# THE DECREASE OF BIODIVERSITY IN AQUATIC HABITATS

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## ABSTRACT

A reasonable amount is known of the potentialities of the factors which determine community structure, but rather less about their actual potencies and the patterns of their action in nature. Discovering the rules through which communities are constructed from populations is one of the many exciting challenges that confronts population ecology today.

Key words: biodiversity, community structure, disturbance, instability, habitat size, habitat diversity.

## RESUMO

Já se acumulou razoável quantidade de conhecimento sobre o potencial dos fatores que determinam a estrutura da comunidade, porém, comparativamente pouco ainda sobre suas potencialidades atuais e os padrões de sua atuação na Natureza. Descobrir as regras segundo as quais as comunidades são constituídas a partir das populações é o desafio com que hoje se defronta a ecologia de populações.

Palavras-Chave: biodiversidade, estrutura da comunidade, perturbação, instabilidade, tamanho do habitat, diversidade do habitat.

## INTRODUCTION

The notion of biodiversity is old; naturalists have always recognized and made a good distinction between communities that are poor and communities that are rich in species. However, our knowledge of phytoplankton diversity is still feeble and the little we have is fragmentary.

The term 'species diversity' is classically used to express the number of populations present in a particular habitat. For convenience these populations are called species populations, but their precise taxonomic nature is very variable. Some animal populations would perhaps be better regarded as subspecies, and some plant populations as ecotypes. The only criterion by which populations can be separated is their genome, which for each population will represent a distinct gene pool; this, while retaining its separate identity, may still engage in gene exchange with neighbouring populations (BOUGHEY, 1968). Species diversity as defined above takes no account of species abundance, that is, the number of individuals in each population.

The composition of phytoplankton communities is commonly related to the trophic stage of lakes. Thus oligotrophic lakes are in general characterized by a relatively low quantity of phytoplankton, and population pulses are uncommon. Eutrophic lakes, on the other hand, support a typically large quantity of phytoplankton composed of only a few species, and the pulses are common and frequent.

Thienemann stated that species number tends to be small and the number of individual specimens of each species very great in habitats that are distant from the conditions considered usual, or conditions that fluctuate and for that reason severe. Periodical fluctuations intervene in the sense that any sample obtained at a given moment contains a few species favoured at that moment and thus represented by many individual specimens, side by side with a series of species that are referred to as rare and that are nothing but remains of the preceeding species or the beginning of some future ones. In a similar manner, the precarious participation of a large number of species is explained by the presence of individuals of species that develop better in other systems; that is, plankton diversity is increased due to the presence of numerous

elements of an accidental plankton — the ticoplankton — especially frequent in not too deep lakes.

## FACTORS AFFECTING COMMUNITY STRUCTURE

Community structure may be affected for a number of reasons, among which the following are significant: (1) interspecific competition, (2) predation, (3) disturbance, (4) instability, and (5) size and diversity of the habitat. The first two of these factors will not be considered here.

### Disturbance

According to CONNELL (1979), disturbance is the indiscriminate, catastrophic removal of all individuals from an area. As such it may take a wide variety of forms: e.g., lightning, storms, landslides or even indiscriminate predation. In general terms, the effect of disturbance will be to prevent communities from reaching an equilibrium; parts of them, at least, will repeatedly return to early, colonizing stages of succession. The more specific effect on species diversity, however, will depend on the nature of the equilibrium community itself; this, in turn, will depend on the other processes discussed here. Nevertheless, a plausible, general relationship between disturbance and diversity has been proposed by CONNELL (1979) — the 'intermediate disturbance hypothesis' — and the role of disturbance in determining community structure can be usefully discussed in this context.

Connell recognized three basic levels of disturbance. At one extreme, where disturbances are frequent and large, the community will tend to be dominated by opportunistic, fast-colonizing species, with, perhaps, a few individuals of intermediate, secondarily colonizing species, probably only present as juveniles. Such a community will consequently have a simple structure and a low diversity. At the other extreme, however, where disturbances are rare and small, the diversity will depend on the importance of what Connell calls 'compensatory mechanisms', i.e., predation, resource-partitioning and so on. As was

already demonstrated, where these are prevalent diversity will be high. In their absence, however, only highly competitive late-succession species will be able to survive, and diversity will be low. At intermediate levels of disturbance, on the other hand, even in the absence of compensatory mechanisms, there will probably be a few adults of fast-colonizing species, many individuals of mid-succession, secondarily colonizing species, and even some individuals, possibly juveniles, of late-succession species. Overall, therefore, diversity will be high; in the comparative absence of compensatory mechanisms, the species-diversity of communities will be highest at intermediate levels of disturbance.

Some of Connell's evidence in support of this hypothesis is shown in Fig. 1, with data from observations on a coral reef off the coast of Queensland, Australia. Disturbance, resulting either from hurricane damage or from effects of anchoring boats on the reef, is measured as the percentage of a site that is devoid of any live coral, and it is indeed apparent that diversity (number of species per sample) is highest at intermediate levels of disturbance. As further evidence, Connell points out that even in tropical rainforests, which are thought of as exhibiting very high diversity, areas that are largely undisturbed (like the Budongo forest in Uganda) come to be dominated by a single species of tree (in this case, ironwood).

Overall, therefore, we can accept that in some cases diversity will be highest at intermediate levels of disturbance; and that large frequent disturbances will tend to decrease diversity. On the other hand, the effects of disturbance on diversity will be much less clear-cut whenever compensatory mechanisms are sufficiently potent to ensure that stable climax communities exhibit a high degree of diversity themselves.

## Instability

As far as the role of instability is concerned, all populations are, to a greater or lesser extent, liable to become extinct. Whenever this occurs, the structure of the the community containing that population will obviously change. However, this liability is bound to be greater in some communities than others, and in this sense some communities must be more unstable than others. Yet the communities with

structures conferring stability are the ones most likely to be observed, because they persist. Structural instability must, therefore, be an important determinant of the community structure observed.

The search for what inherently leads to instability has been the province of theoretical ecologists, and, to paraphrase MAY (1979), two interconnected conclusions have emerged:

(1)     In 'randomly constructed' model ecosystems, an increase in the number of species in a community is associated with an increased dynamical fragility and a diminished ability to withstand a given level of environmental disturbance. Thus relatively stable or predictable environments may permit fragile, species-rich communities to exist; while relatively unstable or unpredictable environments will support only a dynamically robust and therefore relatively simple ecosystem.

(2)     Real ecosystems are not assembled randomly. They are the products of long-running evolutionary processes. We are therefore bound to ask: what special structural features of real ecosystems may help to reconcile community complexity with dynamical stability? In other words, since instability will tend to simplify communities, what observable features of community structure can be deemed to exist by virtue of the stability they confer on complex, species-rich systems? The proposed 'role of instability' will then be the 'selection' of these features.

The attempt to discover what these features might be has also been the province of theoretical ecologists; and, as yet, such attempts have been largely speculative. Nevertheless, there are several interesting possibilities (MAY, 1979). MAY (1972), for instance, and more recently GOH (1978) have suggested (from the analysis of models) that ecosystems will be more robust if they consist of 'loosely coupled subsystems'. This term describes a situation in which a community consists of several parts ('subsystems'), *within* which there is considerable biological interaction, but *between* which there is very little interaction. This, according to LAWTON & PIMM (1978) and BEDDINGTON & LAWTON (1978), is at least consistent with the observation that most insect herbivores are monophagous or

oligophagous, giving rise to relatively discrete food chains even in species-rich plant communities. However, empirical evidence generally fails to give positive support to the hypothesis (PIMM & LAWTON, 1980).

Another feature of natural communities possibly subject to selection by instability is the length of food chains, which rarely consist of more than four or five trophic levels. The conventional explanation for this is that length is limited by inefficiency of energy-flow from one trophic level to the next (there is insufficient energy left to support the higher trophic levels). Yet, as PIMM & LAWTON (1977) have pointed out, this cannot, by itself, explain why food chains are about as long in the tropics (where energy input is high) as they are in the barren Arctic (where energy input is low). An alternative explanation, however, was provided by PIMM & LAWTON themselves. By studying the stability properties of various Lotka-Volterra models, they argued that long food chains may typically result in population fluctuations that are too severe for top predators to exist. In other words, only relatively short food chains are sufficiently stable to be observed in natural communities.

Finally, PIMM & LAWTON (1978) have explored the relationship between omnivory and stability by studying model ecosystems based on Lotka-Volterra equations. Broadly speaking, they concluded that omnivory and overall dynamical stability are easier to reconcile if the omnivores and their prey are of similar size and population density, a situation that most commonly pertains to insect parasitoids. As MAY (1978, 1979) suggested, this may account for the diversity of insects in general and the diversity of parasitoids in particular.

To summarize: while its precise role remains largely the subject of theoretical speculation, it is quite clear that instability can play a crucial part in determining the structure of natural communities.

## Size and diversity of habitat — the role of habitat

As GORMAN (1979) has pointed out, Great Britain has 44 species of indigenous terrestrial mammals, extant or recently extinct, but

Ireland, just 20 miles further into the Atlantic, has only 22; and while this might conceivably reflect the difficulties the mammals have in crossing water, it actually affects bats as much as any other group: only 7 of Britain's 13 species breed in Ireland. Furthermore, of Britain's 171 species of breeding birds, only 126 are recorded as breeding in Ireland, and 24 of these do so only occasionally. For example, there are no woodpeckers in Ireland (though there are plenty of trees), no little or tawny owls, and no marsh or willow tits.

The most likely explanation is that Great Britain is far larger than Ireland. But size can exert its effects in two quite separate ways. Perhaps the most obvious explanation is that differences in habitat size are important because large habitats are more diverse. But there is a second explanation that applies whenever habitats can be thought of as islands (either real islands, or 'habitat islands' of one type surrounded by a 'sea' of another habitat type). Larger islands support larger populations that have a relatively low probability of becoming extinct. In addition, larger islands represent a larger 'target' for colonization by species not already present (MacARTHUR & WILSON, 1967). On two counts, therefore — extinction and immigration — we can expect larger islands (i.e. larger habitats) to support more species. Note, too, that this is an explanation for the fact that (small) islands generally support fewer species than a nearby (larger) mainland.

A typical relationship between the number of species living on an island and the island's area is illustrated in Fig. 8.6 (BEGON & MORTIMER, 1986), for the amphibians and reptiles living on oceanic island in the West Indies (MacARTHUR & WILSON, 1967). The logarithm of species number rises with the logarithm of island area in a remarkably linear fashion, and the slope of 0.30 is very much in line with those obtained in other examples. For organisms ranging from birds to ants to land plants, in both real and habitat islands, the slopes of such log-log plots mostly fall within the range 0.24-.034 (GORMAN, 1979). The role of island (i.e. habitat) size as a determinant of species number (and thus community structure) is, therefore, well-established.

An indication of the fact that size acts through two mechanisms is provided by data in Fig. 8.7 (WILLIAMS, 1964). This, too, is a plot of log species number against log habitat size, but size in this case

pertains to arbitrary sampling areas within a mainland. Once again, on this log-log plot, the number of flowering plants rises linearly with the size of sampling areas in England. But the slope — around 0.1 — is noticeably lower than those from the island examples, and falls near the rance typical for mainland studies: 0.12-0.17 (MacARTHUR & WILSON, 1967). The crucial point is that habitat size can only act via habitat diversity in such cases. These arbitrary areas are continually exchanging organisms with surrounding areas, and they are not, therefore, subject to the considerations of extinction and colonization that apply to isolated islands. Thus, mainland slopes from 0.12 to 0.17 reflect the effects of habitat diversity, while the increased slopes on islands reflect the additional size-effects peculiar to island biogeography.

Overall we can see that an increase in habitat size will lead to an increase in species number, and thus to an increase in the complexity of community structure. This may result from the indirect effects of habitat diversity, or from effects peculiar to the island nature of many habitats; and while it is often difficult to partition the total effect into these two components, there is no doubt that both are of very widespread importance.

## CONCLUSIONS

We have seen that a variety of factors can influence community structure. Yet in truth it has to be admitted that precise statements as to their relative potencies must await further advances in our knowledge and understanding. Nevertheless, certain tentative conclusions can be drawn. Perhaps the most significant of these is that a good case can be made for the constancy, predictability and productivity of the abiotic environment being of absolutely crucial importance in determining community structure. This conclusion stems from a number of considerations: (a) in general terms, diverse, basically fragile ecosystems appear to be relatively stable in constant, predictable environments; (b) more specifically, niches can be stably packed more tightly in predictably productive environments. This suggests that

interespecific competition will be most potent as a mechanism promoting diversity under such circumstances; (c) equally specifically, the stable existence of top predators will be favoured in predictably productive environments (PAINE, 1966). It is, therefore, in such cases that they will be most potent in keeping potential competitors below their carrying capacities, and thus promoting diversity still further; (d) finally, these other mechanisms will tend to reinforce one another. High diversity at a lower trophic level will certainly provide for niche-diversification (and thus increased diversity) at the next highest trophic level; and it is possible that this will lead to an increased intensity of predation, and thus a further increase in diversity, at the lower trophic level. Small 'inherent ' differences in community structure are, therefore, likely to become exaggerated. Note, however, that this reinforcement will occur whatever the cause of the inherent differences. Note, too, as another aspect of this reinforcement, that those effects of habitat size that are attributable to habitat diversity will themselves be influenced by increases in the diversity of the biotic aspects of a habitat.

In short, there is good reason to believe that the constancies, predictabilities and productivities of abiotic environments are crucial, underlying determinants of community structure; and that competition, predation and ecosystem instability are mechanisms through wich they exert their influence. This is almost certainly the explanation for the single most important cline of increasing diversity: from the poles to the tropics.

This view is opposed, to some extent, by Connell's 'intermediate disturbance hypothesis', since a constant, predictable environment is likely to be one with a low level of disturbance. On the other hand, Connell's 'disturbance' requires the indiscriminate removal of species from an area, and an environment can be inconstant and unpredictable without this happening. It is, therefore, possible that this hypothesized mechanism acts independently of the other factors considered.

Finally, the 'island' effects of habitat size are likely to superimpose their influences on community structure wherever they occur; and, to the extent that all environments are patchy, they are likely to occur everywhere.

## ACKNOWLEDGEMENTS

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