# FORUM

## THE INTERMEDIATE DISTURBANCE HYPOTHESIS AND ITS APPLICABILITY TO PLANKTONIC COMMUNITIES: COMMENTS ON THE VIEWS OF PADISÁK AND WILSON

C.S. REYNOLDS
Freshwater Biological Association
NERC Institute of Freshwater Ecology
Ambleside
Cumbria LA22 0LP
United Kingdom

**The relevance of Connell's Intermediate Disturbance Hypothesis (IDH) to explanations of diversity and co-existence among plant species generally and in the phytoplankton in particular has been debated recently. Compared to terrestrial vegetation, planktonic communities experience distorted time and space scales. Generation times are in the order of days, not years to decades. Advective fluid transport raises the critical patch size to the order of kilometers. Within these scales, species survival and growth, community assembly and successional development in the phytoplankton conform to all the standards (compositional, strategic, thermodynamic) of conventional community organisation. These processes are known to move toward competitively excluded outcomes. Equally, they are liable to be interrupted by externally imposed disturbances, which reset the succession or alter its potential outcome. These findings are not only illustrative of intermediate disturbance but are instructive in the nature of diversity-disturbance relationships generally. IDH has considerable potential to explaining persistent species co-existence.**

## Introduction

Several ecologists have recognised the paradox that, while our planet is populated by a vast number of different and distinct species (fashionably, its biodiversity), most relevant theories and experimental evidence point towards the progressive competitive exclusion of all but the most robustly adapted species in each niche. The problem exists in almost all described plant associations, including the phytoplankton (Hutchinson, 1961). The best-known attempt to explain the paradox is the Intermediate Disturbance Hypothesis (IDH). This was elaborated by J.H. Connell (see especially Connell, 1978, 1983), although similar ideas had been expressed previously, notably by Grime (1973). In essence, frequent disturbance excludes all but fast-maturing species. Very infrequent disturbance allows competitive exclusion to reduce diversity. Maximum diversity is thus maintained at intermediate disturbance frequencies.

In his thoughtful analysis of the mechanisms which might have had the effect of maintaining persistent coexistence among the plant communities of New Zealand, Wilson (1990) considered intermediate-timescale disturbances would help to explain the paradox if there was a good mix of patches having different disturbance-ages to sustain among-patch diversity. He concluded IDH to be probably unimportant to within-community co-existence, except in small forest gaps, of less than 1000 m$^2$.

The deduction is of great consequence to diversity considerations elsewhere. Padisák's (1995) article did not explicitly challenge this or any other of Wilson's conclusions. Her concern was that ecologists might be persuaded to reject the applicability of IDH to issues of diversity before its implications had been fully investigated. Her arguments invoked her own observations on the day-to-day and year-to-year variability of the phytoplankton composition in Lake Balaton and the findings of a group of contemporary plankton biologists who discussed the utility of IDH at a colloquium of the International Association for Phytoplankton Taxonomy and Ecology (IAP) in Baja, Hungary, 1991 (Padisák, Reynolds and Sommer, 1993). Wilson's (1995) reply to Padisák's (1995)

commentary may not have taken full account of these developments, whereas I suspect that Padisák may have interpreted terms differently from their original definitions. Yet this is much too important an issue to be lost in an argument about semantics. In fact, the similarities between the views of Padisák and Wilson far outweigh their differences.

The debate provides an opportunity to rehearse those concepts which apply equally to plants evolved to live on the land surface and to those adapted to life in a dense, non-compressible, three-dimensional liquid (Reynolds, 1980, 1987). However, the differences in the spatial and temporal scales at which the plants function influence profoundly what constitutes a patch and what might then be recognised as a disturbance. Here, I argue against Wilson (1995) and for the distinction between GCC (Global Climate Change) and IDH as agents of floristic change. Lastly, I venture a comment on the role of intermediate disturbance, *sensu* Connell, and its role in maintaining the diversity of New Zealand's vegetation.

## Planktonic vegetation and its scales

Wilson's (1995) perplexity with the application of IDH to planktonic communities invokes the generation and re-colonisation of patches at the relevant scales. That Connell specifically excluded plankton from his hypothesis is not an argument that it cannot be applied, or should not be applied. Which scales matter to plankton? Despite the vastness of the pelagic habitats of large lakes and, especially, the open ocean, plankton itself is strictly small-scale. The plants, the phytoplankton, are generally less than 2 mm in size; they rarely comprise more than a few thousands of cells in a loose colony, while many are unicellular. As the only significant primary producers in pelagic habitats, planktonic plants also share with land plants the ability to harvest light, to fix carbon in sugars and to build amino acids. The requirement to maintain a photosynthetic surface in open water, in near-continuous, three-dimensional and substantially turbulent motion, and where there are no surfaces for attachment, has favoured specialised adaptive traits. Planktonic plants inhabit the viscous range of the eddy spectrum and their sizes are smaller than the size of the smallest turbulent eddies (generally < 2 mm, sometimes < 0.5 mm; Reynolds, 1994).

The supposed structural simplicity of the planktonic plant, the exemption from the requirement to allocate resources to mechanical tissue, the small size and the high surface-to-volume ($s/v$) ratio, all contribute to an ability to attain rapid rates of replication and biomass increase ($r'$), when compared with higher plants (Nielsen and Sand-Jensen, 1990). For instance, the replication rates attainable at 20°C under resource-saturating conditions are well predicted by Reynolds' (1989) equation:

$$[r' = 1.142 \ (s/v)^{0.325}]$$

This corroborates natural species-specific rates of biomass-doubling of between one per week to nearly two per day. Depending on species and conditions, a doubling of species-specific biomass every two to five days is a realistic estimate of the typical range of time scales of *in situ* planktonic population replication. Padisák (1985) and I (Reynolds, 1984) have advanced the generation time as the key unit of temporal scaling in succession.

It is interesting that Wilson (1995) does not dispute the application of "succession" to phytoplankton; neither does he reject the cross-scaling argument, for he views the frequency of disturbance in the context of generation times. However, terrestrial plant ecologists have not always clearly distinguished that which happens to individuals from that which happens to successive generations. Acceptance of this point may be crucial to those who doubt that phytoplankton can undergo ecological succession at all (Reynolds, 1988). Once this notion is established, it is then easy to appreciate that planktonic successions may be interrupted or altered by the intervention of external, density-independent forcing, just as they are on land. However, the scales are inevitably different, as a function of organismic complexity and size (Nielsen and Sand-Jensen, 1990). Nevertheless, it is extremely important to recognise that individual cells of planktonic algae may experience similar constraints of (say) photon capture, photosynthesis or intracellular transport as individual vegetative cells of a terrestrial herb or tree and, moreover, within absolutely similar time spans. Thus, one should not assume, as Wilson (1995) implies, that the temporal scaling of phytoplankton and of terrestrial vegetation are simply shifted one against the other. At the level of cytology and biochemistry, the scales more or less coincide; the higher the process the greater the divergence between them (Reynolds, *in press*; see also Fig. 1).

## Spatial scales and patch sizes

The relevant spatial scales are governed by the buoyant entrainment of phytoplankton, or its embedding in the advective medium. Roughly, plankton goes where the water takes it. In the vertical plane, the key dimension is the depth of the surface mixed layer, which can range between zero and
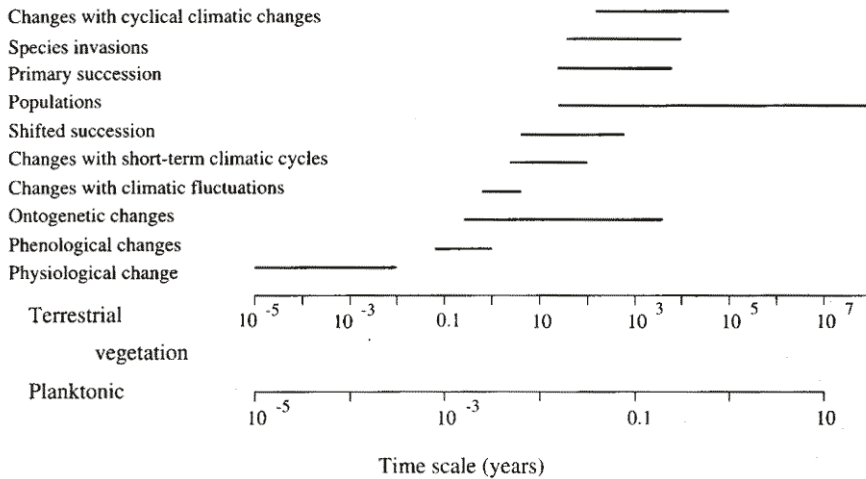
Figure 1: *Major vegetation processes occurring in terrestrial and planktonic plant communities shown in relation to their respective time scales; note the logarithmic scales and that they coincide in the region of $10^{-5}$ years ($\approx 300$ s). Modified after Reynolds,* in press.

250 m in thickness. The time taken for the wind-mixing to turn over this layer averages little more than 45 minutes (Denman and Gargett, 1983). This is much less than an algal generation time. Where the lower boundary is the lake bottom or a thermoclinic density gradient, the mixing time will be still shorter.

To the cell entrained within a mixed layer with a steep underwater gradient of light attenuation with depth, there is a probabilistic alternation between day and effective night every three-quarters of an hour or less, due to its vertical transport. An increase in mixing depth may result in a larger trajectory from the surface, in a shorter aggregate period spent in the light, a poorer net energy-harvest through the thirty or so probable excursions made through the mixed layer every 24 hr and, hence, a lowered capacity to fuel the temperature-dependent potential rate of replication. Conversely, a sharp increase in the light received by cells left in the near-surface layer following a reduction in mixing intensity may subject them to damaging light levels. Differing abilities of phytoplankton species to intercept and harvest light at low aggregate light income, as well as their differing capacities to photoadapt to high intensities of radiation, are important factors in species selection (Reynolds, 1987).

In the horizontal plane, the mixed layer often extends basinwide ($L$); the time taken for a surface drift current ($u$) of from 1 to 100 mm s$^{-1}$ to circulate the layer is related to the length of its downwind axis ($L / 0.5u$), and can be shown to be in the order of

days to weeks, that is, predictably longer than generation times.

Variability in the intensity and duration of hydrographical forcing generates many opportunities for patchiness of the plankton to develop (Platt and Denman, 1980); the most familiar is associated with Langmuir rotations (3-15 m: Leibovich 1983), which physically segregate organisms according to their buoyant or entrainability properties. At scales of 0.5-5 mm, however, the content of each viscous patch is likely to be only briefly different from that of the adjacent one; at a few micrometers, patchiness resolves to the presence or absence of a cell (Reynolds, Padisák and Kóbor, 1993). Patches generated by and maintained by the reproductive activities of organisms have to be much larger: the minimum radius of a patch which can recruit cells by reproduction faster than they can be diluted by erosion at the perimeter of the patch is calculable by the model of Joseph and Sendner (1958): for advective current velocities of 20 mm s$^{-1}$ and algae dividing daily, the minimum patch radius ($d/2$) may be calculated to be over 6 km. The radius diminishes with advection rate but increases with slower rates of phytoplankton replication. The inference is clear: the size of a pelagic patch whose dynamics would be relevant to the application of IDH is in the order of $[\pi(d/2)^2 =]$ 100 km$^2$ and, perhaps, up to 250 m in thickness. This is far from the 10 cm x 10 cm patch-size deduced by Wilson (1995). With this alternative figure to compare to Wilson's standard of $10^3$ m$^2$ for

terrestrial patches, the vulnerability of open-water patches to differentiation by disturbance and re-invasion from adjacent areas is at once more appreciable.

Among relatively modest-sized lakes with persistent environmental gradients, permanent horizontal discontinuities have been described: a classic example is that of Lac Memphrémagog, described by Watson and Kalff (1981). However, many smaller lakes are less extensive than the critical patch size and, on this basis, should be regarded as reproductively unique patches. If patches are not contiguous but merely lacustrine islands in a terrestrial sea, it might be argued that they would fail Wilson's (1995) IDH criterion of post-disturbance re-colonisation coming from adjacent sites. Planktonic biota are, in general, remarkably cosmopolitan and move relatively freely between suitable habitats (Reynolds, 1991). Besides, IDH does not stipulate that the re-establishment of vegetation is limited to the seedbanks and propagules that survived within the area; neither does it specify over what distance the invasive propagules shall have been dispersed.

## Successional change

The hypothesis of Connell freely embraced the idea that the advance of an internally-driven progression towards a competitively-excluded outcome could be interrupted by the intervention of primarily external forcing (e.g., by fire or earthquake) and with sufficient power to disrupt the existing structure and functional organisation. The analogues in lakes and seas are storms and strong winds which, within the space of a few hours, can greatly extend the depth of the mixed layer. Small lakes with large catchments may be similarly sensitive to high rainfall events. The abrupt onset of thermal stratification may provide no less of a shock to phytoplankton adapted to a deep, mixed, poorly insolated layer. Whatever are the relative merits of IDH or GCC or any other explanation of the recovery period in the wake of the event, the trigger itself need be no less abrupt or disruptive than those said to affect terrestrial systems.

Much of my own work has sought to establish commonality between the processes of rebuilding planktonic assemblages and those transforming terrestrial plant communities from pioneer stages to climactic vegetation. Provided that the distinction is made between the processes of change which are driven internally (or autogenically - e.g., by growth and replication, through depletion or spatial segregation of nutrient resources and through self-imposed shading) and those allogenic factors which

are forced from the outside (precisely those mixing and flushing events referred to above), then it is possible to demonstrate that ALL of Odum's (1969) characteristics of autogenic succession apply in planktonic ecosystems. Whether succesional progress is measured in terms of species composition (Reynolds, 1988), of the functional adaptations and life-history "strategies" of the participants (Reynolds, 1995b), or of the thermodynamic complexity of the ecosystem (Reynolds, *in press*), the same conclusion is reached. Pelagic conformity to the successional template is revealed in increasing complexity, species representation and resource partitioning (Reynolds, 1992); increasingly elaborate trophic interconnectedness and more severe interspecific competition accompany the departure further and further from thermodynamic equilibrium (Reynolds, *in press*). Moreover, it has been shown that species diversity increases through the early stages of a planktonic succession but in the later stages, species equitability (= evenness) and, ultimately, diversity collapse, in the way that climactic competitive exclusion predicts (Hardin, 1960).

Planktonic successions require some 12 to 16 generations to reach competitive exclusion. The time span is between 35 and 60 days (Reynolds, 1988). During this period, some gradual environmental change is inevitable, just as it would be over a comparable number of tree generations, but the species displacements during the ascendancy of the dominant are not necessarily the outcome of gradual climate change. What generally happens before competitive exclusion has occurred is that the next atmospheric front or storm or windy day impedes the growth of the potential dominant. Other species may be selected at once, or after they have used their greater capacity to adapt to the new conditions, or after they have arrived from a nearby patch; the response at the community-composition level may follow several days after the trigger event, as species which tolerate the new conditions establish themseves through the recruitment of further generations. If sustained, a new succession, with new dominants and a new potential steady state outcome may be predicted. Such events follow the major "shock periods" of the year, especially those which establish or destroy thermal stratification. The supplanting of one succession by another is referrable to a climate-change response. The broad mechanisms of succession are unaltered but the species now selected and the potential climax vegetation are altered. I have suggested that these changes in the potentially-dominant planktonic vegetation are analogous to those which have occurred in the terrestrial vegetation of higher

northern latitudes since the last glaciation (Reynolds, 1993). Coincidentally, the number of arboreal generations that might have been accommodated in the last 10 000 years is comparable to the number of phytoplankton generations accommodated through the changing seasons of just one year.

What are we to make of those many occasions when the new conditions are *not* sustained and the storm is followed by calm and, several days later again, by the passage of the next disruptive event? The controlled experiments and measurements that were undertaken by my group (Reynolds *et al.*, 1983) and the application of the results to the interpretation of species selection in lakes (Reynolds, 1993) reveal the frequent alternation of advantage among the species present. At any given point, some will be ascendant while others are in decline; yet within days, the selective advantage may be reversed. Depending upon the frequency of the forcing, these alternations are likely to maintain a high diversity of pioneers and mid-successional species in a state of apparent co-existence. The less frequent the alternations, the further the potential succession advances. At very frequent ($\approx$diel) alternations, at the scale of generation times or less, successful species have to be adapted to tolerate the disturbances (i.e., they are ruderals in the terminology of Grime, 1979).

## Applicability of IDH

IDH provides limnologists with an attractive explanation for Hutchinson's "paradox" of a diverse phytoplankton. If the arguments about pelagic patch size and dynamics are accepted, IDH does not fail in its applicability to plankton, nor in its pertinence to the question of maintainance of biodiversity.

However, IDH is not without a critical weakness (Juhász-Nagy, 1993): it is measured purely as the response to an unmeasured event. Without adequate quantification of the external forcing or of the resilience to forcing acquired during succession, this drawback cannot be readily overcome, either for aquatic or terrestrial disturbance (Reynolds, *in press*). Now that the selection of different morphological traits by given hydrographic conditions are being recognised, it is becoming possible to attribute qualitative explanations for altered community structure to preceding weather events. It ought then to be possible to ascribe the same energetic units to the source of the disturbance as to the energy required to maintain the community function (Reynolds, *in press*). For the present debate though, the point needs making that a successional sequence, truncated at a primitive stage in its development, is likely to be followed shortly by another, perhaps

involving many of the same contesting species and only a week or two later on. This is still less likely to be subject to explanations of gradual climate change. GCC *is* invoked, however, especially among temperate lakes, when the potential successional outcome, in terms of the dominant species to be eventually favoured, is not constant through the year. Indeed, it may alter from being likely to culminate in a dominant, near-monoculture of *Oscillatoria* spp. under isothermal conditions, to one of *Microcystis* in a shallow mixed layer, or of niche-separated specialists on a stable density gradient. Both kinds of outcome can be achieved in the same lake in the same year. Here, the explanation is that different dominants with different traits are each selected by seasonally differing environmental conditions. These may be analogous to the vegetational responses to postglacial climatic amelioration and deterioration in northern high latitudes which is supposed to have resulted in recorded changes in the dominant tree species selected.

## Conclusion

My reading of Connell is that he did not confine his explanations of the non-steady state of ecosystems to patchiness but brought them in as only one of the arguments about how supposedly advanced communities have failed to reach complete competitive exclusion. He did anticipate that succession would reduce the number of abundant species, though not their regional total number. Plant ecologists show us that the potential dominant terrestrial vegetation varies according to the interaction of numerous factors, mostly relating to climate and geology. Palaeoecologists show that the identity of the potential dominant species over vast tracts of continental land masses has altered in tune with gross (Milankovitch-scale) cyclical fluctuations in the relative global extent of the Holocene ice cover. IDH remains a powerful potential working hypothesis to explain the non-exclusion, wide species diversity and co-existence of many supposed competitors, in water every bit as much as on land. The hypothesis accounts for the compositional diversity in both low- and high-frequency disturbance ranges but not the totality of species present. It arguably accommodates a view of generalised events, through some broad appreciation of the operation of an overall disturbance regime, as a "within-patch" mechanism (*sensu* Wilson). The Intermediate Disturbance Hypothesis is much too useful to reject prematurely, even if (as we are all agreed) it does require some refinement. IDH does accord with observations on plankton biology but planktonic time-scales assist us to find resolutions to

ongoing debates about the significance of competition in advancing plant community structure, simply because planktonic generation times and species' successions lend themselves to complete study and meaningful experimentation.

As a final word, I venture a comment back to Wilson's (1990) deductions about the diversity of the New Zealand flora. I agree that IDH can have played little part in lengthening the list of species found there - those which are present have had both to arrive there and (at some time at least) to thrive there. What is important, however, is that each species that *has* entered the New Zealand flora (by whatever means) and *has* continued to find the space and the conditions necessary to its continued survival has also been provided with the opportunity to maintain its presence in the country. It is an essential extension of that logic that the requisite array of tangible pieces of land area *has been maintained by intermediate disturbance*. It is a powerful mechanism to maintain the existing compositional diversity against the tendency of the potential dominants progressively to reduce it.

## Acknowledgement

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