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A MARINE SCIENCE ODYSSEY INTO THE 21st CENTURY. *J.M. GILI, J.L. PRETUS and T.T. PACKARD (eds.)*

Emergence in pelagic communities*

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SUMMARY: Pelagic systems, those based on the open waters of large lakes and seas, provide excellent opportunities for ecological study. This is because, the vastness of the oceans apart, pelagic ecosystems operate on short space and time scales. This affords important opportunities to study the emergence of ecosystems and the basis of striking high-order patterns of ecosystem behaviour. The essay seeks an outline of the processes by which the biologies of individual organisms - the largest functional, controlled units in the ecosystem - interact and bias the outcomes in favour of particular network structures recognised by ecologists. Populations build, communities assemble, ecosystems function but always in ways that relate to the match between the adaptations and performances of individual species and the capacities of the environments in which they find themselves. The paper attempts to discern the linkages between the biology of individual and the ways that ecosystems are put together, between organisms and organisation. Drawing on the advantages of absolutely short generation times among the producers, consumers and heterotrophs of the pelagic, I seek to sample the ascendant pathways of ecosystem synthesis, noting the energetic decisions which select for particular outcomes. However, the simple organisational state of many pelagic communities reminds us that ascendancy is frequently restrained by a scarcity of resources and tempered by the frequent intervention of abiotic factors. The presentation does not seek to prove any point about systems: it attempts to re-affirm what is known about organisational hierarchies; then, using approximate quantities, the points of bifurcation between alternative organisational structures are nominated; drawing upon suppositions about the dissipation of energy, the organisational underpinning of function at the level of the whole ecosystem is proposed. Corroboration from observations from the real world is sought throughout.

Key words: community organisation, assembly rules, pelagic, phytoplankton, zooplankton, bacterioplankton, energy thresholds.

INTRODUCTION: FROM PELAGIC ORGANISMS TO PELAGIC ORGANISATION

Like the other papers presented at the 36th European Marine Biological Symposium (held in Maó, Minorca, Balearic Islands, 17-22 September 2001), mine is intended as a tribute to the shining example and monumental inspiration that the work of Dr Ramón Margalef bequeaths to us. Of the many specific reasons for celebrating his scientific career, I select two above all others. One is his pursuit of robust ecological theory: as his ECI Prize Publica-

tion (Margalef, 1997) makes abundantly clear, a grasp is required, urgently and correctly, of the mechanisms by which the Earth's ecosystems regulate themselves. Without this knowledge, we are failing to anticipate the impact of our own over-populous, aspirant, manipulative, destructive species on the resilience of the world's ecosystems. Without an understanding of their regulatory mechanisms or the consequences of their exceedence, how can we hope to determine what is necessary for us to recover a genuinely, ecologically sustainable tenancy in the biosphere?

The second reason is the linkage between the lucidity of Margalef's theories and his own deep

understanding of pelagic systems. This is far from having been a unique combination –one immediately recalls the careers of other famous ecological theorists like G.E.Hutchinson, the Odums and David Tilman– but it conforms to a belief of mine that aquatic systems make inspiring subjects for ecological study. The supposition consolidates the valid claim that, aside from the vastness of the oceans themselves, aquatic ecosystems function on sufficiently short spatial and temporal scales for their high-order workings to be amenable to observation and meaningful experiment (Reynolds, 1998a). All that is needed is an acceptance of the analogies and of the basis for their interpretation and quantification.

This being so, the first priority is to establish vertical connectivities –the nature of the linkages among the behaviours of individuals and the structures evident at the level of ecosystems and biomes. Some species-specific autecologies of aquatic organisms are relatively well-known, often with a clear understanding of their population dynamics and the features of the environments which most influence them. Good examples include fish (Elliott, 1994), invertebrates (such as the "keystone" water fleas of the genus *Daphnia*: Haney, 1985) and some planktic autotrophs (a fine case is the biology of *Cylindrospermopsis*: see Padisák, 1997). At the other end of this spectrum are some recent concepts explaining how ecosystems are organised and regulated (see, e.g., Straškraba *et al.*, 1999, and other papers in the same series). Such contributions add value to the developing sub-discipline of macroecology (Brown and Maurer, 1989; Brown, 1999) which identifies within the large-scale statistical patterns of species distribution, abundance and richness of species, the processes governing the structure and dynamics of complex ecological systems. Exciting as macroecology has become, some ecologists remain uncomfortable with a deductive but practically untestable model that pitches itself above the real-world complexitities of variable population dynamics and other small-scale assembly processes in fluctuating communities. Crucially, however, macroecological approaches to questions about the operation of the intermediate organisational level –that of the local assemblage of species and its structural regulation– seem to promise legitimate and verifiable insights into the ways that the ecologies of individual species slot together into recognisable, functionally viable ecological communities (Lawton, 1999). The broad challenge accepted here is to develop an overview on how pelagic communi-

ties (those of the open water of large lakes and the sea) are assembled.

Thus, the specific aim of this essay is to contribute towards the eventual synthesis of a "rule book" of ecosystem organisation and function. The sequence of ideas to be developed is founded on a "bottom-up" view of biotic sequestration of raw materials by constituent autotrophs and the energetic potential that is harvested from sunlight. The adaptations of individual species of autotrophs and the respective fitness features these impart in the face of intensifying environmental constraints are argued to influence strongly both the directionality of autogenic succession and the responses to allogenic environmental forcing. The analogous behaviour of the phagotrophs and other microbial consumers of primary products are treated in a lesser detail, sufficient only to characterise the interactions among the community's producers and consumers of organic carbon. The relevance of carbon intensity to the structure of distinctive pelagic communities is considered towards the end of the essay.

These are large areas of ecology. It is desirable to adopt some overall framework into which to interface concepts from ecosystem theory with knowledge of the specific adaptations and autecologies of individual species and functional groups. The model I have adopted to provide that framework is an adaptation of the species exergy plots of Nielsen (1992).

EMERGENCE AND EXERGY

An earlier draft of this paper was titled "The self-organisation of pelagic communities". It was changed to the present one because any implication that the striking robust and consistent patterns evident in system development conform to some supra-organismic control is a source of deep concern among practising ecologists. One does not have to go as far as adopting a Gaian interpretation of the biosphere (Lovelock, 1979) before the supposition of some internal design to assembling ecosystems is implicated. The use of terms such as "goal function" (Straškraba, 1980) or, indeed, "self-organisation" (Pahl-Wostl, 1995) to describe the development of complex, networked communities of interrelated producers and consumers risks the misattribution of a system property to some systemic driver. The high-order patterns in pelagic communities are clear enough, with well-rehearsed attributes and processes (see Reynolds *et al.*, 2000) which are not in dis-

pute. However, it has to be rigorously emphasised that the patterns are exclusively contingent on the behaviours and mutual interactions among the biotic components of the ecosystem, that is, the individual organisms making up the specific populations and the putative multi-species communities. The ecosystem is the sum of the component processes carried out by the aggregate of constituent individuals. Organisms, indeed, are the largest self-regulating units of assembly with any kind of controlling, reproducible set of genomic instructions. In the delightful phrase of Lampert and Sommer (1997), we need look "no further [..for system properties..] than the activities of individual organisms".

This being so, self-organisation is a collective outcome (or "emergent property") of the aggregate of the independent dynamic responses of individual organisms to the external environmental conditions obtaining. These act as a kind of filter, admitting the growth of tolerant individuals of suitably pre-adapted species while excluding those that are poorly suited. Changing environments may result in changing filters which lead towards alternative outcomes, when the identities of the best-fit of the species available may also be varied (Harris, 1986). How such small-scale responses and interactions of individuals become aggregated and assembled into recurrent, emergent, high-order structures provides the central theme of this essay. To build this around a thermodynamic model permits an approach to community assembly that relates primarily to the fulfilment of functions rather than to the explanation of any particular assemblage. A starting assumption is made that ecosystems do not necessarily comprise the species that happen to be the best adapted to the particular habitat. A preferable analogy is the creation of a series of vacant employment opportunities, each waiting to be filled by able applicants. Changing conditions of employment might determine that only the fittest or most dogged of the applicants will survive. Yet, here again, we must reject at once any implication that such opportunities arise other than as a consequence of the infrastructural requirements for efficient organismic processing of the resources available: there is no central "employment policy". In this sense, emergent ecosystems have much in common with modern market-driven macroeconomies. Founded on a sound base of natural resources, economies expand through the application of labour and the accumulation of controvertible wealth. Wealth accumulation permits diversification as primary products are exchanged for secondary manufactures and goods are exchanged for services. Each activity requires specialist personnel and each is supported by the primary resource.

The balance of opportunities depends upon the resource availability, the rate of its processing through the economy and the burden of non-primary activities that can be borne. Given an adequate resource base of nutrients ($=K$), ecosystems harvest primary energy (E) to sustain production (P) and to accumulate biomass (B). Trading in organic carbon as currency (C_{org}), primary products support the secondary production of phagotrophic animals and heterotrophic organisms, within the supply limits that the primary ("wealth") generation can fufil. At the systemic level, expansion proceeds as a function of the capacity of the flux of organic carbon ($\{C_{org}\}$'), the concentration base of other elements or nutrients involved ($[K]$'), and the integral of harvestable energy flux ($\{E\}*$). Thus, assembly may be summarised:

$$A = f\,(\{C_{org}\}', [K]', \{E\}*) \qquad (1)$$

It is well understood that whereas energy can be stored chemically, its ability to support work is not. Ecosystems run almost exclusively on the short-wavelength solar flux, which is harvested and invested in high-energy carbon bonds through the remarkably conserved process of photosynthesis. Provided the supply of nutrients, water and inorganic carbon are each adequate to match the potential rate of fixation, primary production yields around 1 kg of carbohydrate per 15 MJ of energy captured (roughly 470 kJ invested per mol C_{org} fixed). Some of this carbohydrate is re-activated in growth, which draws on the store of C_{org} in the synthesis of proteins and new cell mass, and will provide the energy to drive the actual building process. All intracellular energy-consuming processes require the controlled oxidation of the organic carbon bonds, which is effected in the synthesis of ATP. This is another process that is highly-conserved among all living organisms, everywhere resulting in an irretrievable loss of energy as heat. Primary-producer biomass may eventually become the carbon substrate of a heterotrophic decomposer or the carbon intake of a phagotrophic consumer. In either case, oxidation of the organic carbon content provides the raw material of the growth and reproduction of the consumer, as well as providing it with the energy to use in the assembly of its biomass and in the (usually) significant effort required to forage for more organic car-

bon. So it is at each link in the food web, residual organic carbon being gradually oxidised away as it is processed through the prey-predator network. At each point, there are decomposer organisms working on the generated wastes or on the corpses and cadavers of expired organismic components and which, thus, eke out the last of the unoxidised carbon to supply their needs. Ecosystems are simply networks for dissipating energy.

The above model illustrates the linkage of macroecological processes to the molecular chemistry of carbon reduction and oxidation, embracing the notions of community structure and function in terms of thermodynamic exchanges. The quantities of energy that are eventually dissipated, either per unit time or per unit area, are influenced by numerous factors, not the least being the rate at which short-wave radiation is captured and transferred to store. Just as the growth of organisms requires an income of energy that, on balance, exceeds the outgoing losses, so assembling communities represent an accumulating wealth of organic carbon as energy income exceeds expenditure. In this respect, ecosystems appear to contravene basic laws of thermodynamics governing the entropic degradation of energy and matter towards the ultimate equilibrium state. Of course, ecosystems are fully open, dissipative systems (Jørgensen, 1992) that operate, like water-wheels in a stream, by exploiting the dissipative flux. More of the flux can be exploited by building more harvesting biomass (more or bigger water wheels) but the capacity of the flux itself cannot be enhanced (the same amount of water runs through the millstream).

A positive balance of energy harvest over the rate of its biotic dissipation may be referred to as *exergy* (Mejer and Jørgensen, 1979). Sometimes termed "negative entropy", or "negentopy", it is a thermodynamic measure of the information content of the system. The state of living systems may be characterised by the level of molecular organisation and information represented by their useful gene content (Jørgensen *et al*., 1995, Jørgensen, 1999). However, it is simpler to adopt the alternative approach of Nielsen (1992) which has the energetic exchanges as its base. Thus, Reynolds (1997a) calculated the exergy-generation capacity of phytoplankton, as a function of radiant energy income and the energetic costs of respiration and maintenance of the alga *Chlorella*. The model, reproduced in simplified form as Figure 1, supposes a maximum flux of photosynthetically available radiation of 60 mol photons
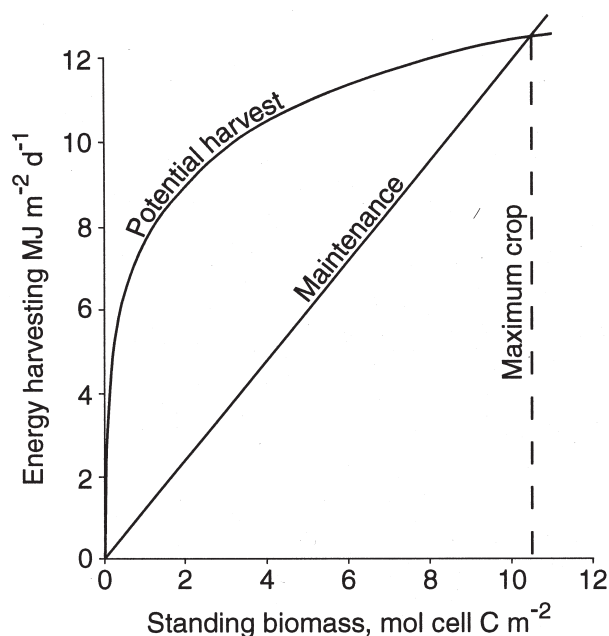

Fig. 1. – The Nielsen-Jørgensen representation of the potential exergy of a system, as the excess energy harvesting capacity relative to the biomass maintenance costs. The quantification is based on the physiology of the alga *Chlorella* (Reynolds 1997b).

m^{-2} d^{-1} (~ 12.6 MJ m^{-2} d^{-1} of photosynthetically available radiation, or PAR) and interpolates the interception of photons up to the areal density of light-harvesting centres that could be simultaneously activated at 20°C (the upper curve, expressed as the equivalent standing-crop carbon). The cost of standing-crop maintenance is calculated as a direct linear function of the basal respiration rate of *Chlorella*. The maximum theoretically sustainable standing crop is that at the point of intersection. The solution given -10.4 mol cell C m^{-2} ($\approx$125 g C m^{-2} or, roughly, 2.5 g chl *a* m^{-2}), compares well to reported natural maximal densities of phytoplankton (~50 g C m^{-2}) and active terrestrial plant biomass (~75 g C m^{-2}: see Margalef, 1997). It is a good deal less than the 20-30 kg C m^{-2} standing crops of forests, though this is, of course, dominated by the accumulated necromass that is wood.

The bow-shaped area enclosed between the energy-harvesting capacity and the maintenance costs of the autotrophic biomass represents the potential compartmental exergy flux. It is a measure of the system's ability to invest in new producer biomass, as represented in eqn (1), and to support the transfer of C_{org} to other levels in the trophic network. The bow also represents the buffering capacity of the system compartment, which enables it to withstand a variable solar energy income as well as consumer-
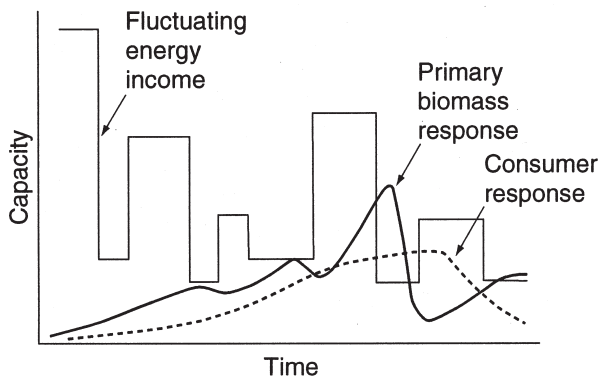
FIG. 2. – Assembly of producer biomass (continuous bold line) in relation to the ability of a fluctuating energy income (thin line) to sustain the mainteance requirements of the biomass. A similar relationship exists between the biomass of consumers and the ability of the food resource to meet its maintenance costs. Based on Figure 65 of Reynolds (1997b).

forced variations in the active biomass present (Mejer and Jørgensen, 1979; see also Fig. 2). So long as the net exchanges are positive, the existing structure has a "cushion" of exergy within which its biomass and its further development are wholly sustainable (Reynolds, 1997a). The economic analogy of exergy is a budgetary surplus that is available to support new growth or to fund the diversification of socially valuable but fundamentally non-productive service activities.

PELAGIC CONSTRAINTS AND THE HABITAT TEMPLATE

From the foundation that emergence is dependent upon a positive compartmental exergy flux, the task is to determine the mechanisms of growth and selection that influence the identity and function of the key players. In order to do this, however, it is necessary to first consider the nature and scale of the formidable constraints and conditions that pelagic environments pose to their exploitation by organisms and putative systems. These are suggested to act like a series of "filters", of differing coarseness, that select candidate species on physical, functional and metabolic criteria.

The "physical constraints" refer to the generic properties of water and of its motion, as it is moved by gravity, atmospheric forcing and gyratory inertia, from one state to another or from one place to another. In a fluid which is simultaneously non-compressible, relatively dense and viscous, mechanical kinetic energy is dissipated through a spectrum of turbu-

lent eddies, the smallest being eventually overwhelmed by the viscosity. The generation and dissipation of turbulent kinetic energy in lakes and seas, relevant to their biology, were quantified successfully over a decade ago (see e.g., Denman and Gargett, 1983; Spigel and Imberger, 1987) and their importance to pelagic ecosystems was quickly diagnosed (Mann and Lazier, 1991; Reynolds, 1994; Catalan, 1999). Contention with the combination of turbulence and the Archimedean properties of water makes rigidity a lower adaptive priority than tensile strength or the ability to escape turbulent shear by exploiting the viscous end of the eddy spectrum (Reynolds, 1998b). It is no coincidence that the dominant life forms of pelagic primary producers should be almost exclusively pico-, nano- or microplanktonic (i.e., < 0.2 mm; the few exceptions occupy rather specialised niches) and that they share this viscous world with most heterotrophs (bacterioplankton) and many species of phagotrophs (microzooplanktonic protists and rotiferans). Mesoplanktonic feeders (0.2-2 mm) that exploit turbulence in their foraging (Rothschild and Osborn, 1988) are built very differently to withstand shear. For larger pelagic foragers, the principal force countering progression through the water is frictional drag, to which end, the simultaneous investment in powerful musculature, streamlined body form and smooth surface is a long-appreciated adaptation, not just of pelagic fish but among other large animals too (Bainbridge, 1961).

The "functional level" invokes the major segregations in pelagic-role fulfilment, with respect to the movement of organic carbon. The essential distinctions are, clearly, among those organisms engaged in its synthesis into primary biomass and those which consume it as a delivered product. It may seem trite to be differentiating plants from animals at this point in the essay but this is an appropriate juncture at which to point out that the interactive, trophic relationships struck among the producer and consumer components –the food web– is generally recognised to represent one of the most important filters in structuring pelagic communities (Carpenter *et al.*, 1985; McQueen *et al.*, 1986), as it is elsewhere (Oksanen *et al.*, 1981). Clearly the interactions go beyond the sequence, carnivore eats herbivore eats plant: in a three dimensional environment, the means of foraging and the accessibility of resources need to be reconciled. Food availability and consumer ontogeny and electivity are prevalent in pelagic food webs (Pahl-Wostl, 1990). The impor-

tant trophic relationships in the pelagic are just as much networks as they are on the land. The components of a *Planktothrix*-Chironomid-Cyprinid food chain are no more interchangeable with those of a microbially-mediated picoplankton-calanoid-salmonid network than are those of a shrub-aphid-coccinellid sequence with those of a grass-zebra-lion linkage. Functional groups of every trophic level have to match the foraging opportunities of the habitat and trophic networks inevitably reflect these.

The "metabolic level" is the finest level of filtration, yet it is possibly the one requiring the greatest flexibility of paradigms held hitherto to explain species selection. In fact, the same principle holds as for the two higher levels, that every species will grow in suitable environments (its spectrum of requirements is satisfied) provided it has the opportunity to do so (a viable inoculum is present). The prominent species are not necessarily the best fitted and, while the opportunity is presented, any of a number of species may increase simultaneously and while individual demands are fully supplied by the collective resources, they are not strictly competitors (Reynolds, 1984a). This is different from the view, implicit in Tilman's (1977) resource-ratio hypothesis, that the species whose optimum requirements match most closely the conditions obtaining will "outcompete" all others in contention. However, once the supply of one or other of the resources fails to satisfy all the demands of co-habiting species, then there is a competition for limiting resource, and for which superior uptake affinities or alternative uptake strategies will single out the fittest competitors. Demonstrable limitation of performance is the essential prelude to competition, when the selectivity of the filtration is tightened against less well-adapted contenders.

The difference between the two ideas is narrow and nearly semantic. The principal distinction of the filtration concept is that it allows more species to function in benign 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. Moreover, the modern view of habitat filtration has much in common with the biocoenotic hypotheses advanced by Thienemann (1918) and others in the early part of the twentieth century (for a convenient summary of which, see Lampert and Sommer, 1997). They recognised the association of low species diversity with "harsh conditions" (i.e, tolerable to relatively few species) but greater numbers of species (albeit, many of them represented by small numbers of individuals) in varied 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 and Keddy, 1995), who was motivated by work on wetland plants, by Kelt *et al*. (1995), working with small mammals, Belyea and Lancaster (1999), inspired by stream fauna, and Rojo *et al*. (2000) analysing phytoplankton assemblages. Belyea and Lancaster (1999) offer a clear definition of what constitutes an "assembly rule" and discuss which of the rules hitherto proposed might have most relevance to emergence. They accept that many factors shape observable communities but that the internal dynamics are the most influential factors in community building, within constraints imposed by the local environment and the pool of species available.

The deductions also bring an exciting complement to the approach to habitat classification, pioneered by Southwood (1977) and Grime (1979). Their templates of available environment anticipate the delimitation of habitat range occupied by species with the appropriate adaptive specialisms. Once again, students of the phytoplankton have not been far removed from these approaches, which find evident analogies in Margalef's delimitation of evolutionary adaptations (life-forms: Margalef, 1978) and habitat representations (the "mandala" of Margalef *et al*., 1979).

My own attempts to discriminate common behaviours among the phytoplankton and match them, on the one hand, to morphological properties and, on the other, to environmental gradients (Reynolds, 1980, 1984a, 1987) are coincidentally allied. These attempted to convey the profound and potentially selective constraints on the growth and development of phytoplankton imposed by the extreme dilution of nutrient resources in open waters and the impact of light absorption through in deep mixed layers. The first characterisations of habitats were set against axes representing "nutrient availability" (y) and "mixed depth" (x). To emphasise the analogy with Grime's (1979) work, these were considered pelagic equivalents of (respectively) "stress" and "disturbance". More recently, they have been quantified in terms of the accessibility of the critical resource (K^{**}, being the

areal concentration of the limiting nutrient, which can be phosphorus, nitrogen, iron or other micronutrient, divided by the product of the depth and the concentration gradient from top to bottom (One is added to the gradient to avoid zero denominators; the units cancel to m) and harvestable processing energy (I^{**}, being the geometric mean daily photon flux divided by the depth of the mixed layer; units: mol photons $m^{-3} d^{-1}$). A wide variety of phytoplankton has been fitted to this template (Reynolds, 1997b, 1999a).

Most recently, the template has been extended to represent a wider range of pelagic habitats, defined by axes describing "resource constraints" and "processing constraints" (Reynolds, 1999b). This widens the conceptual representation to embrace the food resources of the consumer trophic levels and the oxidative potential which is required for organically stored energy content to be realised. The extended template established "domains" separated by the agent most likely to regulate the metabolism of the system. In this way, the constraint of functioning of the whole system is interpretable, not just as a prob-lem of nutrient supply but also of energy input, of carbon sourcing and whether the system redox inhibits the cycling of primary products.

This habitat template is invoked (see Fig. 3a) here to illustrate the patterns of constraint filtration, primarily as they apply to phytoplankton. To move rightwards, in the x direction, continues to represent the increasing severity of the processing constraints, or, in this instance, diminishing access to photo-chemical energy; this makes adequate photosynthet-ic productivity progressively more difficult to achieve. 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 the other nutrients is able to sustain a rate of biomass synthesis which consumes carbon dioxide at a rate which exceeds the rate invasion into the water across the surface (it has been calculated that this route can supply no more than 90-100 g C $m^{-2} y^{-1}$: Reynolds, 1999b). Even that rate depends upon the mainte-nance of a steep solution gradient. Smaller water bodies, in which the direct invasive pathway is
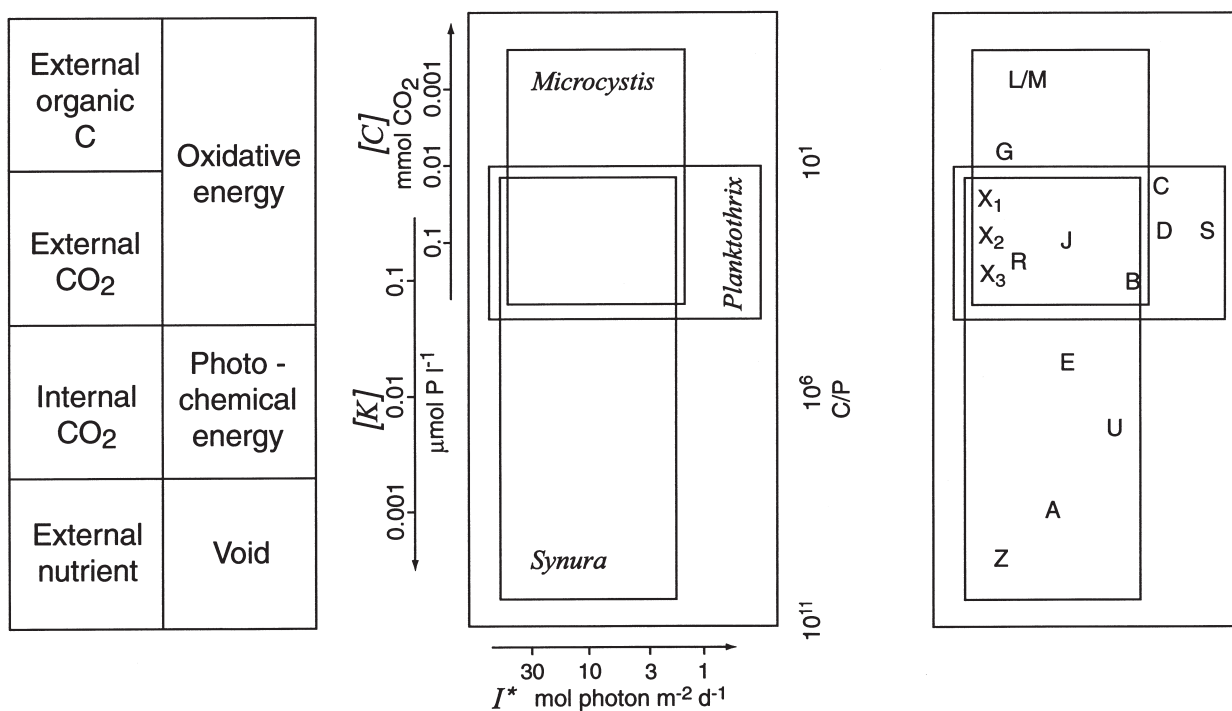

FIG. 3. – Development of a habitat template for phytoplankton. The left hand shape is based on the matrix of limnetic metabolic sensitivities (Reynolds, 1999b) in terms of carbon resource (vertical axis) and the rate of its processing (horizontal axis). Starting at a point half way up the left-hand axis, 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 con-strained by oxidative potential. Quantifying in terms of carbon, phosphorus availability and the harvestable photon flux, the physiological ranges of plankton algae can be represented (the middle shape). Each of the three shown is particularly well-adapted to contend with defi-ciencies in the supply of one of the requirements. At optimal supply rates, all three species perform to the best of their abilities. The right hand shape is identical to the centre one but now serves as a habitat template that is populated by functional species associations. These are identified by the alphanumeric coda developed by Reynolds (1997b).

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 (Maberly, 1996; Thomas, 1997; Whitehead *et 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.

The template is an aid to recognition of the constraints obtaining in a habitat and provides an index to the intensity of selective filtration operating and of its sensitvity to variation. Moreover, from co-ordinates representing a starting position, the impact of emergent assembly on the habitat might also be tracked. To improve its usefulness in this context, the template can be further tuned to the specific site sensitivities, which, for many freshwater habitats, may reduce to the supply of bioavailable phosphorus, the maximum flux of inorganic carbon and the harvestable light flux in the mixed layer. This rationale is followed in the construction of Figure 3b. The revised template accommodates 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 Figure 3b 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 relative 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 obtaining. Outside these bounds, the organism is unable to grow.

To show the principle, three filter boxes are inserted in Figure 3b. The range for *Microcystis* reflects its shortcomings as a light antenna and of its relatively weak affinity for phosphorus at low concentrations. However, *Microcystis* is one of the Cyanobacteria known to contend with high pH levels and micromolar concentrations of carbon dioxide (Moss, 1973; Talling, 1976), which ability is now known to be attributable to a very sophisticated carbon-concentrating and transport mechanism (Kaplan *et al*., 1980; Miller *et al*., 1991; Espie *et al*., 1991). The range of *Microcystis* penetrates deeply into the low-CO$_2$ regions of Figure 3b.

By analogy, some of the solitary, filamentous forms, like *Planktothrix agardhii*, are not just demonstrably good light interceptors (Kirk, 1976; Reynolds, 1989) but they have great flexibility in the amount of photosynthetic pigment they contain and, in some species and subspecies, in the amounts of accessory pigments too (Tandeau de Marsac, 1977). The experimental results of Post *et al*. (1985) provide the data to construct the range of *P. agardhii* inserted in Figure 3b.

The represented tolerance of low phosphorus environments by *Synura* is not due just to the alga's high affinity for phosphorus (data of Saxby-Rouen *et al*., 1997) but to its capacity to live phagotrophically on bacteria (Riemann *et al*., 1995). It should be said that the capability does not provide a complete explanation (at 10^{-9} mol l^{-1}, how do the bacteria take up sufficient phosphorus?). In the small, vegetal pools in which *Synura* thrives, however, sources of terrestrially-formed organic debris are generally disproportionately plentiful.

Just to emphasise the point, it is rehearsed again that *Synura* cannot even use bicarbonate, *Microcystis* is a very poor light antenna (Reynolds, 1989) and *Planktothrix* is, relatively, a phosphatophil. For each of the specialisms, one of the organisms is superbly well-adapted but it turns out to be a poor competitor in the other domains. Thus, totality of habitats is subdivided into subsections in which the environment sets up functional funnels or "filters". The "filtration" is entirely analogous to classical set theory wherein subsets of datapoints (= organisms) may be grouped together but separated from others by the inserted boundaries. The filter is analogous to the Venn diagram of classical set theory and which is passed only by species with appropriate adaptations and which*, of course, happen also to be present*. The first rule of emergent assemblages is that *the component species must be available in substantial numbers ("viable inocula") and that the habitat conditions obtaining must be adequate to sustain their minimal requirements for net biomass increase*.

Even without good quantitative data for any but a handful of other species, experience with designing other templates and accommodating named species conforming to one or other of the (alphanumeric) functional classifications (see above and Reynolds,

1997b) permits their distribution in the new template to be plotted provisionally (Fig. 3c). This version of the template is included to assist the next task, which is to establish the properties of individuals of the various species of phytoplankton which contribute to the emergence of the functional guilds of species upon which community structures are founded.

POPULATION GROWTH AND COMMUNITY ASCENDANCY

An important feature of the habitat template is that the ranges of species overlap in a domain which represents a general adequacy of resources and processing energy, wherein almost all species can operate without stretching their specialist adaptations. The converse is that, in such benign environments, just about everything else is capable of attaining its its maximal performance too. Nevertheless, these are appropriate co-ordinates at which to observe the mechanisms of emergence. With metabolic filtration at its least exacting, it is predictable that the most successful organisms, of a pool populated by many potential contenders, will be those that furnish the largest inocula (N_0) or those that achieve the fastest rates of assembly (r). The connotation, "r-selection" (McArthur and Wilson, 1967), is transparent in the logistic growth Equation (2):

$$N_t = N_0 e^{rt} \qquad (2)$$

where e is the base of natural logarithms and t is a period of time through which r holds. The appropriate strategic adaptation under such circumstances is invasiveness, with the ability to invest in propagule production and the capacity to achieve short generation times distinctive attributes. Invasiveness is synonymous with the competitive C strategy in Grime's (1979) vegetation theory. Usage of the terms, "competitive ability" and "a power to outcompete other species" is not consistent among terrestrial and plankton ecologists (the latter attribute the title to the eventual "winner" –Æsop's tortoise, not the hare, is the better competitor). The vital recognition is the communal effect of individual species responding idiosyncratically to the growth opportunity with which they are confronted. At this point in the template, where nearly all species are able to perform well, the fastest-growing among them are likely to emerge dominant. This view of "fitness" is preferable to suppositions about "competitive" outcomes.

The fastest growing representatives of the planktonic C-strategists are the smaller, usually unicellular species, having the high surface-to-volume ratios that favour rapid assimilation and conversion of resources with minimal temperature sensitivity (Reynolds, 1997b). Difficulties persist in the determination of in-situ cell replication rates growth, being generally understood to exceed, sometimes considerably, the observable rates of population increase $[r = \{\ln (N_t / N_0)\}/t]$. The latter are net of all losses befalling intact cells, including mortality, settlement and advection. On the other hand, the measurement of nutrient-uptake or photosynthetic carbon-fixation rates, provide supportive capacities: they cannot be, on average, lower than the rate of growth actually achieved but they are naturally capable of supplying the fastest attainable rates of cell growth and replication. The latter are best determined in controlled cultures in which all needs are supplied in excess, under conditions of continuous saturating light. Species-specific replication rates measured thus are reassuringly consistent. and they are now known to be reliably predictable from morphological properties of the algae (Reynolds, 1989; Reynolds and Irish, 1997). An obvious corollary is that, so long as the supply of resources (*sensu lato*, taken to include carbon and the harvestable photon flux) exceeds the demands of the assembling biomass, individuals will grow and populations will assemble at the fastest rates that the temperature and photoperiod will allow.

These assembly rates are simulable by adequately sensitive and verifiable models (see Elliott *et al.*, 1999a,b). They readily uphold published observations made under optimal conditions: many of the familiar small, unicellular phytoplankters are capable of doubling their mass in under 12 hours, principally as a correlative of their relatively high surface-to volume ratios. Reported resource-saturated replication rates of laboratory strains of *Chlorella* at 20°C are in the region of $r = 1.84$ d^{-1} (21.3 x 10^{-6} s^{-1}: Reynolds, 1990), which is equivalent to a doubling of biomass every 9.05 hours. Analogising growth to carbon dynamics, doubling the mass is equivalent to fixing, assimilating and deploying 1 mol of new carbon for every 1 mol of cell carbon represented in N_0. The same alga has been shown to be capable of photosynthesis that will provide this amount of reduced carbon in under 7 hours and to be able to absorb sufficient carbon dioxide at the air-water solubility equilibrium in 38 minutes (Reynolds, 1997b). Moreover, the affinity for phosphorus is such that it would require only 7 minutes at

its maximal uptake rate to assimilate sufficient phosphorus to maintain the stoichiometric equivalence with carbon in the daughter cells.

The solar energy required to reduce 1 mol of inorganic carbon dioxide to carbohydrate is not less than 8 mol photons (Falkowski, 1992), while there is a further energy cost attaching to protein synthesis. Empirical determinations of photoautotrophic biomass yields do not much exceed the 0.07-0.09 mol C (mol photon)$^{-1}$ measured by Bannister and Weidmann (1984). Supposing that the formation of 1 mol cell C requires the capture of 13 mol photons (2.8 MJ) and that the area projected by a single *Chlorella* cell (diameter, ~ 4 x 10^{-6} m, containing about 0.6 pmol C) is 12.6 x 10^{-12} m^2, then the solar flux required to saturate its maximum growth rate at 20°C, calculated as 7.8 x 10^{-12} mol photon per 12.6 x 10^{-12} m^2 per 9.05 h, solves to about 19 μmol photon m^{-2} s^{-1} (or ~ 4 W m^{-2} of photosynthetically-active radiation). While these benign conditions persist, the equivalent carbon-specific resource demand will be close to 0.01 mol P and 0.16 mol N per mol new photoautotroph carbon formed. At the same time, each mol of autotroph C added also represents the addition of 0.2-0.3 g chlorophyll *a* pigment and a commensurate increase in the potential exergy-flux capacity of the assemblage.

A positive exergy flux is essential to building autotrophic communities. Just as the most powerful sectors of the buoyant economy are those which generate the most wealth, so the species contributing most to the carbon flow through emergent communities need not be the ones with the greatest mass but those which are the most productive (*sensu* carbon flux per unit mass per unit time). Analyses of the early assembly stages (e.g., Rojo *et al*., 2000) reveal no clear patterns in terms of the identity of the main species. While the environmental filter remains coarse, however, "fitness" (as defined above) soon becomes the most important determinant of dominance. Besides *Chlorella* and similar unicellular chlorococcal nanoplankters, such genera as *Ankyra*, *Chlamydomonas*, the cryptophyte *Rhodomonas*, the haptophyte *Chrysochromulina* and the xanthophyte *Monodus,* have all been observed at times to increase in natural plankton at rates exceeding one doubling per day (Reynolds, 1984b). Some larger microplankters, including the diatom *Fragilaria*, whose morphology maintains a high surface area-to-volume ratio, are believed to achieve comparable rates of replication. Interestingly, the fastest rates of autotroph replication measured in the laboratory (Kratz and Myers, 1955) have been on picoplanktonic species. On the other hand, the in-situ replication rates of larger microplankters and colonial algae are rather slower than *Chlorella* (at best, doubling every 1-5 days). Even dividing twice in the time that smaller algae divide three times results in only half the biomass, assuming initial parity. Overall, *early assembly mechanisms are biassed towards species traits favouring rapid resource acquisition and conversion.*

The "early-successional"-stage community is characterised by processes leading to the accumulation of biomass which, in turn, delivers the means of further growth and development of the assemblage. This is, of course, a re-statement of long-held understanding the role of *r*-selection in early succession (Odum, 1969). Species garnering and allocating the most resource contribute most to the increase in carbon biomass, to the replication of new generations and to the communal exergy flux. Subject to the continued satisfaction of demand by the resource and processing fluxes, the cells of other, subdominant, species may behave in an analogous manner way, each building its own population and, so, contributing to the overall producer biomass, without risk of being excluded by resource competition. *The more photosynthetic biomass that is built, the greater is the aggregate ability of the developing assemblage to intercept energy. The richer is the species representation the more varied is the network of energy flow and the greater is the information content.*

The coupling of these statements corresponds, approximately, to the principle of optimal ascendancy, as formulated by Ulanowicz (1986). The main reason for invoking it in the context of assembly rules is that it emphasises again that emergent structures rely wholly on the performances of the component organisms. It is necessary to point out, however, that it is the "fittest" of the developing populations, developing the biggest share of the total biomass, which most influence the mathematical (Shannon-type) diversity of the assemblage. Diversity may decrease even while species richness is accumulating.

SELECTIVE DIRECTIONALITY OF EMERGENCE

Still concentrating on phytoplankton, this section attempts to account for emergence trends in sub-

ideal environments when resource or processing constraints are operative and a more rigorous filtration of adaptive traits applies. The constraints may be characteristic of the habitat anyway (it is chronically poor in nutrients or energy or both) or it may be imposed, autogenically, as a consequence of the impacts by the emergent community. However, the outcomes are not necessarily the same, and the pathways to their realisation may differ substantially. Common to all, however, is the selective drive of ascendant processes being biassed towards species contributing strongly to the overall exergy flux.

Let us take the example of chronically nutrient-deficient environments. Of those available, the species with the fastest metabolism and the highest biomass-specific potential replication rates, for the necessary high aspect ratio of cell surface area to cell volume confers the same advantages in the uptake and assimilation of resources: diffusion boundary layers are small and intracellular transport distances are short (Chisholm, 1992; Reynolds, 1997a; Agawin *et al*., 2000). In large oligotrophic lakes, the main autotrophic biomass continues to be represented by picoplanktic and nanoplanktic size fractions, for long periods of time. Part of this depends on their escape from herbivory (see later) but a part is simply that too little scarce resource is sequestered by, transferred to or otherwise available to, larger algae. *High nutrient affinity and potentially rapid translation of energy into functional producer biomass provide ready and plausible explanations for the ascendancy of small algal species in open pelagic habitats, especially in warm water and under conditions of high solar flux and resources in excess of uptake demand.*

So, how is it that, in many water bodies, larger algae or colonial species do dominate frequently? When is larger body size a material advantage? When do large units make the biggest contribution to the exergy flux? There are certainly several contributory causes, all of which are consequences of ascendancy. The most cited and most readily understood is to do with the relative immunity conferred from non-selective feeding by zooplankton (e.g., Ferguson *et al*., 1982). Another is the easier disentrainment from turbulent eddies –which is another way of saying that they have greater powers of self-directed movement (migratory velocity and distances travelled in unit time). This permits self-regulation with respect to the underwater light field (Heaney and Talling, 1980; Whittington *et al*., 2000) and the possibility of gleaning the more remote

nutrient reserves in stabilising water columns (Reynolds, 1976; Ganf and Oliver, 1982; Bormans *et al*., 1999; Nakano *et al*., 1999). Yet another is that, in kinetic environments in which disentrainment is difficult but mixing depth forces phytoplankton to spend a substantial proportion of the daylight period beyond the depth of growth-saturating irradiances, attenuated form (that is, size increases in only one, possibly two dimensions, manifest in needle-like cells or chain-forming coenobia) is demonstrably beneficial to prolonged entrainment and improved antennal qualities (Kirk, 1976).

In this way, *community ascendancy brings in its wake, consequent, or "self-imposed", environmental changes that alter which organismic properties are decisively advantageous.* Rapid, opportunistic, exploitative life history strategies are fine for building biomass but increasing augmentation leads to vulnerability to the population responses of filter-feeding phagotrophs; alternatively or additionally, depletion of nitrogen or phosphorus or other nutrient from the most attractive parts of the trophogenic layer will favour the more explorative, gleaner-type strategies of larger, motile plankton (Anderies and Beisner, 2000) and for which large size and lowered mortality compensate the erstwhile disadvantages of slow growth rates. They are the planktic equivalents of Grime's (1979) stress-tolerant S strategists. Or again, restrictions on energy harvesting through the imposition of truncated photoperiods, as a consequence of seasonally short day-length, increased turbidity or deeper vertical mixing, favour antennal species. The restricted opportunities for processing the available resources into new biomass are argued to be analogous to the frequent habitat disturbance tolerated by terrestrial ruderals, Grime's (1979) disturbance-tolerant R strategists. Relevant planktic traits amount to facultative antennal enhancement - surface-area attenuation, augmentation of photosynthetic and accessory pigment deployment.

The point is that the traits which define the fitness of individuals and species apply under a restricted set of contingencies. When conditions change, the advantage moves with the changing habitat constraints towards species with the appropriate alternative fitness or competitiveness. The only constant is that success tends to move among the alternative species available as the adaptations required to develop the highest exergy are also updated by environmental variation. Dynamic advantage is often transient, provided at certain times to C-type strategists, capable of rapid biomass

expansion and, at others, towards the alternative S-strategist adaptations for efficient resource scavenging and biomass conservation. Yet again, the (R-type) ability of certain organisms to maximise exergy gains within truncated or intermittent processing opportunities identifies the conditions providing relative fitness over less efficient light-harvesting species or poor conservers of biomass. Each of the broad adaptive strategies can be represented in the context of the exergy buffering capacity (Fig. 1), where the filtering role of the habitat constraints is strongly apparent as an energetic analogue to the habitat template, and wherein *relative competitiveness is a transient determinand of the environment and not a constant of some species-specific trait.*

Habitat conditions are changed autogenically by emergence: *community ascendancy brings in its wake, consequent, or "self-imposed", progressive environmental changes that alter the organismic traits most advantageous to sustaining growth.* The progression implies a directionality of trait selection which, of course, may lead to a sequence of distinct functional types that is recognised as a species succession. "Autogenic ecological succession" could just as easily be styled "emergent directionality".

Successional sequences in the phytoplankton are rarely predictable in the sense that species composition can be reliably anticipated in advance (save in extremely well-characterised assemblages over very proximal timescales). However, it is often possible to account for the sequence of population responses to environmental changes on the basis of an eco-physiological knowledge of the performance capabilities of individual species available (Reynolds, 1989, 1998c). The reactivity and sensitivity of extant assemblages to further variability should therefore be generally predictable from the size of the resource pool and the possible opportunities for its processing, afforded in terms of the exergy flux.

Examples of current understanding may be appreciated within the context of equation (1). So far as assembly of the autotrophic community is concerned, the flux of organic carbon ($\{C_{org}\}'$) is, of course, predominantly self-driven and, at least so long as photosyntetic reduction and carboxylation rates saturate the growth requirement and the supplies of nutrient resources are plentiful, self-limited, at least during daylight (see, e.g., Tortell, 2000). However, the more severe is the diminution of the nutrient pool $[K]'$ –or, more strictly, the diminution of the nutrient least available relative to demand– or the more severe is the restriction of the integrated

energy flux ($\{E\}*$), then the more selective the assembly process becomes. The "filtration" exerted by the intensifying environmental constraints refines the species-specific performance criteria for continued function and, thus, on the structure of the emergent community. Depending upon the property in contention, competition favours those fitter species with relevant functional traits.

The traits themselves are also reasonably understood. Resource constraints ($[K]'$ low) invoke two groups of adaptive specialisms. One of those is primarily to do with resource affinity. Excepting the uptake requirements to supply the building of such specialist skeletal structures as the siliceous frustules of diatoms or the calcareous tests of coccolithophorids, the elements needed to assemble protoplasm are broadly similar for all aquatic organisms and, in the main, have to be derived from the common source of the adjacent medium in which they are in (often very dilute) solution. There is little evidence to suggest that that any given species is less dependent on the common resource than any other. There are obvious caveats to this statement, such as the important additional resource opportunity presented to fixers of dissolved atmospheric nitrogen. In general, there is little reason to suppose that the fitness of species is differentiated on the basis of their resource *requirements*. However, it is equally clear that concentration gradients and the laws of molecular diffusion demand that most nutrients have to be actively captured and transported into the cell. The plasmalemma (cell wall) is equipped with specialised, ligand-specific receptor structures that bind the target molecule, pending its biochemical transfer to an internal biochemical pathway (see Simon, 1995). These facilities carry energetic costs, both in construction and operation; quite naturally, their evolution is subject to natural selection, favouring some resource-uptake specialisms –in which species have a relatively high affinity for certain target molecules, but not others– or generalism, in which uptake affinity is relatively poor.

Emphasis here should be on the adverb, since the ability of all planktonic algae to deplete external nutrient concentrations of certain key ligands to close to the limits of their analytical detection is enduringly impressive. The concepts of nutrient limitation and its role in species selection have been refined progressively through physiological experimentation and model development (Dugdale, 1967; Droop, 1973; Tilman and Kilham, 1976; Tilman *et al*., 1982; Rhee, 1982). However, because the criti-

cal behaviour occurs at such low external concentrations, the functional understanding of affinity has come mainly through the fields of biochemistry and molecular biology. For instance, Falkner *et al.* (1989) applied force-flow functions derived by Thellier (1970) to show that the external concentrations of phosphate below which cells of Cyanobacteria fail to balance its minimal maintenance requirements fall within a range of 1-50 nmol l^{-1} (0.03-1.5 µg P l^{-1}). Moreover, the same species of Cyanobacteria are known to maintain full growth down to external concentrations of 100 nmol P l^{-1} (~3 µg l^{-1}) without producing any of the regulator proteins that signal cell starvation and trigger cell reactions thereto (Mann, 1995; Scanlon and Wilson, 1999). A new radiobioassay technique (Hudson *et al.*, 2000) concurs with the view that the amount of phosphorus in the medium supporting active phytoplankton populations can fall to <1 nmol l^{-1}. The study emphasises the importance of the affinity of uptake mechanisms and of the opportunism to invoke them in the face of erratic supplies (Aubriot *et al.*, 2000).

Some of the species of freshwater phytoplankton that are found typically in lakes with chronically low phosphorus concentrations and which, presumably, have high affinity of phosphorus uptake, include the diatoms *Urosolenia eriensis*, *Cyclotella comensis* and *Aulacoseira distans*; desmids of the genus *Cosmarium* and *Staurodesmus* and many Chrysophyte genera such as *Dinobryon* and *Synura* (Rodhe, 1948; Rawson, 1956). However, the low levels tolerated by some Chrysophyceae is, in part, facilitated by their phagotrophic capabilities (Riemann *et al.*, 1995). To be capable of ingesting organic particles is an incomplete explanation, in so far as a nutrient-poor habitat is nutrient-poor for all its components - in other words, everything else in the habitat suffers the same debility. On the other hand, particulates produced outside the water body and imported to it impart a distinctive metabolic carbon base and an equally distinctive user community.

Analogous arguments presumably apply to the ability to sequester other nutrients at low concentrations. They hold for the scavenging and concentrating mechanisms for carbon uptake (noted in several Cyanobacteria and other diatoms and dinoflagellates that can continue to function successfully into the pH range 9.5-10: Talling, 1976). Nitrogen sequestration is likely also to be subject to specialisation, although phagotrophy and the ability to fix gaseous nitrogen are important contributions to the ability to be able to maintain growth. This recognition has supported a perception that nitrogen availability acts more as a selective agent (favouring dinitrogen fixers, for instance) than as a capacity limitation on biomass (Schindler, 1977). However, this supposes that the atmospheric or organic sources are exploitable: there is clear evidence that the extreme oligotrophy of some lakes in Patagonia owes only partly to their depth and low concentrations of dissolved phosphorus, for producer biomass appears to be constrained first by nitrogen availability, which shortfall is not compensated by external loads of organic nitrogen or by fixation of atmosperic nitrogen (Soto *et al.*, 1994).

The second group of adaptive specialisms for coping with diminishing resources involve adaptations to improve accessibility to reserves in the water column beyond the principal sites of autotrophic uptake. Thus as nutrients are worked out from the surface layers of a stratified system by the generalist phytoplankton, an increasing advantage accrues to the species able to undertake substantial migrations to the greater depths where the availability of nutrient resources may well persist. In fact, the only algae known to be able to do this are the larger, late-successional species of dinoflagellate (*Ceratium*, *Peridinium*), motile chlorophyte (*Volvox*) and Cyanobacteria (some *Anabaena*, *Gloeotrichia*, *Gomphosphaeria*, *Microcystis*); in only in a few of these cases has the access been demonstrated to be nutritionally beneficial (see above). On the other hand, the familiar "successional" pathways frequently observed do tend towards ultimate dominance by one or other of these larger, self-regulating organisms.

It has already been acknowledged that ascendant communities can just as easily experience constraints upon processing rates ($\{E\}^*$ low), which, for planktonic algae, at least, are mainly governed by the photon flux rate and the efficiency of energy harvesting. As with resources, the adaptive advantages for low-light species are not about being less energy dependent –the energetic investment into one mol cell carbon is almost invariable– but in being much more effective in intercepting capturing and gathering the modest fluxes of energy available. Also as with resources, separate specialisms seem to distinguish adaptations for harvesting photons from continuously low fluence rates and those for harvesting photons in the alternating high and low irradiances received by individuals entrained in deep convective vertical mixing. However, these properties ovelap

somewhat, to the extent that among the most efficient of both types can belong to closely allied taxa.

The generality is that the life forms are measureably good light interceptors. In the underwater world of scattering light, the best antennae (in the sense of photon-interceptive surface per unit of cell carbon) are maintained among small or attenuated cells and by filamentous coenobia (Kirk, 1975, 1976; Reynolds, 1989: $> 10 \text{ m}^2 \text{ [mol cell C]}^{-1}$). The more densely populated with light harvesting centres is the area projected, then the greater is the potential energy harvest from the flux of photons. Species that have lower light-dose thresholds for the initiation and maintenance of net growth in mixed layers, which include the diatoms *Asterionella formosa* and *Aulacoseira subarctica*, the xanthophyte *Tribonema aequale* and, especially, the cyanobacterium, *Planktothrix agardhii* (Kirk, 1976; Reynolds, 1989) also demonstrate considerable flexibility in the amount of photosynthetic pigment they maintain (by a factor of up to 9: Reynolds, 1997b). Conversely, the greater is an alga's specific chlorophyll-*a* complement, the lower is the daily light dose required to support its net growth.

Where light levels are continuously low, as in stable, deep chlorophyll maxima, the relevant specialism is to exploit as much of the spectrum of usable energy as possible. This is expressed in the support of accessory photosynthetic pigments, especially the phycobilins, which capture the energy of photons not absorbed by chlorophyll *a*. The burgundy-red colour attained by deep-stratified populations of *Oscillatoria rubescens* is one of the most familiar examples of chromatic adaptation (Tandeau de Marsac, 1977): the positive contribution to the growth of such populations has been measured, as well as successfully simulated, by Bright and Walsby, 2000).

Emergent directionality is subject to environmentally imposed inhibitions as well as to inadequacies, when tolerance is the selective criterion. Thus, adaptations to withstand or neutralise toxic substances can be highly relevant. High acidity of lakes is sufficiently encountered for distinctive groups of acid-tolerant species to have been recognised (most happen to be Chlorophytes or Euglenophytes). Biochemical adaptations for regulating internal pH have been described (e.g., Lane and Burris, 1981) but mechanisms to deal with mobilised aluminium species (see, for instance, Nakatsu and Hutchinson, 1988) may be decisive.

Subjected to increasing severity of constraints set by resource availability or accessibility, or by the energy available to convert resources to biomass, *organismic preadaptations and facultative adaptabilities of individual species become increasingly influential in determining the relative (competitive) abilities of individual species to continue functioning and to determine the structure of the appropriate ecosystem component. Moreover, the more severe the constraint, the more selective is its impact and the more robust is the direction of assemblage ascendency. However, the succession of events and their eventual outcome outcome is anticipated by the attributes and performance limits of the species that are available.*

HETEROTROPHS AND PHAGOTROPHS

Returning to the analogy of a national economy, we have followed development to a state of accumulating wealth and labour diversification to a point where it can support exchange of products for services with other sections of society. However, within a finite productive capacity, itself liable to fluctuation in supply, conditions for ongoing communal ascendency clearly cannot be satisfied indefinitely. Eventually, consumptive demand may come to exceed the supply side of the economy and the socio-political organisation becomes strained by its inability to sustain continuous economic growth. Before progressing to the ways that emergent biological structures react to a recession in the currency flow of individuals, it is useful to consider the role of the heterotrophic members of the pelagic community who are not employed in the primary wealth-generating industries.

Pelagic heterotrophs gain energy in two main ways. The more readily comprehended of these is *phagotrophy*, which is exemplified by the familiar supposition that zooplankters feed on planktic algae and fish then feed on zooplankton. So they do but, as a summary of how pelagic systems work, it is dangerously unrepresentative of the array of carbonflow pathways. Many species of the fish to be found commonly in the open water, especially in their juvenile stages, do feed heavily on crustacean plankton if the opportunity arises and is adequately attractive. However, in all but very large lakes, it is evident that the macroinvertebrates of the littoral and sub-littoral areas represent a more attractive energetic return for foraging effort. Piscivorous predators also

tend to follow their prey species to the inshore regions of the water. Globally, there are other ways in which lacustrine fish may be nourished –from filter-feeding, surface scraping, scavenging and semi-parasitism. Primary planktivory is reduced from an option to an obligation mainly in very large and very deep lakes, where, as in the sea, evolutionary adaptations to maximise the area of foraging for what are typically sparse resources are prominent.

There is an enormous range of preferred foods and feeding adaptations among the zooplankton, even in freshwaters where the phyletic representation in the plankton is rather poorer than in the sea. Cladoceran filter-feeders are capable of consuming large numbers of planktic algae, provided they are of filterable size and adequately concentrated, but they consume all manner of organic particles, including bacteria and fine detritus. Calanoids are more selective of foods occurring in lower concentrations than could satisfy the needs of obligate filter feeders. Few of the many species are exclusively herbivorous. Diaptomids feed extensively on the ciliates and flagellates of the microzooplankton, mainly protistans in the size range 20-200 μm. The fascinating diversity of form and feeding adaptations among the phagotrophic protists themselves is only now becoming realised (Finlay et al., 1999) but it is already clear that the organisation of pelagic food webs that result in its concentration into large macroplankters and nekton is consequent upon the limited opportunities for gathering organic carbon in dilute environments and the ways in which organisms have evolved to exploit them (see Sorokin, 1999).

The other main heterotrophic pathway for second-hand carbon involves the activities of microbes. Once again, functional diversity among the bacteria, archeans and other aquatic microorganisms is striking. Not all of them are strictly heterotrophs: besides a handful of photoautotrophs, there are many chemoautotrophs who make their living by oxidising sulphur or nitrogen compounds (see e.g. Atlas and Bartha, 1993). Space and the central theme necessarily confine the consideration here to the aerobic bacteria that are mainly engaged in the assimilation and oxidation of organic carbon. Some live freely is suspension (bacterioplankton) while others attach themselves to the surfaces of dead and decomposing fragments of plant and animal cadavers and voided wastes. Mineralisation through microorganismic activity is important to the recycling of inorganic nutrients and the renewal of carbon dioxide within the water column.

Of particular interest is the abundance of colloidal and dissolved organic carbon in solution in lakes and in the sea. Often exceeding 1 mg organic C l^{-1} (Thomas, 1997), it is rarely appreciated that the major fraction of the organic carbon present in aquatic ecosystems is not in biomass but in solution (Wetzel, 1995). Much of this DOC, even in the sea, is refractory –mainly humic and fulvic substances derived originally during the breakdown of terrestrial plants. All natural planktic assemblages also comprise substantial numbers of free-living bacteria, typically in concentrations covering about two orders of magnitude, $10^{5.5}$-$10^{7.5}$ ml^{-1} (Vadstein et al., 1993). However, there is some doubt about the ease or extent to which bacterial populations exploit the largest pool of organic carbon: bacterial biomass is scarcely correlated to total DOC availability so much as to phytoplankton productivity (Bird and Kalff, 1984). Moreover, on the premise of experiments by Goldman and Dennett (2000), the C:N ratios for oceanic bacterial biomass that are commonly reported (4.5:1 to 7:1; e.g. Kirchman, 1990) rather indicate that natural bacterial growth is limited by the supply of DOC. It is wrong to suppose that all planktic bacteria use the same organic substrates as carbon sources or that all are simultaneously abundant and simultaneously active. There is abundant evidence for the photolytic breakdown of refractory DOC into assimilable forms in surface waters under high irradiance and for positive responses of bacterial biomass thereto (reviews of Thomas, 1997; Cole, 1999). Equally, the numbers of free-living bacteria increase in response to the production of organic carbon produced by phytoplankton (Nakano et al., 1998; Ziegler and Benner, 2000). The implied "leakiness" of organic products from algal cells seems, at first sight, unduly profligate and unhelpful to primary anabolism. On the other hand, it is necessary to recognise that, in an oligotrophic environment, chronically deficient in other raw materials, the potential production of carbohydrate cannot be invested automatically into proteins or new protoplasm, much less into new biomass. Instead, primary photosynthate (or, more likely, PSI intermediates and alternative metabolites, such as glycollate) is necessarily voided from cells as a self-regulatory measure. This low-molecular weight organic carbon is, nevertheless, readily assimilated by proteobacteria, flavobacteria and other organisms in the bacterioplankton. Note that Chlorophytes actually oxidise ("photorespire") glycollate back to carbon dioxide, which consumes excess intracellular

photosynthetic oxygen in the cell, though this process but does little to benefit heterotrophs in the extracellular neighbourhood!).

The heterotrophic bacteria of the plankton are no less dependent than photoautotrophic algae upon a supply of nutrients such as phosphorus and nitrogen, and which bacteria are able to take up at least as efficiently as the algae, if not more so (e.g., Gurung and Urabe, 1999). Potentially, a mutualism develops between a carbon-limited bacterioplankton and a nutrient-limited phytoplankton. The bacteria comprise an essential sector of the pelagic community, accounting for as much as 25% of the organismic carbon present in oligotrophic systems (Weisse and MacIsaac, 2000).

Following the recognition of the pivotal participation of microbes in the flow of organic carbon to the higher trophic levels ("the microbial loop": Azam *et al*., 1983), the need to revise the view of energy capture and flow in aquatic ecosystems has become progressively apparent. Only in truly pelagic systems (of large, deep lakes and the open sea) is there a substantial reliance on *in-situ* photoautotrophic energy capture. The same systems generally operate under a chronic shortage of bioavailable phosphorus (owing to its ready immobilisation on metal oxides, hydroxides and clay minerals) and, in the oceans and in lakes in arid regions and low latitudes, of nitrogen. Biological dinitrogen fixation can overcome one of these deficiencies, but it is itself an energy-expensive process and requires the intervention of iron-and molybdenum-based enzymes (Rueter and Peterson, 1987). That these metals tend also to be scarce in the same types of water rather excludes oceanic nitrogen-fixers (Falkowski, 1997), leaving the prospect of a meagre producer biomass, chronically dilute and almost continuously resource-deficient. Under such conditions, it is advantageous to primary producers to be able to minimise sinking and grazing losses: this works in favour of relatively large buoyancy-regulating or swimming microplankters (including the large dinoflagellates), or to be very small and nearly neutrally buoyant (as are the picoplankters). In fact, in seas and lakes where the resource capacity is habitually insufficient to support a biomass of more than 50 μg C l^{-1} (4 mmol C m^{-3}), picophytoplankton are generally the main primary producers. The biomass of co-existent bacterioplankton is in a comparable range (20 to 100 μg C l^{-1}, or $\leq$8 mmol C m^{-3}; Lee and Fuhrman, 1987).

The trophic relationships among planktic autotrophs, heterotrophs and phagotrophs impact upon the relative importance of the carbon pathways through the pelagic. Productive investment in microplankton is most likely to lead to the export of primary carbon as a sedimentary flux of moribund and increasingly bacterised algae biomass and/or as the faecal pellets of the copepods and other planktic consumers of primary product. The microbial network flourishes on (a part of) the relatively very large pool of recalcitrant DOC, the downward dispersion and slow oxidation of which produces most of the dissolved inorganic carbon (DIC). Near-surface photochemical transformation of DOC also produces DIC as well as some low-molecular weight carboxylic acids (Bertilson and Tranvik, 2000). The balance of these processes determines the extent of the internal cycling of the fixed carbon and nutrient resources as opposed to its export to depth. In the deep ocean, with its global-scale circulation, mineralised carbon and nutrients are ultimately returned to sustain new productive cycles. In lakes between 5 and 200 m in depth, the interception of the vertical flux by the profundal sediments interrupts the aquatic part of the regeneration cycle by retaining significant fractions of the export flux, at least at the ecologically-relevant physiological and biogeochemical scales. Of the organic carbon, some is reprocessed by benthic detritivores, subject to the constraint of oxidative capacity but the return of some sedimentary nutrients to the pelagic, especially silicon and, often, phosphorus too, may be very slow indeed. This is the main reason why the average phytoplankton biomass of many such lakes is reasonably correlated to the external nutrient load.

More abundant or more freely recycled nutrients lift the ceiling on pelagic primary production. Higher carrying capacity permits a wider functional width to the types of producer organisms that are supportable and to the variety of animal consumers that can forage successfully. In turn, generic differences in food-web structure are evident, with consequent variance in the principle avenues of carbon transfer.

STRUCTURAL THRESHOLDS IN CARBON FLOW THROUGH FOOD WEBS

The recurrent supposition is that reproducible patterns in the structure and function of pelagic communities to differing fluxes of carbon, nutrients and processing energy remain the aggregate of the responses of individual organisms to the driving

variables. This section attempts to show how critical quantities constrain the activities of major functional groups of aquatic species and thus influence the achieveable structures of communities.

One such threshold that is well attested provides an illustration of the concentration of appropriate food particles that must be available to meet the metabolic demands of an active planktic filter feeder, such as *Daphnia*. The maximum volume of water that can be processed by an individual animal depends upon its size and the water temperature (Burns, 1969). The amount of water actually filtered is variable but it is close to maximum when all the food particles are readily filterable but the concentration is insufficient to deliver the food requirement for maximum growth. The size of food particles ingested by *Daphnia* is also a function of animal size (Burns, 1968). From a classical series of measurements, Lampert (1977) showed that the food concentration required to meet the full requirements of growth and fecundity of the *Daphnia,* at 20°C, is similar over a quite wide range of animal size, close to 0.5 mg C l^{-1}. This is equivalent to a population of some 800 *Cryptomonas* ml^{-1}, or 70 000 *Chlorella* ml^{-1}, or around 4×10^7 free-living bacteria ml^{-1}. Above saturating food concentrations (0.5-0.7 g C m^{-3}; see also Jones *et al*., 1979: 20-28 mJ ml^{-1}), filtration rates may slow. On the other hand, food concentrations of less than 0.08 mg C l^{-1} fail to satisfy even the basic respiration and maintenance requirements of *Daphnia*: animals starve and young ones soon die (Ferguson *et al*., 1982). Where food concentrations habitually fall below 0.1 mg C l^{-1}, *Daphnia* spp. are effectively excluded.

Supposing there to be even as much as 100 µg biomass C l^{-1} available (say, 200 µg dry mass l^{-1}; with an energy value of ~ 20 kJ per g; Cummins and Wuychek, 1971), the potential energetic yield (≤ 4 mJ per ml water filtered) scarcely compensates the harvesting effort. On the other hand, the continuation of the microbial loop, through the browsing of bacteria by phagotrophic nanoflagellates (< 20 µm) and the feeding by small ciliates (generally, << 200 µm in length) achieves an experimentally demonstrable emergy and functioning trophic cascade (see, e.g., Šimek *et al*., 1999). The close coupling and functional integrity of the microbial loop are known to achieve a high ecological efficiency of trophic carbon transfer (10-35%: Gaedke and Straile, 1994). Now, reduced even to 25 µg C l^{-1} (~1mJ ml^{-1}), a substantial fraction of the productive capacity is packaged in a size range and at a concentration likely to

satisfy the minimum food requirements of calanoid selective browsers (0.005 to 0.08 g C m^{-3}: Hart, 1996). In contrast, at concentrations that are sufficient to sustain efficient filter feeding, *Daphnia* can grow and multiply rapidly –sufficiently to increase the aggregate feeding rate by 20% each day, until twenty large animals per litre, each filtering 50 ml of lake water per day (or 200 small ones, each filtering 5 ml d^{-1}) are statistically capable of sweeping the water clear not just of its nanoplanktic algae but most of the components of the microbial loop as well (Lampert, 1992; Jürgens and Jeppesen, 2000). Plainly, the characteristic structure of the zooplankton reflects the abilities of the most successful species present which, in turn, are likely to be those best able to fulfil their own requirements against the sustainable food supply. The structure originates entirely from the activities of the species present.

The functional distinction between the calanoid-microbial loop and *Daphnia*-nanoplankton associations coincides broadly with the separation of oligotrophic and eutrophic systems. Annual primary production in lakes where the biomass of phytoplankton is constrained by a nutrient-controlled carrying capacity of 0.1 mg C l^{-1} may nevertheless turn over some 50-100 g C m^{-2} y^{-1} (Kirk, 1983), representing ~2000 to 4000 kJ m^{-2} y^{-1}. Most of this is processed by bacteria and the microzooplankton of the lake. Supposing a ten-metre productive layer (containing up to 1 g C m^{-2}), the implied power yield exceeds 2 MJ (g C)$^{-1}$ y^{-1}. However, the tangible biomass that is transferable to trophic levels beyond the internal cycle cannot, on average, exceed the stoichiometric limit of the nutrient-regulated export flux: an annual loading of 20 mg P m^{-2} y^{-1} is scarcely capable of supporting a net yield of new producer biomass much greater than 1 g C m^{-2} y^{-1}. The C:P ratio of the phytoplankton in these circumstances, as well as of the dependent heterotrophs and the chain of phagotrophic consumers will tend to reflect the poverty of the limiting nutrient.

The phosphorus-determined threshold for lake eutrophy is generally accepted to be equivalent to a concentration of 30-35 mg P m^{-3} which, if fully biologically available, will support a maximum biomass of primary producers of 1.5 g C m^{-3}. Annual primary production in eutrophic lakes is generally estimated to fall within a range 200-800 g C m^{-2} y^{-1} (say, 8-32 MJ m^{-2} y^{-1}), and it is often manifest as contributing to the sedimentary flux (Jónasson, 1996). Again, supposing a 10-m productive layer with an average fixation of 20-80 g C m^{-3} y^{-1}, the

annual power yield may well fall below 2 MJ (g C)$^{-1}$ y^{-1} but the transferable new biomass is now quite substantial. Salomonsen's (1992) calculations indicated the orders of magnitude of volume-specific phytoplankton production in oligotrophic (~100 kJ m^{-3} y^{-1}) and eutrophic (~1000 kJ m^{-3} y^{-1}) lakes.

Different relationships govern power transfers among planktic organisms in smaller, shallow water bodies, where the availability of resources and the opportunities for processing them are substantially influenced by the proximity of the upper trophogenic zone to the profundal deposits, to the interface with the land surface and, especially, to the resources supplied from the hydrological catchment. The latter offers a potential yield of solutes (including nutrients and gases) and particulates (including organic derivatives); warm, insolated shallows allow faster transformations by a greater variety of life-forms. Beyond a trite statement that such contrasts may be manifest, there is no ready basis for summarising community structure and function in these "smaller water bodies". Key biota and dominant processes are almost infinitely variable among water bodies, responding to such factors as latitude and altitude, contiguity and proximity to others; morphometry and hydrology; relative transparency, alkalinity and nutrient content; and the efficiency of internal resource cycling.

Two general assertions, however, are possible. One is that the system function ceases to be centred exclusively on planktonic primary production: apart from the fact that the impact of organic carbon transported from terrestrial ecosystems becomes areally more concentrated, the potential development of submerged macrophytic marginal swamps and wetlands represents a quite different aquatic primary product. Accordingly, the range of exploitable food materials available to phytophagous and detritivorous phagotrophs, as well as of substrates available to fungal and microbial heterotrophs, is much wider in these smaller bodies of water. The extent to which these alternatives supplement or subsume the contribution of planktonic primary production to the nutrition of the aquatic consumer community depends upon the relative magnitudes of the sustaining flows of carbon and energy.

This is not merely a matter of relating productivity to nutrient loading but rather of understanding the second assertion: that there is an important functional balance to be struck between, on the one hand, the supportive capacity of the open water (not just in terms of the fluxes of nutrients and dissolved gases but also of the driving solar energy) and, on the other, the biotic involvement of the benthic, littoral and catchment in the economy of the plankton. This alternative approach to the organisation of aquatic communities provides a means of rationalising the large number of quantitative studies of the trophic structures in numerous studies of individual water bodies or of given functional constituents.

The division between sites whose productivity is dominated by their littoral or benthic communities as opposed to their plankton is certain to be blurred. Even quite small water bodies (< 1 km^2) seem as likely to be dominated by a chlorophyte- or *Planktothrix*- phytoplankton as by a macrophytic community, with its associated fauna (Scheffer *et al.*, 1993). Of considerable current interest are the mechanisms that trigger state changes among them (Scheffer, 1998; see also contributions in Jeppesen *et al.*, 1998). Provided the habitat is amenable, macrophyte dominance is favoured by the ability of plants to sequester and retain nutrient resources in biomass (thus to deny it as resource to phytoplankton) and to provide refuge for filter-feeding microinvertebrates (especially plankton-feeding cladocerans). The advantage is lost to phytoplankton at levels of phosphate saturating the sequestering power of macrophytes (>150 μg P l^{-1}; Søndergaard and Moss, 1998).

Elsewhere, water depth, substratum type and exposure to wave scour may be decisive in selecting against macrophytes. Except where they are in uniformly or predominantly shallow and, hence amenable to macrophytic establishment across the entire area, the dominance of the limnetic ecology by littoral primary production might persist in lakes in the range 1-10 km^2. However, my calculations in respect of the annual net production of phytoplankton (75-90 g dry mass m^{-2}) in Crose Mere, England, (a small, mainly steep-sided eutrophic lake having a maximum depth of 9 m and an area of only 0.15 km^2) and the annual biomass generation of macrophytes in its narrow fringing reedswamp (1.5 kg m^{-2}) were quite comparable when extrapolated to the entire lake (Reynolds, 1979). With progressively larger area, the overall contribution of the littoral must diminish but it is significant that, in the Bodensee (Lake of Constance, 540 km^2; maximum depth: 250 m), Müller (1967) was able still to demonstrate the influence of littoral production in the pelagic food web.

Of course, the scale of the food resource available to planktic herbivores among smaller lakes subject to overriding external nutrient inputs or littoral

processing contrasts with the severe capacity restrictions of the true pelagic. If the levels of bioavailable phosphorus and nitrogen can be maintained by inflows and by internal recycling at > 3 µg P l^{-1} and > 25 µg N l^{-1}, then it is inferred from the ideal stoichiometry of algal cells that it is possible to accumulate a standing crop of photoautotrophs equivalent to 0.1 mg C l^{-1}, that is, just sufficient to satisfy the minimum requirements of cladoceran filter feeders (Lampert, 1977, 1992). As already indicated, a growing aggregate concentration of cladoceran filter feeders compromises the net recruitment rate of phytoplankton. Against a cell replication rate in the order of a doubling per day (r' ~0.7 d^{-1}), algal increase cannot be contained until aggregate filtration imposes a removal rate of a comparable or greater magnitude (-0.7 d^{-1}), demanding an aggregate filtration rate of more than 500 ml l^{-1} d^{-1}. In turn, this requires the activity of equivalent of up to 1 mg *Daphnia* mass l^{-1}, represented by some 10 large (~2 mm) individuals of *D. galeata* or *D. pulicaria*, or perhaps, 100 smaller animals (< 1.0 mm) per litre.

Should the aggregate filtration rate exceed the algal recruitment rate, however, rapid depletion of the planktic food resource soon follows, with starvation of the filter feeders and with mass mortalities, especially among the younger animals (George and Reynolds, 1997). Having zooplankton exhaust the phytoplankton to relative clarity of open water is an unstable outcome that must be followed by some restucturing of the community. On the other hand, if there is a substantial alternative supply of detrital and bacterial carbon, originating from the littoral macrophytes or from adjacent terrestrial habitat, starvation is not inevitable and mass mortalities may be spared. The quality of food may be poorer but so long as it can support their minimum maintainenace requirements, the aggregate filtration rates of large cladoceran filter feeders (*Daphnia* and other species distinctive littoral species, such as *Sida* and *Simocephalus* spp.) can stop the algae from becoming abundant again.

This behaviour may contribute to the upkeep of the low phytoplankton - high water clarity that is associated with the macrophyte-rich state. However, it is clearly far from being the full story, for the high concentration of cladocerans comes to constitute an attractive food opportunity for planktivorous fish. From the dry mass-length relations collected by Bottrell *et al*. (1976), the numbers of large or small *Daphnia* needed to filter 500 ml per litre of water each day are calculated to be equivalent to approximately 1 mg dry mass l^{-1}. Again approximating from Cummins and Wuychek (1971), such a population offers to an appropriate planktivore, a resource of some 20 J l^{-1}.

Now, supposing the measurements of Elliott (1975a,b; Elliott and Hurley, 1999) on captive brown trout (*Salmo trutta*) to be representative of the daily energetic requirements of active fish (between 330 J per gram fresh weight per day for a 250-g fish and 570 J g^{-1} d^{-1} for one of 11 g), then the larger fish needs to crop the zooplankton from ~4 m^3 of water each day, while the smaller one requires the harvest from ~300 litres. Given pelagic populations of cladocera or calanoids offering perhaps only one hundredth of this concentration, the assertion that planktivores must forage very large volumes of water ($\geq$400 m^3 d^{-1}) or, if the opportunity is open to them, to switch to browsing benthic or littoral macroinvertebrates is powerfully upheld. Conversely, large populations of *Daphnia* may be attractive to foraging fish; consumption may be voracious, leading to abrupt diminution in *Daphnia* numbers (Mills *et al*., 1987). Thus, structural thresholds have significance in both directions. Planktic *Daphnia* concentrations of the magnitude required to control the phytoplankton are sustainable only if planktivorous fish are scarce or absent (Kasprzak *et al.*, 1999; Scheffer *et al*., 2000), certainly less than 10 g ww m^{-3}, or if the zooplankton gains adequate protection from planktivorous predators from macrophytic refugia (Irvine *et al*., 1990, 1991; Søndergaard and Moss, 1998). In all cases, the sustainability of cladoceran filter feeders remains dependent upon the simultaneity of the minimal threshold of filterable algal, bacterial and detrital particles of $\geq$0.1 g C m^{-3}. This may be fulfilled frequently (Kamjunke *et al*., 1999) but, away from shallow margins, the scaling difficulties of striking and holding a steady state are strongly apparent.

It becomes clear that deliberate manipulation of the food web to control phytoplankton abundance can be usefully applied only if the phytoplankton ceases to be the major vehicle of primary carbon transfer. Alternatives are identifiable in small, shallow ponds with a high input of organic carbon and supplemented by macrophytic autotrophy but not in the open, unpolluted water of the pelagic. The essential deduction is that *the structure of the community that may be assembled and the manner in which the limnetic food-web processes its carbon supply are wholly consequential on the resource flux and on the processing capacities of individual organisms that happen to be present and fitted to the task.*
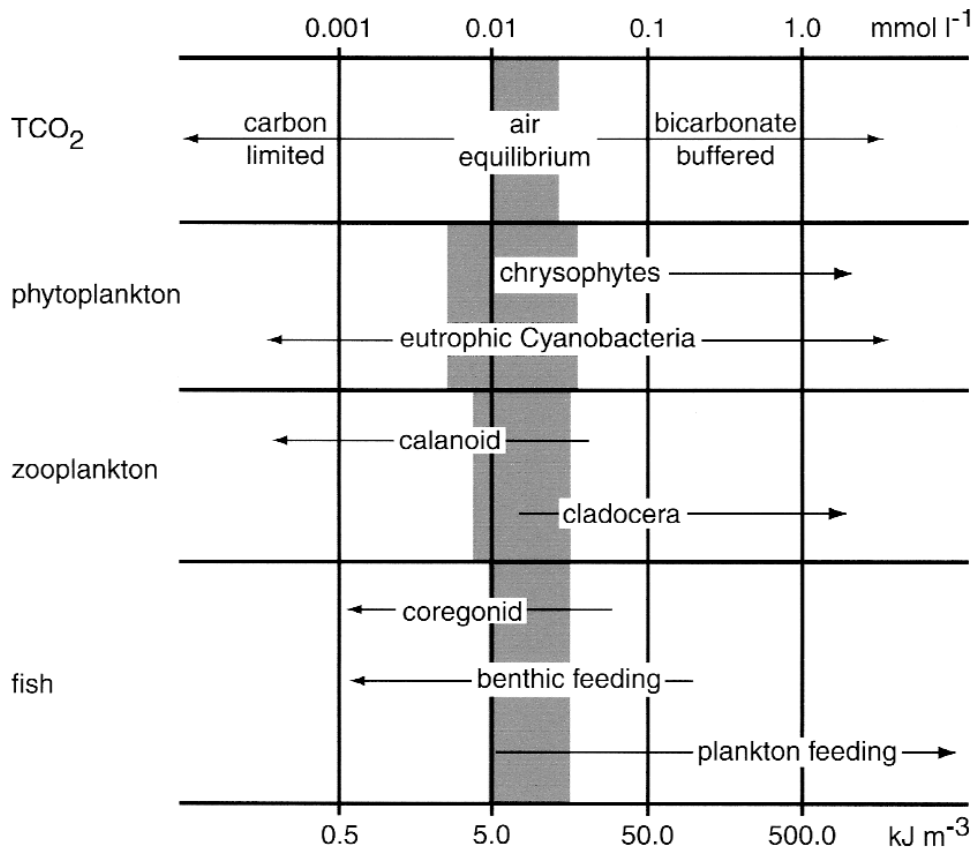
FIG. 4. – Carbon- and energy-flow constraints in the structuring of emergent pelagic communities. Accepting that the amount and distribution of native carbon sources vary over several orders of magnitude, phytoplankton composition varies with the carbon dynamics, while the concentration of food particles determines the type and productivity of the zooplankton and, in turn, the resource and its relative attractiveness to fish. Shaded areas represent the transition but is generally close to a carbon availability of 0.01 mmol l^{-1} in each instance.

This principle is fully consistent with the concept of a functional habitat template populated by appropriately-adapted species and according to contingent rules of assembly. The community structure is reasonably predictable from the supportive capacity of the habitat (Southwood, 1977; Lamouroux *et al.*, 1997).

A provisional guide to the carbon thresholds in the structuring of pelagic ecosystems is presented in Figure 4. The various trophic levels are shown against a logarithmically-scaled spectrum of useable carbon. The entries conform to the discussion in the text.

DISSEMBLY PROCESSES AND THE MAINTENANCE OF DIVERSITY

Emergent communities acquire a structure and organisation dominated by the best-adapted, highest-exergy species under the environmental conditions obtaining. The principles of maximum ascendency and the maximum power determine the struc-tural and functional make-up of the community. Thus it is that the best-fit species in each tangible niche is expected to rise to a steady-state dominance that, theory demands, excludes all inferior competitors, though always within the abiotic resource- and processing-rate limits. Usually, this means that *K*-selected "gleaners" begin to exclude the *r*-selected "opportunists" (Tilman, 1977; Anderies and Beisner, 2000).

The fact that most of the living world and, most obviously, the conspicuously variable environment of the plankton, fails to comply with any such predicted ideal has long been a fascination to ecologists. The short temporal scales that characterise the lives of planktic organisms have perhaps contributed most to the recognition of what Hutchinson (1961) referred to as the "paradox of the plankton" –it actually applies to all immature (*sensu* being far short of self-determined steady state) biotic communities–although they have also facilitated the development of several explanative hypotheses. In essence, these acknowledge that food-web interactions promote

co-existence (Paine, 1966); that co-existence is possible through the simultaneous physical or physiological niches (Tilman, 1977); and that temporal variability keeps renewing some resource or processing capacity (Connell, 1978).

These explanations are not mutually exclusive. However, conspicuous variability in the physical habitat and the sometimes quite rapid restructuring of the planktic components of the community are intuitively supportive that periodic restructuring of the habitat is symptomatic of "disturbance". The ordered progress of emergent community assembly is stopped, diverted or completely usurped by the decisive intervention of external factors. Moreover, this can happen repeatedly, so that the frequency of directional change becomes a factor favouring the coexistence of an unexpectedly large number of potentially competing species. Infrequent disturbances allow community emergence to progress towards a competitive exclusion of all but the most successful "gleaner" species and very frequent disturbances are tolerated only by a few opportunists. At intermediate frequencies, a larger number of species are permitted to co-exist.

This is the essential provision of Connell's (1978) intermediate disturbance hypothesis (IDH); the idea does have earlier provenance (Wilkinson, 1999), it is Connell's articulation by which it is best known. There is little difficulty in understanding the intervention of catastrophes, from fires and storms to volcanic eruptions and lava-flows, arresting, not to say obliterating, the development of self-organising terrestrial vegetation and re-opening the land surface to colonist plants. The pelagic analogues of severe flood and storm events as mechanisms re-setting pelagic successions were promoted in Reynolds (1980). Stochastic, smaller-scale forcing may create just the fluctuating environment which prevents the exclusion of opportunist ("C") strategists by (R- or S-strategist) gleaners Anderies and Beisner, 2000). However, these possibilities invoke an assumption that there remain simultaneous sources of invasive species, which also rather implies that there has to be a continuity of disturbances and a continuum of patches in different stages of maturation, among which invasive species may migrate. It is self-evident that were this not true, opportunism (*r*-selection) would have no viability as an adaptive strategy. This view of patch dynamics is explicit in Connell's (1978) hypothesis and it is implicit in Hutchinson's (1961) proposed explanation of the diversity paradox, which refers to "contemporaneous disequilib-

ria". Thus, dispersal constraints are as important to community assembly as are the inevitability of self-organisation and the stochasticity of external disturbances.

Careful analysis of structural changes in the phytoplankton has uncovered other interpretative complexities. Not the least of these is that external forcing has no unique scale and certainly no unique response. Storm events do not necessarily break the current species dominance while, elsewhere, relatively trivial events lead to upheavals of species composition (see, for instance, Jacobsen and Simonsen, 1993). Indeed, external forcing relevant to the planktic organisation comes with variable intensity and at a variety of temporal scales. Some, associated with the shift of seasons and interannual differences, occur at scales (100-1000 d). Equally, *individuals of a single generation may be subjected to the variability in the intensity of wind mixing and to day-time cloud cover, as well as the alternation between night and day. It is at this scale that planktic light-harvesting takes place and thus, it is this scale which most affects the dynamics of the species present* (Huisman *et al.*, 1999). The way these factors are integrated over a generation or two clearly do influence the environment perceived by the individuals, which will set distingishing limits to growth, which will shape the ascendant community and which may well constitute decisive environmental selectivity. Quite manifestly, such developments are *not* self-organised, but are allogenic consequences of environmental variability.

Two other contributions serve to improve the generality of a theory of ecological disturbance. One concerns the importance of distinguishing clearly between the biotic response –the observed disturbance– and the external forcing that precipitates it (Juhász-Nagy, 1993). For example, wind-mixing may have much less effect on the functioning of phytoplankton in a clear, nutrient deficient lake than in a turbid, eutrophic one. Equally, strong mixing will have little lasting effect on the species composition of a turbid, eutrophic lake if it blows for one day compared to the effect of the same wind if it persists for a week. Arguments concerning the distinctions among the intensity, frequency and persistence of disturbance can be addressed, not merely by separating cause and effect but to compare them in comparable units. To be able to make preliminary evaluations of the energy harvest of pelagic photosynthesis and its simultaneous losses to maintenance and, thus, to estimate the margin of exergy buffering

against external forcing (Reynolds, 1997b) provides the second promising dimension to modelling disturbance reactions in the plankton.

These developments also offer the prospect of testing quantitatively the relationship between disturbance and the structural re-setting that favours a more primitive and less self-selected community. The present hypothesis indicates that by resisting severe or continuous resource competition or any bias in favour of a particularly efficient processing, species filtration can also be less exacting and any selective advantage is traded through the assemblage as a whole, before any has the opportunity to exclude others.

The diversity thus maintained provides may alternative options and pathways for moving carbon through the ecosystem, while the relative immaturity of the system (where potential exergy is much higher than maintenance costs) favours its ready return to net productivity after each critical forcing. These communal traits are frequently advanced as the benefit of efforts to maintain a high species richness but it is just as probable that diversity and high areal productivity (*sensu* conversion of resource to biomass per unit area per unit time) are consequential upon a variable but positive exergy flux. The distinction is not entirely academic but with the current focus, quite properly, on the mechanisms and ecological importance of a high natural biodiversity (e.g., Huston, 1994; Lawton *et al*., 1998; Waide *et al*., 1999), the small temporal scales of the diversity fluctuations in relation to the internal organisation of planktic communities seem apposite and worthy of further detailed study.

CONCLUSION

This dissertation has sought an explanation of the ways in which planktic communities are assembled, essentially on the backs of the biological responses of individuals of particular species attempting to grow and multiply in environments that are not necessarily altogether favourable to them. The short generation times of planktic organisms provide appropriate and sensitive indicators of the ways in which assemblages respond to a background of fluctuating resource constraints and processing opportunities. Analysis at the appropriate timescales reveals that planktic systems generally operate in conspicuously variable environments which are, by degrees, sometimes replete in meet-

TABLE 1. – Emergence in planktic communities. Summary of statements

1. Component species must be present in substantial numbers ("viable inocula") and that these must find the conditions obtaining to be adequate to meet their minimal requirements for net biomass increase.

2. Early assembly is biassed towards species-specific adaptive traits favouring rapid resource acquisition and conversion; that is, *r*-selection predominates in early succession (Odum, 1969).

3. The more photosynthetic biomass that is built, the greater is the aggregate ability of the developing assemblage to intercept energy. The richer is the species representation the more varied is the network of energy flow and the greater is the information content.

4. Relative high nutrient affinity and potentially rapid translation of energy into functional producer biomass provide ready and plausible explanations for the ascendancy of small algal species in open pelagic habitats, especially in warm water and under conditions of high solar flux and resources in excess of uptake demand. Invasive, opportunistic nanoplanktic or small microplanktic species are frequently found to dominate.

5. The advantages of small size persist under a wide range of circumstances. However, larger, more conspicuous components of the plankton often emerge to account for relatively more of the planktic producer biomass than do the nanoplankton.

6. Community ascendancy brings in its wake, consequent, or "self-imposed", progressive environmental changes that alter the organismic traits that are decisively beneficial to growth.

7. Organismic preadaptations and facultative adaptabilities of individual species become increasingly influential in determining the relative (competitive) abilities of individual species to continue functioning and to determine the structure of the appropriate ecosystem component. Moreover, the more severe is the constraint, the more selective is its impact and the more robust is the direction of assemblage ascendancy. However, the succession of events and their eventual outcome is anticipated by the attributes and performance limits of the species that are available.

8. The structure of the community that may be assembled and the manner in which the limnetic food web processes its carbon supply are wholly consequential on the resource flux and on the processing capacities of individual organisms that happen to be best fitted to the task.

9. The filter behaves as does the Venn diagram of classical set theory: it is passed only by species with appropriate adaptations and which, of course, happen also to be present.

10. Individuals of a single generation may be subjected to variability in the intensity of wind mixing and to day-time cloud cover, as well as the alternation between night and day. It is at this scale that planktic light-harvesting takes place and, thus, it is this scale which most affects the dynamics of the species present

ing biotic demands placed upon them, sometimes stressed by resource inadequacy and sometimes so disturbed that the exploitative opportunities are short or intermittent. Thus, emergent behaviour is correspondingly shaped by species responses that invest maximum ascendant power into biomass, or that are efficient in resource uptake and conservation, or those that are efficient in processing resources during very limited opportunities.

While the relatively simple organisational state of many pelagic communities reflects their vulnerability to change and emphasises the fragility of internal processes in the face of a physically dynamic, abiotic environment, the patterns are sufficiently clear for it to be possible to abstract some draft rules of emergence. The statements in Table 1 are culled from sectional conclusions or observations italicised in the text. Refinement of these statements may be helpful to the interpretation of emergence in other systems. For the present, it will be sufficient to have its proposed application to pelagic communities explored and tested, by real experiments and realistic simulations.

REFERENCES

Agawin, N.S.R., C.M. Duarte, and S. Agustí. – 2000. Nutrient and temperature control of the contribution of picoplankton to phytplankton biomass and production. *Limnol. Oceanogr.*, 45: 591-600.

Anderies, J.M. and B.E. Beisner. B.E. – 2000. Fluctuating environments and phytoplankton community structure: a stochastic model. *Am. Nat.*, 155: 556-569.

Atlas, R.M. and R. Bartha. – 1993. *Microbial ecology* (Third edition). Benjamin/Cummings Publishing, Redwood City.

Aubriot, L., F. Wagner and G. Falkner. – 2000. The phosphate uptake behaviour of phytoplankton communities in eutrophic lakes reflect alterations in the phosphate supply. *Eur. J. Phycol.*, 38: 255-262.

Azam, F., T. Fenchel, J.G. Field, J.S. Gray, A. Meyer-Reil and F. Thingstad. – 1983. The ecological role of water-column microbes in the sea. *Mar. Ecol. Progr. Ser.*, 10: 257-263.

Bainbridge, R. – 1961. Problems of fish locomotion. *Proc. Zool. Soc. London*, 5: 13-32.

Bannister, T.T. and A.D. Weidmann. – 1984. The maximum quantum yield of photosynthesis. *J. Plankton Res.*, 6: 275-294.

Belyea, L.R. and J. Lancaster. – 1999. Assembly rules within a contingent ecology. *Oikos*, 86: 402-416.

Bertilsson, S. and L.J. Tranvik. – 2000. Photochemical transformation of dissolved organic matter in lakes. *Limnol. Oceanogr.*, 45: 753-762.

Bird, D.F. and J. Kalff. – 1984. Empirical relationships between bacterial abundance and chlorophyll concentrations in fresh and marine waters. *Can. J. Fish. aquat. Sci.*, 41: 1015-1023.

Bormans, M., B.S.Sherman and J.T. Webster. – 1999. Is buoyancy regulation in Cyanobacteria an adaptation to exploit separation of light and nutrients? *Mar. Fresh. Res.*, 50: 897-906.

Bottrell, H.H., A. Duncan, Z.M. Gliwicz, E. Grygierk, A. Herzig, A. Hillbricht-Ilkowska, H. Kurasawa, P. Larsson and T. Weglenska. – 1976. A review of some problems in zooplankton production studies. *Norwegian J. Zool.,* 24: 419-456.

Bright, D.I. and A.E. Walsby. – 2000. The daily integral of growth by *Planktothrix rubescens* calculated from growth rates in culture and irradiance in Lake Zürich. *New Phytologist*, 146: 301-316.

Brown, J.H. – 1999. Macroecology: progress and prospect. *Oikos*, 87: 3-14.

Brown, J.H. and B.A. Maurer. – 1989. Macroecology: the division of food and space among species on continents. *Science*, 243: 1145-1153.

Burns, C.W. – 1968. The relationship between body size of filter-feeding cladocera and the maximum size of particle ingested. *Limnol. Oceanogr.*, 13: 675-678.

Burns, C.W. – 1969. Relation between filtering rate, temperature and body size in four species of *Daphnia*. *Limnol. Oceanogr.*, 14: 693-700.

Carpenter, S.R., J.F. Kitchell, and J.R. Hodgson. – 1985. Cascading interactions and lake productivity. *Bioscience*, 35, 634-639.

Catalan, J. – 1999. Small-scale hydrodynamics as a framework for plankton evolution. *Japanese J. Limnol.*, 60: 469-490.

Chisholm, S.W. – 1992. Phytoplankton size. In: P.G.Falkowski and A.Woodhead (eds), *Primary productivity and biogeochemical cycles in the sea*, pp. 213-237. Plenum Prss, New York.

Cole, J.J. – 1999. Aquatic microbiology for ecosystem scientists: new and recycled paradigms in ecolgical microbiology. *Ecosystems*, 2: 215-225.

Connell, J.H. – 1978. Diversity in tropical rain forests and coral reefs. *Science*, 199: 1302-1310.

Cummins, K.W. and J.C. Wuychek. – 1971. Caloric equivalents for investigations in ecological energetics. *Mitteilungen der internationale Vereinigung für theoretische und angewandte Limnologie*, 18: 1-158.

Denman, K. and A.E. Gargett. – 1983. Time and space scales of vertical mixng and advection of phytoplankton in the upper ocean. *Limnol. Oceanogr.*, 28: 801-815.

Droop, M.R. – 1973. Some thoughts on the nutrient limitation in algae. *J. Phycol.*, 9: 264-272.

Dugdale, R.C. – 1967. Nutrient limitation in the sea: dynamics, identification and significance. *Limnol. Oceanogr.*, 12: 685-695.

Elliott, J.A., A.E. Irish, C.S. Reynolds, and P. Tett. – 1999a. Sensitivity analysis of PROTECH, a new approach to phytoplankton modelling. *Hydrobiologia*, 414, 45-51.

Elliott, J.A., A.E. Irish, C.S. Reynolds, and P. Tett. – 1999b. Exploring the potential of the PROTECH model to investigate phytoplankton community theory. *Hydrobiologia*, 414, 37-43.

Elliott, J.M. – 1975a. The growth rate of brown trout (*Salmo trutta* L.) fed on maximum rations. *J. Anim. Ecol.*, 44: 805-821.

Elliott, J.M. – 1975b. The growth rate of brown trout (*Salmo trutta* L.) fed on reduced rations. *J. Anim. Ecol.*, 44: 823-842.

Elliott, J.M. – 1994. *Quantitative ecology of the brown trout.* Oxford University Press, Oxford.

Elliott, J.M. and M.A. M.A. Hurley. – 1999. A new energetics model for brown trout, *Salmo trutta*. *Freshwater Biol.*, 42: 235-246.

Espie, G.S., A.G. Miller, R.A. Kandasamy and D.T. Canvin. – 1991. Active HCO_3^- transport in Cyanobacteria. *Canad. J. Bot.*, 69: 936-944.

Falkner, G., R. Falkner and A. Schwab. – 1989. Bioenergetic characterization of transient state phosphate uptake by the Cyanobacterium *Anacystis nidulans*. *Arch. Microbiol.*, 152: 353 -361.

Falkowski, P.G. – 1992. Molecular ecology of phytoplankton photosynthesis. In: P.G. Falkowski and A. Woodhead (eds.), *Primary productivity and biogeochemical cycles in the sea*, pp.47-67. Plenum Press, New York.

Ferguson, A.J.D., J.M. Thompson and C.S. Reynolds. – 1982. Structure and dynamics of zooplankton communities maintained in closed systems with special reference to the algal food supply. *J. Plankton Res.*, 4: 523-543.

Finlay, B.J., G.F. Esteban and T. Fenchel. – 1999. Protozoan diversity: converging estimates of the global number of free-living ciliate species. *Protist*, 149: 29-37.

Gaedke U. and D. Straile. – 1994. Seasonal changes of the quantitative importance of protozoans in a large lake. An ecosystem approach using mass-balanced carbon flow diagrams. *Mar. Microb. Food Webs* 8: 163-188.

Ganf, G.G. and R.L. Oliver. – 1982. Vertical separation of light and available nutrients as a factor in causing replacement of green algae by blue-green algae in the plankton of a stratified lake. *J. Ecol.*, 70: 829-840.

George, D.G. and C.S. Reynolds. – 1997. Zooplankton-phytoplankton interactions; the case for refining methods, measurement and models. *Aquat. Ecol.*, 31: 59 -71.

Goldman, J.C. and M.R. Dennett – 2000. Growth of marine bacteria in batch and continuous culture under carbon and nitrogen limitation. *Limnol. Oceanogr.*, 45: 789 -800.

Grime, J.P. – 1979. *Plant strategies and vegetation processes*. John Wiley and Sons, Chichester.

Gurung, T.B. and J. Urabe. – 1999. Temporal and vertical difference in factors limiting growth rate of heterotrophic bacteria in Lake Biwa. *Microb. Ecol.*, 38: 136-145.

Haney, J.F. – 1985. Regulation of cladoceran filtering rates in nature by body size, food concentration and diel feeding patterns. *Limnol. Oceanogr.*, 30: 397-411.

Harris, G.P. – 1986. *Phytoplankton ecology. Structure, function and fluctuation*. Chapman and Hall, London.

Hart, R.C. – 1996. Naupliar and copepodite growth and survival of

two freshwater calanoids at various food levels: demographic contrasts, similarities and food needs. *Limnol. Oceanogr.*, 41: 648-658

Heaney, S.I. and J.F. Talling. – 1980. Dynamic aspects of dinoflagellate distribution patterns in a small productive lake. *J. Ecol.*, 68: 75-94.

Hudson, J., D.W. Schindler and W. Taylor. – 2000. Phosphate concentrations in lakes. *Nature*, 406: 54-56.

Huisman, J., P. van Oostveen and F.J. Weissing. – 1999. Species dynamics in phytoplnkton blooms: incomplete mixing and competition for light. *Am. Nat.*, 154: 46-68.

Huston, M.A. – 1994. *Biological diversity: the coexistence of species in changing landscapes*. Cambridge University Press, Cambridge.

Hutchinson, G.E. – 1961. The paradox of the plankton. *Am. Nat.*, 95: 137-147.

Irvine, K., B.Moss and J.H. Stansfield. – 1990. The potential of artificial refugia for maintaining a community of large-bodied Cladocera against fish predation in a shallow eutrophic lake. *Hydrobiologia* 200/201: 379-389.

Irvine, K., J.H. Stansfield and B. Moss. – 1991. The use of enclosures to demonstrate the enhancement of *Daphnia* populationswhen isolated from fish predation in a shallow eutrophic lake. *Mem. Istit. ital. Idrobiol.*, 48: 325-344.

Jacobsen, B.A. and P. Simonsen. – 1993. Disturbance events affecting phytoplankton biomass, composition and species diversity in a shallow, eutrophic, temperate lake. *Hydrobiologia*, 249: 9-14.

Jeppesen, E., M. Søndergaard, M. Søndergaard, M. and K. Christoffersen. – 1998. *The structuring role of submerged macrophytes in lakes*. Springer Verlag, New York.

Jónasson, P.M. – 1996. Limits for life in the lake ecosystem. *Verhandlungen der internationale Vereinigung für theoretische und angewandte Limnologie* 26: 1-33.

Jones, H.R., T.J.Lack and C.S.Jones. – 1979. Population dynamics and productionof *Daphnia hyalina* var. *lacustris* in Farmoor I, a shallow eutrophic reservoir. *J. Plankton Res.*, 1: 45-65.

Jørgensen, S.-E. – 1992. *Integration of ecosystem theory: a pattern*. Kluwer, Dordrecht.

Jørgensen, S.-E. – 1999. State-of-the-art of ecological modelling with emphasis on development of structural dynamic models. *Ecol. Model.,* 120: 75-96.

Jørgensen, S.-E., S.N. Nielsen and H.F. Mejer. – 1995. Emergy, enviiron, exergy and ecological modelling. *Ecol. Model.*, 77: 99-109.

Juhász-Nagy, P. – 1993. Notes on compositional diversity. *Hydrobiologia*, 249: 173-182.

Jürgens, K. and E. Jeppesen. – 2000. The impact of metazooplankton on the structure of the microbial food web in a shallow, hypertrophic lake. *J. Plankton Res.*, 22: 1047-1070.

Kamjunke, N., A. Benndorf, C. Willbert, M. Opitz, J. Kranich, M. Bollenbach and J. Benndorf. – 1999. Bacteria ingestion by *Daphnia galeata* in a biomanipulated reservoir: a mechanism stabilizing biomanipulation? *Hydrobiologia*, 403: 109-121.

Kaplan, A., M.R. Badger and J.A. Berry. – 1980. Photosynthesis and the intracellular inorganic pool in the blue-green alga, *Anabaena variabilis*: response to external CO_2 concentration. *Planta*, 149: 219-226.

Kasprzak, P., R.C. Lathrop and S.R. Carpenter – 1999. Influence of different-sized *Daphnia* species on chlorophyll concentration and summer phytoplankton community structurein eutrophic Wisconsin lakes. *J. Plankton Res.*, 21: 2161-2174.

Keddy, P.A. – 1992. Assembly and response rules: two goals for predictive community ecology. *J. Veget. Sci.*, 3: 157-164.

Kelt, D.A., M.L. Taper and P.L. Meserve. – 1995. Assessing the impact of competition in community assembly. *Ecology*, 76: 1283-1296.

Kirchman, D.L. – 1990. Limitation of bacterial growth by dissolved organic matter in the subarctic Pacific. *Mar. Ecol. Progr. Ser.*, 62: 47-54.

Kirk, J.T.O. – 1975. A theoretical analysis of the contribution of algal cells to the attenuation of light within natural waters. II. Spherical cells. *New Phytologist*, 75: 21-36.

Kirk, J.T.O. – 1976. A theoretical analysis of the contribution of algal cells to the attenuation of light within natural waters. III. Cylindrical and sphaeroidal cells. *New Phytologist*, 77: 341-358.

Kirk, J.T.O. – 1994. *Light and photosynthesis in aquatic ecosystems* (Second Edition). Cambridge University Press, Cambridge.

Kratz, W.A. and J. Myers. – 1955. Nutrition and growth of several blue-green algae. *Am. J. Bot.*, 42, 282-287.

Lamouroux, N., J.-M. Olivier, H. Persat, M. Pouilly, Y. Souchon and B. Statzner. – 1999. Predicting community characteristics from habitat conditions: fluvial fish and hydraulics. *Freshwater Biol.,* 42: 275-299.

Lampert, W. – 1977. Studies on the carbon balance of *Daphnia pulex* De Geer as related to environmental conditions. IV. Determination of the threshold concentration as a factor controlling the abundance of zooplankton species. *Archiv Hydrobiol. (Supplementband),* 48: 361-368.

Lampert, W. – 1992. Zooplankton vertical migrations: implications for phytoplankton-zooplankton interactions. *Ergeb. Limnol.*, 35: 69-78.

Lampert, W. and U. Sommer. – 1997. *Limnoecology*. Oxford University Press, Oxford.

Lane, A.E. and J.E. Burris. – 1981. Effects of environmental pH on the internal pH of *Chlorella pyrenoidosa*, *Scenedesmus quadricauda* and *Euglena mutabilis*. *Plant Physiol.*, 68: 439-442.

Lawton, J.H. – 1999. Are there general laws in ecology? *Oikos*, 84: 177-192.

Lawton, J.H., S. Naeem, L.J. Thompson, A. Hector and M.J. Crawley. – 1998. Biodiversity and ecosystem function; getting the Ecotron experiment in its correct context. *Funct. Ecol.*, 12: 848-852.

Lee, S. and J. Fuhrman. – 1987. Relationships between biovolume and biomass of naturally-derived marine bacterioplankton. *Appl. environ. Microbiol.*, 53: 1298-1303.

Lovelock, J. – 1979. *Gaia: a new look at life on Earth*. Oxford University Press, Oxford

Maberly, S.C. – 1996. Diel, episodic and seasonal changes in pH and concentrations of inorganic carbon in a productive lake. *Freshwater Biol.*, 35: 579-598.

MacArthur, R.H. and E.O. Wilson. – 1967. *The theory of island biogeography*. Princeton University Press, Princeton.

Mann, K.H and J.R.N. Lazier. – 1991. *Dynamics of marine ecosystems*. Blackwell Scientific Publications, Oxford.

Mann, N.H. – 1995. How do cells express nutrient limitation at the molecular level? In: I. Joint (ed.), *Molecular ecology of aquatic microbes*, pp. 171-190. Springer Verlag, Berlin.

Margalef, R. – 1978. Life forms of phytoplankton as survival alternatives in an unstable environment. *Oceanol. Acta*, 1: 493-509.

Margalef, R. – 1997. *Our biosphere*. ECI, Oldendorf.

Margalef, R., M. Estrada and D. Blasco. – 1979. Functional morphology of organisms involved in red tides, as adapted to decaying turbulence. In: D.L. Taylor and H.H. Seliger (eds.), *Toxic dinoflagellate blooms*, pp. 89-94. Elsevier, Amsterdam.

McQueen, D.J., J.R. Post and E.L. Mills. – 1986. Trophic relationships in freshwater pelagic ecosystems. *Can. J. Fish. aquat. Sci.*, 43: 1571-1581.

Mejer, H. and S.-E. Jørgensen. – 1979. Exergy and ecological buffer capacity. In: S.-E..Jørgensen (ed.), *State-of-the-art in ecological modelling, Vol. 7*, pp. 829-846. International Society for ecological Modelling, København.

Miller, A.G., G.S.Espie and D.T.Canvin. – 1991. Active CO_2 transport in Cyanobacteria. *Can. J. Bot.*, 69: 925-935.

Mills, E.L., J.L. Forney and K.J. Wagner. – 1987. Fish predation and its cascading effects on the Oneida Lake food chain. In: W.C. Kerfoot and A. Sih (eds.), *Predation: direct and indirect impacts on aquatic communities*, pp. 118-131. University Press of New England, Hanover (New Hampshire).

Moss, B. – 1973. The influence of environmental factors on the distribution of freshwater algae: an experimental study. II. The role of pH and the carbon dioxide-bicarbonate system. *J. Ecol.*, 61: 157-177.

Müller H. – 1967. Eine neue qualitative Bestandsaufnahme des Phytoplanktons des Bodensee-Obersee mit besonderer Berücksichtigung der tychoplanktischen Diatomeen. *Archiv für Hydrobiol. (Supplementband)*, 23: 206-236.

Nakano, S.-I., N. Ishii, P.M. Mange and Z. Kawabata. – 1998. Trophic roles of heterotrophic nanoflagellates and ciliates among planktonic organisms in a hypereutrophic pond. *Aquat. microb. Ecol.*, 16: 153-161.

Nakano, S.-I., T. Nakajima, K. Hayakawa, M. Kumagai and C. Jiao. – 1999. Blooms of the dinoflagellate *Ceratium hirundinella* in large enclosures placed in Lake Biwa. *Japanese J. Limnol.*, 60: 495-505.

Nakatsu, C. and T. Hutchinson. – 1988. Extreme metal and acid tolerance of *Euglena mutabilis* and an associated yeast from Smoking Hills, Northwest Territories and their apparent mutualism. *Microb. Ecol.*, 16: 213-231.

Nielsen, S.N. – 1992. *Application of maximum energy in structural dynamic models*. Miljøministeriet, København.

Odum, E.P. – 1969. The strategy of ecosystem development. *Science*, 164: 262-270.

Oksanen, L., S.D. Fretwell, J. Arruda and P. Niemalä. – 1981. Exploitation ecosystems in gradients of primary productivity. *Am. Nat.*, 118: 240-261.

Padisák, J. – 1997. *Cylindrospermopsis raciborskii* (Woloszynska) Seenaayya *et* Subba Raju, an expanding, highly adaptive Cyanobacterium: world-wide distribution and a review of its ecology. *Archiv für Hydrobiol. (Suppl.),* 107: 563-593.

Pahl-Wostl, C. – 1990. Temporal organisation: a new perspective on the ecological network. *Oikos*, 58: 293-305.

Pahl-Wostl, C. – 1995. *The dynamic nature of ecosystems*. John Wiley and Sons, Chichester.

Paine, R.T. – 1966. Food complexity and species diversity. *Am. Nat.*, 100: 65-75.

Post, A.F., R. de Wit, and L.R. Mur. – 1985. Interactions between temperature and light intensity on growth and ohotosynthesis of the Cyanobacterium, *Oscillatoria agardhii. J. Plankton Res.*, 7: 487-495.

Rawson, D.S. – 1956. Algal indicators of trophic lake types. *Limnol. Oceanogr.*, 1: 18-25.

Reynolds, C.S. – 1976. Sinking movements of phytoplankton indicated by a simple trapping method. II. Vertical activity ranges in a stratified lake. *British phycol. J.*, 11: 293-303.

Reynolds, C.S. – 1979. The limnology of the eutrophic meres of the Shropshire-Cheshire Plain. *Field Studies*, 5: 93-173.

Reynolds, C.S. – 1980. Phytoplankton assemblages and their peridicfish in stratifying lake systems. *Holarctic Ecol.*, 3: 141 – 159.

Reynolds, C.S. – 1984a. Phytoplankton periodicity: the interaction of form, function and environmental variability. *Freshwater Biol.*, 14: 111-142.

Reynolds, C.S. – 1984b. *The ecology of the freshwater phytoplankton*. Cambidge University Press, Cambridge.

Reynolds, C.S. – 1987. Community organization in the freshwater plankton. In: J.H.R. Gee and P.S. Giller (eds.), *Organization of communities, past and present*, pp. 297-325. Blackwell Scientific Publications, Oxford.

Reynolds, C.S. – 1989. Physical determinants of phytoplankton succession. In U. Sommer (ed.), *Plankton ecology*, pp. 9-56. Brock-Springer, Madison.

Reynolds, C.S. – 1994. The role of fluid motion in the dynamics of phytoplankton in lakes and rivers. In: P.S. Giller, A.G. Hildrew and D.G. Rafaelli (eds.), *Aquatic ecology: scale, pattern and process*, pp. 141-187. Blackwell Scientific Publications, Oxford.

Reynolds, C.S. – 1997a. Successional development, energetics and diversity in planktonic communities. In: T. Abe, S.R. Levin and M. Higashi (eds.), *Ecological perspectives of biodiversity*, pp. 167-202. Springer, New York.

Reynolds, C.S. – 1997b. *Vegetation processes in the pelagic; a model for ecosystem theory*. ECI, Oldendorf.

Reynolds, C.S. – 1998a. The state of freshwater ecology. *Freshwater Biol.*, 39: 741-753.

Reynolds, C.S. – 1998b. Plants in motion; physical-biological interaction in the plankton. *Coast. Mar. Stud.*, 54: 535 – 560.

Reynolds, C.S. – 1998c. What factors influence the species composition of phytoplankton in lakes of different trophic status? *Hydrobiologia*, 369/370: 11-26.

Reynolds, C.S. – 1999a. With or against the grain; responses of phytoplankton to pelagic variability. In: M.J. Whitfield, J.R. Matthews and C.S. Reynolds (eds.)*, Aquatic life-cycle strategies: adaptations for a variable environment*, pp. 15-43. Marine Biological Association, Plymouth.

Reynolds, C.S. – 1999b. Metabolic sensitivities of lacustrine environments to anthropogenic forcing. *Aquat. Sci.*, 61: 183-205.

Reynolds, C.S., M. Dokulil and J. Padisák. – 2000. Understanding the assembly of phytoplankton in relation to the trophic spectrum: where are we now? *Hydrobiologia,* 424: 147-152.

Reynolds, C.S. and A.E. Irish. – 1997. Modelling phytoplankton dynamics in lakes and reservoirs: the problem of in-situ growth rates. *Hydrobiologia*, 349: 5-17.

Rhee, G.-Y. – 1982. Effects of environmental factors on phytoplankton growth. In: K.C. Marshall (ed.), *Advances in microbial ecology*, p. 33-74. Plenum Press, New York.

Riemann, B., H. Havskum, F. Thingstad and C. Bernard. – 1995. The role of mixotrophy in pelagic environments. In: I. Joint (ed.), *Molecular ecology of aquatic microbes,* pp. 87-114.

Springer Verlag, Berlin.

Rodhe, W. – 1948. Environmental requirements of freshwater plankton algae: experimental studies in the ecology of phytoplankton. *Symbolae Botanicae Upsaliensis*, 10: 5-149.

Rojo, C., E. Ortega-Mayagoitia and M. Alvarez Cobelas. – 2000. Lack of pattern among phytoplankton assemblages. Or, what does the exception to the rule mean? *Hydrobiologia*, 424: 133-139.

Rothschild, B.J. and T.R. Osborn. – 1988. Small-scale turbulence and plankton contact rates. *J. Plankton Res.*, 10: 465-474.

Rueter, J.G. and R.R. Peterson. – 1987. Micronutrient effects on Cyanobacterial growth and physiology. *New Zeal. J. mar. fresh. Res.*, 21: 435-445.

Salomonsen, J. – 1992. Examination of properties of exergy, power and ascendency along a eutrophication gradient. *Ecol. Model.*, 62: 171-181.

Saxby-Rouen, K.J., B.S.C. Leadbeater and C.S. Reynolds. – 1997. The growth response of *Synura petersenii* (Synurophyceae) to photon flux density, temperature and pH. *Phycologia*, 36: 233-243.

Scanlan, D.J. and W.H. Wilson. – 1999. Application of molecular techniques to addressing the role of P as a key effector in marine ecosystems. *Hydrobiologia*, 401: 149-175.

Scheffer, M. – 1998. *Ecology of shallow lakes*. Chapman and Hall, London.

Scheffer, M., S.H. Hosper, M.-L. Meijer, B. Moss and E. Jeppesen. – 1993. Alternative equilibria in shallow lakes. *Trends Ecol. Evol.*, 8: 275-279.

Scheffer, M., S. Rinaldi and Yu.A. Kuznetsov. – 2000. Effects of fish on plankton dynamics: a theoretical analysis. *Can. J. Fish. aquat. Sci.*, 57: 1208-1219.

Schindler, D. – 1977. Evolution of phosphorus limitation in lakes. *Science*, 196: 260-262.

Šimek, K., P. Kojecká, J. Nedoma, P. Hartman, J. Vrba and J.R. Dolan. – 1999. Shifts in bacterial community composition associated with different microzooplankton size fractions in a eutrophic reservoir. *Limnol. Oceanogr.*, 44, 1634-1644.

Simon, M.I. – 1995. Signal transduction in microorganisms. In: I. Joint (ed.), *Molecular ecology of aquatic microbes*, pp. 205-215. Springer Verlag, Berlin.

Søndergaard, M. and B. Moss. – 1998. Impact of submerged macrophytes on phytoplankton in shallow lakes. In: E. Jeppesen, M. Søndergaard, M. Søndergaard and K. Christoffersen (eds.). *The structuring role of submerged macrophytes in lakes*, p. 115-132. Springer Verlag, New York.

Sorokin, Yu.I. – 1999. *Aquatic microbial ecology*. Backhuys Publishers, Leiden.

Soto, D., H. Campos, W. Steffen, O. Parra and L. Zuñiga. – 1994. The Torres del Paine lake district (Chilean Patagonia): a case of potentially N-limited lakes and ponds. *Archiv Hydrobiol. (Suppl.)*, 99: 181-197.

Southwood, T.R.E. – 1977. Habitat, the templet for ecological strategies? *J. anim. Ecol.*, 46: 337-365.

Spigel, R.H. and J. Imberger. – 1987. Mixing processes relevant to phytoplankton dynamics in lakes. *New Zeal. J. mar. fresh. Res.*, 21: 361-377.

Straškraba, M. – 1980. Cybernetic categories of ecosystem dynamics. *J. int. Soc. eco. Model.*, 2: 81-96.

Straškraba, M., S.-E..Jørgensen and B.C.Patten. – 1999. Ecosystems emerging: 2. Dissipation. *Ecol. Model.*, 117: 3-39.

Talling, J.F. – 1976. The depletion of carbon dioxide from lake water by phytoplankton. *J. Ecol.*, 64: 79-121.

Tandeau de Marsac, N. – 1977. Occurrence and nature of chromatic adaptation in Cyanobacteria. *J. Bacteriol.*, 130: 82-91.

Thellier, M. – 1970. An electrokinetic interpretation of the functioning of biological systems and its application to the study of mineral salt absorption. *Ann. Bot.*, 34 , 983-1009.

Thienemann, A. – 1918. Untersuchungen über die Beziehungen zwischen dem Sauerstoffgehalt des Wassers und der Zusammensetzung der Fauna in norddeutschen Seen. *Archiv Hydrobiol.*, 12: 1-65.

Thomas, J.D. – 1997. The role of dissolved organic matter, particularly free amino acids and humic substances, in freshwater ecosystems. *Freshwater Biol.*, 38: 1-36.

Tilman, D. – 1977. Resource competition between planktonic algae: an experimental and theoretical approach. *Ecology*, 58: 338-348.

Tilman, D. and S.S. Kilham. – 1976. Phosphate and silicate uptake and and growth kinetics of the diatoms *Asterionella formosa*

and *Cyclotella meneghiniana* in batch and semi-continuous culture. *J. Phycology*, 12: 375-383.

Tilman, D., S.S. Kilham and P. Kilham. – 1982. Phytoplankton community ecology: the role of limiting nutients. *Ann. Rev. Ecol. Syst.*, 13: 349-372.

Tortell, P.D. – 2000. Evolutionary and ecological perspectives on carbon acquisition in phytoplankton. *Limnol. Oceanogr.*, 45: 744-750.

Ulanowicz, R.E. – 1986. *Growth and development - ecosystems phenomenonology*. Springer, New York

Vadstein, O., H. Olson, H. Reinertsen and A. Jensen. – 1993. The role of planktonic bacteria in lakes - sink and link. *Limnol. Oceanogr.*, 38: 539-544.

Waide, R.B., M.R. Willig, C.F. Steiner, G. Mittelbach, L. Gough, S.I. Dodson, G.P. Juday, and R. Parmenter. – 1999. The relationship between productivity and species richness. *Ann. Rev. Ecol. Syst.*, 30: 257-300.

Weiher, E. and P.A. Keddy, P.A. – 1995. Assembly rules, null models and trait dispersion: new questions from old patterns. *Oikos*, 74: 159-164.

Weisse, T. and E. MacIsaac. – 2000. Significance and fate of bacterial production in oligotrophic lakes in British Columbia. *Can. J. Fish. aquat. Sci.*, 57: 96-105.

Wetzel, R.G. – 1995. Death, detritus and energy flow in aquatic ecosystem. *Freshwater Biol.*, 35: 83-89.

Whitehead, R.F., S. de Mora, S. Demers, M. Gosselin, P. Monfort and B. Mostajir. – 2000. Interactions of ultraviolet-B radiation, mixing and biological activity on photobleaching of natural chromophoric dissolved organic matter: a mesocosm studty. *Limnol. Oceanogr.*, 45: 278-291.

Whittington, J., B. Sherman, D. Green and R.L. Oliver, – 2000. Growth of *Ceratium hirundinella* in a subtropical Australian reservoir: the role of vertical migration. *J. Plankton Res.*, 22: 1025-1045.

Wilkinson, D.M. – 1999. The disturbing history of intermediate disturbance. *Oikos*, 84: 145-147.

Ziegler, S. and R. Benner. – 2000. Effects of solar radiation on dissolved organic matter cycling in a subtropical seagrass meadow. *Limnol. Oceanogr.*, 45: 257-266.