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Pelagic community assembly and the habitat template

Abstract

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The representation of habitats against axes of relative stress and relative disruption of growth opportunities, as conceived by Southwood and by Grime, provide helpful templates to which organisms may be fitted according to their abilities to cope with the habitat constraints. More than that, the template may be developed as a kind of "filter", whose porosity is set by the habitat, and the species whose traits allow them to pass the filter will be candidate components of the community structures likely to emerge.

Introduction

Theoretical ecology continues to wrestle with several fundamental issues about natural systems. Of general and pressing importance is the conceptualisation of ecosystem function and, in particular, the factors governing their assembly and the role of biodiversity in their maintenance. A common requirement is the diagnosis of the attributes of organisms that fit them to their environments and to their ecosystem roles, which information may be used to feed models of the effects of environmental change upon the structure and dynamics of the functioning system in its entirety. Much of the intractability of these problems relates to the complexity of ecosystems, the large temporal and spatial scales at which most of them operate, and the difficulties of observing or experimenting with system function and control. Often the main tools available are the recognition and analysis of patterns and the formulation of models to test hypotheses about their development. In this article, I take the opportunity to reiterate a view that pelagic ecosystems conform to patterns analogous to those of other systems but, because the biotic components are founded upon microbial producers and involve relatively small and generally short-lived metazoans, the absolute temporal scales of ecosystem processes are observable and amenable to practical experiment (Reynolds 1997, 1998a). All that is really needed is to establish the transferability of the patterns and the analogies of the high order assembly processes shared by all dissipative systems.

In this article, I seek to make these points through reference to the development of a framework for the organisation of ecological facts, in which the variety and variability of habitats provide a sort of matrix, or template, to which the survival requirements and evolutionary traits of organisms are stipulated and to which the names of pelagic biota are fitted, according to their physiological attributes. Much is based upon many years of studying the ecology and dynamics of the pelagic vegetation - the phytoplankton - but data on the decomposer and consumer components (including the bacteria, microzooplankton and fish) are also invoked.

The chequered history of the habitat template

The notion of devising a habitat template is credited to Southwood (1977: he actually used the word "templet"), although he attributed its initial foundation upon a matrix of breeding success to the influence of other ecologists. Moreover, the template he designed (see Fig.1) had little practical utility but, in fitting accommodating concepts of species strategies and community processes into a matrix of spatial and temporal heterogeneity, it has provided inspiration for many others.

The Oxford Dictionary definition of a template (or templet) refers to a thin board or plate used as a guide in cutting or drilling. It would be used by an artisan to ensure that a sequence of output products conformed to an identical, interchangeable pattern. In the ecological sense, species with similar functional and morphological traits, physiological attributes and adaptive life-history (*r, K*) strategies will conform to distributions in relation to habitat availability, duration, resource availability in generally consistent and reproducible ways. The most successful early application of this approach came in Grime's (1979) graphical linkage of the reproductive strategies of plants to the patterns of development of the vegetation of which they were a part. I am not sure that Grime ever used the term "template". Moreover, his main axes were differently labelled but the variable stress (due to resource shortage) and the frequency of disturbance (due to mechanical forcing) have obvious analogies to the Southwood dimensions, "resource level" and "durational stability" (see Fig.1). Of special interest is the fact that, on a 2 x 2 contingency table setting high or low resource accessibility against high or low frequency disturbance, Grime (1979) recognised that the combination of resource poverty and habitat impermanence was practically untenable as habitat. The remaining options provided environment for plants either able to invest strongly in biomass and dense vegetation ("competitors", or C species), or for specialists adapted to withstand severe abiotic resource deficiencies, including of water ("stress tolerators", or S species) or for specialists whose short lives and heavy investment in propagules facilitated exploitation of temporary or frequently disturbed habitats ("ruderals", or R species). Although the scheme envisaged many intergrades, the extremes of C, S and R adaptation afforded three apices of what quickly became known as Grime's "C-S-R triangle" (Fig. 2).

It is fair to point out that the triangular representation attracted severe criticism (Loehle 1988), while its central concept of trait-based differentiation of life-history strategies and their contribution to plant-community structure has been fiercely debated against Tilman's (1982) rival resource-based competition theory which predicts community outcomes that are a function of the concentrations of limiting resources. Despite the arbitration of other contributors (see Grace 1991), the debate was more exhausted than finally resolved.

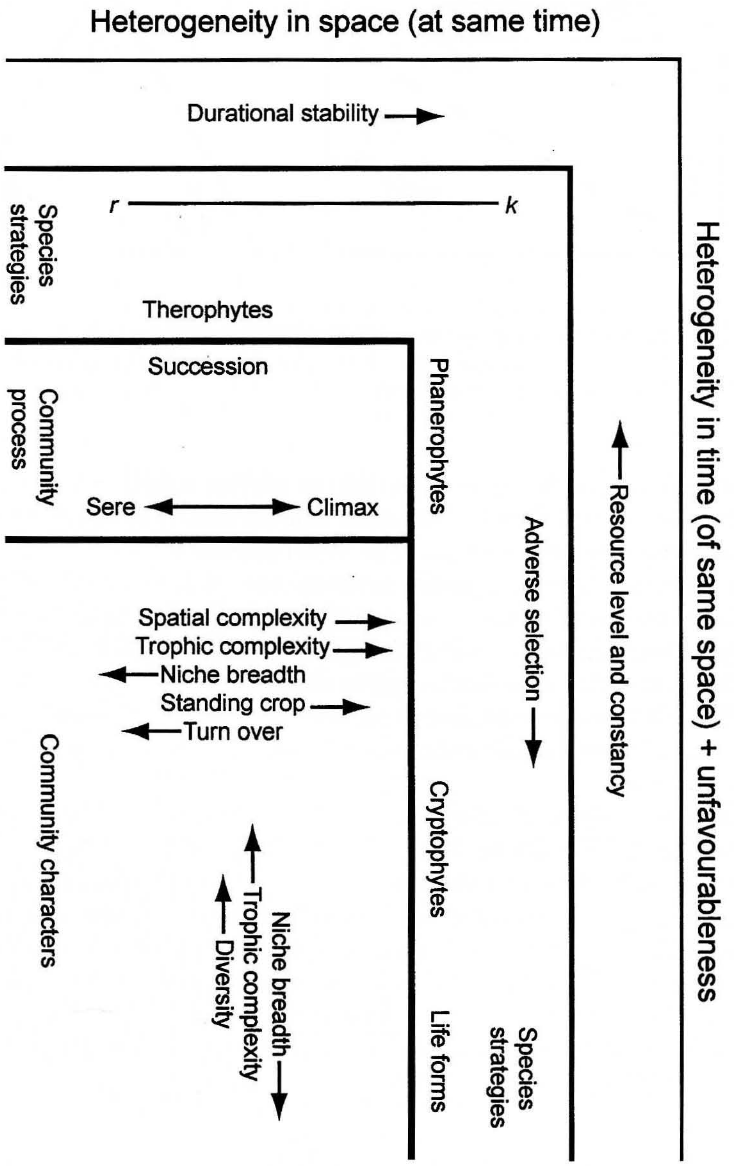

Fig. 1. Southwood's (1977) proposal for a habitat template to accommodate ecological strategies.

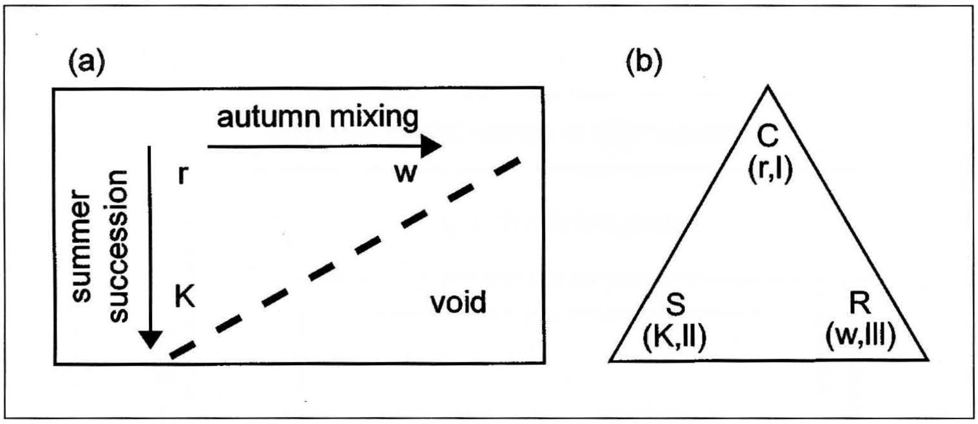

Fig. 2. (a) An early representation of the primary strategies of phytoplankton (r, K, w, as proposed by Reynolds & al. 1983), arranged to accommodate observeable the periodic changes in phytoplankton composition. This was later adapted to fit (b) Grime's (1979) CSR triangle of primary strategies.

Arguments centred more on the classification than on whether similar specific attributes of species really suited them to similar ecological distributions. Only much later, did the Integrated Screening Programme (Grime & al. 1997) demonstrate powerful evidence for the existence of primary functional groups, including the C, S and R types. Grime's vision is also vindicated by other recent efforts to develop classifications of species that relate them directly to function through shared biological characteristics (Lavorel & al. 1997). Implicit in the quest is that plant species can be classified into functional groups, whose ecologies and sensitivities are indicative of the state of the local ecosystem and to which whose underpinning physiological attributes are deterministic - more or less as Grime had argued in the first place.

One further line of support for the tenability of the C-S-R representation comes from an unexpected quarter, in a paper by Romanovsky (1985) on the life-history strategies detectable among the planktonic cladoceran crustaceans. He distinguished among species (like *Diaphanosoma brachyurum*) that invest in high survivorship rather than in juvenile growth, those ultimately large- bodied species that sustain rapid rates of juvenile recruitment and development (typified by *Daphnia galeata*) and those smaller-bodied but fast reproducing occupants of transient habitats, like *Moina* spp.). Following a terminology he attributed to L.G.Ramenskiy, he referred the three types as representing "patient", "violent" and "explerent" life-history strategies; their respective analogies to Grime's S, C and R plants are transparent.

The habitat template for phytoplankton

Reference to planktic life forms is the opportune point to bring the essay back to community assembly in the open water of lakes and seas. Here, the formulation has been relatively non-controversial, because the separation of species on the basis of spatial and tem-

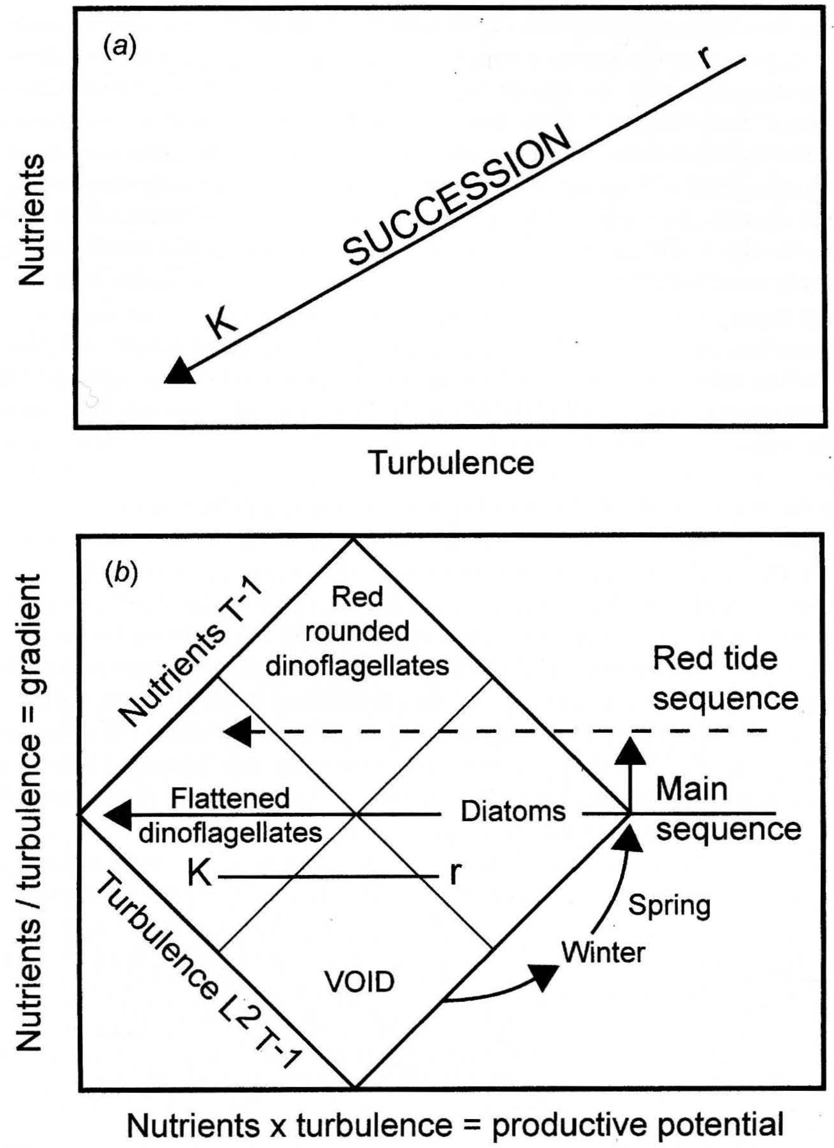

Fig. 3. (a) Simplified version of Margalef's (1978) representation of the response of phytoplankton assemblages to seasonal changes in structure ("turbulence") and resource accessibility ("nutrients") and the main course of succession. (b) The later mandala of Margalef & al. (1979) separated the implied mutual dependency of nutrient availability and structure and allowed trajectories other than the main sequence to favour other types of phytoplankton.

poral distributions was readily related to functional distinctions among the algae. Moreover, species showing similar ecologies share many morphological and physiological characters in common (Reynolds 1997).

Margalef (1978) produced one of the earliest diagrams to represent annually reproducible sequences in the species composition and dominance of the phytoplankton, based upon his observations in the Ria de Vigo, north-west Spain. Against quantified axes of "turbulence" and "nutrients" (Fig. 3a), he plotted the change from a spring assemblage (dominated by the diatoms, *Thalassiosira* and *Chaetoceros*) in the upper right-hand corner as being associated with mixed, unstratified conditions with relatively abundant nutrients. In direct contrast, he represented the summer assemblage (of *Ceratium*-like dinoflagellates) in the lower left corner, signifying their ability to thrive under conditions that were not simply stratified ("low-turbulence") but strongly differentiated into a very nutrient-deficient upper layer and a richer but light-deficient deeper layer. The diagonal between them simultaneously traces the trend in the changing environment and the "main sequence" of alternate species selected. In the text, Margalef (1978) developed the idea that the adaptations required for survival in the seasonally altered conditions had necessitated the switch to another life form which is not reliant on turbulent entrainment or maintenance near the surface and which has sufficient self-regulatory powers to be able to exploit the stratification and, thus, to self-organise the task of gleaning sufficient resources. The penalty for sophistication is a slow growth rate: the sequence, as is also marked on his diagonal, Margalef took to be a classical succession from fast-growing, *r*-selected species to slower growing, *K*-selected species, garnering the diminishing resource base and conserving the assembled biomass (cf. MacArthur & Wilson 1967; Pianka 1970).

A year or so later, Margalef & al. (1979) presented a redesigned matrix to accommodate some of the morphological diversity of the predominant phytoplankton and alternative tracks in the main sequence that might result in red-tide formation. This they styled a "mandala" (Fig. 3b). Its redesigned axes now showed the link between life-form and the physical environment for the first time. However, it was the simpler figure from Margalef (1978) that became the better known.

At about this time, students of the freshwater phytoplankton were seeking graphic means to organise ecological information. My first attempt (Reynolds 1980) was a "possibility matrix", inspired by Margalef's (1978) diagram, but defined by axes of nutrient availability and column stability. In to this, the ranges of twelve types of phytoplankton ("association") were fitted, with respect to their apparent preferences for nutrient-rich or nutrient-poor systems and for stratified or mixed conditions. It was envisaged that natural succession ("main sequences") followed a rightward drift but changes of mixing were externally forced, requiring separate representation as "perturbation" or "reversion". The twelve groups had been identified beforehand using a long-hand adaptation of the classical approach of phytosociology to define groups of consistently co-occurring species that wax or wane in abundance. They could have qualified for a proposal to name them according to formal phytosociological nomenclature ("Asterionelletum", "Dinobryonetum" etc.) but, from then until present, they have been distinguished only by alphanumerics.

From that time, there has been a steady progress, both in the design of the matrix and the delimitation of the species associations. There is little point in cataloguing the development in its entirety but some steps were linked to important conceptual advances. The

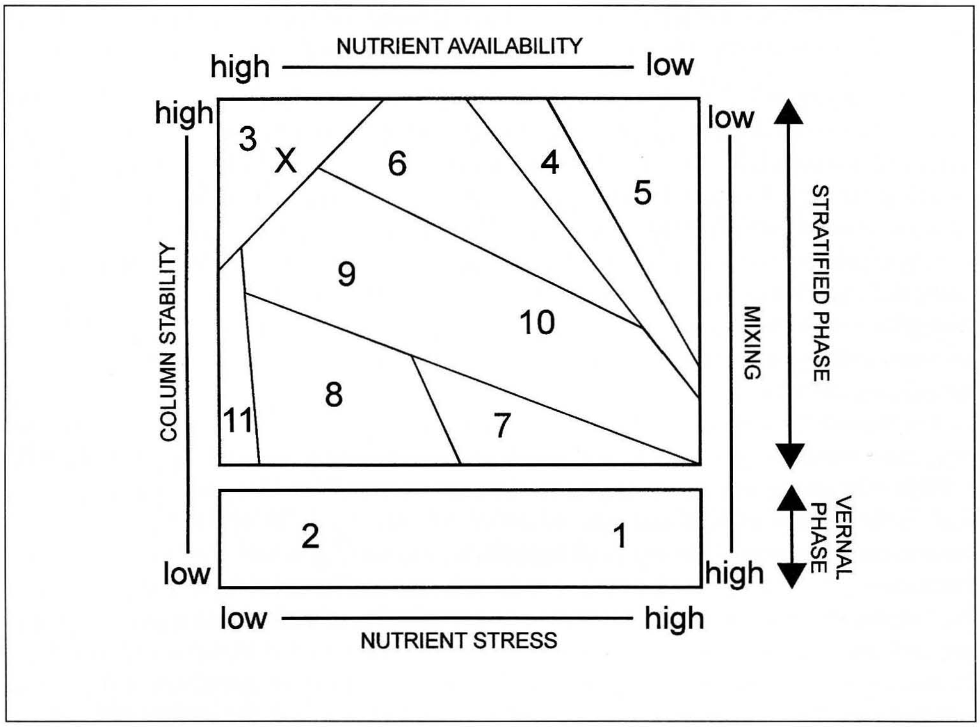

Fig. 4. Part of Reynolds' (1980) "possibility matrix", showing the distribution, against axes again representing nutrient availability and stratification, of phytosociological groups of phytoplankton species separated according to their seasonality. The group identifiers correspond to what are now B (for 1), C (2), G (3), F (4), E (5), H (6), P (7), N (8), LM (9), LO (10), R/S (11).

first of these (in Reynolds 1984) was the recognition of the strong morphological coherence of species with similar ecologies and, often (where such data were available), similar physiologies too. Three, rather than four generic patterns were noted:

- Type I organisms corresponded to small, nanoplanktic algae, generally unicellular and capable of the rapid, invasive growth expected of *r*-selected species, especially early in the stratification when nutrients were still readily available in the insolated upper water column.
- Type III organisms were generally much larger, often (but not exclusively) colonial, motile (having evident self-regulatory capacity) and loss-resisting but slow growing, like Margalef's *K* species. These species are prominent in late successions in highly stratified and resource segregated environments. They are directly and successionally linked to *r*-selected Type-I organisms.
- Type II organisms were mostly non-motile, but distorted from the spherical form (high surface-to-volume) which supports efficient light interception and growth. These are species favoured by, if not dependent upon, a finite mixing depth for suspension. They populate mixed layers and sink from stratified ones. They do not belong to the Type-I

→ Type-III succession but stand apart from it through the linkage of external forcing of mixing and or stratification. Reynolds (1984) distinguished them as *w*-strategists.

Although originally developed in ignorance of Grime's work, the delimitation of three main phytoplankton groupings has self-evident analogies with both Grime's (1979) categories of terrestrial life-history strategies. Reynolds (1988) formally substituted C-S-R labelling for the *r-K-w* terminology. With hindsight, the fitting was perhaps unduly forced in the interest of consolidating conceptual unification of concepts. However, acceptance of the three primary strategies of the Grime triangle remains explicit, as is the bridge to the Margalef model (Fig 2). A re-styled template accommodating the alphanumeric phytosociological categories was devised (Reynolds 1987: see Fig. 5) and to which explicative fits of representative physiology (Reynolds 1989) and morphology (Reynolds 1993) were added progressively.

Subsequent refinements to this line of development were to introduce, finally, quantitative axes which would define the ranges of alphanumeric representatives (Reynolds 1999a). The energy (x) axis is scaled by the derived unit $I^{**} = I^{*}/h_m$ and where $I^{*} = (I'_0\ I_m)^{1/2}$ is the integral of light through the mixed column, h_m, I_m being the light level at its base and a proportion of the light just beneath the surface (I'_0, in mol photons m^{-2} d^{-1}), calculated as $I_m = I'_0 \exp(-\varepsilon h_m)$, where ε is the relevant coefficient of light extinction. I^{**} is thus sensitive to light deprivation whether as a result of poor surface irradiance, deep mixing or high turbidity; the units are mol m^{-3} d^{-1}. The resource (y) axis is substituted by a "resource accessibility" term, $K^{**} = [K_0]/\delta[K]$, $[K_0]$ being the concentration of the critical nutrient (say, biologically-available phosphorus, in mmol m^{-3}) at the surface and $\delta[K]$ is the mean concentration gradient (in mmol m^{-3} m^{-1}) through the trophogenic zone. The idea is that K^{**} (units, m^{-1}) not only distinguishes high and low initial nutrient concentrations, but that it is also responsive to successional resource segregation. The template in Fig. 6 is populated with generalised freshwater habitats but the alphanumeric boundaries in Fig. 5 fit comfortably and correctly into the relevant habitats. The procedures invoked look simple but the significance of using a habitat template to predict the structure of a biotic assemblage should not be overlooked. The approach has been emulated for the phytoplankton of the sea and the first indications are that it works extremely well (see Smayda & Reynolds 2001).

Other improvements have been to the algal categories themselves. Although originally recognised from their co-occurrences, it is now evident that it is the selective trait which is crucial and that similar niches in distant lakes may be filled by quite different species. For instance, it is apparent that the turbid, nitrogen deficient habitat should be occupied by a solitary, photo-adapting, filamentous Cyanobacterium - like *Cylindrospermopsis,* in fact, in the palaeotropical and neotropical regions (Padisák 1997) but *Anabaena minutissima* in New Zealand (Pridmore & Reynolds 1989). Several other examples have persuaded me to drop the reference to "species associations" in favour of another term implying "narrowly-defined functional group", though, as yet (at the time of writing), without finalisation. At the same time, the list of alphanumeric groups has been lengthened, sometimes by splitting, to accommodate more ecologically-distinct types of plankton. The list published in Reynolds (1997) has already been modified by Padisák & Reynolds (1998) and Huszar & al. (2000), and the nucleus of an international forum for the classification and naming of

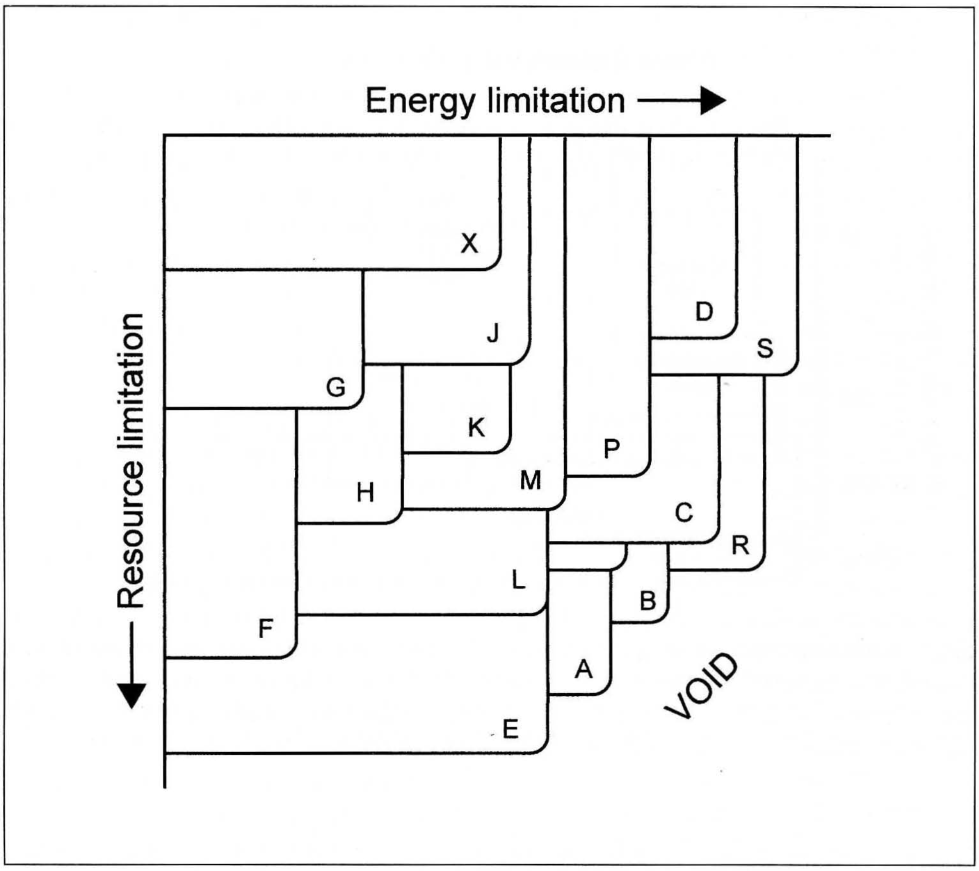

Fig. 5. Improved matrix of plankton Reynolds (1987) accommodating an increased number of phytosociological functional group-associations (now identified by letters) and fitted to axes of critical resource limitation and energy limitation (the principal effect of deep entrainment).

the phytoplankton functional groups already exists. Finally, a means of representing the adaptations of the functional-group representatives, in the form of a hexacle has been devised (see Reynolds 1997, 1998b), although they are already known as "umbrellas" on account of their shapes.

The habitat template and the assembly of communities

In the final part of this article, I hope to show how the simple concept of a habitat template has matured into a fundamental model of the process of community assembly. Like all supra-organismic processes, the observable behaviour can only be emergent: the general patterns and probabilities inherent in developmental outcomes are manifestly non-chaotic responses to environmental cues and which are substantially biased by the programmed reactivities provided by intraorganismic traits. Such outcomes fall within the

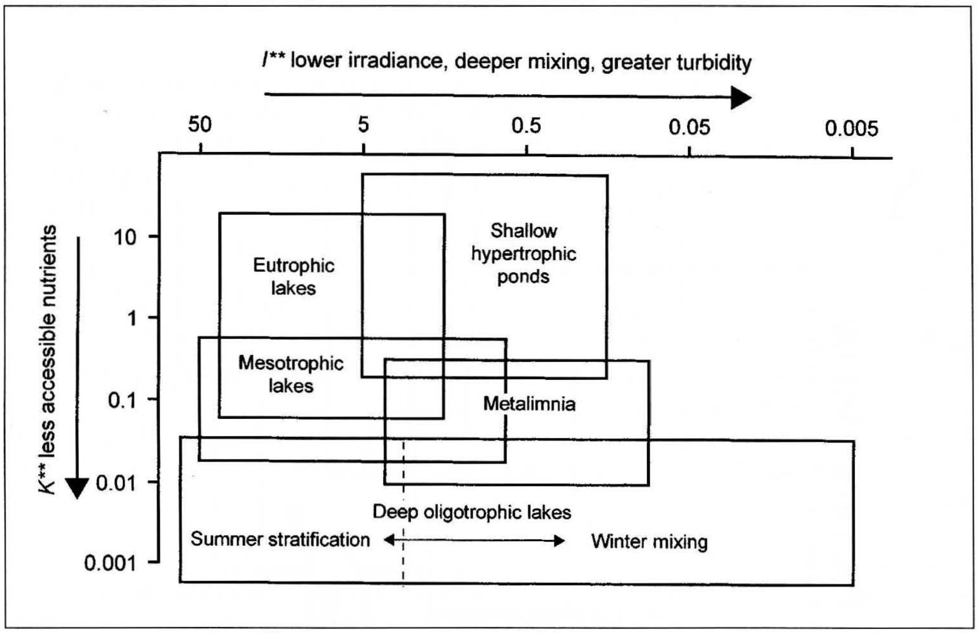

Fig. 6. Habitat template, scaled against quantified (logarithmic) gradients of energy and resource accessibility, developed in Reynolds (1998a), and to which the phytoplankton distribution in Fig. 5 can be fitted. The habitats shown are generalised but, potentially, co-ordinates for any lake or reservoir can be defined to identify the likely functional types of phytoplankton to be found there.

understanding of contingency - the probabilistic result of the coupling of deterministic processes to stochastic events (Berlow 1997). Thus, variations in community structure of the emerging community cannot be predicted precisely or repeated exactly. However, as responses to a given sequence, duration and intensity of variability, they may be interpreted retrospectively from a sound knowledge of how particular organisms, or types of organisms, respond to controlled changes in their environments. Like some giant board game, there are rules for its conduct and they may be deployed to gain advantage over other contestants but what happens may still hang substantially on the roll of the dice.

Many ecologists have been interested to establish the rules of community assembly. So far as the pelagic vegetatio- the phytoplankton- is concerned, some progress towards the compilation of a "rule book" has been made, mainly through workshop discussion (see Rojo & al. 2000: Reynolds & al. 2000). It is not known how well accepted or widely shared its views might be but it is recognised that, in order to be generally useful, rules of assembly need to relate to a mathematical framework, to a contingency matrix, in fact.

The most familiar representation in the mathematics of logic is the Boolean truth table, in which statements of the kind "if A is so, then B is also so but C is not" can be represented as binary tabulations in a 2-d table. In the contingency table, it is the strength of the dependency of B or C on A which is evaluated. Clusters of high positive or high negative values denote consistent positive or negative influences, while their delimitation defines the identity of a group, or set, of similarly contingent outcomes.

Going one stage further, the Venn Diagram used in classical set theory affords an appropriate model upon which the candidacy for an available species for participation in the assembly of a community suited to the particular environmental constraints might be tested. The universal set (usually symbolised by the notation, $\mathscr{E}$) represents the totality of habitats, among certain of which the totality of organisms lives and thrives. We might refine this initially to represent the totality of aquatic habitats (from which all terrestrial species would normally be excluded) or just those of inland waters (so excluding all marine species). By diminishing the scope and sharpening the focus of the biospheric compartment of interest, we rapidly eliminate the candidacy of huge numbers of known species to be able to inhabit any part of the environmental set retained. This process can be continued into habitats that are more and more finely delimited, each time "filtering out" the species lacking the fundamental traits that would allow them to live there. Moreover, the process begins with quite coarse filters but, eventually, candidate species are selected on finer and finer criteria.

So far as the freshwater plankton is concerned, the intensification of selectivity moves from the physical constraints set by the generation and dissipation of turbulent kinetic energy through the water mass, through the level of trophic function and participation in carbon transport (producer, consumer, decomposer) and, finally, to the metabolic level where the minimal requirements of individual species can be met within the temporal opportunities to gather them (Reynolds 2001). Carried to its logical extreme of sufficiently narrow habitat constraints, the filtration concept should finally identify the best-fitted species. However, it also allows more species to function in less severe (more "benign"; Reynolds 2001) environments. This is important to understanding how species that are not equally competitive nevertheless co-exist and, indeed, how a high diversity of potentially redundant species can be maintained. The notion of habitat filtration is not especially new either-it has much in common with the biocoenotic hypotheses advanced by Thienemann (1918) and others to explain the faunistic composition of particular kinds of lake, with special reference to the low species diversity associated with "harsh conditions" (i.e, tolerable to relatively few species) and to the greater numbers of species in environments permitting many species to approach their optimal performances.

The idea that communities might comprise not merely the best-fitted species but that they are, rather, near-random assemblages of all but the non-fitted species, is now strongly advocated by, *inter alia*, Keddy (1992: see also Weiher & Keddy 1995), who was motivated by work on wetland plants, by Kelt & al. (1995), working with small mammals, and by Belyea & Lancaster (1999), inspired by stream fauna.

The conclusion of Belyea & Lancaster (1999), that internal dynamics would always be the most influential factors in community building but necessarily within the constraints imposed by the local environment and the pool of species available, is an exciting complement to Southwood's (1977) valuation of habitat classification and of the environmental "sets" that the template approach provides.

Drawing these lines of reasoning together, it is still to plankton biology where we may look for examples of how the template carries the information necessary to predict the functional groups likely to be suited to the environment in question, as well as those likely to survive intensification of the selective constraints. In Fig. 7, I show a recent revision to the template layout that accommodates habitat domains distinguished according to how difficult it is to convert available carbon into specific, functional biomass (Reynolds 1999b). The primary handicaps on conversion, "resource constraints" and "processing constraints", now define the axes. These have their roots in the corresponding axes of Figs 3a–6 but the conceptual breadth is widened to embrace the carbon sources and sinks in limnetic habitats generally and to acknowledge explicitly the role of redox as a factor regulating the mobility of fixed carbon. To move rightwards (in the x direction) in Fig. 7a continues to represent the encounter of increasingly severe constraints on the processing opportunities, which include the diminution of access to incoming photochemical energy, as a growing constraint on the capacity of photosynthetic production. Moving in the y direction from the bottom left-hand corner follows a gradient of alleviating severity of traditional nutrient limitation, to a point where the supply of nitrogen, phosphorus and all other nutrients is able to sustain a rate of biomass synthesis which consumes carbon dioxide at a rate similar to the maximum rate of invasion into the water across the surface (it is supposed that this route can supply no more than 90-100 g C m^{-2} y^{-1}: Reynolds 1999b). Even that rate depends upon the maintenance of a steep solution gradient. Smaller water bodies, in which the direct invasive pathway is matched or exceeded by carbon dioxide dissolved in the inflowing water, or is enhanced by the release of gas through the photolysis dissolved organic matter (Maberl 1996; Thomas 1997; Whitehead & al. 2000), are represented towards the top of the template, as are the effects of an organic input that exceeds the capacity for its re-oxidation. Thus, the sub-habitat boxes in Fig. 7a are identifiable by the dominant limitation of carrying capacity (Reynolds 1999). Note that the bottom four squares are analogous to the four squares of the mandala (Fig. 3b).

In Fig. 7b, the representation is modified to a Venn Plot to which the distributon limits of named examples of organisms or functional types can be fitted according to the physiological limits of their biological traits. The axes (note the log scales) accommodate the maximum photon flux ($\{E\}^* \sim 60$ mol m^{-2} d^{-1}) and a range of carbon dioxide concentrations influenced by the solution flux to open water systems ($\{C\}$). Capacity limitation by the supply of phosphorus (it could just as easily have been nitrogen or any other nutrient) is inserted on the carbon axis in the appropriate stoichiometric equivalence (1 mol P :106 mol C). To move downwards from this point is to imply increasing risk of phosphorus deficiency; to move upwards increases the system dependence on external supplies of inorganic or organic carbon. To move rightwards implies the increasing limitation by light energy.

The perimeter of Fig. 7b can be taken to represent the totality of planktic habitats (at least, with respect to these three dimensions) and to cover all eventualities from relative plenty to virtual famine. The plot is then amenable to the insertion of the operational ranges and tolerances of particular species. Where the species plot embraces the habitat co-ordinates, it may be deemed to be filterable and, thus, its growth is tolerant of the environmental conditions.

To illustrate the principle, details of three phytoplankters are entered in Fig. 7b. The limits shown for *Microcystis* summarise its inadequacies as a light antenna and its relatively weak affinity for phosphorus concentrations but emphasise its superior affinity for carbon dioxide at the micromolar concentrations found at high pH (Moss 1973; Talling 1976;

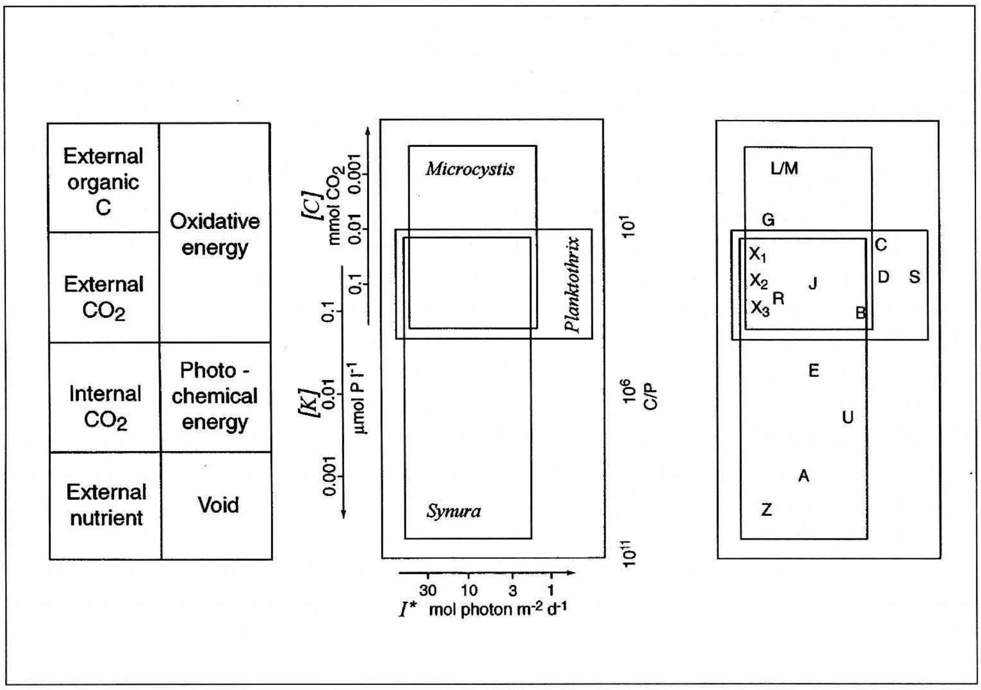

Fig.7. Habitat template development for community assembly. (a) Simplified matrix of limnetic metabolic sensitivities as proposed in Reynolds (1999b), with carbon resource (vertical axis) and the rate of its processing (horizontal axis) as the constraining factors. Starting at a point half way up the left-hand axis, it is supposed that the supply of carbon and nutrients will saturate the fastest rate of carbon fixation. In the downwards direction, nutrient resource availability constrains the biomass assembly; rightwards, the system becomes limited by photosynthesis; upwards, carbon dioxide is the most serious constraint; if the system is relieved by an alternative supply of fixed carbon, processing rates are often constrained by oxidative potential. (b) Quantifying in terms of carbon, phosphorus availability and the harvestable photon flux, the physiological ranges of given plankton algae can be represented by Venn boundaries. Each of the three shown is particularly well-adapted to contend with deficiencies in the supply of one of the requirements. At optimal supply rates, all three species perform simultaneously: their Venn plots overlap and, at these co-ordinates, any or all may be anticipated contributors to the community structure. (c) as (b) but (provisionally) populated with the potential assemblages of phytoplankton likely to thrive at the relevant co-ordinates, shown by functional-group identities. Redrawn from Reynolds (2001).

Kaplan & al. 1980). The range of *Microcystis* penetrates deeply into the low-CO_2 regions of Fig. 7b. By analogy, *Planktothrix agardhii* is not just a good light interceptor but shows great capacity for photosynthetic adaptation (Tandeau de Marsac 1977). Data from Post & al. (1985) allow us to insert a range of opportunities for *P. agardhii.* Finally, the tolerance of low phosphorus environments by *Synura* is not only a consequence of the alga's high affinity for phosphorus (data of Saxby-Rouen & al. 1997) but also to its capacity to live phagotrophically on bacteria (Riemann & al. 1995).

Each of the three specific rectangles now defines a series of habitats in which the alga can live. Note that all can live in the area of overlap, where benign levels of carbon, light and phosphorus obtain. None of them is excluded in this area of the filter but this will be true for a large number of other planktic species. The filter does not say which will dominate but we already know that dominance is likely to pass to species which are dynamically fit, that is, to the fastest growing species of those present or, if not, the one fielding the largest inoculum.

Even without showing comparable data for other species groups (where such are available) it is easy to recognise that the concept will readily embrace the filtration criteria for the traits of other functional types. As a provisional step, the alphanumeric codes to some of the other functional types are inserted in the areas likely to be reached by their respective Venn-sets, and where the ability to survive the filtration is adequate to qualify them for passage into the assembling community (Fig. 7c).

The template-cum-trait filter will not predict species composition (save, perhaps, at the extremes), which will continue to be subject always to species availability, relative fitness and the "seed banks" of system memory. Mutual antagonisms, genuine competition for limiting resource (where applicable) and the effects of the food web (selective consumption) will remain powerful influences on the outturn, in the terms of species abundance and composition. What the filter does is to narrow the probabilities considerably and, in many instances, to identify the trait characters likely to provide the greatest benefit to species survival.

Conclusions

The essence of this presentation is that habitat templates provide a helpful and very useful approach to the classification and prediction of community structure, based upon the functional requirements of their occupancy. Templates assist us to understand the rigours posed by given environments and to determine the adaptive criteria of the tolerant organisms. This, in turn, validates the recognition of traits, encourages their quantification and, not least, opens the door to the classification of organisms according to their ecological tolerances and preferences. The approach is not unique to phytoplankton, nor is it original in this context. However, it is once again possible to point out the powerful scaling advantages of studying community ecology in the plankton that are demonstrated in the clear patterns of distributions that emerge from biological traits.

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