suggested that most diversity indices are relatively insensitive to changes in community structure and, thus, they have limited value in defining the severity of pollutant stress.

Perhaps the most universal criticism of the Shannon diversity measure is the misleading interpretation evoked within depauperate communities due to the large influence of the evenness component (Gray, 1976; Letterman and Mitsch, 1978; Godfrey, 1978; Marshall and Mellinger, 1980). Equitability drastically increases the importance of rare species in the index's value and at the low population densities associated with toxic pollution, this influence is immense. In contrast, the evenness effect would be relatively insignificant at normal population levels.

Displeasure with the standard diversity indices has prompted several researchers to offer alternative quantitative measures of structure. Hurlbert (1971) argued that the term 'species diversity', having been defined in a variety of disparate ways, did not provide clear information on community structure. As an alternative to diversity measures he proposed two indices that take the form of probability theory relationships: *PIE* and *E(S)* (see Table 5.2); but these indices

have been applied only in a limited way to field data. Read *et al.* (1978) compared the *PIE* index with diversity measures (α , H' , E) in an analysis of intertidal pollutant gradients. They found that these indices were closely correlated with one another, *PIE* values being nearest to the median.

The application of log-normal distribution analysis to the number of individuals per species has been proposed as another alternative structural measure (Gray, 1979, 1980; Gray and Mirza, 1979; Åkesson, 1983). Figure 5.7 illustrates the response of invertebrate populations to increased inputs of pulp and paper mill effluents. The data are distributed over three phases, a pre-pollution phase, a transitory phase and a polluted phase. In a nonpolluted system, the community has a log-normal distribution with data spanning few geometric classes. The transitory phase is characterized by a bend in the straight line distribution and an increase in the number of geometric classes spanned. The stressed community has a straight line distribution at a less steep angle. The log-

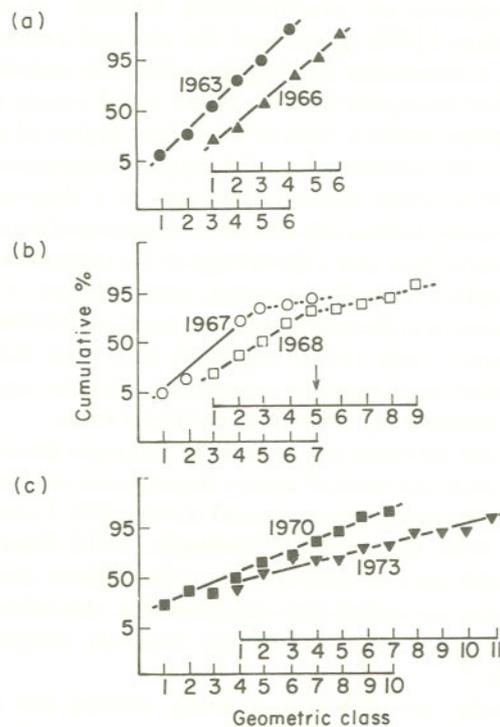


Figure 5.7 Log-normal plots of benthos from Loch Eil, Scotland: (a) unpolluted phase 1963–1966; (b) transition phase 1967, 1968; (c) polluted phase 1970–1973. (From Gray and Mirza, 1979. Reproduced with permission from Pergamon Press Ltd)

normal distribution for the transition phase illustrates the importance of the response of species with an intermediate number of individuals (16 to 128). Gray and Mirza (1979) concluded that although there is no single underlying biological property behind this distribution pattern the method is effective in demonstrating pollution. However, they could not define the critical degree of slope separating non-polluted from polluted systems and this technique has had very limited application in studies of toxic chemicals.

5.4.2 Similarity

Temporal and spatial changes in environmental stress may be assessed through the comparison of two or more community structures. Similarity indices have been developed primarily by plant ecologists in order to distinguish community organization in space or successional time (reviewed by Whittaker, 1972). Several common similarity indices are described in Table 5.2. These measures may be particularly applicable in identifying pollutant-induced discontinuities among communities which are located at varying distances from a source of contamination or in detecting changes in a community with time (Hellowell, 1977). Most similarity indices compare either joint species presence or presence and proportional abundance. Clustering techniques are then used to group 'like' assemblages (see Williams, 1971). Haedrich (1975) stressed that diversity and overlap measures should be employed simultaneously to provide a clearer interpretation of community response to changes in environmental quality.

Similarity indices and clustering techniques have, in fact, been used for some time to identify aquatic communities affected by organic and industrial wastes (Burlington, 1962; Dean and Burlington, 1963; Cairns and Kaesler, 1969). Brock (1977) emphasized the importance of these techniques in facilitating meaningful comparisons of reference areas with those receiving effluent. Crossman *et al.* (1974) separated macroinvertebrate assemblages with respect to the deleterious impacts of an acid spill using presence-absence data, and documented the recovery process. They also found cluster analysis useful in determining the effects of natural factors (e.g. substrate, flooding) on community structure. Vander Wal (1977) defined two major ecosystems in Nipigon Bay as generally related to distance from a pulp mill effluent outfall using similarity comparisons. Researchers have used these techniques to define distinct community types along pollutant gradients. Beckett (1978) demonstrated a gradient of macroinvertebrate community structural change in a multistressed river system. Similarly, Hummon *et al.* (1978) identified distinct microfaunal communities in sandbars of acid-rain-polluted streams.

There is evidence to indicate that similarity indices are more sensitive, and, therefore, more indicative of structural differences, at low levels of stress than are diversity measures. Marshall and Mellinger (1980) successfully demonstrated changes in zooplankton community response (*PS* and *CC*) to several levels of cadmium pollution $< 5 \mu\text{g l}^{-1}$. *PS* was significantly reduced by 1.2, 0.6, and

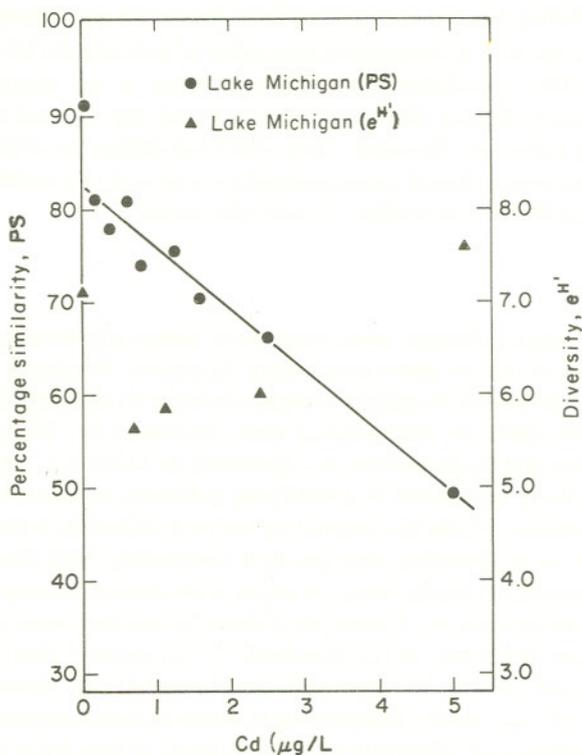


Figure 5.8 Effects of cadmium on percentage similarity (PS) and diversity (H') of planktonic crustacean communities, 3 weeks after cadmium enrichment of enclosures in Lake Michigan. (Data from Marshall and Mellinger, 1980. Reproduced by permission of the *Canadian Journal of Fisheries and Aquatic Sciences*)

$0.2 \mu\text{g l}^{-1}\text{Cd}$ while diversity indices were not significantly lowered at these levels and displayed an inconsistent pattern in relation to Cd concentration (Figure 5.8). In evaluating changes in a deciduous forest exposed to air pollution, McClenahan (1978) reported a significant relationship between coefficient of community and combined air pollutant index (relative exposure of stands to Cl^- , F^- and SO_2). Similarity decreased along the gradient of increasing pollutant exposure, while diversity was depressed only near the source.

Monitoring pollution-caused changes in complex terrestrial plant communities is a difficult task. In examining changes in relation to distance from a large source of smelter emissions, Scale (1982) found that a combination of indices was useful but that each type had specific drawbacks (see Figure 5.9).

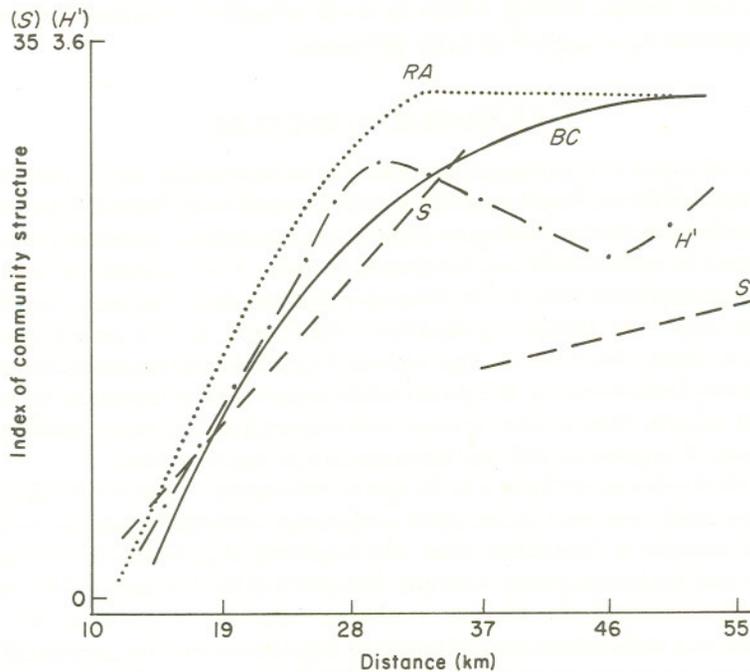


Figure 5.9 Comparison of potential monitors of change in plant communities due to air pollution: Shannon's diversity of ground flora (H'), species richness of ground flora (S), Bray-Curtis similarity to reference sites (BC), reciprocal averaging (RA). (Data from Scale, 1982)

Complex changes in diversity occurred in all plant strata with a transient increase observed over the transect. The diversity pattern of ground flora (plotted) failed to signal enormous changes in the community and did not show either a linear or a logarithmic relationship with distance. The species richness pattern was also a relatively poor indicator of fume damage. Reciprocal averaging (RA) measures and the Bray-Curtis similarity index (BC) were capable of discerning certain changes but were less effective as indicators of more subtle changes at greater distances. Scale also found that Principal Component Analysis (PCA) reflected the dramatic elimination of shrubs, and in this sense it was a powerful analytical tool for describing community response.

Considering the numerous drawbacks of diversity indices, their use in pollution evaluation is probably best limited to the demonstration of gross changes, and their interpretation must be approached with care and a thorough understanding of the ecology of the system. To the contrary, similarity measures would appear to have a more proven utility, and analytic techniques such as PCA , RA and discriminant analysis should be more commonly applied to future

quantitative studies relating effects to levels of specific pollutants in systems contaminated by a number of toxic substances.

5.5 SPATIAL STRUCTURE

Spatial structure is a universal characteristic of ecosystems and is particularly meaningful in forest, desert, grassland, coral reef and rocky intertidal systems. It has also been studied in freshwater plankton communities. Spatial structure can be defined by both vertical and horizontal patterns. For example, the unit layer concept as applied to forests comprises several strata including trees, shrubs and ground cover. The spatial organization of terrestrial flora is generally a very visible attribute; therefore, changes induced by pollutant stress should be readily recognized. Unfortunately, the spatial relationships of most terrestrial fauna and of most aquatic communities are not well defined due to species mobility, the small size of organisms and the heterogeneity of microhabitats.

Pollution-associated changes in the spatial heterogeneity of a terrestrial system are most easily observed in the plant community, although there are certainly parallel changes in associated fauna. Heterogeneity is generally reduced in the vertical and horizontal planes with any disruption of the tree canopy. Woodwell (1970) demonstrated that chronic irradiation of a late successional oak-pine forest led to a well-defined zone of modified vegetative structure, correlated with gamma-ray exposure varying between 1-200 Rads per day. He described this pattern as a systematic dissection of the forest with removal of successive vertical strata. A similar pattern of simplification following radiation damage was reported for desert shrubs near nuclear explosives testing areas (Ragsdale and Rhoads, 1974). Woodwell (1970) indicated that this pattern was not peculiar to radiation but common to many forms of environmental stress, including fire and toxic chemical pollution. Mangrove communities, which are particularly sensitive to herbicides, displayed significant simplification of vertical structure after exposure (Odum and Johannes, 1975). Similar observations were made of the defoliated triple canopy jungles in Vietnam which reverted to a bamboo monoculture after a large scale US military spraying effort using Agent Orange (a combination of 2, 4, 5-T and 2, 4-D) and other herbicides (Odum, 1976). Due to the differential sensitivity of plants to herbicides, less dramatic reductions in vegetation have led to characteristic shifts in plant community morphometry. Willis (1972) documented such changes in roadside vegetation sprayed with 2, 4-D for 12 years. Control plots were characterized by a stable cover of grasses (50 per cent by volume) and numerous dicotyledonous plants, averaging 90-95 cm in height. After consecutive annual sprays, grasses became strongly dominant (\approx 90 per cent by volume), forming a community with an average height of about 50 cm. The spraying of herbicides can also have deleterious effects on animals' habitats and food. Several examples of changes in animal distribution as a secondary effect of vegetative loss were described in an extensive review report on phenoxy herbicides (NRCC, 1978).

Several authors have reported significant changes in forest structure induced by sulphur dioxide pollution (e.g. Knabe, 1976; Freedman and Hutchinson, 1980a; Scale, 1980). Trees were shown to be generally sensitive to SO_2 and, therefore, were killed at sites close to a source, removing the upper level of vegetative structure. Dawson and Nash (1980) found a very different set of changes in spatial structure associated with copper smelter effluent, which also contained high SO_2 concentrations. Changes in the distributional patterns of plants were related to the interaction of copper toxicity and soil acidification as it affected rooting depths and life history strategies. Deep-rooted woody shrubs were less affected than shallow-rooted grasses and they became the dominant structural forms.

5.6 STABILITY

Ecosystems are not naturally constant. Apparently, they do not have a single stable equilibrium structure, nor does recovery from a disturbance always follow a pre-determined pattern. However, ecosystem characteristics do persist, within certain bounds, despite small perturbations. This situation raises some complex questions in relation to the assessment of 'stability' of an ecosystem as affected by the stress of chemical pollution.

Various aspects of the general concept of stability have been studied for many years in connection with mechanical, electrical and similar systems, and analogous concepts from these fields have been applied to ecosystems. To begin with, stability does not necessarily refer to the maintenance of a static situation; periodically fluctuating behaviour can be thought of as stable provided that the same cycle is repeated constantly. The general concept of stability relates to the question of how a system will respond to a small perturbation (in mathematical theory, infinitesimally small). If there is a natural tendency to return to its previous state (or its previous pattern of fluctuation) the system is called stable. If any small perturbation is magnified by natural causes, the system is called unstable. The intermediate case, where small changes are not naturally either magnified or depressed, is called neutral in mathematical literature; in ecosystem applications, where perturbations of all magnitudes are assumed to be occurring at all times, such a system would deviate more and more from its original state by random variations, and would in effect be unstable, so there is no need to consider an intermediate situation.

In environmental applications, in fact, we must modify the concept of an infinitesimal perturbation. The disturbances suffered by any ecosystem are not at all vanishingly small, and it is necessary to think in terms of the response of the system to changes that may be quite large. Thus, a new concept has to be introduced, namely the concept of the maximum size of perturbation that can be tolerated, after which the ecosystem will return to normal on its own. Furthermore, there is the possibility that certain systems, once perturbed in a certain way, may re-stabilize in a different configuration (for example, some

species may be extinct and others start to perform their role or occupy their niche), so that yet another kind of stability must be introduced, namely the ability to continue to exist but in a different form, rather than to collapse if the original form cannot be re-achieved.

In order to deal with these concepts, ecologists have adopted many terms from their fields, and have invented some new ones. In some cases, meanings have had to be modified to fit the new situations. The usages do not all agree, and many contributions have been made to the literature (Holling, 1973; May, 1973, 1975; Orians, 1975; Cairns and Dickson, 1977; Westman, 1978). Thus we are not able to summarize all approaches, but will simply quote some examples.

The basic definition of *stability*, as applied to ecosystems, was stated above. Also used are the ideas of *constancy*, the more strict requirement of lack of change, in other words, the static version of stability. The ability of the system to resist perturbation at all is referred to as *inertia*, while the speed of recovery, which is vital in the real environment because subsequent perturbations may occur at any time, is called *elasticity* (Bourdeau and Treshow, 1978; Westman, 1978). It should be noted that different measures of the structure and function of an ecosystem may give different values for the recovery time. Thus, it is not enough to refer to the elasticity of a system; one must also specify how it is measured. *Persistence* simply means the survival of the ecosystem through time, without reference to its condition (Westman, 1978).

The concept of how much perturbation a system can absorb and eventually return to a stable existence is called *resilience* by Holling (1973), and he and his co-workers have developed an extensive network of ideas of ecosystem dynamics around this theme. Critical to the approach is the idea that after some perturbations, the system will be able to return to its original state (which, of course, is not necessarily static; a stable state can involve fluctuations around a mean value), while after other, larger, perturbations the system may recover by achieving a different stable configuration. The idea is that there may be many discrete stable 'points' in parameter space, and under violent perturbations the system might move from one to another. The approach is therefore 'global', to borrow a term from the theory of differential equations, while most of the other work in this area refers to perturbations from a single equilibrium point. The corresponding concept for the local case is what Westman (1978) calls *amplitude*.

More recently, work has appeared which attaches a quantitative measure to the degree to which the recovery of a system does not match its history of degradation; this is called *hysteresis*, while *malleability* describes the degree to which the ecosystem has been permanently altered (Westman, 1978). Table 5.3 summarizes some of these concepts. It is to be expected that usages will change as the approach continues to develop.

Traditionally, fluctuations in ecosystems have been discussed in terms of population densities of certain species, but there appear to be good reasons for examining short-term changes in other structural and in some functional

Table 5.3 Measures of ecosystem dynamics and examples of their application (after Holling, 1973; Westman, 1978).

Characteristic	Definition	Example: Ecosystem subjected to oil spill
Inertia (ecological buffering capacity)	Resistance to change	Amount of oil that must accumulate over a given area in a given time period to cause a given level of ecosystem damage (such as local extinction of species <i>X</i> and <i>Y</i>)
Elasticity	Rapidity of restoration of a stable state following disturbance	Time required to recover initial structure or function following ecosystem damage (e.g. restoration of populations <i>X</i> and <i>Y</i>)
Amplitude	Zone from which the system will return to its original state	Maximum amount of oil that can accumulate in an area such that damage sustained can be fully repaired (e.g. restoration of populations <i>X</i> and <i>Y</i>)
Resilience	Zone from which the system can return to a stable configuration, perhaps different from the original	Maximum pollutant level after which populations will stabilize at <i>some</i> level
Hysteresis	Degree to which path of restoration is an exact reversal of path of degradation	Degree to which pattern of secondary succession is not an exact reversal of the pattern of retrogression experienced following impact (e.g. were the last species to disappear the first ones to return?)
Malleability	Degree to which stable state established after disturbance differs from the original steady state	Degree to which new climax ecosystem resembles the initial climax state (e.g. how closely do the species composition and equitability of new climax state resemble the old?)

characteristics (e.g. similarity, diversity, species richness, total biomass, primary productivity, essential element retention). These properties reflect system-wide changes which may not be obvious from single species results, and thus they should better demonstrate the dynamics of stressed systems.

Constancy, in the strict sense of a system at rest, is not a viable ecological concept (Botkin and Sobel, 1975; Botkin, 1980). However, the fluctuation of ecosystem structure within a prescribed range of variation is an index of departure from constancy which, theoretically, would be affected by pollution. It has been postulated that the lower the variation in ecosystem characteristics, the greater the stability of the system (Wilson, 1969; Fishelson, 1977); therefore, pollutant perturbation would act to decrease the regularity of both structure and function. It should be noted that under conditions of drastically reduced numbers of an organism, the probability of chance playing a significant role in sample abundance and distribution is increased. Fluctuations in such systems are highly erratic and their relation to the level of pollutant stress is uncertain. Gray and Mirza (1979) suggested that the statistical problem in measuring population variation below a sample size of 20 individuals is enormous.

Fishelson (1977) described waste heat perturbation as inducing increased

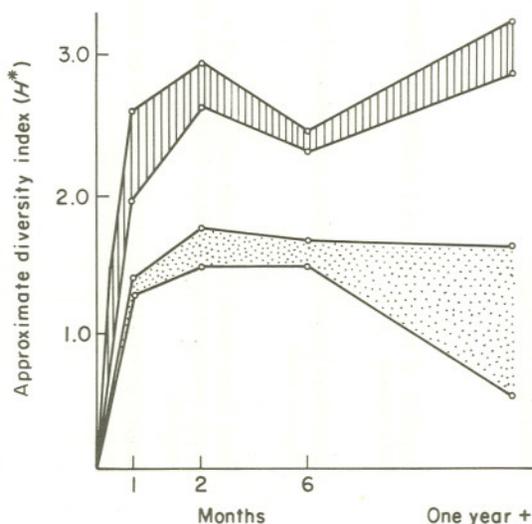


Figure 5.10 Development and succession of an animal-plant community on coral skeletons implanted in a clean (lined) and in a polluted (dotted) area in Eilat shallow-water littoral. H^* is based on identification of higher taxonomic units and is highly correlated with the Shannon index (Reproduced by permission of Professor Lev Fishelson and Biologische Anstalt Helgoland, Hamburg)

sample variability in the proportions of epiphytic worms associated with the alga *Ulva lactuca*. In other experiments he demonstrated that the diversity of organisms which colonized coral skeletons implanted in oil-contaminated habitats was lower and more variable than that of the colonizers in uncontaminated areas (Figure 5.10). The disturbed micro-ecosystems did not achieve a stable pattern of fluctuations and, in addition, they displayed wide variation in species composition, reflected in the range of diversity values measured. Jacobs (1980) reported that both diversity and evenness of littoral assemblages fluctuated abnormally after the *Amoco Cadiz* spill. The increased fluctuations were described as rapid changes in dominance associated with the expansion of opportunistic species.

There is some evidence, however, which conflicts with the postulate that stress increases the variability in structural indices. Winner *et al.* (1980) found that copper pollution damped the variability in community composition, over time, among sequential macroinvertebrate samples. In fact, they reported that the affinity among samples increased with the growing dominance of chironomids at the higher concentrations of copper. Read *et al.* (1978) observed that the smallest temporal changes in PIE (see Table 5.2) were found in assemblages inhabiting a grossly polluted beach, whereas the largest changes occurred in a relatively unstressed beach community. It is not clear to what extent these conflicting reports can be explained by a difference in the severity of stress. The great simplification in structure of highly stressed communities suggests that temporal variability would be damped as resident species come to be controlled more by the pollutant than by natural biological factors.

5.6.1 Inertia

The inertia of an ecosystem, i.e. its capacity to resist change, is a measure of that system's resistance to pollution. In the context of ecological modelling, inertia has been called buffering capacity (Jørgensen and Mejer, 1977, 1979) and the inverse of inducible adaptability (Conrad, 1976). An ecosystem's inertia is a function of several basic properties:

1. The resistance of the organisms to environmental fluctuations.
2. The degree of functional redundancy within the system.
3. The self-cleansing capacity.
4. The chemical buffering capacity.
5. The proximity of its parameters to ecological threshold values for factors such as temperature and salinity (Cairns and Dickson, 1977).

Accordingly, it has been suggested that ecosystems with a high degree of specialization and little history of fluctuating environmental parameters have low inertia and are highly vulnerable to pollution damage (Boesch, 1974; Jernelov and Rosenberg, 1976).

To assess the inertia of an ecosystem, the degree of chemical contamination must be related to some measure of change. Westman (1978) proposed a measure of damage of 50 per cent change in composition and relative abundance of species, using the percentage similarity index (*PS*). This measure would be patterned after well-known bioassay techniques. The quantity of a chemical which causes a 50 per cent change in *PS* (between the before-exposure and after-exposure values) would be the measure of inertia. This technique has been used to measure the inertia of an oak-pine forest exposed to chronic gamma radiation (Woodwell, 1967), although the characteristic chosen was species richness. The criterion of a 50 per cent reduction in macroinvertebrate richness (excluding the chironomid taxa) was used by Sheehan (1980) to estimate the impact of metal pollution on the structure of a stream system. This analysis demonstrated that high seasonal influxes of copper were annually effective in overwhelming the inertia of the system, depressing species richness to a level below 50 per cent of that in the reference community.

5.6.2 Elasticity

The elasticity of an ecosystem is a measure of its ability to recover, within acceptable limits, after being perturbed. It is best related to restoration time, and is affected by a variety of factors.

The relationships of species abundance interactions, and vegetative structure to community elasticity have been examined experimentally, through selective plant removals from an old field community (Allen and Forman, 1976). Recovery was inversely correlated with the per cent cover of species removed. The recovery response was also highly dependent on the particular species removed, emphasizing the importance of species interactions and of the species' ability to reproduce rapidly and fill gaps in community function. High elasticity was positively correlated with vertical stratification (belayered with dense ground cover), horizontal patchiness (many low diversity patches), and the abundance of species which were capable of rapid vegetative reproduction. In particular, this study emphasized that spatial heterogeneity of biota was essential to ensure community recovery from perturbation. This characteristic has been linked also to the maintenance of stable population interactions through its provision of cover, refuge and patches of potential immigrants for dispersal (Stenseth, 1980).

The mobility of juvenile recruits and potential immigrants is a major factor in the rapid recovery of animal communities. Leppäkoski (1975) suggested that migrating populations can contribute significantly to ecosystem elasticity. When exposed to increasing pollution, such a group can move away from the source while maintaining its structural integrity. Thus, these populations are always available to contribute immigrants to the rapid recovery of a system when the toxic stress has abated. This idea developed from observations of the effects of

pollution in estuaries; it is not known yet to what extent it can be applied to other situations.

Elasticity, as measured by restoration time is not a simple concept. It can be defined in terms of various characteristics each of which will provide a different estimate of community recovery. Rosenberg (1976) showed that baseline levels of faunal density and biomass were regained more rapidly than were the numbers of species, but both the biomass and density of the fauna showed erratic fluctuations during the early recovery period. Therefore, the predictability of the recovered state must be considered. Westman (1978) proposed that recovery time to reach 85 per cent similarity to the original composition be used, emphasizing that achievement of 100 per cent agreement is an unrealistic expectation. Restoration rates have also been assessed in terms of species-shifts from reproduction-oriented to competition-oriented strategists (Opler *et al.*, 1977). The use of colonization data and appropriate mathematical model curves (Sheldon, 1977) might offer a rapid appraisal of stream recovery. However, care must be taken to confirm that the colonizers do indeed survive throughout their vulnerable life history stages and then reproduce successfully within the recovering system.

There are several obvious difficulties in estimating elasticity. Stochastic as well as deterministic processes contribute to successional recovery and, thus, to the nature of the climactic structure. Recovery time may be long, and the rate of change might not be linear, so there is no guarantee that early estimates can be extrapolated to predict long-term progress towards restoration of either structure or function. Also, as previously mentioned, ecosystem characteristics do not necessarily recover at concurrent rates.

5.6.3 Amplitude

Amplitude, as used by Westman (1978), is that maximum amount of perturbation from which an ecosystem can still recover. The critical question with regard to the 'brittleness' of a polluted system is whether sufficient structural organization and biotic interaction has been maintained to allow it to persist. This question is far from simple and forms the crux of the problem of establishing protective standards for an ecosystem.

A number of environmental factors and species characteristics have been shown to increase the amount of stress that an ecosystem can bear before becoming permanently impaired (Orians, 1975). These include intraspecific variability of component species, capacity for long-distance dispersal, broad physical tolerance limits, and low density-dependence in birth rates.

The measurement of amplitude involves the determination of a threshold, if there is one, beyond which recovery to the original state can no longer occur (Westman, 1978). The necessity of estimating amplitude has long been recognized with respect to recovery in agricultural systems from over-grazing or

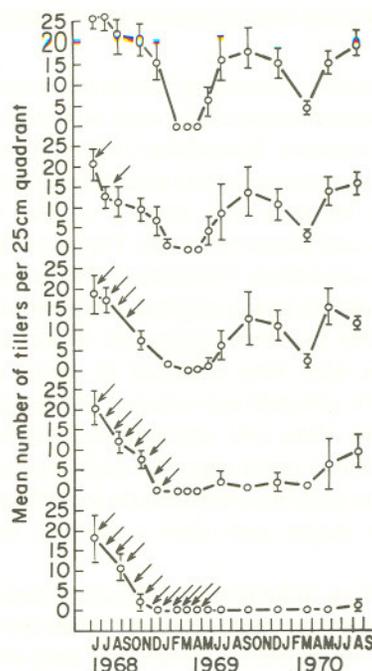


Figure 5.11 The results of successive oilings of plots of *Spartina anglica*. Oil was applied on the dates arrowed; 95 per cent confidence limits (t -test) are indicated. (from Baker, 1971. Reproduced by Permission of the Institute of Petroleum, London)

nutrient stresses. The relationship between system amplitude and chronic or successive inputs of toxic pollutants is less well documented. Baker (1971) examined the successive inhibition of recovery with increasing duration of oil stress in the salt marsh grass *Spartina anglica* (Figure 5.11). From her data, she concluded that approximately 12 successive oilings, with 90 per cent crude oil over a 14-month period, would exceed the system's threshold of self-repair. The application of repeated doses of No. 2 fuel oil as slicks on a salt marsh grass community resulted in similar long-term reductions in plant vigour and productivity (Hershner and Lake, 1980). Although neither of these studies was of sufficient duration to demonstrate long-term inhibition of recovery, field observations by Hampson and Moul (1978), following a No. 2 fuel oil spill, indicated that the inability of grasses to reestablish themselves either by reseeding or by rhizome growth would be aggravated by increased erosion, preventing any likely short-term recovery. There is little data on the amplitude of pollutant

damage which a system can sustain for periods approximating those of normal succession. Examples of continuous disruption by fire preventing reestablishment of normal composition patterns in forests have been documented for extended periods (Vale, 1977).

5.6.4 Hysteresis and Malleability

Hysteresis is a measure of the degree to which an ecosystem's pattern of recovery is not the reversal of the pattern of species loss. There is very little data comparing the disappearance and reappearance of species in relation to effluent release and abatement. Westman (1978) suggested that hysteresis could be measured by such a comparison, using techniques such as Spearman's rank correlation coefficient, and that this information should be of considerable interest to environmental managers.

Malleability is a measure of the ease with which a system is permanently altered to a new stable state. An ecosystem can possess a multiplicity of stable states (May, 1977). The problem facing the ecotoxicologist is demonstrating that the system is indeed new and stable. In the initial stages of recovery from a disruption, a system might be expected to display large differences in community composition (*PS*) from year to year. Small changes in *PS* over several years would indicate that a stable configuration had been achieved. Malleability could then be assessed by analysis of the differences between characteristics of the original and the new states, in relation to the extent of pollution.

5.6.5 Persistence

The ultimate criterion in pollution assessment is the persistence of a functioning ecosystem. It would appear to be more practical to define persistence in terms of primary productivity, organic decomposition rate, or nutrient recycling capability, since these processes are central to ecosystem function. Studies of ecosystem restoration have indicated that essential processes involving nutrient conservation and cycling are exceptionally difficult to reestablish. Bradshaw *et al.* (1978) reported that the overriding problem in restoration of a terrestrial ecosystem is the provision of adequate inorganic nitrogen. Therefore, the breakdown of essential nutrient cycles may provide a key to evaluating a system's persistence under stress. Likens *et al.* (1978) noted that the recovery of deforested ecosystems was dependent upon nutrient availability and the reestablishment of biological regulation of nutrient cycles. In the experimentally logged forest, 28 per cent of the total pool of nitrogen was lost, and it was estimated that this would require 20 years to be replaced by natural processes (mineralization and N-fixation).

The above field observations on the sensitivity of nutrient cycles to system stability are generally in agreement with predictions using the Liapunov Direct

Method (mathematical stability model). This method was used by Lasalle and Lefschetz (1961) to predict that damage to decomposers or to nutrient pools is a potentially stronger cause of instability than are disturbances to predator-prey components of the system. Similarly, the relative stability of a generalized linear ecosystem model was found to be influenced by the efficiency of nutrient recycling processes (Webster *et al.*, 1975; Halfon, 1976). Closed-looped nutrient cycling was also shown to have great influence on the homeostasis of a modelled ecosystem (Waide *et al.*, 1974).

Although there appears to be a growing interest in the practical assessment and modelling of ecosystem resilience and persistence under various conditions of stress, the use of stability criteria in pollution-effects research is still in its infancy.

5.7 SUCCESSION AND RECOVERY

5.7.1 Terrestrial Succession

Ecological succession has recently been defined as a less directed process than originally conceived. MacMahon (1980) defined succession as merely the change in an area of the earth's surface and its inhabitants over a moderate period of time (i.e. tens to hundreds of years), during which environmental conditions remain relatively constant. He assumed no inherent order to the process and no precisely defined time schedule. Succession is usually characterized as changes through time in species composition and community structure, but other ecosystem attributes such as community energetics (Odum, 1969) and chemical budgets (Woodwell *et al.*, 1975; Vitousek and Reiners, 1975; Gorham *et al.*, 1979) may respond to seral change.

Although some changes in species composition take place in all systems after a disturbance, succession is most obvious in terrestrial systems which are not under severe environmental stress. MacMahon (1980) concluded that in harsh environments such as desert or tundra, following a disturbance, the only viable colonists were the limited numbers of tolerant species previously resident. Even for forest ecosystems, for which successional changes in vegetative structure have been well documented, there have been few studies encompassing changes in both plants and animals.

The successional state of a system has been described as an inverse function of stress (Regier and Cowell, 1972). The sequence through which community structure is simplified by chronic stress has been suggested to be the reverse of succession, that is, retrogression (Whittaker and Woodwell, 1973). Odum (1969) listed several trends descriptive of developmental and mature stages. The usefulness of many of these general descriptors has been questioned. However, those specifically dealing with the decrease in the productivity to biomass ratio (P/B), the accumulation of organic matter, heightened nutrient retention, and increases in species richness, with time, seem to have general applicability at the

ecosystem level (MacMahon, 1980). The reverse of these trends would then be evidence of retrogression.

A pattern of simplification has been documented for forested ecosystems in proximity to SO₂ emission sources (Guderian and Kueppers, 1980). Under high dosage, near the source of contamination, the tree stratum is destroyed, followed by subsequent die-back of shrubs, herbs, mosses or lichens, one after another until the zone is barren. The denuded zone is surrounded by a transition zone containing isolated clusters of grass and resistant ground cover. This area adjoins the outer stunted forest zone. Less severe changes in composition are found under low to intermediate pollutant dosage. Kercher *et al.* (1980) have forecast from models that SO₂ pollution would increase white fir (*Abies concolor*) dominance at the expense of ponderosa pine (*Pinus ponderosa*) stands in a western coniferous forest. The reduced vigour of the stressed pines would provide the fir with a substantial advantage even at non-necrotic SO₂ levels. It is also evident that air pollutants influence the community makeup of later series by influencing reproductive success (Keller, 1976).

Gradient studies in forested systems have demonstrated retrogressive trends in biomass and species richness associated with increasing levels of pollutants (e.g. McClenahan, 1978; Freedman and Hutchinson, 1980a; Scale, 1982). There is less definitive evidence on P/B trends. The elimination of large tree species, as frequently reported in cases of severe stress, could raise the ratio of productivity to biomass in the remaining undergrowth community. However, the effects of the pollutant on photosynthesis might significantly retard primary productivity in these normally more rapid growing species.

5.7.2 Recovery in Aquatic Ecosystems

There is little defined theory describing successional patterns in freshwater and marine systems. However, there exists very good information on the successive recovery of ecosystems following pollution abatement and oil spill cleanups (e.g. Rosenberg, 1976; JFRBC, Special Issue, 1978; Turnpenny and Williams, 1981).

Much of the emphasis in recovery studies has been on the sequence of species recolonization. The general pattern of rocky shore community reestablishment after the *Torrey Canyon* oil spill was observed to be similar to that found after small scale removal experiments (Southward and Southward, 1978). However, the time scale of recovery of the oil-polluted system was significantly longer due to: (1) residual toxicity, (2) the extent of widespread mortality which restricted potential adult immigration and (3) the nearly complete removal of the herbivore community. Loya (1976) found that low level residual oil toxicity slowed the rate of recovery for a Red Sea coral community and may, in fact, have prevented the community from returning to its former configuration. Climate also affects recovery time. For example, oil spilled in colder water degrades more slowly, thereby retarding recolonization (Vandermeulen *et al.*, 1977). Conversely, spills

in the tropics, even though the oil may degrade more rapidly, can lead to higher water temperatures through increased absorption of solar radiation by the contaminated ocean surface (Chan, 1977). The compounded effects of temperature and oil toxicity can further stress intertidal communities. Southward and Southward (1978) noted that the temperate climate of Cornwall may have mitigated the effects of the *Torrey Canyon* spill on marine life.

Recovery from pollution can be separated into two phases: (1) colonization, (2) reestablishment of biotic interaction. During the colonization phase a species' capacity to immigrate, rapidly reproduce, and disperse young are essential attributes (Rosenberg, 1976), along with a resistance to persistent toxicity. The early colonizing community therefore consists of opportunists and forms highly resistant to pollution (Grassle and Grassle, 1974; Leppäkoski, 1975; Leppäkoski and Lindström, 1978). These species display many of the characteristics attributed to the reproduction-oriented strategist and may have been members of the original assemblage, although at relatively low population densities. The polychaete *Capitella capitata* exemplifies such a species in temperate estuarine environments, having widely dispersing pelagic larvae, an opportunistic benthic stage, and a short life cycle (Grassle and Grassle, 1974). Rosenberg (1976) reported *C. capitata* to be the dominant early successional colonizer, following abatement of pulp mill effluent. This 'opportunist' colonized unoccupied space rapidly under conditions of reduced competition, and comprised more than 90 per cent of the individuals in the benthic community during the first year of recovery.

In intertidal systems, shifts in the spatial patterns of species are common for the period prior to the development of strong biotic interactions. This is due primarily to the differing time scales of resettlement for different species. Southward and Southward (1978) reported that the rapid regrowth of macroalgae high in the intertidal splash zone was due to the absence of grazing pressure by limpets, which were drastically reduced in numbers by the *Tsesis* spill and cleanup. The lack of biological interaction appeared to be more important than was physical dessication in establishing the upper limit of algal growth on rocks.

The latter recovery phase is dominated by density-dependent population regulation. Specialists become more common following the displacement of early dominant opportunists. An obvious indication of this phase is the reestablishment of population equilibriums, through trophic and competitive interactions. Fluctuations in population densities of predators and prey are slowly damped as balance is restored in the pollution-disrupted cycle. Figure 5.12 demonstrates the restoration of these relationships for the limpet *Patella*, one of its major food sources, the alga *Fucus*, and its major competitors for space, barnacles. A decrease in both herbivore and algal density occurred between 1975 and 1976, at which time *Fucus* cover was reduced and *Patella* populations stabilized at a relatively lower density. With *Fucus* removed, competition for

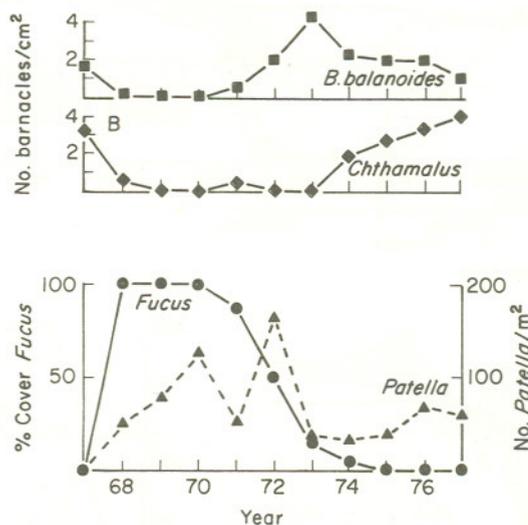


Figure 5.12 Population fluctuations during recolonization of flat rocks at mean tide level, at Trevone, from 1968 to 1977. Lower section: circles indicate percentage cover by *Fucus*; triangles, no. of *Patella vulgata* m⁻². Upper section: squares indicate no. of *Balanus balanoides* cm⁻²; diamonds, no. of *Chthamalus stellatus* cm⁻². (From Southward and Southward, 1978. Reproduced by permission of the *Journal of the Fisheries Research Board of Canada*)

attachment space increased between the barnacles, *Balanus* and *Chthamalus*. The recovery of the barnacle population when, by 1973, *Fucus* cover had been reduced by 75 per cent from the maximum levels attained during the early recovery phase, can be seen in Figure 5.12. This figure exemplifies not only the restoration of balance among populations, but also the effects of earlier stages on establishment of the eventual equilibrium. The importance of assessing recovery through both the recolonization and interaction phases has been repeatedly emphasized (Grassle and Grassle, 1974; Rosenberg, 1976; Leppäkoski and Lindström, 1978).

5.8 AN ILLUSTRATIVE CASE STUDY

Ecosystem recovery following the introduction of abatement measure in chronically polluted systems can illustrate many changes in structural characteristics common to the original sequence of degeneration. Many of these principles of structural destabilization were exemplified in the comprehensive study

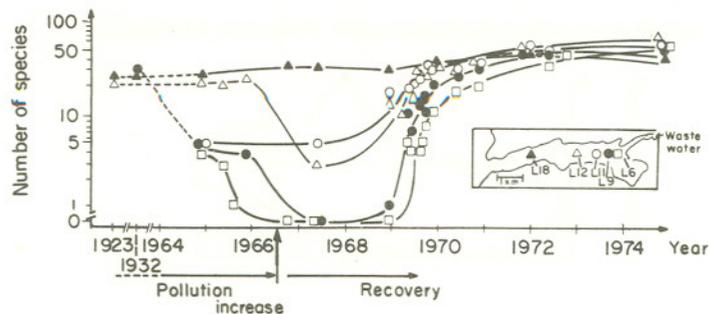


Figure 5.13

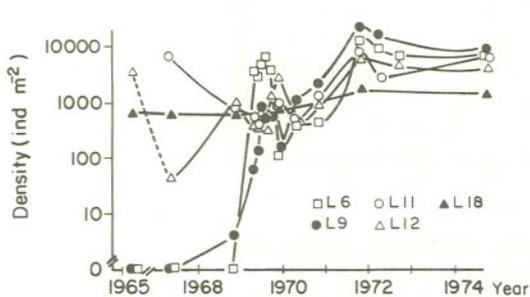


Figure 5.14

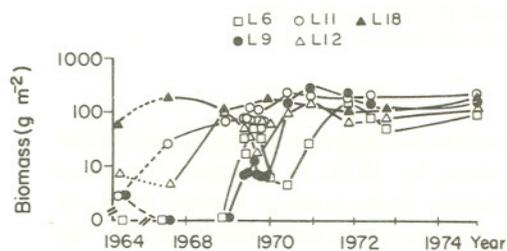


Figure 5.15

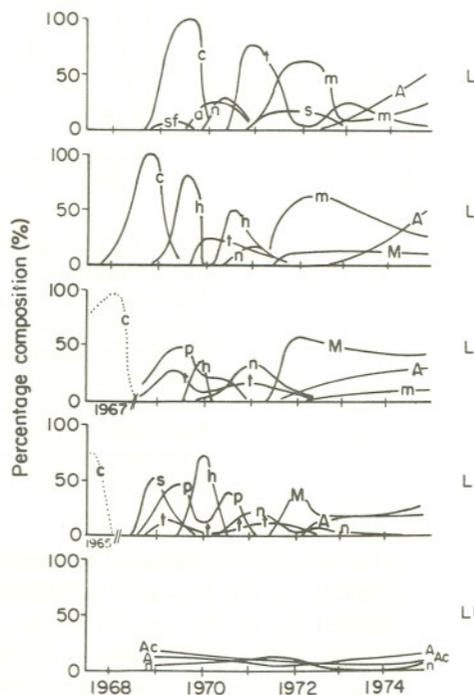


Figure 5.16

Structural characteristics describing the recovery of a pollution-perturbed estuarine system. (From Rosenberg, 1976, by permission of *Oikos*, Munksgaard, Copenhagen)

Figure 5.13 The succession of benthic species at five stations in the Saltkallefjord. The arrow indicates the time of pollution abatement

Figure 5.14 Dynamics of faunal density during 1965 to 1974

Figure 5.15 Benthic faunal dynamics of biomass (wet weight).

Figure 5.16 Percentage composition of some abundant populations during succession in the Saltkallefjord. c: *Capitella capitata*, a: *Abra alba*, S: *Scalibregma inflatum*, A: *Amphiura filiformis*, M: *Myriochele oculata*, Ac: *Amphiura chiajei*, n: *Abra nitida*, sf: *Scololepis fuliginosa*, t: *Thyasira spp.*, m: *Mysela bidentata*, h: *Heteromastus filiformis*, p: *Polyphysia crassa*

(Rosenberg, 1976) of benthic faunal dynamics following abatement of sulphite and pulp mill effluent into the Stalkallefjord in Sweden. Unfortunately, as with many pollution studies, good records of community characteristics were unavailable for the periods prior to and during much of the degeneration. During the period of severe pollution stress, the number of macroinvertebrate species was inversely related to the pollutant concentration, which decreased with distance from the effluent source. Figure 5.13 illustrates the increased time delay prior to recovery in species number at the more severely polluted sites. The indices of density and biomass (in Figures 5.14 and 5.15, respectively) show heterogeneity and discontinuity in the development of early recovery assemblages. Faunal density rose rapidly at all sample stations but there was a delay of approximately 2 years before species recruitment began at the most polluted sites. The graph of the number of individuals shows two peaks, 1969 and 1972, which appear to be representative of an estuarine recovery pattern (Leppäkoski, 1975). The data showed a primary maximum indicative of marine assemblages and a secondary maximum for freshwater-tolerant groups. Biomass (wet weight) also increased rapidly after an initial delay but continued to fluctuate throughout the colonizing phase of recovery. Biomass levels appeared to stabilize after 1971. The fluctuations in density and biomass characteristics were in contrast to the continuous trend of species recruitment in the early recolonizing phase. This emphasizes the predictability of the latter of these simple indices and is in accord with earlier discussions (sections 5.1 and 5.2).

Successive changes in dominance are displayed in Figure 5.16. With decreasing distance from the pollution source, the early dominance of the opportunistic polychaete, *Capitella capitata*, was evident from its higher percentage of relative abundance. In general, amplitude changes in relative abundance are larger and take longer to approach equilibrium in more severely polluted systems. The short duration of dominance displayed at site L12 is typical of the pattern expected for opportunistic populations which are able to expand rapidly into 'empty' niches created by pollution stress (Grassle and Grassle, 1974).

The information provided by the more complex indices of diversity and evenness, H' and J in this case, was somewhat confusing (Figure 5.17). An understanding of the biology of the estuarine system, and a great deal of care, must be exercised in interpreting these diversity trends. Although the species diversity at the reference site (L18) was high and relatively stable, as expected, the values calculated for polluted sites did not show a regular trend. Diversity at these sites peaked early in the recovery period and then declined by the third year. There was also some unexpected ordering of sites according to diversity during the early recolonization phase. For example, site L6, closest to the pollutant source, was more diverse than the less polluted site L12, in 1970. Some of the contradictions contained in the Shannon diversity data were associated with the equitability component. The evenness data showed that the relative abundance at several polluted sites was higher than that of the reference community during

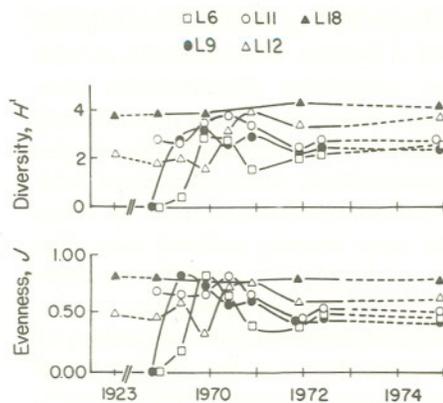


Figure 5.17

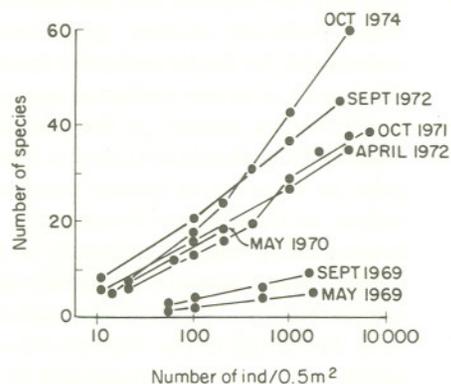


Figure 5.18

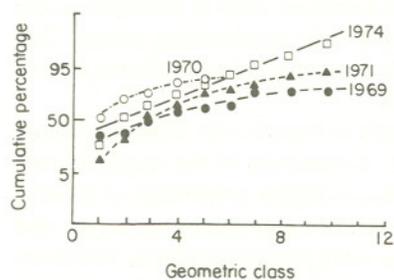


Figure 5.19

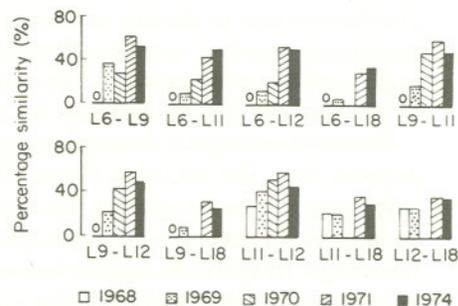


Figure 5.20

Structural characteristics describing the recovery of a pollution-perturbed estuarine system. (Figures 5.17, 5.18 and 5.20 from Rosenberg, 1976, by permission of *Oikos*, Munksgaard, Copenhagen; Figure 5.19 from Gray, 1979, by permission of The Royal Society)

Figure 5.17 Diversity according to Shannon (H') and evenness (J), at five stations in the Saltkallefjord

Figure 5.18 Diversity at station L6 according to Sanders' rarefaction technique

Figure 5.19 Log-normal plots of individuals per species during recovery from pollution in the Saltkallefjord. Reproduced with permission from Gray (1979)

Figure 5.20 Percentage species similarity of benthic fauna between pairs of stations in the Saltkallefjord. Data from L18 in 1970 is missing. 0 indicates no similarity

the early abatement period. High evenness values are frequently found for moderately stressed communities containing reduced numbers of species and individuals (Gray, 1979).

Rosenberg (1976) suggested that the Sanders' rarefaction technique provided a clearer picture of diversity trends (Figure 5.18) than the more complicated Shannon index. Gray (1979) reported that log-normal plots of Rosenberg's data (Figure 5.19) demonstrated a continuous pattern of recovery. The shape of the curves changed from a polluted pattern, through the transition form, to a typical clean-water distribution, through five years following abatement (see Gray and Mirza, 1979, for an explanation of log-normal plots).

Similarity measures such as percentage similarity (*PS*) were used both to order communities according to the magnitude of change due to the severity of sulphite pulp effluent stress and to establish community elasticity (Figure 5.20). In 1968 no similarity was found between communities at the two most polluted sites (L6, L9) and any other community. There was successive increase in *PS* from 1968 to 1970, and a specific trend towards increasing similarity was apparent during the later seral stages (1970–1971) as compared to the previous period. However, the pattern was not one of successive step increases as with the earlier recovery phase. The inability to define succession stages from 1971 to 1974, using the *PS* index, probably indicates that either (1) natural fluctuations were too large to permit separation of successive change in species number and abundance or (2) the pollutant concentration was no longer the factor controlling relative population abundance. This would infer that biological regulation of community processes had been reestablished.

The usefulness of similarity measures for distinguishing seral recovery through the initial recolonization phase appears to be greater than that of the complex diversity indices and, therefore, it complements the simple characteristic of species richness, which also shows an unambiguous trend with ecosystem recovery. The Rosenberg study also provided insight into several aspects of the stability–pollution relationship in an estuarine ecosystem. The reduced fluctuations in species number and fauna density from 1972 to 1974 indicated that the system had returned to a state of 'constancy'. The rather rapid recovery (5–7 years) and the fact that eleven of the fifteen species recorded at site L9 before pollution had reappeared in significant numbers by 1974, suggests that the system was highly elastic. High inertia and elasticity are properties expected of a physically and chemically varying ecosystem with an extensive history of pollutant stress. This example is an effective summary of the usefulness of structural characteristics in describing the ecosystem-level effects of pollution.

