

**WATER QUALITY AND STRESS INDICATORS
IN MARINE AND FRESHWATER ECOSYSTEMS:
LINKING LEVELS OF ORGANISATION
(INDIVIDUALS, POPULATIONS, COMMUNITIES)**

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The effects of stress on benthic algal communities

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The effects of stress on both microalgal and macroalgal communities are considered. On one hand the contrasting approaches of studies of these two communities reflect intrinsic differences in plant size, longevity and ease of handling. On the other hand they reveal that biological monitoring of the potentially deleterious effects of man's activities has focused largely on freshwater environments in which macroalgae only occasionally dominate. Large conspicuous plants can be readily investigated as individuals, whereas it is virtually impossible to trace effects of stress on an individual cell of a vegetatively-reproducing microalga; a population approach is almost inevitably necessary. However, rapid turnover rates, a spectrum of ecological characteristics distributed between many taxa, and the potential for statistical analysis, have facilitated the use of microalgae in environmental impact studies. Failure to extend such investigations into marine systems rests as much on man's ability to ignore environmental deterioration until it affects his quality of life as on the visual dominance of seaweeds around our coasts. However, large gaps remain in our knowledge of both large and small algae; some reported community changes over time are suspect, and the causes of even blatant changes are not always apparent.

Introduction

Stress is an imprecise concept, the definitions of which reflect the interests and points of view of their authors. For example, one of us chose the definition: "Stress may be said to occur when physiological (or other) processes are altered in such a way as to render the individual less fit for survival" (Brett 1958), while the other likes Grime's (1989) definition that invokes the term "stress" to describe "external constraints limiting the rates of resource acquisition, growth or reproduction of organisms". Certainly the most obvious symptoms of stress are alterations in the plant's performance.

Algae always live within the constraints imposed by their environment. When those constraints become extreme, the plants are stressed. Thus, stress is not caused only by pollution. It can also be an effect of a range of environmental conditions, e.g. pH, temperature, insolation and salinity, whether constant or fluctuating. Even predictable, characteristic fluctuations in light, temperature and exposure can stress the organisms exposed to them if the necessary physiological adjustments have a deleterious effect on photosynthesis, growth rate, tissue or thallus integrity, susceptibility to epiphyte colonisation, etc. Anthropogenic sources of stress in aquatic communities may also act by inducing extreme conditions, for example by increasing the concentrations of particular compounds or mixtures (such as organic compounds, heavy metals, and nutrients such as nitrates and phosphates), or by modifying the physical environment, e.g. altering temperature or flow regimes.

The different habitats colonised by algae subject them to a variety of stresses: fresh water poses different problems from sea water, and the conditions on the shore contrast with those in

the subtidal zone. Even more important is the variation in plant size. Clearly microalgae, often confined within the boundary layer, experience a different world from that inhabited by the larger seaweeds in the turmoil of the waves (Table 1).

Table 1. *Characteristics and adaptations of algae exposed to various environmental stresses in nature.*

Variable	Type of stress	Characteristics of microalgae	Characteristics of seaweeds
Hydrology	Shear stress/drag Desiccation Abrasion by sand	Morphological adaptation Drought resistance or persistence Morphological adaptation	Morphological adaptation Drought tolerance and rapid recovery Morphological adaptation and thallus 'toughness'
Substratum	Instability Siltation	Morphological adaptation Mobility	Ephemeral, opportunistic lifestyle —
Light	Seasonal changes Turbidity	Light adaptation, seasonality Shade adaptation	Shade tolerance, adaptation Shade tolerance
Water chemistry	Variability of pH, hardness and nutrient content	Physiological adaptation or indifference	Anatomical adaptation
Temperature	Diurnal and seasonal variations	Seasonality, persistence	Seasonality, life history changes
Other biota	Infection by bacteria or fungi Grazing Shading by canopy vegetation	Resistance to infection Chemical and anatomical adaptations Seasonal shade adaptation	? Chemical and anatomical adaptations Shade tolerance

In general, algae seem ill-prepared to meet the stresses that confront them. They evolved suspended in or protruding up into water, bathed in all the raw materials they need and buffered from the extreme vagaries of weather and climate. However, the necessity of having no obstacle to the absorption of nutrients means that the plants also have no outer barriers for protection. Some freshwater species have resting stages resistant to environmental extremes, but most benthic species do not, and such a device is unknown to the seaweeds. Algae are therefore particularly vulnerable to stressful conditions.

Stress operates on individual organisms, but its effects may be recognised at a variety of levels: molecular, physiological, population and ecosystem. Although we will chiefly address the effects at community level, these are essentially the outcome of differing physiological responses of interacting individuals. In studying effects on communities one should not forget that these are the result of differential physiological responses of the component species and their interaction.

Microalgae

Stress induces qualitative and quantitative changes in the structure and functioning of algal communities. Structural changes are usually assessed by analysing species diversity and/or composition (with or without reference to biomass or density). Functional effects are less frequently monitored, but various metabolic processes, biochemical assays and measures of growth rate can be used. The assumption is that structural and functional integrity are linked; if one is modified the change will be reflected in the other. However, some authors argue that functional capacity can be maintained even if structural changes occur when one species takes over the "role" of another (cf. Schindler 1987; Forbes & Forbes 1993).

Effects on community function

Because algae are autotrophic organisms, methods measuring photosynthesis or chlorophyll concentration can be used to monitor algal activity. Phytoplankton chlorophyll-*a* has been used as an estimate of trophic status in lakes or large rivers, such as the Rhine (Friedrich 1991), but wide seasonal fluctuations occur and only broad relationships between algal chlorophyll and nutrient loading can be drawn. When applied to benthic algae on contrasting substrata, pigment or biomass assessments are less suitable for resolving specific pollution problems because they are subject to differing velocities and spate events (Marker & Collett 1991). Biggs (1990) found that increases in chlorophyll-*a* concentration and specific growth rates of stream periphyton paralleled an increase in dissolved reactive phosphate. However, given the innate spatial and temporal variability of natural systems, only comparative measures between sites within particular aquatic systems are possible. It is not possible to make simple deductions about trophic status from chlorophyll-*a* concentration or primary production alone, but moderate organic pollution usually has a stimulatory effect on algae and raises their productivity in freshwater systems (Butcher 1947).

Other measures of metabolic activity, e.g. carbon fixation, can also be applied at the community level but, without information on the composition and density of that community, cannot show the direct effect of a stressor on photosynthesis. Fisher (1975) demonstrated that carbon fixation by diatoms in the presence of PCBs and DDT was reduced, not because carbon fixation per cell was lower, but because cell densities (compared to controls) were lower because of reduced cell division rates. Algal biomass had decreased although photosynthetic activity had not been impaired. Biomass has also been found to change in a species-specific manner in the presence of contaminants such as oil (McCauley 1966). Dennington *et al.* (1975) showed that *Euglena gracilis*, which could be abundant at polluted sites, showed no significant reduction in population size or growth rate in the presence of diesel or lubricating oil, whereas growth of *Scenedesmus quadricauda* (from cleaner sites) was reduced in 10% lubricating oil and halted by any concentration of diesel oil (0.1% to 10%).

Acidification has a negative effect on photosynthesis, probably mediated by the availability of dissolved inorganic carbon (DIC). Turner *et al.* (1987) found that epilithic net photosynthesis declined early in the experimental acidification of a lake, as DIC decreased and H⁺ increased, but epilithic dark respiration did not decline. Associated changes in algal community composition were probably due to interspecific differences in the competitive ability for DIC uptake.

Enzyme activity is another metabolic function with a potential monitoring role. As surface phosphatases are inducible under moderate phosphate limitation, the presence of phosphatase has been suggested (Whitton 1991) as an indicator of limiting phosphorus supply. Reichardt *et al.* (1967) and Healey (1978) have suggested its use as an indicator of phosphorus status in natural waters, but this may be unreliable since phosphatase activity is affected by phosphorus concentration in the organisms rather than in the environment (Whitton 1991). Although dissolved phosphate concentrations in streamwater may be low, supply to the organisms may be more than adequate because of constant replenishment in flowing waters (Biggs 1990; Schmidt, *pers. comm.*). Benthic communities may also be able to take up phosphate from sediments (Cox 1988); phosphorus-loading of sediments and the concentration in the overlying water are not always correlated.

Effects on community structure

Stress can modify the structure of algal communities by altering species complement, relative abundance of individual taxa, diversity and evenness of the community. Pearsall (1924) linked

phytoplankton assemblages with the physico-chemical characteristics of the lakes in which they occurred, but even earlier, one of the first attempts to monitor the effect of organic pollution on water quality incorporated algae (Kolkwitz & Marsson 1908). This "Saprobien system" and its developments rested on autecological knowledge of the component species, an approach followed by virtually all water quality assessments, except those based on diversity values only.

While the first saprobien indices gave indicator species for the different zones, Fjordingstad (1964, 1965) not only modified the assessments of species tolerance but also moved towards using community composition rather than single indicator species, and tried to improve the resolution of the zonation. He argued (Fjordingstad 1964) that communities should be used because "life is only possible in co-existence with other species". Therefore if all species are constrained by the environment it should be possible to integrate ecological information on all members of the community, in order to assess water quality. Other community indices of water quality based on the same argument include: organic pollution (Leclercq & Maquet 1987; Watanabe *et al.* 1988), diatoms (Leclercq 1988), community (Descy 1979) and river pollution (Watanabe *et al.* 1988). In slight contrast, Lange-Bertalot (1978) suggested a scheme in which the occurrence of certain species is used to distinguish between levels of pollution. However, all indices attempt to give a numerical value to water quality based on the composition of the diatom flora and the available ecological information on component taxa. Some involve elaborate mathematical equations (Knöpp 1954; Pantle & Buck 1955), although these methods are not without their critics (Caspers & Schulz 1960), while more recently, computer programmes incorporating ecological information on many taxa have been devised to analyse community data and automatically calculate several indices of pollution (Prygiel *et al.* 1991). Although the expansion of field databases linking species and water-chemistry variables reflects an attempt to calculate individual species "tolerances" and "optima" more objectively, they effectively rest on correlation between the frequency of occurrence at particular relative abundances in relation to measured water chemistry (Descy 1979, 1984), an approach with intrinsic shortcomings (see below).

Algal communities also vary with pH regime. Hustedt (1937-39) initiated the use of diatoms to estimate pH, based on the perceived "preferences" of the dominant taxa. His designations, "acidophilic", "alkaliphilic", etc., were based on observed species occurrence in relation to measured pH and implied ecological optima. Subsequent palaeolimnological pH predictions incorporate entire assemblages and various equations to calculate predicted pH (cf. Battarbee 1984). More recently, pH reconstruction studies have involved multiple stepwise regression of selected predictor taxa to pH, and the use of ordination techniques (Battarbee & Charles 1987; Flower 1987).

Changes in community diversity as a pollution indicator (advocated by Patrick 1949) seems to have developed from numerical inventories of taxa occupying different trophic levels in ecosystems, but has its roots in Thienemann's (1920) ideas about communities, with the implication that stability is a function of diversity. Another conclusion was that communities from unpolluted habitats are naturally diverse, while pollution causes a reduction in diversity and increasing dominance by one or a few species. Patrick (1949), Patrick *et al.* (1954) and Patrick & Hohn (1956) developed the use of diversity indices and deviations from log-normal curves as monitors of pollution, but their failure to consider the autecologies of the component species has invited criticism. Archibald (1972), for example, argued that a low diversity community in the Vaal River could not be caused by organic pollution as the dominant species, *Achnanthes minutissima*, requires highly oxygenated water for good growth. Also, although pollution eliminates sensitive taxa and reduces diversity, mildly polluted waters can have high diversity values when organic pollution increases the tolerant species without causing loss of

sensitive ones. Low diversity is not inevitably a function of pollution although many intrinsically species-poor communities in unpolluted habitats, e.g. low pH waters and high mountain lakes, probably are stressed.

Deducing species optima

Although diversity estimates which utilise artificial substrata or defined area sampling can be expressed as cells per unit area, this is not inevitably the case, and information related to community density may be ignored. Furthermore, relative abundance (= per cent abundance) is often used without recognition that this measure is density independent but affected by the number of taxa in the sample. By percentage abundance a taxon may be strikingly dominant, but not have achieved its maximum density; alternatively, lower percentage abundance may coincide with higher cell density (Cox, unpublished). Therefore high relative abundance should not necessarily be taken to imply optimal growth when assessing species tolerance and ranges.

There are two main difficulties in deducing ecological tolerance and optima from field data: firstly, species are probably often growing under suboptimal conditions; secondly, the reliability of designations from field distributions, even when statistically evaluated, depends upon the size, evenness and inclusivity of the environmental variables data-set (cf. Descy 1984). Furthermore, the use of terms such as "successful" or "dominant" may be inappropriate when based only on numerical superiority, without allowance for intrinsic differences in growth rate, survival strategies or relative size (Cox 1991). Nevertheless, most modern methodologies for assessing water quality, predicting past pH or salinity, continue to use field correlations based on percentage abundance. Intriguingly, while consideration of the entire diatom assemblage is generally encouraged, Round (1993) reverts to the explicit use of dominant, indicator species to recognise water quality zones in British rivers.

The indicator species concept rests on taxa having clear, narrow field ranges or presenting a characteristic response to particular conditions, allowing identification of those conditions from the presence of a taxon. Although Round (1993) uses indicator species to monitor general deterioration in water quality, they have more frequently been used to demonstrate extreme pH or metal pollution (Whitton 1970; Besch *et al.* 1972; Say & Whitton 1980), especially where tolerant strains have been identified, although tolerance may be dependent on other environmental variables (Whitton & Diaz 1981). Morphological changes in widespread species may also be indicative of pollution or nutrient deficiency. For example, many diatoms produce teratological forms in high metal environments (Carter 1971); *Stigeoclonium tenue* produces long hairs under conditions of phosphate deficiency (Gibson & Whitton 1987); some Rivulariaceae produce tapered trichomes and colourless hairs in the absence of combined nitrogen (Sinclair & Whitton 1977). The indicator species approach primarily records species present under differing contamination, noting those which remain and are presumed tolerant, although some authors, e.g. Besch *et al.* (1972), also take abundance into account. Whilst sometimes presented as opposing, mutually exclusive systems, even within a community approach, some species are recognised as being of good or poor indicator value, according to whether they have a wide or a narrow ecological amplitude (Fabri & Leclercq 1986).

Seaweeds

Seaweeds inhabit two contrasting stress regimes. Species found in the subtidal zone inhabit a predictable environment bereft of extremes. Conditions in the sea are very stable over time. For example, the salinity of the oceans has changed little over the last 600 million years (Seibold & Berger 1982). Seasonal changes in conditions are also very slight. Around the British Isles, sea surface temperature varies by only 7–8°C throughout the year.

In contrast, intertidal seaweeds are no strangers to stress. Indeed it is difficult to think of any other habitat in which the plants spend so much time out of their "natural" environment. The intensity of the stress is extreme. Waves ravage the coast and, allowing for the density of water, a storm wave is equivalent in effect to a wind gust of almost 430 m s^{-1} (950 miles h^{-1}). It would brush aside an oak tree, yet the seemingly fragile seaweeds thrive on all but the most exposed shores. How they manage this feat is discussed by Norton (1991). Even so, some species are more wave-tolerant than others, indeed the seaweed communities are sufficiently different on exposed, intermediate and sheltered shores to provide an indicator of wave exposure (Lewis 1964).

When the tide withdraws it exposes innately marine organisms to rapid fluctuations in aerial conditions. Animals seal off their shells, hunker down or seek out damp havens, but seaweeds must take the brunt of desiccation, not only for themselves but on behalf of the diverse community that shelters beneath their canopy.

Stress operates at the level of the individual plant and the effects on seaweeds of air and water temperature, insolation, pollution and disease are detailed by Kinne (1970, 1971), Andrews (1976), Norton (1985) and Kain & Norton (1990). In general, characteristically subtidal plants have much narrower tolerances to most abiotic environmental stresses than do intertidal species (see Norton 1985). Indeed many intertidal plants exhibit an extravagant tolerance range and are able to withstand some conditions far more extreme than they are likely to encounter in nature. Some other species, however, avoid seasonal extremes of conditions by perennating in the most resistant phase of their life history. Yet others can rapidly "harden off" as conditions change, so that they have increased frost tolerance in winter (Parker 1960; Bird & McLachlan 1974) and desiccation tolerance in summer (Schonbeck & Norton 1979).

The effects of water quality are difficult to evaluate. It is not always clear what represents "poor" or "good" water quality for seaweed communities. Although nutrients, especially nitrogen, are present in the sea only in low concentrations, it was assumed that the large volume of water that could be sampled by a seaweed would compensate for this. Some seaweeds in calm-water sites, however, have been shown to be under nutrient stress, and the addition of nitrogen to the water stimulates seaweed growth in some coastal waters (reviewed by Norton 1991). Sewage outfalls may therefore supplement the nutrient supply and enhance the growth of local seaweeds rather than depress it. Ephemeral green seaweeds often benefit most, for all their characteristics favour rapid nutrient uptake and growth (Norton 1991), indeed they have been used for stripping nutrients from overenriched waters (e.g. Vandermeulen & Gordin 1990) and some, such as *Ulva lactuca*, can double in thallus area in only 3–4 weeks (Kanwisher 1966). Indeed the growth rates of *Ulva* have been proposed as an indication of various sorts of pollution (e.g. Burrows 1971).

Water-borne toxins may of course have adverse effects on seaweed communities, which can be disrupted by a variety of chemicals from industrial effluent (e.g. Edwards 1972a; North *et al.* 1972; Hoare & Hiscock 1974; Wilkinson *et al.* 1980). Also the growth of certain seaweeds, either in nature (Widdowson 1972) or in water samples collected from the sea, has been tested as possible bioassays of water quality (Clendenning & North 1960; Burrows & Pybus 1970, 1971; Burrows 1971; Edwards 1972b; Hopkin & Kain 1978). It remains a problem, however, to determine exactly what is affecting the growth of the plants. The growth of *Laminaria saccharina* in culture, for example, is depressed by detergents, filtered sewage sludge and industrial waste, as well as by non-toxic silt, reduced salinity and dim light (Burrows 1971).

The most dramatic changes in seaweed-dominated communities are brought about by stress adversely affecting either the dominant canopy-forming plants or the grazers that prey on them. Many benthic marine communities are dominated by large plants of one or few species.

Because of their large surface areas and complex shapes such plants harbour a rich epifauna and flora (Kain & Norton 1990; Norton 1992). Moore (1973), for example, found that 72 holdfasts of *Laminaria hyperborea* yielded 90,000 animals from 387 species. Clearly any reduction in the abundance of such a plant has immense repercussions for the entire community.

Seaweed-dominated communities are also stratified, like a tropical forest (e.g. Dayton *et al.* 1984; Foster & Schiel 1985). Thus if there is a loss of the canopy-forming species, obligate understorey species may decline (Dayton 1975a,b), but other plants that had been inhibited by the overshadowing canopy may be released to thrive in the sun (Dayton *et al.* 1984; Hill & Norton unpublished). Canopy loss may also allow the ingress of many species that are normally excluded (Kain 1975; Deysner & Norton 1982).

If eliminated or drastically reduced by a single event, the canopy may take between 2 and 7 years (or considerably longer in the exceptional case of *Ascophyllum*) to re-establish itself (reviewed by Kain 1975; Kain & Norton 1990). Piecemeal loss of canopy plants may result in a mosaic, with each patch at a different stage of canopy restoration (Dayton *et al.* 1984).

Grazers such as limpets, chitons and snails on the shore, or urchins and fish in the subtidal zone, can truncate seaweed zones, influence species diversity or even eliminate all but the most resistant species (reviewed by Kain & Norton 1990). Major community disruption may occur when a minor catastrophe such as a severe rain storm (Littler & Littler 1987), ice scouring (Keats *et al.* 1985) or pollution (Southward & Southward 1978) eliminates grazers, allowing many normally suppressed species to flourish. The repercussions of such events may be felt for many years (e.g. Burrows & Lodge 1951; Kitching & Thain 1983; Novacek & McLachlan 1986).

Pollution provides an additional stress, of which seaweeds have only limited evolutionary experience. Although their short generation time sometimes enables algae to rapidly develop a resistance to some pollutants (Russell & Morris 1973), this is not invariably the case.

For seaweeds, the main adverse effects of sewage are thought to be increased water turbidity (reducing light penetration and therefore photosynthesis) and the siltation of sewage-derived sediment. Even a very thin layer of silt can smother attached germlings and prevent the attachment of settling propagules (Norton 1978). Sometimes plants are eliminated not by the effluent itself but by grazers attracted to the outfall (Kirkham & Young 1981). It should also be remembered that sewage enters the sea in fresh water which is itself a stressor of marine algae. It is noteworthy that the pattern of community change approaching a sewage outfall is very similar to that occurring within a river estuary (Table 2), and in both situations the euryhaline green seaweeds dominate in the region of highest stress.

Table 2. Species richness and the composition of seaweed communities along a salinity gradient (Great Pond Estuary, Massachusetts, USA) and a pollution gradient from a sewage outfall (Sydney, Australia).

Calculated from data in Conover 1958 and Borowitzka 1972.

Seaweeds	Mouth of estuary	Decreasing salinity →				Upper tidal limit
Total number of species	40	45	34	34	25	8
Percentage of chlorophyta	10	18	29	32	48	100
Seaweeds	"Unpolluted"	← (Decreasing pollution)			Outfall	
Total number of species	41	39	28	15	6	2
Percentage of chlorophyta	17	26	25	33	67	100

Seaweed communities are most at risk from pollution in sheltered bays and lagoons where effluents are more poorly dispersed than on the open coast. Often, as with microalgae, there is a reduction in species richness, algal biomass and also community stratification in proximity to outfalls (Table 2, and Borowitzka 1972; Hoare & Hiscock 1974; Littler & Murray 1975). However, in contrast to the situation with microalgae, diversity indices for seaweed communities have few adherents.

Chronic pollution stress can substantially deplete seaweed communities. In the Firth of Forth, for example, a hundred years ago the shore at Joppa was clean and had luxuriant algal growth but Johnston (1972) found it silted, with sewage in the pools. There had also been a 41% reduction in algal species and 55% of the once most common species had been lost, whereas unpolluted shores nearby showed no such impoverishment (Johnston 1972; Wilkinson & Scanlon 1987). The progressive reduction of sewage discharged at Joppa from 1978, led to a 16% increase in species richness (Wilkinson & Scanlon 1987). A similar pattern of decline and recovery in response to changes in water quality has been reported for many polluted sites, notably Oslofjord (Bokn *et al.* 1992).

A reduction in seaweeds allows other communities to prosper in polluted sites e.g. mussels and barnacles (as at Joppa) or mats of benthic diatoms, cyanobacteria or sedentary polychaetes. The seaweeds that survive are usually crustose or low turf-forming species and opportunistic green algae. In general they tend to be highly productive, early successional forms with simple, short life histories (Littler & Murray 1975).

In general, oil spills affect the dominant brown seaweeds less than marine animals (Notini 1978; Bellamy *et al.* 1967). The elimination of grazers such as limpets and periwinkles, which often results from the dispersants used to clear the oil rather than the oil itself, allows the shores to become swamped by ephemeral green seaweeds, to be replaced within a year or two with dense communities of fucoids. It takes 10 years or more for some of the shores to return to their pre-oiled state (Southward & Southward 1978). A feature of these dense fucoid communities, following disturbance, is that the ordered zonation of the plants may be lacking, with many plants occurring "out of zone" until environmental factors and competition progressively restrict their distribution (Burrows & Lodge 1951).

An abundance of ephemeral green algae is often an indication of any stress-related disruption of benthic communities. In heavily polluted sites, algae such as *Ulva*, *Enteromorpha* and *Monostroma* cease to be the friendly "sea lettuce" and form instead great floating green "tablecloths". Such "green tides" have been reported world-wide and are specially troublesome in the Venice Lagoon where they produce over a million tonnes fresh weight of tissue per year (Sfriso *et al.* 1989). This material sinks, to decay on the lagoon floor where it deoxygenates the water and generates hydrogen sulphide, which eliminates many benthic invertebrates that would otherwise survive in the eutrophic conditions.

Determining the causes of change

Change in algal communities is complex and our understanding often inadequate. Natural, seasonal changes may be substantial and difficult to differentiate from those induced by man. Organismal responses are many and varied, and affected by external environmental factors and intrinsic physiological processes. The effect of a particular stressor may be modified by temperature, or light regime, but will also depend upon the age and health of the algae; juvenile plants are often more susceptible than adults.

Although field manipulations can demonstrate community differences in relation to some factors, the underlying processes remain obscure. Some significant changes may not have any obvious cause. For example, on the Berwickshire coast in Scotland we have evidence that there

was a dramatic decline in the abundance of *Mastocarpus stellatus* (= *Gigartina stellata*) between 1941 and 1961. The decline occurred at sites where there was no apparent pollution and no corresponding decline in other species. On the North Wales coast, *Nemalion helminthoides* mysteriously vanished for many years and then reappeared equally inexplicably years later in the same places as before (Jones 1974). Insufficient information on natural turnover rates, the growth and loss processes acting on each component, and the influence of interspecific competition, prevents us from identifying causes of such fluctuations in species composition.

Correlation between an environmental change and a shift in community composition is not proof that they are causally linked. In 1977 a flush of green seaweeds swamped the shore at Dounreay, Scotland, after 17,000 gallons of oil had leaked from a storage tank and been cleared with dispersant. It seemed to be a typical pollution event. However, the green algal bloom was not caused by this pollution incident, but followed the death of large numbers of algae, barnacles and limpets after an exceptionally hot dry spell prior to the oil leak (Bowman 1978). Elsewhere it may be difficult to identify the stressor responsible even for blatant community changes, particularly if there is a delay between the application of the stress and the appearance of the symptoms. Summer pruning of seaweed zones on the shore, for example, occurs 3 weeks after the causal conditions (Schonbeck & Norton 1978). Clearly, response times are shorter for microalgal communities in which turnover rates are faster, but even so, field correlations are often inadequate to explain change (Cox 1993).

The effects of one stress may not eliminate a plant directly but render it more vulnerable to another stress. For example, nutrient-enrichment pollution may promote heavy growths of epiphytes on some seaweeds (Bokn *et al.* 1992) and this may reduce the growth of the "host" plant by shading its thallus and stealing its nutrients (Norton 1992). The greater susceptibility of some species to epiphytization may alter the competitive balance between canopy-forming species (Bokn *et al.* 1992). Desiccation-stressed individuals of *Padina gymnospora* were twice as susceptible to grazing as were unstressed plants, presumably as a result of a loss of chemical defences (Renaud *et al.* 1990). Conversely, in other species, desiccation or previous grazer attack may increase defences and thereby reduce their palatability (Van Alstyne 1988; Renaud *et al.* 1990). Microalgae may also be deleteriously affected by particular conditions when combined with another stress. The diatom *Meridion circulare* is typically found in the spring, in cool shady waters, although it can occur under brighter light in the summer. Experimental studies revealed that although it can grow under high light at low temperatures, growth ceases when water temperatures are also raised (Cox 1993). Such subtle effects presumably alter the competitive abilities of the species and thereby influence communities but, even for macroalgae, they are very difficult to unravel in the field.

Still less is understood of the competitive interactions between microalgae. Light attenuation and self-shading have been demonstrated in dense populations, but it is often assumed that microalgal species do not compete for essential nutrients or gases. Yet differing abilities among planktonic diatoms to take up particular elements (Tilman 1982) can explain why one rather than another predominates. Survival (and dominance) of a few species in extreme environments may not be because they are "better suited" to the conditions, but simply because there is less competition. If cell density rather than abundance were used to assess "success" this question might be resolved.

Reports of long-term reductions in species richness are sometimes exaggerations and, even where a real decline is identified, a variety of conditions may be responsible. For example, *Fucus vesiculosus* has progressively declined on the southern coast of Finland as a result of a natural rise in salinity and nutrient concentrations, and the consequent increase in epiphytes

and herbivorous isopods (Kangas *et al.* 1982). Changes in diatom communities with increasing lake acidity may be the outcome of natural weathering processes or changes in land use, rather than acid deposition (Battarbee 1984). Caution is called for in the interpretation of field observations, with an awareness that hypotheses erected on the basis of correlations always require rigorous testing before the causes of change are clear.

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