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Intermediate disturbance in the ecology of phytoplankton and the maintenance of species diversity: a synthesis

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Abstract

This paper concludes a collection of contributions presented at the 8th Workshop of the International Association of Phytoplankton Taxonomy and Ecology. It derives a consensus as to the virtues and strengths of J. H. Connell's Intermediate Disturbance Hypothesis (IDH), its applicability to phytoplankton ecology and its theoretical and practical weaknesses. The view is expressed that the IDH is too useful a concept to reject and that, as a word model, it provides a powerful link between diversity and disturbance. The more robust investigations that are necessary to consolidate the tenancy of IDH need to concentrate upon the separation and quantification of the stimulus- and response-components of disturbance.

Introduction

The purpose of this short paper is to conclude the collection of articles contributed to the IAP Workshop on The Intermediate Disturbance Hypothesis, or IDH, (Padisák, Reynolds & Sommer, 1993) with particular reference to its applicability in plankton ecology. Here we attempt to summarize the general thrust and direction of the individual contributions. This article is not, however, intended to be an abstract of abstracts, or some convenient review of those papers. Rather, it is our joint statement of how the utility of the concept, founded in community ecology, is currently viewed by a group of contemporary plankton biologists. Moreover, our principal concern is not the concept itself, which is extensively discussed in the foregoing articles (Sommer *et al.*, 1993), by Connell (1978) himself and by others prior to that, albeit without the 'IDH' title (see e.g. Grime, 1973). We are concerned with its applicability to current problems in pelagic ecology. These include the extent and outcome of interspecific resource-based competition, the question of regulation by higher trophic levels, and the mechanisms contributing to the high biodiversity among planktonic organisms.

This discussion is arranged in four sections: first, why it is necessary to adopt an intermediate disturbance hypothesis (or something like it) into pelagic biology; second, to examine the relative merits of IDH; third, to consider its relative weaknesses; and, finally, we offer some deductions and recommendations.

The need for conceptual explanations

A part of modern biological science is directed towards the more subtle interrelationships of individual species with their environments and how these might respond to imposed change. Such questions assume increasing importance to the future of planetary ecosystems overexploited by our own species or damaged in consequence of changes wrought elsewhere. The answers generally involve, or imply, a level of understanding of ecosystem functioning which turns out to be mainly theoretical, unverified and (usually) hotly debated. One of the attractions of pelagic ecosystems for study is that, the vastness of the open-water habitats apart, they function at predominantly small spatial and temporal scales. Organisms are small (generally 10^{-2} to 10^{-7} m) and live short lives (generally 10^4 to 10^7 s) so that it is quite possible to follow, observe and experiment with the development of planktonic individuals, populations and communities. Curiously, this opportunity seems not to have attracted the attention of theoretical ecologists although several plankton biologists, for instance, G. Evelyn Hutchinson, Ramón Margalef & David Tilman became renowned theorists.

However, it is equally clear that the real world does not conform, either continuously or consistently, to the sum of experimentally-validated growth-, competition- and exclusion models. Yet, it is sufficiently structured and its processes are sufficiently reproducible for it not to be a fortuitous assembly of disorder and, in the common sense of the word, chaos. This apparent paradox reflects the tenous balance between biological organization, at every level from molecules to populations of organisms, and the counterposing entropic laws of dissipation (diffusion and thermodynamics). At the supraindividual level, the balance is poised between the organization of individuals into communities and variations in disruptive physico-chemical forcing.

Connell's (1978) Intermediate Disturbance Hypothesis is a fulcrum in this respect. It represents a mature and reasoned expression of the interactions among, on the one hand, the internally driven progress towards community organization and energetic equilibrium (*sensu* Odum, 1969) and, on the other, the externally-imposed stochasticity of environmental variability, operating at a variety of temporal (and, we infer, spatial) scales.

Strengths of the IDH concept

Two outstanding merits of the IDH concept come immediately to mind. One is the ease of its comprehension: as a word-model it is readily understood that, whereas natural communities under unchanged external conditions tend to become uniform, their progress towards the anticipated, equilibrated, competitively-excluded outcome can, at any time, be slowed, interrupted or overridden by forces emanating from outside and which are beyond the capability of the existing community to absorb. This first merit survives even the semantic differences of comprehension of Connell's view of intermediacy, *viz.* whether it refers to disturbances of intermediate strength or duration, as considered by Sommer *et al.* (1993), or of a disruptive event inserted firmly into the sequence of an internally-directed succession, prior to its conclusion, to the extent that it is halted, shifted or reversed. The second virtue of IDH is that it provides an explanation for the uncomfortable gulf that lies between what we expect to happen on the basis of controlled experimentation and what we generally observe. Simply, most recognizable ecosystems are far from being at steady state. Has not sufficient time elapsed for the majority of them to have come close to ecological equilibrium? Why have they not done so? Why do they support so many species? Can it be that, hitherto, their structures have been so frequently or extensively 'disturbed' in the recent past that they have failed to establish more than the elements of an equilibrated system? If equilibrium is, in fact, unusual, many of the contentious issues, like that of the 'top down vs. bottom up' control, become symptomatic dependents of the immaturity of the ecosystems in which they feature (Reynolds, 1993).

The problem may be viewed in the terms of the 'three patch' analogy. In this, a single hillside is envisaged, having a single aspect, macro-climate and geological foundation: a first vertical band is clothed by mature forest; a second was clear-filled and ploughed some years previously but was then abandoned to recolonization and has already developed the appearance of shrub and immature woodland; a third continues to be subject to regular livestock grazing. The appearances of the three areas are mutually contrasted, carrying communities corresponding approximately to Grimes (1979) S, C and R categories of plant species. Yet their differences lie essentially in the time that has elapsed since each was last 'disturbed' (in this case, by management). The first has progressed farthest towards its climactic condition. The second has begun to resemble the first, with conspecific juvenile trees developing within a richly diverse herb/shrub flora; the third looks quite open and its species composition is limited to species tolerant of the imposed management. In other words, each has acquired a species composition and an internal organization which is a function of the frequency of disturbance applied. If specific examples are preferred to this rather generalized consideration, then Grime's (1973) analysis of flowering-plant richness in herbaceous vegetation should be consulted. The idea works just as well for phytoplankton (Reynolds, 1993). Immaturity becomes a recognizable attribute of systems; equally, disturbance becomes a valid factor contributing to their productivity, species structure, biomass and organization.

Weakness of the IDH concept

Ranged against the deceptive simplicity of the Intermediate Disturbance Hypothesis are some quite fundamental questions of logic and/or practicality. Until they are adequately answered, the utility of the IDH remains in doubt. The difficulties are incisively exposed in Juhász-Nagy's (1993) paper, though certainly not in a manner which sought to discredit IDH in any way. On the contrary, any preconception that may be betrayed is supportive of IDH.

As discussed at the outset (Sommer *et al.*, 1993), the principal difficulty concerns the recognition and measurement of disturbance. This point is emphasized in most of the contributed papers (notably Rojo and Alvarez-Cobelas, 1993). Although it is becoming increasingly straightforward to measure a force imposed on an ecosystem, it is quite another thing to relate quantitatively the extent of the impact, if any, to that force. Whereas a sudden storm, or a flash flood attributable to sharply-enhanced summer rains, would be anticipated to have an immediate effect upon the biomass, species composition and productivity of a respondent system, it is in no way 'guaranteed'. Such a storm event might, for instance, be expected to interrupt abruptly the summer phytoplankton succession and stimulate the development of a diatom-desmid association (Reynolds, 1993). Yet the strength of stimulus to attain this is generally more effective in disturbing the development of (say) a midsuccessional *Sphaerocystis* population than of a well-established *Microcystis* bloom: its eradication may require more drastic and more persistent disturbance, although the same intensity of disturbance applied earlier in the development of the *Microcystis* could have delayed its establishment, perhaps indefinitely (Reynolds *et al.*, 1984). In other words, the imposition of the same external forcing may well invoke quite different community responses, depending upon the resilience shown by the development stage achieved and the strength of the internal linkages already established at the instant when it is applied (Padisák, 1993). For instance, Jacobsen & Simonsen (1993) showed that heavy rainfall and storms increased the loss from an *Aphanizomenon* population in Lake Godstrup but failed to break its dominance. The role of this acquired late-successional complexity in governing the responses to (e.g.) external forcing is highlighted in the papers contributed by Moustaka-Gouni (1993) and Eloranta (1993). In general, the sooner in the succession that a given stimulus is imposed, then the greater and more immediate is the compositional response. Late successional, senescent communities can become again more sensitive to environmental disturbances; however, senescence is difficult to observe in phytoplankton communities (cf. Sommer, 1991).

Similarly, the same forcing, even supposing it to be quantified in the appropriate vector units, can impact quite differently upon two adjacent systems. Several of the papers in this volume (Sommer, 1993; Trifonova, 1993; Holzmann, 1993; Chorus & Schlag, 1993), in fact, contrast the effects of what are assumed to be the same stimuli acting upon pairs of nearby lakes, in each case differing mutually either in area, depth or exposure. In the sites contrasted by Holzmann (1993) the responses in the oligotrophic Kautsee differ from those in the eutrophic Pelhamer See. In this instance, a more exacting or more persistent control (that of low nutrient concentration) acts on species structure and abundance throughout and which the external stimulus fails to disturb. Olrik & Nauwerck (1993) describe another case in which the reaction to external forcing was suppressed by internal conditions: severe carbon limitation brought to an end the dominance of a large *Limnothrix* population in Hjarbæk Fjord and, eventually, the initiation of a new successional sequence dominated by *Scenedesmus*. Olrik & Nauwerck (1993) and Padisák (1993) point out that stress and disturbance can produce similar outcomes. There were occasions, too, when the systems studied by Rojo & Alvarez-Cobelas (1993) and by Chorus & Schlag (1993) did not respond to forcing as expected.

These are truly instances when the pool of potential respondents may be viewed as being either 'squeezed into an apex' of a C.S.R. triangle (Reynolds, 1993) or the enforced matrix co-ordinates are encompassed by the Venn envelopes of a diminishing number of species (cf. Juhász-Nagy, 1993). The community becomes more specialist with fewer species of non-common behaviour (Kullback, 1959).

These concerns lead to a further, more fundamental difficulty to the tenancy of IDH. It is inescapable that disturbance is a phenomenon recognized and measured only as an effect: the stimulus may be generally external but its nature is judged exclusively by the reaction it engenders. This property is implicit in the definitions of Pickett *et al.* (1989): disturbance is a change in the minimal structure of an ecological object caused by a factor external to the level of interest (individual, population, community, etc.). It is equally clear that, since the 'minimal structure' is a system of lower entities permitting the persistence of the object, the application of the disturbance concept will always depend upon the perception of the structure of the ecological systems concerned.

The contributions on river communities remind us that it is less the intensity of the physical forcing that is critical to the development of ecological structure so much as the frequency with which it is applied. Intuitively, rivers may be regarded as highly kinetic and open systems in which structure will be difficult to elaborate. Not so, for the organisms tolerant of the conditions obtaining perceive them as being uniform and therefore undisturbed. Descy (1993), Carvajal-Chitty (1993) and Ács & Kiss (1993) all properly treat disturbance as an abrupt shift in the status quo. The intuitively disturbed state turns out to be structurally constant, pending flood events or, presumably, in the opposite direction, impoundment in a reservoir.

A similar cautionary remark has to be made for lakes:

Lake planktonologists tend to perceive sustained thermal stratification as the 'undisturbed state' of a lake. This preconception is for example apparent in Reynolds' (1987) adoption of Grime's plant strategy typology. Phytoplankton taxa characteristic for mixed water columns (e.g. diatoms) are termed 'ruderals' in analogy to terrestrial plants from disturbed sites. However, if vertical mixing is continuous the environment of the phytoplankton may be perceived as a more or less constant low light-high nutrient one. As long as at least some phytoplankton are still able to grow and to influence the transparency of the water there will be competitive exclusion of all species but those with minimal light requirements. Therefore, permanent circulation can be a low-disturbance status. Sudden stratification would then be a disturbance of this status. The results of Chorus and Schlag (1993) could best be interpreted this way.

Applications of the IDH concept

In spite of its unresolved weaknesses, the concept of intermediate disturbance remains too useful in its potential to reject. Its application to current problems in ecology and in management of ecosystems can advance as the understanding of the structural linkages is strengthened (Pickett *et al.*, 1989). The latter invokes the importance of selecting the correct spatial and temporal scales at which structure is established, information is assembled and entropy is diminished. As is made clear in several of the contributions, the scales are set by the organisms concerned. Within the context of seasonal change in phytoplankton species composition, our workshop agreed a working definition that '*disturbances are primarily non-biotic, stochastic events that result in distinct and abrupt changes in the composition and which interfere with internally-driven progress towards self-organization and ecological equilibrium; such events are understood to operate through the medium of (e.g.) weather and at the frequency scale of algal generation times*'.

In this sense, it is evident that undisturbed successions should eventually approach competitive exclusion and ecological equilibrium. This may well require the 12–16 generations suggested by Reynolds (1993) and hence occupy periods of 35–60 days (Sommer, 1985). On the other hand, external events interfering with that progress will promote a mix of contemporaneously occurring species, even though some may be decreasing while others are increasing. Several contributors (Padisák, 1993; Sommer, 1993) are agreed that the diversity – roughly the number of species over the numbers of individuals represented in a given space – is also highest early in successions, probably around the second-third generation (i.e. ~5–15 days) before any achieves eventual dominance. Disturbances occurring at similar frequencies are adequate to explain both the failure of competitive exclusion and how the diversity might be maintained. At the same time, a plausible mechanism for driving contemporaneous disequilibrium (Richerson *et al.*, 1970) and for the 'paradoxical' structure of planktonic communities (Hutchinson, 1961) is projected.

However, despite the demonstrably close correlation between diversity and disturbance they are only indirectly linked, through the hierarchical structure of ecological systems. The bridging condition depends, on the one hand, upon the abilities and/or specialisms of individual species to process environmental signals and, on the other hand, the time taken by them to respond. While the external signals are perceived as being constant, succession proceeds towards competitive exclusion; when they alter frequently, early successional stages are supplanted by alternative early successional stages!

In this way, it is possible to substantiate the connectances in the general deductions presented in this volume:

– Diversity is high or increases when species replacement rates are rapid, as, for instance, in warm water; these are neither necessarily nor exclusively driven by disturbances, although communities repeatedly destabilized at frequencies in the order of three generation times are likely to support a high diversity of species. Diversity is promoted when fast-growing (i.e. usually small-sized) algae are abundant.

– Diversity is low or declines in advanced successions where a large biomass is dominated by a single, generally 'large' ($>200\ \mu$m) algal species. Diversity is rarely high in strongly selective environments, such as highly flushed systems or in lakes characterized by extremes of acidity, alkalinity, turbidity, oligotrophy or physical constancy (save by spatial niche differentiation). Without disturbance of the status quo, equilibrium dynamics predict an eventual total suppression of diversity.

Final remarks

The deductions and opinions advanced in this discussion are those of the authors and not necessarily shared by the contributors to this volume. Nevertheless, we are most grateful to them for the stimulus of their information and ideas. Besides, the topics of disturbance and diversity are scarcely exhausted; we hope that this article serves as a catalyst for further, more robust investigations that may consolidate the tenancy of the Intermediate Disturbance Hypothesis.

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