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## Hutchinson's heritage: the diversity-disturbance relationship in phytoplankton

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### Abstract

This paper introduces a collection of contributions presented at the 8th Workshop of the International Association of Phytoplankton Taxonomy and Ecology. It compares the substance of with what to limnologists is the more familiar 'paradox of the plankton' posed by G. E. Hutchinson. The utility of Connell's Intermediate Disturbance Hypothesis in plankton ecology is, potentially, more instructive but inherent difficulties in relating response to stimulus have to be overcome. A copy of the brief distributed to contributors before the workshop is appended.

### Preamble

All modern students of limnology will have benefited from the influence of the late Professor G. Evelyn Hutchinson. The thoroughness and erudition of his monumental *Treatise on Limnology* (Hutchinson, 1957a, 1967, 1975a) imparted knowledge, understanding and inspiration to all engaged in the study of limnetic and lotic ecosystems. Those of us who have specialized in pelagic ecology hold a special regard for Hutchinson's challenge that the high diversity of species present in limnetic plankton is inconsistent with the assumptions of competitive exclusion in the supposed uniformity of pelagic environments. Indeed, the dilemma has become widely known as the 'paradox of the plankton' (Hutchinson, 1961).

Hutchinson was intrigued by the fact that ep-

ilimnetic phytoplankton coexist in a well mixed environment and compete for a very small number of common limiting resources (light and a few nutritional elements). Nevertheless, even in small samples of water, it is not unusual to find more than 30 species of phytoplankton present. Equilibrium concepts predict that competition would eventually select the best fit species to the exclusion of all others (Hardin, 1960) and that only as many species can coexist as there are limiting factors. The search for solution to this apparent paradox has occupied plankton biologists ever since.

Going into a bit deeper into Hutchinson's heritage, it is interesting to observe the thread of reasoning running through his masterly book 'An Introduction to Population Ecology' (Hutchinson, 1978). This begins with a consideration of

temporal processes, enriched by a very deep feeling for science history, and goes on to cover such exciting topics as 'Living Together in Theory and Practice' (Chapter 4) or 'How Is Living Nature Put Together?' (Chapter 6). The book is full of very interesting examples and speculations on the possible interconnections between limnic and terrestrial ecology.

In making his perceptive generalizations, it may be noted that, in addition to his own deep intentions, Hutchinson was influenced by a number of friends, students, including Charles Elton, David Lack, R. H. MacArthur, R. H. Whittaker & J. L. Harper. It is interesting to observe, however, that his attitude is always critical, as is shown, for example, in his questioning comments on some statements of Lack (1954) or Slobodkin (1961).

We believe that at least three closely related topics, have been relevant in motivating Hutchinson's appreciation:

- (i) the nature of ecological patterns,
- (ii) the nature of niche,
- (iii) and the nature of coexistence.

Topic (i) can be followed reasonably well from Hutchinson (1953) through MacArthur (1965) to Hutchinson (1975b). Topic (ii), the story of 'niche-ology', is also fairly well accepted, started, in a sense, by Hutchinson (1957b) and continued by the activities of R. H. MacArthur, R. K. Colwell, I. Emlen, I. Futuyama, M. E. Gilpin, I. Roughgarden, who are, directly or indirectly, students of Hutchinson.

The third topic (iii) is the most difficult one: it was also the most pertinent problem of Hutchinson. Following his publications carefully, from the rather early papers (e.g. Hutchinson, 1948, 1951, 1953, 1954) to his most famous syntheses (Hutchinson, 1959, 1961, 1978), we discern a recurrent view that the rebuses of coexistence would be solved through the search for potential optima, the recognition and definition of moving patterns and where the interpretation of which remained within the context of evolutionary ecology.

Needless to say, all the components of such a reasoning have induced several divergent lines of further investigations (e. g. Levins, 1968, 1979; Lewontin & Cohen, 1969, etc.).

In his seminal paper, Hutchinson (1961) suggested several possible explanations for his planktonic paradox of diversity. Among them was the idea that the boundary conditions of competition change frequently enough to revert competitive hierarchies before exclusion occurs. The proposal was reformulated by Richerson *et al.* (1970) as 'contemporaneous disequilibrium'. Later attempts to solve the paradox include theoretical analyses (Grenney, 1973; Armstrong & McGehee, 1976; Levins, 1979, Ebenhöh, 1988; Grover, 1990) and experimental approaches (Turpin & Harrison, 1980; Robinson & Sandgren, 1983; Sommer, 1984, 1985; Gaedeke & Sommer, 1986; Grover, 1988, 1989, 1991). In spite of these considerable efforts, no universally accepted explanation for the paradox has been forthcoming.

Although freshwater biologists associate the problem of species diversity with Hutchinson, it is fair to say that analogous questions have been prevalent among terrestrial ecologists. For instance, Grime (1973) was among the first to recognize that although competition can be a major causal factor in the maintenance of low diversities in herbaceous vegetation, there is nevertheless a low incidence of competitive species in floristically rich habitats. Wilson (1990) considered twelve possible mechanisms to account for species coexistence in New Zealand plant communities: most of these are equilibrium concepts, including niche diversification and stabilizing coevolution; his non-equilibrium explanations assumed that there had not been enough time for competition to completely exclude relevant species before sudden or gradual alterations intervene to arrest or shift back the development of the association of species.

Still more perplexing is the astonishing diversity observed among tropical forests and in coral reef communities in which an equilibrated climax condition is intuitively anticipated; competitive exclusion appears, again paradoxically, not to have been effective. Connell (1978) argued that, even here, the time taken to recover from damage through change of climatic conditions, landslides, fires or violent storms is such for it to be difficult for competitive exclusion to occur finally. Thus

the intervention of factors delaying progress towards, or preventing the attainment of, an equilibrium condition is supposed to be responsible for the maintenance of the diversity. This has become widely known as ‘Connell’s Intermediate Disturbance Hypothesis’.

### **The Intermediate Disturbance Hypothesis and its applicability to phytoplankton**

Connell’s (1978) hypothesis states:

(1) In the absence of disturbance (eternal steady state), competitive exclusion will reduce diversity to minimal levels.

(2) Under very intense disturbance only few populations of pioneer species could establish themselves after each disturbance event. This would also lead to minimal diversity.

(3) If disturbances are of intermediate frequency and/or intensity there will be repeated opportunities for the re-establishment of pioneer populations which would otherwise be outcompeted and the populations of the successful competitors could withstand the disturbance without completely taking over the community. Thus, a peak of diversity should be found at intermediate frequencies and intensities of disturbance.

In his original paper, Connell conceived disturbances as primarily originating from internal processes (e.g. treefall gaps caused by the death of senescent trees). However, there is no *a priori* reason why disturbances of external origin should have different consequences on species diversity. Obviously, there are instances, when the contribution of internal and external factors cannot be separated easily. For instance, senescence of a tree might not make a tree fall by itself but it may increase its susceptibility to windfall. For our present discussion, we have assumed that the distinction between external or internal origin of disturbance is less important than the occurrence of disturbance *per se*.

It is implicit in IDH that the post-disturbance recovery of communities is strongly directional, in accord with successional theory (Odum, 1969, 1971). Habitats newly- opened by, for instance,

storm damage are likely to be recolonized first by invasive species. These will generally be those which can provide the largest number of propagules or which can expand their biomass the most rapidly, assuming that the new conditions are adequate to meet their requirements. In time, however, these colonist species will be replaced by others which are better equipped to live close to the limits of the available resources (McArthur & Wilson, 1967). As the community is assembled, the ratio between the production and the biomass falls simultaneously until, ultimately, the biomass supported is the maximum achievable with the energy available.

The application of successional theory to the seasonally changing structure of phytoplankton assemblages has been attempted by Reynolds (1988). His approach depended upon the recognition of the importance (a) of the temporal scaling, which relates primarily to the life spans of consecutive generations of algae (measured in hours to days rather than months to decades), and (b) that different species of phytoplankton show adaptations to exploit particular parts of the spectrum of environmental variability. Just as on the land, colonist weeds and equilibrial dominants are recognizable in the plankton (see Padisák & G. Tóth, 1991).

Sommer (1991, see also Padisák, 1992) has argued strongly that succession of phytoplankton is analogous to the succession of terrestrial vegetation rather than being a purely seasonal phenomenon. The several months of the plankton growing season, accommodating dozens of generations of phytoplankton, correspond to tens of years in grassland, and to centuries in forest. Variations in growth conditions should necessarily be viewed at a similar scale. Under favourable physical conditions, the intrinsically transient nature of early- and middle phases of planktonic successions, and the self-sustainability of final stages have been demonstrated (Sommer, 1991). It is only the external cycle in climatic and hydrological conditions which resets the plankton succession each year.

As a consequence of short generation times, however, plankton communities are responsive to

meteorological variability. The 'weather' experienced by terrestrial vegetation is the 'climate' perceived by phytoplankton. The fluctuations are especially pronounced in shallow, polymictic lakes where apparently random population variations often make the main trend unrecognizable.

### **Developing the utility of the Intermediate Disturbance Hypothesis**

It seemed to us germane to take advantage of the small temporal scales of phytoplankton dynamics to explore the operation of intermediate disturbance and its role in maintaining species diversity. These issues were considered by participants at the 8th Workshop of the International Association of Phytoplankton Taxonomy and Ecology convened at Baja, Hungary, held between 5–15 July 1991. This volume contains the individual contributions presented at the workshop. All authors were expressly asked to address their presentations within the context of the Intermediate Disturbance Hypothesis (IDH). Because IDH had not been widely accepted as a basis for viewing phytoplankton ecology and, in consequence, compliance with our request may have involved authors in unfamiliar conceptualization, we considered it important to append (Appendix 1) to this introductory paper the brief issue to participants prior to the workshop.

The particular problems upon which resolution was sought included the distinction of disturbance from the undisturbed, the timescales involved and the quantification of their impacts on diversity. However, we were anxious not to impose too rigid a definition of disturbance. In everyday usage, 'disturbance' implies a stimulus whereas the formal attempts to recognize and quantify ecological 'disturbance' (e.g. Pickett *et al.*, 1989) lie exclusively in the response to that stimulus. In order to make the hypothesis testable, the magnitude and frequency of environmental change and of the disturbance-responses have to be quantified. Change can be found in many environmental properties which may be measured on different scales. As long as all fac-

tors other than that to be tested are held constant, no problem of commensurability arises. This is usually the case in experimental design. In the analysis of collected field data, however, commensurability becomes a prominent problem. On what basis, for example, does one equate simultaneous changes in incident radiation, temperature, nutrient loading or flushing rate, etc.? Obviously, generally valid conversion factors for empirical measurements cannot be found. By quantifying the biotic response rather than the stimulus, the problem of commensurability is circumvented but it is replaced by a danger of circular reasoning in that the strength of the disturbance is the strength of the biotic response. Does the lack of a measurable response indicate that there was no measurable stimulus? Without appreciation of these serious difficulties of interpretation it is unlikely that meaningful application of the intermediate disturbance concept or its assimilation into ecological theory can be usefully achieved.

### **Dedication**

For many plankton ecologists, Hutchinson's paradox has been a more familiar and a more challenging problem than Connell's hypothesis. Among the significant attempts to address the issue (see above), the tendency for phytoplankton diversity to be increased by environmental variability has been strongly evident. In this respect Connell's Intermediate Disturbance Hypothesis represents a workable framework for superimposing non equilibrium explanations for Hutchinson's paradox.

We acknowledge this close empathy between Hutchinson's and Connell's views. Because of our perception of the prevalence of non-equilibrium dynamics in plankton ecology, we recognize the potentially greater utility of Connell's hypothesis to our understanding of pelagic ecosystems. Nevertheless, the inspiration and challenge to plankton ecologists will long remain that of Hutchinson.

It is sadly ironic that our workshop should have coincided with G. Evelyn Hutchinson's un-

timely death and with the thirtieth anniversary of the publication of his paradox. It is no less than with a profound sense of duty that we respectfully dedicate this volume to his memory.

## Appendix 1

### *The intermediate disturbance hypothesis*

The question of diversity has been one of the most controversial issues in succession theory in general. According to the classical (e.g. Clements, 1916: *Plant Succession: an Analysis of the Development of Vegetation*. Carnegie Inst. Washington Publ. 242, 1–517) view, diversity of communities increases towards the late phases of succession, while the competitive exclusion theory (if several species compete for the same resource one of them excludes all the others: Hardin, 1960: *Science*: 131: 1292–1297) predicts that the process should be towards the establishment of a low-diversity equilibrium. The Intermediate Disturbance Hypothesis (IDH) was originally elaborated by Connell (1978: *Science* 99: 1304–1310) to interpret the high species diversity that can be observed in tropical rain forests and coral reefs. The theory was adapted to phytoplankton succession by Reynolds (1988: *Verh. int. Ver. Limnol.* 23: 683–691).

Phytoplankton of temperate lakes has been rarely limited simultaneously by more than 1–3 main resources (N, P, Si alone or in any combination, light). Competitive exclusion theory allows the phytoplankton succession to tend towards an equilibrium of 1–3 species, at any phase of its seasonal development. This is obviously inconsistent with the great species richness and high species diversity that can be observed in most cases (e.g. the paradox of the plankton, Hutchinson, 1961: *Am. Nat.* 95: 137–147). Theoretical approaches (e.g. Tilman, 1982: *Resource Competition and Community Structure*. Princeton Univ. Press.) and chemostat experiments (Sommer, 1985: *Limnol. Oceanogr.* 30: 335–346; 1989: *Plankton Ecology: Succession in Plankton Communities*. Springer; Gaedeker & Sommer, 1986: *Oecologia* 71: 98–102) indicated that fluctuations in resource availability makes possible the coexistence of more species than is predicted by the competitive exclusion theory. Several field observations indicate the same (e.g. G.-Tóth & Padisák, 1986: *J. Plankton Res.* 8: 353–363; Padisák *et al.*, 1988: *J. Plankton Res.* 10: 249–265; 1990: *Hydrobiologia* 191: 249–254). As follows from the aforementioned theories, experiments and observations, the frequency of disturbances has an essential influence on the diversity of the phytoplankton and on the establishment of the equilibrium state.

According to Reynolds (1988: *Verh. int. Ver. Limnol.* 23: 683–691):

(1) at frequencies in order of a few hours (< 1 generation time) the responses are physiological;

(2) low frequency pulses, separated by intervals of 10 days or more, can initiate a successional sequence;

(3) progressively smaller intermediate scales (200–20 h) interact with the growth rates of phytoplankton species and tend to preserve high species diversity. The attainment of equilibrium is delayed at a sort of ‘plagioclimax’ (Reynolds, 1984: *Freshwat. Biol.* 14: 111–142).

Because the above outlined IDH seems to be very useful in understanding many phenomena that we are used to observing in phytoplankton time series, the participants of the last IAP round-table (Munich, August 1989) agreed to hold a detailed discussion on the topic. In order to make this discussion as useful as possible we summarize here the outcome of our several hours of talk about the IDH and about the possibilities of its test.

### *Long term data series*

In order to test the IDH it is necessary to have phytoplankton data (species composition) with weekly, biweekly (but only if the sampling was really very regular over many years) or shorter sampling intervals over several years. In order to identify the frequency of disturbances data on appropriate physical parameters are needed, such as mixing depth, water column stability. Contributions with insufficient data series should not be admitted, except for experimental and theoretical papers relevant to the topic.

### *Identification of disturbances*

In stratifying lakes, increase in the mixing depth would be the ideal indicator of physical disturbance. If meteorological data are used as ‘independent variables’, it has to be noted that not every wind or cooling event qualifies as a ‘disturbance’. In very stably stratified lakes, even a major meteorological event may lead to only a small increase of mixing depth and may be quite ineffective in terms of its impact on succession. The identification of disturbances in nonstratifying lakes is more problematic. Besides physical variables (changes in transparency, turbidity, etc.), biological variables (for example, the contribution of non-planktonic algae to some population measure, the number of diatom frustules, etc.) can register the physical disturbance.

It should be mentioned that ‘disturbances’ are not necessarily physical in nature. In the context of the IDH and its relation to the competitive exclusion principle, any event that interrupts the approach toward the eventual exclusion is a disturbance. Generally, disturbances would be recognised by a decrease of phytoplankton biomass and probably by an increase in the availability of resources.

### *Identification of equilibrium*

In natural phytoplankton communities, it is often difficult to determine whether a given ‘phase’ in a seasonal sequence can be considered to be in an equilibrium state or not, due either to a lack of chemical data, or to insufficient sampling frequency, or to any other cause. For practical purposes, provided that (i) 1, 2 or 3 species of algae contribute more than

80% of total biomass, (ii) their existence or coexistence persists for long enough (more than 1–2 weeks) and (iii) during that period the total biomass does not increase significantly, then that phase can be considered to be at equilibrium. Since our knowledge on the nature of equilibrium state in natural phytoplankton is very limited, contributions (for example: how many generations are involved?) to this aspect of the IDH are also invited.

#### *Definition of diversity*

In appreciation of the fact that usually data on the dominant species are more reliable than data of the rare species, an index should be used which gives more weight to the dominant species. Therefore, we ask that the Shannon-Weaver Index be used. Some people have strong opinions about whether this index should be based on cell-numbers, 'units' (one colony being one unit) or biomass. We shall not be strict on this point, because we have to use old data and different contributors may well have documented them differently and they will not always be able to reconvert them. If cell number is used, unidentified picoalgae should be excluded, otherwise even a very massive bloom of some large alga (e.g. *Ceratium*) will be 'drowned' by  $10^4$  to  $10^5$  picoalgae per ml. Alternatively, partial diversity indices of conventionally defined size-classes could be calculated. Participants with appropriate data sets are encouraged to try numbers-, unit-, biomass- and surface area-based indices in order to test whether they show the same pattern or not. However, use of biomass data is recommended wherever possible. Because the Shannon-Weaver Index is sensitive to the final number of coexisting species, please indicate on your graphs, how many species (in general 1, 2 or 3) provided the final equilibrium.

#### *Time scale of disturbance*

This is the most problematic part of our enterprise. We think that most of the contributors (including ourselves) have an insufficient knowledge of the potentials and pitfalls of the different statistical procedures of time-series analyses. We do not think that we should try to solve this problem by sending out 'recipes'. This problem should be discussed at the workshop. This means, that our workshop will not be the end of the discussion procedure but only an intermediate step.

ULRICH SOMMER and JUDIT PADISÁK"

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