The role of biota in shaping the phosphorus cycle in lakes

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Abstract

Although phosphorus is an abundant element on Earth, its low availability often constrains the growth and/or biomass of aquatic biota. Introducing large quantities of available P into the biosphere, humans have opened up the relatively closed biogeochemical cycle of P, resulting in the eutrophication of many types of aquatic ecosystems worldwide. A thorough understanding of the P cycle is needed, therefore, to both understand the structure and functioning of aquatic ecosystems and to preserve the quality of our aquatic resources.

In this review, we deal first with the often misused concept of ‘nutrient limitation’. The rather general use of P uptake kinetics as an indicator of nutrient deficiency requires a discussion on methodology. Since metabolic rates and nutrient demands scale with the size of organisms, coexistence of aquatic osmotrophs relies on unique adaptations and is controlled by the whole network of ecological interactions. Some of these adaptations and interactions are reviewed, with a focus on P cycling. Finally, a case study demonstrates that the complicated P cycle must be simplified to extremes to predict eutrophication-related changes in a shallow lake.

Keywords: Global P cycling; eutrophication; growth limitation; capacity limitation; P uptake; coexistence; allometric scaling; grazing; stoichiometry.

Introduction - Why is the P cycle so important?

Phosphorus (P), as a constituent of phosphate rocks (primarily of apatite) is the 11th most abundant element in the Earth's crust. Its abiotic cycling is bound up with the sedimentary-tectonic cycle, in which weathering slowly brings phosphate ions into solution as restricted by the low solubility of apatite. Most of the liberated phosphate is adsorbed on iron and aluminium oxy-hydrates and clay minerals. Diagenetic transformations into insoluble compounds decrease the pool of mobile (dissolved and adsorbed) P. Erosion and runoff transport P to river systems and ultimately to the ocean, where the particulate forms rapidly sink into the sediments. Tectonic uplift completes the geochemical cycle by re-exposing the minerals to denudation over time-scales of tens of millions to hundreds of millions of years (Smill, 2007).
Ever since the appearance of life on Earth, the geochemical cycle of P has been inseparably interconnected with the biotic cycling of this essential element. P is universally needed by every organism for storing and handling chemical energy (ATP) and genetic information (DNA and RNA), for enveloping cells and their organelles (phospholipid membranes), and for coordinating metabolic processes (signal transduction cascades). The chemical basis of the unique role of phosphates in the living world is the ability of phosphoric acid to link two nucleotides and still ionise. The negative charge stabilises the phosphomono- and phosphodiesters against nucleophilic attack, most importantly hydrolysis. The associated low thermodynamic stability ensures reactivity in the presence of organic and inorganic catalysts. Simultaneously, the charged phosphoesters can be retained within the lipid membrane (Westheimer, 1987). Besides its current metabolic functions, P is also thought to have played a crucial role in the creation of life (Arrhenius et al., 1997).

The global mean P content of the Earth’s crust slightly exceeds 0.1 %. Although the amount of biologically available P is not well quantified and varies in both time and space, no more than 10 % to 30 % of total P can be potentially available (Froelich, 1988; Compton et al., 2000). Compared to the abundance of available P in the environment, both aquatic and terrestrial biota concentrate P in their biomass by two to three orders of magnitude (Redfield, 1958; Cleveland & Liptzin, 2007). To characterise the efficiency of uptake, microbial P demand has been shown to control partitioning of P into biotic and geochemical pools in soils, where inorganic surfaces available for adsorption are orders of magnitude more than in water (Olander & Vitousek, 2004), while P uptake affinity in aquatic osmotrophs may approach the theoretical limit set by diffusion (Thingstad & Rassoulzadegan, 1999; Section 3).

In addition to efficient P uptake, osmotrophic organisms may directly enhance the liberation of phosphate from inorganic sources. Examples include enzymatically mediated bacterial dissolution of iron-bound P in aquatic sediments (Hupfer et al., 2007) and micorrhizae that selectively enhance P weathering from primary minerals through the release of organic acids (Lenton & Watson, 2004). The composite metabolic activity of organisms modifies the availability of P indirectly by altering redox and pH conditions in the environment, by releasing organic chelators that reshape the chemical behaviour of P-binding metal ions, and by inducing precipitation/dissolution of carbonate minerals (calcite, aragonite) during photosynthesis/respiration. The influence of biota on the water status of the soil is an indirect control mechanism specific for terrestrial ecosystems. The background to these indirect interactions is the quick uptake/release of the charged phosphate ions by/from a wide variety of inorganic surfaces that together build up an effective abiotic phosphate buffer mechanism (Froelich, 1988).

Biotic communities efficiently recycle and rapidly reuse most of the P lost from the living biomass both in dissolved and particulate forms. The need for efficient recycling is obvious when we consider that terrestrial plants annually assimilate some 30 to 50 times more P than supplied by the present, biologically enhanced rate of P weathering (Lenton & Watson, 2004; Smill, 2007). Faster biomass turnover in aquatic communities results in a lower overall recycling efficiency over the same time span in the aquatic environment. Conservation mechanisms also include the reduction of abiotic losses of P. Most conspicuously, terrestrial plant coverage diminishes erosion and alters the seasonal pattern and magnitude of runoff thereby decreasing the transport of P to waters. During succession, mineral nutrient cycles become increasingly closed, a growing proportion of the available nutrients is incorporated into the biomass, and thus the share of nutrient regeneration from detritus increases within the total nutrient supply in both terrestrial and aquatic ecosystems (Odum, 1969).

Despite the conservation mechanisms operative across various time scales in various ecosystems, P cannot escape the ultimate fate of being withdrawn from the biosphere and ‘reborn’ millions of years later through tectonic processes. Analysis of soil chronosequences has indicated that highly weathered and leached old soils are deprived of available P (Walker & Syers, 1976) while the oceanic loss of available P has been estimated as between
1 × 10^12 and 2.5 × 10^12 g yr^-1 (Compton et al., 2000). Due to this loss and to the virtual absence of an atmospheric reserve, P has been the limiting nutrient to global biological productivity over geological time-scales during cool periods (Saltzman, 2005). It is worth noting that the P cycle is tightly coupled to the biogeochemical cycles of all other elements that make up living organisms. Through the interaction between the stoichiometric nutrient demands of biota and chemical processes, these cycles merge into the co-evolution of biota and their environment (Redfield, 1958; Bergman et al., 2004; Lenton et al., 2004).

Humans have considerably increased the amount of P available in the biosphere. Global mining of phosphate rocks with a mean P content of about 10 % varied between 130 million and 150 million tonnes per year in the last decade. Some 85 % of the mined P is used in agriculture, accumulates in soils and finds its way to aquatic ecosystems. Phosphorus-containing detergents, manufactured from the bulk of the remaining 15 % of mined P, end up in sewage. Flow of food materials through households is estimated to add as much P to the water as leaching of fertilisers (Steen, 1998). In sharp contrast with traditional agricultural societies, urbanisation, intensive and industrialised agriculture have greatly reduced the efficiency of P recycling. Although the uncertainty of estimates is very high, the modern flux of total P to the oceans (18 × 10^{12} to 31 × 10^{12} g year^{-1}) certainly exceeds pre-human losses (11 × 10^{12} to 18 × 10^{12} g year^{-1}). For potentially available P, as opposed to total P, the difference is even greater (3.4 × 10^{12} to 10.1 × 10^{12} g year^{-1} modern flux, as compared to 3.1 × 10^{12} to 4.2 × 10^{12} g year^{-1} pre-human losses; Compton et al., 2000).

Enrichment of waters with excess plant nutrients, primarily P and N, has resulted in eutrophication, i.e. enhanced vegetation growth and imbalance of the aquatic ecosystem. A worldwide survey by the International Lake Environmental Committee (http://www.ilec.or.jp) indicated that in the 1990s, some 40 % to 50 % of our lakes and reservoirs were eutrophicated. Wetlands, large rivers, estuaries, coastal zones and inland seas are also subject to eutrophication. This undesirable process results in a significant loss of many ecosystem services. To illustrate the economic scale of this loss, the damage and management costs of freshwater eutrophication in England and Wales were estimated at between 182 million and 237 million US dollars per year in the 1990s (Millennium Ecosystem Assessment Synthesis Report, 2005).

Since P plays a basic role in both eutrophication and determining or modifying coexistence and trophic interactions among various species, a vast number of studies have focused on aquatic P cycling, covering diverse aspects. In this review, we first discuss what the often misused term ‘nutrient limitation’ means (Section 1). The P status of osmotrophic organisms has frequently been assessed from P uptake measurements using the convenient radiotracer method. Due to the widespread, but theoretically not fully justified, reliance on this method, next we ask what we really measure with the radiotracer (Section 2). The volume and the surface area-to-volume ratio of aquatic osmotrophs vary over 11 and 4 orders of magnitude, respectively. Since metabolic rates and nutrient demands scale with the size of organisms, the question arises as to why small microorganisms do not invariably outcompete the large ones for P (Section 3). To illustrate the role of P in trophic interactions, we examine the consequences for crustacean zooplankton of grazing on a P-deficient diet (Section 4). Finally, a case study demonstrates how much the complicated P cycle can be simplified to predict eutrophication-related changes in a shallow lake (Section 5).

### 1. What does ‘nutrient limitation’ mean?

According to what Turchin (2001) calls the ‘first law of population ecology’, organisms are inherently capable of exponential growth. In a finite world, however, exponential growth is sooner or later constrained by the decreasing availability of resources or other vital conditions such as space or suitable habitat. When net growth rate (the difference between production and loss rates) drops to zero because of the limited resource availability, the supportive (carrying) capacity of the environment is said to have been filled. Evidently, net growth may also approach zero due to increases in loss rates (sedimentation, grazing, etc).
The term ‘limiting nutrient’ is often used to mean two distinct, though interrelated, concepts: growth-limiting and capacity-limiting. The concept of limitation dates back to Liebig’s ‘Law of the Minimum’ (1840), according to which the yield of a plant is proportional to the amount of nutrient in the shortest supply relative to the plant’s demand. This concept is relevant to its original application, agricultural production, where the main concern is to achieve the highest yield in a monoculture over the growing season. In natural ecosystems, however, many players (populations) participate in the game. While the object of each player is to maximise its own yield, this game has two peculiar features: both rules (absolute and relative supply rates of various resources) and players may change during the play. The actual rules re-define the biomass capacity (the maximum yield that the players can jointly achieve) and simultaneously define the identity and severity of growth limitation, thereby selecting among the individual players. Besides this, a second variable subset of rules (biomass loss) can also selectively influence and even exclude players from the game. As in other games, the success of players depends on both their skills (adaptations) in exploiting the periods when the rules provide them the opportunity to grow and their good luck of having high abundance at the onset of this opportunity.

While resources are abundant, an idealised organism at constant temperature harvests and allocates various resources in exact proportion to its stoichiometric demand that sustains the maximum growth rate. Since uptake and storage of nutrients need energy, any deviation from a perfectly balanced resource acquisition and allocation would unnecessarily suppress the growth rate. However, without a tight control over the availability of resources, this organism would be extremely sensitive to the slightest environmental change.

As resources become increasingly scarce, individuals and populations are forced to compete with each other. From an evolutionary perspective, each species must cope with the problem of ‘finding’ its own optimal combination of traits within the constraints of allometry, biochemical kinetics (a function of temperature) and biochemical stoichiometry (Brown et al., 2004) with the ‘objective function’ of maximising its fitness. From an ecological perspective, scarceresource availability selects for species with a suitable set of traits to maintain positive net growth under the actual conditions. The realised net biomass yield determines the competitive rank of these species. Traits can be classified arbitrarily into two broad categories: 1. those that primarily influence resource gathering and 2. those that directly influence the rate of net growth.

One should, however, always keep in mind that metabolism is a highly coordinated hierarchical network of processes, in which the state of pools and the rate of metabolic pathways propagate their feedback to the functioning of the whole network and to the manifestation of metabolism in maintenance, growth and reproduction.

Osmotrophic organisms gather various resources individually though not independently, while phagotrophic ones consume ready-made packages of energy and nutrients. This difference is not absolute. When inorganic P is depleted, many osmotrophs, such as mixoticflagellates, consume P-rich bacteria with the additional benefit of ‘killing’ their competitors (Stibor & Sommer, 2003). Carnivorous plants are thought to evolve in extremely nutrient (nitrogen, P, potassium) depleted environments (Ellison, 2006). Phagotrophic organisms may also have options to compensate for their deficiency by absorbing individual nutrients from the medium. Protist grazers, for example, can take up ortho-P (Hadas et al., 1992), and even cats and dogs preferentially visit puddles for a good drink to avoid microelement deficiency.

Despite the difference in their feeding habits, similar adaptations provide competitive advantage to both osmotrophic and phagotrophic organisms. Concerning resource acquisition, adaptations include low consumption thresholds in chronically resource depleted environments (Sommer, 1985; Lampert, 1994); high rates of resource acquisition during transiently high resource availability (Sommer, 1985; Hansen et al., 1997); buffering the fluctuating external availability of resources by storage (Sommer, 1985; Kirk et al., 1999); quickly sensing environmental fluctuations and re-adapting uptake rates and resource allocation accordingly (Plaetzer et al., 2005; Thomas & O’Shea, 2005; Stelzer, 2005); keeping the ‘memory’ of past adaptive
events and transferring this information to daughter generations (LaMontagne & McCauley, 2001; Plaetzer et al., 2005); and exploiting spatial resource gradients or forms of nutrients not available for the competitors.

The ultimate measure of competitive success, however, is not the amount of resources an organism can gather but the economy of using these resources to produce new biomass. In this respect, adaptations include reducing the loss of acquired resources associated with both the loss of biomass (sedimentation, grazing, etc) and the efflux of nutrients caused by the enormously high concentration gradients across the cell envelope (for example in unicellular organisms, the intracellular phosphate pool may exceed the extracellular one by a factor of 10^6; Button et al., 1973). Further adaptations may include a low growth demand (e.g. minimum cell quota) for the potentially limiting resource; switching to alternative metabolic pathways that ensure rapid internal recycling of the limiting nutrient (Theodorou et al., 1991); a short time lag (‘nutrient processing time’) before growth is resumed following a nutrient pulse (Davidson & Cunningham, 1996; Spijkerman & Coesel, 1998); and enhanced production of allelopathics under nutrient stress to suppress the growth of competitors (Leflaive & Ten-Hage, 2007).

Although trade-off relations restrict the number of combinations in which the above traits co-occur among species, the range of adaptive variability is virtually inexhaustible. So is the dynamic variability in the environment. This complexity, as well as the interactions between various growth-limiting factors, makes it extremely difficult to identify which resource actually limits growth. In osmotrophic organisms, the kinetics of P uptake (Section 2) and alkaline phosphatase activity (Fitzgerald & Nelson, 1966; Pettersson, 1980) have been used as P deficiency indicators for many years. Growth, however, is rarely a direct function of external nutrient concentration and uptake rate as proposed by the early models of nutrient limited growth (Monod, 1942; Dugdale, 1967). Therefore it is somewhat disappointing that contrary to the rapid development of molecular techniques that provide us with an arsenal of increasingly faster, more species- and resource-specific tools for quantifying stress reactions, La Roche and co-workers (1999) predicted that molecular markers of P (and N) limitation are likely to remain related to acquisition – a prediction which appears equally valid today. Since the P status of organisms, among other factors, plays a key role in regulating the cell growth cycle (Vaulot et al., 1996; Reynolds, 1997; Scanlan & Wilson, 1999; Kulaev & Kulakovskaya, 2000), there may come a time when we will be able to assess in a direct way to what degree P limits the growth of various aquatic populations under natural conditions.

When the composite biomass of a community, such as the phytoplankton, cannot increase any more due to the shortage of a resource, the system is said to have exhausted the supportive capacity of the environment. Contrary to what the etymology of the often used term ‘carrying capacity’ suggests (Sayre, 2008), capacity is not a constant value but an ever fluctuating limit. Reynolds (1992, 1997) elaborated several methods to compare the potential maximum biomass of phytoplankton supported by various resources, most importantly light and nutrients. The P-determined capacity can be calculated from regressing the biomass yield (chlorophyll concentration) against P supply (derived from the external load as described by Vollenweider & Kerekes, 1982, from the measured concentration of available P). Alternatively, a P capacity can be estimated from a community average minimum P quota and the available P supply. This capacity should then be compared to biomass capacities determined by other resources to find out which resource limits the yield. While the concept is simple, its application to real lakes and particularly to shallow ones is not always straightforward (Section 5). Nevertheless, Reynolds’ analysis and the associated lake typology clearly indicate that apart from a few lake types, the identity of the capacity-limiting resource changes at varied time-scales including both smooth seasonal shifts and rapid, stochastic fluctuations.

The chlorophyll = f(P) regressions indicate that integrated over a year, P is the nutrient that most frequently or most stringently limits the growth of algae in many temperate lakes. This, however, does not mean that P is always growth-limiting in a particular lake or that P determines the biomass capacity in each lake.
Consequently, reduction in the external P load is not the single possible or the universally applicable approach to eutrophication management. Load management must be assessed in each individual lake, and this assessment should consider the whole network of ecosystem processes (Vollenweider & Kerekes, 1982; Sas, 1989; Reynolds, 1992).

In conclusion, growth- and capacity-limitation should be clearly distinguished in ecology. When the growth rate of a species is suppressed below its maximum temperature-dependent intrinsic value due to the shortage of a vital resource, the growth is limited by that resource. Growth limitation (and resistance to loss) selects for species that are capable of maintaining positive net growth under the given conditions. When no species can be selected that could convert the limiting resource to new biomass more efficiently than its competitors, the community fills the supportive capacity and biomass becomes limited by that resource. The supportive capacity of the environment varies widely in time within the same lake as well as among lakes.

2. What do we measure with the radiotracer method?

As mentioned in Section 1, the P acquisition properties of osmotrophic microorganisms have been widely used to assess their P status. Application of the radiotracer method in limnology dates back to Hutchinson & Bowen (1947) and Rigler (1956). Since low concentration and rapid flow of available P are the symptoms of P shortage, the radiotracer method is the most convenient and often the single possible approach to measure the rate of uptake.

Besides performing whole lake radiotracer studies, Rigler (1956) experimentally investigated both the uptake and regeneration of P under laboratory conditions. This work led him to two influential discoveries that, according to subsequent studies, applied to a diverse range of aquatic habitats. First, P deficient plankton keep the turnover time ($TT$) of ortho-P in the water ($[P_e]$, nM P) as low as a few minutes, while low demand or excessive supply increases $TT$ by orders of magnitude. Second, the chemical method overestimates the ambient concentration of $P_e$ by up to an order of magnitude.

To appreciate the importance of Rigler’s first discovery, we must recall that early limnologists perceived the pelagial of lakes as a more-or-less closed system where summer phytoplankton gradually convert phosphate brought in by the spring overturn to organic P. Although Juday and co-workers (1927) observed that algal blooms might develop when the external concentration of phosphate is very low, the lack of appropriate methods prevented them resolving this paradox. Rigler’s kinetic data revealed that the unexpectedly fast turnover of P might maintain a sufficiently large flux of P when $[P]$ is low ($flux = [P_e]/TT$, nM P min$^{-1}$). He replaced the concept of a unidirectional flow of P with the kinetic concept of a two-directional exchange between the epilimnion and the littoral, as well as between each compartment within these habitats. Giving an overview of the history of limnetic P research, Rigler (1975) pointed out that:

‘Studies of phosphorus kinetics… did change our attitude to lakes by helping to free us from the static concept and to see lakes as dynamic open systems.’

His ‘kinetic thinking’ has remained a paradigm for modern limnology. It is worth noting that introduction of the radiotracer method stimulated a similar paradigm shift in physiology just a little earlier. The Hungarian chemist, György Hevesy, who first developed the radiotracer method and first used $^{32}$P in physiological research, emphasised in his Nobel prize presentation (Hevesy, 1944):

‘The most remarkable result obtained in the study of the application of isotopic indicators is perhaps the discovery of the dynamic state of the body constituents.’

An analogy may help us to understand better both the essence of the new paradigm and eutrophication. Eutrophic lakes are enriched with excess nutrients, but what does ‘enrichment’ mean? A unidirectional flow of unproductive goods to his Treasury made King Dareios rich. In contrast, the Rockefellers’ wealth originated from a rapid turnover of a comparatively low amount of capital. External P load accumulates primarily in the sediments of lakes. However, it is the fast sediment–water or littoral–pelagial exchange and the rapid turnover of P in the water that supports the enhanced growth of phytoplankton. The concentration of available P may
remain low and algae P-deficient during most of the eutrophication trajectory (Sections 3 and 5). At the extreme end of enrichment, when the carrying capacity is no longer P-determined, lakes become P-rich in a Dareian sense.

Rigler’s other important observation about overestimating the ambient concentration of ortho-P by the chemical method might appear to be a mere technical problem. Since the numerous subsequent studies failed to elaborate an appropriate method to measure low concentrations of ortho-P, we still use Rigler’s operative terminology ‘soluble reactive P’ (SRP). More importantly, the observation has theoretical implications.

Rigler (1966) studied the dependence of P uptake kinetics on the P concentration by adding various amounts of cold P ([P]s, nM) simultaneously with the tracer. He suggested using Michaelis-Menten (MM) kinetics to analyse the results (Fig. 1):

\[
TT = \frac{[P]_s + K_p}{V_{max}} + \frac{1}{V_{max}}[P_i] 
\]

where \(V_{max}\) (nM P min\(^{-1}\)) is the saturated rate of P uptake and \(K_p\) (nM P) is the half saturation constant. The x-axis intercept of the \(TT = \frac{[P_i]}{[P_s]}\) line provides an upper limit of \([P_i]\). When planktonic microorganisms are P deficient and therefore \([P_i]\) is low, the SRP concentration substantially exceeds this limit.

Although MM kinetics have been used widely in studies of P uptake kinetics, a systematic deviation at zero added P puzzled the researchers. In 10 % to 15 % of cases, \(TT\) at \([P_i] = 0\) was higher than expected. This type of deviation might be caused by diffusion limitation of uptake (Mierle, 1985). However, in the majority of cases, a negative deviation has been observed (Fig. 1b). Several mechanisms may explain the latter deviation. First, multiphasic uptake systems are involved in P uptake (Jansson, 1993). Recent thermodynamic and genetic studies identified the presence of two (high and low affinity) P transporters in Cyanobacteria, both with the stoichiometry of one phosphate molecule taken up per ATP (Ritchie et al., 2001). Second, \(K_p\) varies among co-occurring planktonic

Fig. 1. A phosphorus uptake experiment and its interpretation.
(a) Disappearance of carrier-free \(^32\)P from the filtrate. The tracer was added at \(t = 0\). The absolute value of the initial slope of the uptake curve (orange line) is an empirical estimate of the uptake rate constant, \(k\) (min\(^{-1}\)). \([P]_s\) is the ambient P concentration; \([P]_i\) is the internal P concentration of the cells. (b) Rigler’s bioassay based on Michaelis-Menten kinetics. Turnover time (\(TT = \frac{1}{k}\)) was determined as shown in (a) but unlabelled ortho-P was added in several concentrations ([P]s) to the sample, simultaneously with the isotope. The absolute value of the x-axis intercept is equal to the sum of \([P]_s\) and the half-saturation constant of uptake (\(K_p\)). The reciprocal of the slope is the saturated rate of P uptake (\(V_{max}\)). A negative deviation (orange dots) can most frequently be observed at \([P]_i = 0\). (c) Schematic presentation of energy-dependent P uptake coupled to the proton flux across the thylakoid membrane (redrawn from Falkner et al., 1989). When the proton flux is perfectly coupled to the P flux, the overall reaction is \(H^+ + P + n_H^+ + H_n + + H^+\) where \(H^+\) and \(H_n^+\) denote external protons, protons in the thylakoid space and in the cytoplasmic space, respectively; \(P_e\) is poly-P containing \(n\) number of P atoms; and \(n_h\) is the number of protons translocated from the thylakoid space to the cytoplasm during P uptake. Passive P leakage leads to the degradation of poly-P. (d) Thellier plot of the uptake experiment shown in (c). \([P]_s\) is the threshold P concentration where net uptake (\(v_{net}\), blue dots) ceases for energetic reasons. The leakage flux (\(v_{leak}\)) remains constant during short-term uptake experiments. The radiotracer method measures the sum of net uptake and leakage rates, i.e. \(v\) (orange dots). The positive deviation of \(v\) in (d) is equivalent to the negative deviation of \(TT\) in (b).
microorganisms. Three orders of magnitude of variability had to be assumed in a modelling study to account for the negative departure observed in Lake Michigan (Tarapchak & Herche, 1989). Such a wide interspecific variability, however, seems to be unlikely. Third, a threshold for net P uptake also leads to negative departure from the MM model at zero added P. I examine this latter mechanism below.

The MM model has been borrowed from enzyme kinetics. Many of the underlying assumptions do not hold true for such complex phenomena as nutrient uptake by cells (Thellier, 1970). Falkner and co-workers (1989) deduced and verified experimentally a new concept of P uptake, the linear force-flow model using the non-equilibrium thermodynamic approach of Thellier (1970). The starting point of this model is that P uptake is an endergonic process (cf. Ritchie et al., 2001) that will cease when the available energy is insufficient to cover the costs of uptake. The lower is \([P_e]\), the more is the energy needed for the uptake. Uptake is ultimately driven by the energy of polyphosphate formation. In photosynthetic organisms, energy is derived from allocating protons across the thylakoid membrane to the cytoplasm (Fig. 1). Since the proton flux is tightly but not perfectly coupled to P influx, there is a passive loss of P from the cells to the medium. The rate of net P uptake \((v_{net}, \mu\text{M P min}^{-1})\) can be described by the simple relationship,

\[
v_{net} = L_r \cdot (\log([P_e]) - \log([P_t]))
\]

(2)

where \(L_r\) (\(\mu\text{M P min}^{-1}\)) is a conductivity coefficient and \([P_e]\) (\(\mu\text{M}\)) is the threshold concentration for net uptake. Maintenance of a steady-state \([P_e]\) requires energy, since at \([P_e] = [P_t]\) cells must counterbalance the passive loss of P by an active uptake. This two directional flux of P is called leakage. Thus, at \([P_e]\) net uptake is zero but leakage is greater than zero. Extremely P deficient planktonic microorganisms have been shown to reduce \([P_e]\) to a few nanomols per litre (Falkner et al., 1989). Comparable ortho-P concentrations have been estimated from kinetic data in the epilimnion of stratified lakes (Hudson et al., 2000).

In light of the linear force-flow model, one should make a clear distinction between leakage and net uptake when using the radiotracer method (Lean & White, 1983; Istvánovics & Herodek, 1995). At zero added P the method measures the rate of leakage, while in samples perturbed by cold P additions the method yields the combined rate of leakage plus net uptake. The net uptake depends on the actual P concentration, while leakage was shown to be constant in short-term uptake experiments and to vary with the physiological status of the microorganisms. Thus, linearity of the \(TT = f([P_e])\) relationship is approximate and the systematic negative deviation at \([P_e] = 0\) becomes evident (Fig. 1). Although the rate of leakage has rarely been estimated, it seems to decrease with complexity of cells. Lean & Nalewajko (1976) found that leakage decreased in the order cyanobacterium (Anabaena flos-aquae) > diatom (Navicula pelliculosa) > green algae (Chlorella pyrenoidosa > Scenedesmus quadricauda). These differences are possibly related to the large evolutionary changes in the functions of polyphosphates (Kulaev & Kulakovskaya, 2000).

The force-flow model helped to highlight the role of planktonic P uptake in the life history of Gloeotrichia echinulata in Lake Erken (Istvánovics et al., 1993). A peculiar feature of this \(\text{N}_2\)-fixing cyanobacterium, which forms spherical colonies of up to 1–2 mm in diameter (Fig. 2), is that a large (40 %) fraction of its planktonic population may originate from benthic recruitment as opposed to epilimnetic growth (Barbiero & Welch, 1992). The P uptake threshold of \(G.\) echinulata exceeded the epilimnetic concentration of SRP by an order of magnitude during most of its summer bloom in 1992 (Fig. 2). Thus, P uptake in the epilimnion could not support the observed increase in the biomass. Recruiting colonies were estimated to translocate some two thirds of the total net internal P load from the sediments to the epilimnion. Since benthic recruitment of \(G.\) echinulata is insignificant in many years (Barbiero & Welch, 1992; Karlsson-Elfgren et al., 2003), interannual variability in the internal P load is highly variable in \(G.\) echinulata lakes.

Summarising this section, the radiotracer method is an essential tool for studying the P uptake kinetics of P deficient planktonic microorganisms. The technique has provided new insight into nutrient cycling in aquatic ecosystems and led to a paradigm shift in limnology some five decades ago. Since limnologists use almost exclusively
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Empirical models (e.g., first order kinetics, Michaelis-Menten model) to analyse the results of their radiotracer experiments, many uncertainties have remained unresolved. Ecological studies of metabolic processes, including uptake and utilisation of nutrients, always present the dilemma of how best to simplify the background biochemical and physiological phenomena to solve the uniquely ecological projections of the problem. In this respect, most advances have been made in photosynthetic utilisation of CO$_2$ (Falkowski & Raven, 1997; Honti, 2007) and more efforts are required in the case of phosphorus.

3. Why do small microorganisms not outcompete the large ones for P?

Since the radiotracer technique provided a rapid, inexpensive and seemingly simple way to measure P uptake (Section 2), and the balanced growth could sufficiently be approximated by the Monod (1942) model, many limnologists came to the erroneous conclusion that a superior P uptake ability ultimately determines the success of osmotrophic microorganisms competing for the shared limiting resource, phosphorus. This would mean that the smallest osmotrophs invariably outcompete the large ones.

Rigler (1956) observed that at ambient P concentration, bacteria incorporate a disproportionately high amount of the tracer relative to their biomass. In Lake Memphremagog, between 97% and 100% of the carrier-free $^{32}$P was taken up by microorganisms <3 µm in size, mostly bacteria (Currie & Kalff, 1984). Other studies confirmed this pattern in a variety of lakes but indicated that the contribution of bacteria decreased to some 20% with increasing trophic status (Currie et al., 1986). Although the lack of distinguishing leakage from net uptake may somewhat underestimate P partitioning by large (potentially less leaky) cells, the observation challenged the classical view of aquatic nutrient cycling. According to this view, autotrophic organisms (phytoplankton) use inorganic nutrients, whereas heterotrophic ones (bacterioplankton) are remineralisers of organic nutrients (Fig. 3). Currie & Kalff (1984)

![Fig. 2. The role of Gloeotrichia echinulata in epilimnetic P cycling during summer 1992 in Lake Erken, Sweden. The threshold for P uptake was too high relative to the soluble reactive phosphorus (SRP) concentration for the alga to acquire P in the epilimnion and to support the increase in biomass and P associated with the colonies a), b); biomass is expressed as concentration of chlorophyll a, Q$_P$ is the P quota of G. echinulata). There was indirect evidence that colonies took up P in the sediments and transported P to the epilimnion where stored P might support three to four doublings. (Redrawn from Istvánovics et al., 1993.)](image-url)
proposed a new model of aquatic P cycling (Fig. 3). Since at low \([P_e]\) small bacteria are superior competitors for inorganic P relative to large phytoplankton, the bacterioplankton are P sufficient and depend on dissolved organic carbon (DOC) excreted mostly by algae. Phytoplankton growth, in turn, is P limited and inversely related to bacterial P utilisation.

The concept of the microbial loop (Azam et al., 1983; Fig. 3) was less intrinsically bound to the analysis of P uptake kinetics and interpreted the interactions between bacteria and phytoplankton in a wider context of trophic dynamics than did Currie & Kalff (1984). In the classical food web, carbon fixed in photosynthesis is channelled by the crustacean zooplankton to fish (Fig. 3). A substantial amount of fixed carbon, however, is lost as DOC. A variable fraction of DOC is re-incorporated into the particulate food web through the microbial loop. Bacteria utilise DOC and efficiently compete with phytoplankton for both inorganic and organic forms of P and N. Microbial grazers (heterotrophic nanoflagellates and ciliates) regenerate inorganic nutrients and serve as food for large zooplankton.

Microbial grazing significantly influences the coexistence of bacteria and algae even when bacteria are DOC limited. A simple chemostat experiment illustrates this point (Rothhaupt, 1992; Fig. 4). The chemostat was inoculated with two algal species (the diatom *Synedra acus* and a strain of small *Cryptomonas* sp.) and their unidentified bacterial contaminants. In about 10 days, steady-state coexistence was attained. The equilibrium biomass of the diatom was determined by silica, while the biomass of bacteria was controlled by the DOC release of the diatom. The cryptomonad was nearly excluded from the system since bacteria utilised the external P supply more efficiently than did *Cryptomonas*. Introduction of the bacterivorous flagellate *Spumella* sp. to the steady-state assemblage forced a radical shift in the equilibrium biomass of both bacteria and the P-limited cryptomonad without an effect on the Si-limited diatom. Grazing substantially reduced the

![Fig. 3. Schemes of competition for P among planktonic microorganisms.](image)

(a) The traditional concept. Phytoplankton use dissolved inorganic P (DIP) and release organic C and P (DOC and DOP, respectively). Bacterioplankton re-mineralise DIP. (b) The hypothesis of Currie & Kalff (1984). Competition for DIP among bacteria and algae leaves the latter P-limited. Bacteria depend on DOC while phytoplankton supplement their P demand from DOP. (c) The concept of the microbial loop. DIP is primarily recycled by protist grazers (heterotrophic nanoflagellates, ciliates). Bacterial growth rate depends on DIP in oligotrophic systems and this shifts to DOC limitation in nutrient enriched ones. Bacteria are superior competitors for both DIP and DOP relative to algae. (d) The idealised three-member food chain as a basic unit that accounts for the coexistence of two competitors. In this specific case, the common limiting resource is P. A trade-off is assumed between affinity (favours small sized, competition specialist) and grazing resistance (favours large sized, defence specialist). (For the sake of transparency, several processes have been neglected. For example, zooplankton also graze on bacteria, recycle DIP and may excrete DOP and DOC).
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biomass of bacteria that, in turn, released the cryptomonad from competition for P. This resulted in an increase in the biomass of Cryptomonas by two orders of magnitude.

In contrast to the hypothesis of Currie & Kalff (1984), a series of observations suggested that bacterial growth is P limited in oligotrophic habitats and a transition to C-limitation occurs with increasing trophic status (Currie, 1990; Thingstad & Rassoulzadegan, 1999). When bacteria and algae compete for the common limiting resource P, stable coexistence cannot be expected unless a selective mechanism controls one of the two groups. An idealised three-member food web is the simplest conceptual unit that accounts for the coexistence of P-limited osmotrophic organisms (Thingstad & Rassoulzadegan, 1999). In steady-state, the resource controlled, defence specialised ‘large’ microorganism coexists with the predator controlled, competition specialised ‘small’ microorganism (Fig. 3d). The balance between the two competitors is resource dependent; the competition specialist dominates at low supply and the defence specialist at a higher one.

Experimental evidence and theoretical considerations led Thingstad & Rassoulzadegan (1999) to question whether heterotrophic bacteria are invariably the superior competitors for P at low external concentration. Specific affinity ($\alpha = \frac{V_{\max}}{K_P}$ litres (nmol P)$^{-1}$ h$^{-1}$) is a measure of the nutrient uptake ability of microorganisms at low [P]. Diffusion to the cell surface sets an upper limit to specific affinity ($\alpha_{\text{max}}$), and the actual affinity of planktonic microorganisms was shown to approach this limit in certain habitats such as the oligotrophic Mediterranean Sea during stratification. For a spherical cell of radius $r$ (µm)

$$\alpha_{\text{max}} = \frac{3D}{\sigma r^2}$$

where $D$ is the diffusion coefficient of phosphate in the medium ($\approx 10^3$ µm$^2$ s$^{-1}$) and $\sigma$ (nmol cellular P µm$^{-3}$) is the volume-specific structural P content of the cells. The theoretical maximum affinity rapidly decreases with increasing size. This is reflected in published affinities of bacteria that tend to be higher than those of phytoplankton.

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Fig. 4. Chemostat experiment illustrating the effect of bacterial grazing on the competition for P between bacteria and algae. See text for further details. Bacteria outcompeted the P-limited Cryptomonas sp. in the absence of grazing but had no effect on the biomass of Si-limited Synedra acus that supplied them with energy (dissolved organic C, DOC). Cryptomonas sp. was released from the competition when Spumella grazing controlled the biomass of bacteria. (POC – particulate organic carbon. Redrawn from Rothhaupt, 1992.)
(in the order of $10^2$ to $10^3$ litres (nmol P)$^{-1}$ h$^{-1}$ and $10^3$ to $10^2$ litres (nmol P)$^{-1}$ h$^{-1}$, respectively; Vadstein & Olsen, 1989). Equation (3), however, also indicates that a decrease in $\sigma$ may, to some degree, counterbalance the reduced $\alpha_{max}$ in larger cells. Although both bacteria and algae are known to store substantial amounts of P in excess to their instantaneous growth requirements, the stoichiometry of the functional machinery (structural P content) is relatively constant (Klausmeier et al., 2004). As an average, bacteria need twice as much P as algae (C:P molar ratio is 50:1 and 10:1, respectively). Small cells with intrinsically rapid growth rates must preferentially invest in the assembly machinery (ribosomes), particularly when they are grazed intensely. Ribosomes are rich in both N and P and thus the investment in the assembly machinery results in a relatively high $\sigma$ and reduced $\alpha_{max}$. The resource acquisition machinery (nutrient transport proteins, chloroplasts for light harvesting) contain N but little or no P. Thus, allocation to the acquisition machinery in slower growing, larger organisms simultaneously increases $\alpha_{max}$ and the actual affinity, $\sigma$.

Considering the idealised 3-member food chain (Fig. 3) and the possibility of adjusting $\alpha_{max}$ by reducing the structural P needs of the cell, Thingstad and co-workers (2005) have recently proposed an exciting hypothesis. They argue that the $\alpha_{max} = f(\sigma)$ relationship (Equation 3) introduces some flexibility into the trade-off between the life strategies of the two competitors. The common assumption is that small cells pay for their high uptake-affinity by high susceptibility to grazing, while the cost of grazing resistance of larger cells is a reduction in affinity. However, using a non-limiting substrate to optimise competitive P-uptake ability and predator defence simultaneously is a feasible win–win strategy. The authors refer to this strategy as Winnie-the-Pooh, quoting Milne:

‘…and when the Rabbit said “Honey or condensed milk with your bread?” he was so excited that he said, “Both”.’

The hypothesis is supported by some experimental evidence (Thingstad et al., 2005). An excess of DOC favours selection for heterotrophic bacteria with high affinity for mineral nutrients. If affinity were a function of size (surface to volume ratio) only, one would expect the dominance of small cells under these conditions. However, Thingstad et al. found that glucose enrichment induced the growth of large colony-forming and filamentous forms in the marine bacterium, Vibrio splendidus during a mesocosm experiment. The C:P molar ratio and linear size of the bacterium increased from a mean of 50:1 to 260:1 and from <1 µm to around 4 µm, respectively. The observed increase in size was sufficiently large to reduce predation by heterotrophic flagellates, while $\alpha_{max}$ remained nearly as high as in small bacteria.

Thingstad et al. (2005) also speculated that high affinity of diatoms relative to their size may be based on an analogous ‘large yet small’ strategy. In diatoms, the vacuole may occupy a major part of the cell and thus the volume-specific structural P content is relatively low. In this case silica is used to build the frustule that serves as a supporting structure for the vacuole. Following this reasoning, desmids may also be candidates for the Winnie-the-Pooh-strategy. Among desmids, a distinct mucous (polysaccharide) layer is found only in species from oligotrophic habitats. Cosmarium abbreviatum var. plancticum, a taxon characteristic of oligo-mesotrophic waters, has been shown to react to severe P limitation with highly enhanced mucilage production (Spijkerman & Coesel, 1996). If mucilage acts as a diffusion barrier for phosphate, the Winnie-the-Pooh assumption does not apply to desmids. Permeability of the mucilage with respect to P is still an unresolved question (Spijkerman & Coesel, 1996; Freire-Nordi et al., 2006).

No Winnie-the-Pooh strategy can, however, override the allometric scaling of P acquisition parameters among planktonic osmotrophs (Wen et al., 1997). Coexistence of small and large organisms vividly demonstrates that competitive hierarchies are not directly related to resource acquisition. The efficiency of using the acquired resources for growth is often thought to counterbalance the inferior P uptake abilities of larger microorganisms relative to the smaller ones. Such differences, however, collapse in the face of allometry. Reynolds (1997) showed that the maximum growth rate of algal species scales with their surface-to-volume ratios to the power of about 1/3. If each species were spherical, the maximum growth rate would

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scale with $r^{-1/3}$. Assuming a constant biomass-specific P content, the total cellular P is a linear function of cell volume. Thus, the total P demand of balanced growth (maximum growth rate times the total cellular P content) increases with $r$ to the power 2.67. This rapid increase in the total P demand with scale indicates that differences in growth efficiency (see Section 1) may be decisive only when the size of competitors is not too different. It is worth noting that most laboratory experiments are aimed at studying the competition between species of similar size.

Several other explanations have also been suggested to account for the coexistence of osmotrophic microorganisms. In their review of the proposed solutions to Hutchinson’s plankton paradox (1961), Roy & Chattopadhyay (2007) classified the possible mechanisms into two main categories: 1. the plankton is out of equilibrium due to either external forcing or self-organised dynamics and 2. additional factors such as predator-prey interactions modify resource limitation.

Three relatively simple examples that focus on the coexistence of P-limited algae may illustrate these broad categories.

The first example concerns external forcing due to spatial and temporal fluctuations of P supply. These fluctuations are highly variable in their amplitudes and frequencies. Wind-induced sediment resuspension in large shallow lakes transports frequent, small pulses of P to the water (Istvánovics et al., 2004). In contrast to this, large, infrequent pulses are associated with upwelling events in stratified lakes (Pierson & Weyhenmeyer, 1994). Microorganisms are also exposed to locally elevated P concentrations, encountering P-rich resuspended particles or faecal pellets of zooplankton. Studies of P uptake kinetics have revealed that even a small transient increase in the phosphate concentration favours uptake by larger microorganisms (Lean & White, 1983; Istvánovics & Herodek, 1995). Microorganisms are also exposed to locally elevated P concentrations, encountering P-rich resuspended particles or faecal pellets of zooplankton. Studies of P uptake kinetics have revealed that even a small transient increase in the phosphate concentration favours uptake by larger microorganisms (Lean & White, 1983; Istvánovics & Herodek, 1995).

Chemostat experiments with natural phytoplankton have indicated that pulsed P supply supports a much more diverse assemblage than continuous supply. Sommer (1985) found that in a pulsed chemostat, with a stable oscillating equilibrium, biomass oscillations of one group of species were synchronised to the pulses. These ‘velocity specialists’ grew rapidly when the pulse increased [$P_e$] and were gradually pushed towards exclusion upon depletion of the pulse. They had high maximum P-uptake velocity ($V_{max}$), high maximum growth rate ($\mu_{max}$, day$^{-1}$) and low affinity. Their size was not restricted to a narrow range but they could not be too large to grow fast. Another group of species maintained a stable biomass in the pulsed chemostat. Some of them were small sized ‘affinity specialists’ that excluded other algae when competing for P under continuous low supply. A few large sized species could also maintain stable biomass in the pulsed chemostat. These were slowly growing ‘storage specialists’, the high $V_{max}$ of which allowed them to acquire P in excess of their instantaneous growth requirements. Stored P was then used for growth during the period of low [P]. It has also been shown that storage specialists maintain high P-uptake rates for a significantly longer time after encountering a pulse of P than small osmotrophs. In the latter, the elevated cellular P content down-regulates the rate of uptake in an hour or so (Suttle et al., 1988).

_Gloeotrichia echinulata_ represents an extreme case among storage specialist species (Section 2). Although less extreme, other bloom-forming Cyanobacteria are also specialists in P storage. This, coupled with buoyancy regulation, allows them to exploit P reserves that are not readily available for other algae. _Microcystis aeruginosa_ is a poor competitor for P but its buoyancy regulation is particularly efficient. Colonies sink to nutrient rich sub-surface waters to replenish their internal P store and to use stored P for growth upon ascendancy into the well illuminated, nutrient depleted surface waters (Reynolds, 1989). The N$_2$-fixing subtropical cyanobacterium, _Cylindrospermopsis raciborskii_ is probably an opportunistic species that has both high affinity and storage capacity for P, relatively high $\mu_{max}$ and efficient buoyancy regulation (Padisák, 1997; Istvánovics et al., 2000).

The second example considers the influence of small-scale turbulence on size-dependent competition for limiting nutrients. Most planktonic osmotrophs are smaller than the Kolmogorov scale ($L_K$, µm), at which inertial and viscous forces equally determine the properties of fluid motion. In well-mixed natural systems, $L_K$ is in the order of a few mm (Spigel & Imberger, 1987;
Reynolds 1994). Below the scale of the smallest eddies (~2π L_K), turbulence creates a laminar shear field that changes in direction at time scales of between 1 s and 100 s (Lazier & Mann, 1989). This temporal scale is relevant to nutrient uptake by osmotrophic microorganisms.

Particles embedded in turbulence are surrounded by a diffusive boundary layer (DBL) through which nutrients are replenished by pure molecular diffusion. The concentration gradient is maintained by the fast cellular uptake that may decrease the concentration of a limiting nutrient to nearly zero. The outer frontiers of DBL are subject to a laminar shear derived either from the smallest eddies or from the motion of organism relative to the water. In a stagnant fluid, the effective DBL thickness around a spherical cell of radius r extends to a distance of 2r from the centre of the sphere. The linear shear flow decreases DBL thickness and enhances laminar advection of nutrients to the cell surface (Ploug et al., 1999). The increment in mass transfer increases with both cell size and flow velocity. For example, a spherical organism of r = 50 µm enjoys a ~50% increment relative to still water conditions at a shear rate of 1 s⁻¹, while the difference is negligible at a shear rate of 0.01 s⁻¹. The respective values are ~450% and ~20% when r = 500 µm. Since, however, the effective DBL thickness is much greater around large than small cells (~600 µm and ~400 µm for the r = 50 µm cells; ~1000 µm and ~4000 µm for the r = 500 µm cells at these shear rates, respectively), the advection-enhanced nutrient flux is insufficient to counterbalance the disadvantage of larger organisms. This effect is still important for colony formation in Phaeocystis since without an enhanced P flux, no large colonies (up to ~500 µm) could form under nutrient deficiency (Ploug et al., 1999).

Theoretical analysis (Karp-Boss et al., 1996) has indicated that the steady, uniform flow arising from swimming or sinking substantially increases P transport to the cell surface for microorganisms with r > 20 µm. To take advantage of laminar advection, cells must be larger than ~60 µm. Rotation of non-spherical cells, particularly of highly asymmetrical dinoflagellates, diminishes this gain. Long chains of diatoms and filamentous Cyanobacteria that span the scale of the smallest eddies are best able to take advantage of advective nutrient transport, although they risk physical damage at high shear rates. In addition to size, cell morphology is a key factor in determining mass transfer of nutrients to osmotrophs, particularly in high flow–low nutrient environments (Karp-Boss et al., 1996, Pahlow et al., 1997).

Size-dependent enhancement of mass transport under turbulent conditions should translate into enhanced growth of large osmotrophs, providing them with a competitive advantage over small cells. In their critical review of experimental data, however, Peters & Marrasé (2000) failed to find evidence for faster growth under turbulent conditions. Among other reasons, this might be due to insufficient knowledge of small-scale turbulence and to the difficulty of studying an inherently random process under fixed, homogeneous conditions. Data showed that turbulence adversely affects the growth of dinoflagellates irrespective of their size. Other osmotrophs grow either slightly faster or slightly slower under turbulence. More recent experiments seem to support theoretical expectations (Cózar & Echevarría, 2005; Peters et al., 2006). For example, in a mesocosm experiment, Cózar & Echevarría (2005) found that turbulence had a marginal and indirect (grazer-mediated) effect on the biomass of picoplankton, while the growth of diatoms was enhanced progressively with their cell size.

The fascinating scaling analysis of Siegel (1998) suggested that turbulence might prevent competition most often among planktonic microorganisms. Although models of planktonic interactions (nutrient acquisition, grazing) implicitly assume continuous distribution of organisms, the validity of this assumption depends on the characteristic spatial distribution scales of ‘particles’ (organisms, molecules of nutrients) relative to characteristic spatial scales in aquatic flows (L_flow, µm). The reference L_flow varies with the type of interaction we would like to study. For nutrient acquisition by osmotrophs, L_flow is the smallest scale where turbulence creates fluctuations in the nutrient field. This corresponds to the Batchelor scale, which is roughly 30 times smaller than 2πL_K. The largest micropatches of nutrients are up to a few hundred µm in size in well-mixed environments and up to a few mm in stagnant water.

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Under most natural flow regimes and abundances, planktonic osmotrophs behave as discrete particles that utilise a continuous nutrient field. For nutrient uptake, discreteness means that each cell occupies a different micropatch of nutrients, while continuous distribution means that cells uniformly and instantaneously are exposed to the concentration decrease caused by the uptake of their neighbours. The prerequisite for competition is a high abundance of large cells characteristic of eutrophic systems during bloom periods. For example, competition among picoplankton (~1 µm) and net plankton (~100 µm) is not expected at abundances below ~5 × 10⁶ individuals ml⁻¹ and ~30 ind ml⁻¹, respectively. Competition among individuals of the latter group is continuous at abundances over ~10⁸ ind ml⁻¹. Thus, competition is unlikely in oligotrophic environments and its probability also decreases under quiescent conditions. Since Siegel (1998) considered only mass transfer by molecular diffusion, the actual values might overestimate the abundances at which discreteness is replaced by competitive interaction. This, however, does not challenge the concept overlooked by most limnologists. The main conclusion of the study recalls the notion of Keddy (2001) that ecologists too often used the term ‘competition’ vaguely without testing that one organism had a negative effect upon the other by influencing access to resources.

Inconvenient for any experimentalist, Siegel (1998) also showed that well-stirred, crowded chemostats and batch cultures represent systems in which small cells are distributed continuously and nutrients discretely. Under these conditions, microorganisms experience an unrealistically high competitive intensity.

The third example explains coexistence of various size classes of phytoplankton by interactions between their size-dependent loss (grazing and sedimentation) and P status along a gradient of P enrichment (E). As a general rule, no species can maintain a steady-state population unless its growth rate (µ, day⁻¹) is sufficiently high to counterbalance the rate of biomass loss (L, day⁻¹). Assuming that algal growth is a hyperbolic function of the phosphate concentration (Monod, 1942), the minimum P concentration ([P]_{min}) that fulfills this criterion is:

\[
[P]_{min} = \frac{\mu_{\text{max}}}{\alpha_{g} (\mu_{\text{max}} / L - 1)}
\]  

(4)

where \(\mu_{\text{max}}\) is the maximum specific growth rate and \(\alpha_{g}\) (litres (nmol P)⁻¹ d⁻¹) is the specific affinity for growth. Both of these variables decrease with size and the composite effect is a rapid increase in \([P]_{min}\). Thus, small phytoplankton can establish themselves at lower \([P]_{min}\) than large algae. Equation 4 also reflects the higher growth rate needed to balance an increased loss and this, in turn, elevates the minimum P concentration where invasion by a competitor occurs. Analogous expressions can be derived for the minimum prey biomass that counterbalances the loss rates of a predator as a function of its resource-dependent growth efficiency.

Various models have been developed to describe the steady-state behaviour of idealised multi-species trophic networks as a function of \(E\), which is defined as the total concentration of a potentially limiting nutrient (Thingstad & Sakshaug, 1990; Armstrong, 1994). The network of transformations (growth, background loss, grazing, recycling, sedimentation) determines the distribution of \(E\) among the pool of free nutrient and the various species. In models of a closed system, the loss term (L) in Equation 4 represents an unspecified background loss since sedimentation is zero and the loss associated with zooplankton grazing is described explicitly. Although various models assume different interactions between species and formulate the same process in slightly different ways, the steady-state behaviours that emerge from the different models converge into a set of generalised patterns of behaviour.

In the hypothetical case when \(E < [P]_{min}\) of the smallest picoalga (A1), no aquatic life is possible. Passing this threshold, species A1 with a high growth affinity and \(\mu_{\text{max}}\) arrives. A further enrichment alleviates P limitation of its growth. Both growth rate and steady-state biomass increase, while the concentration of the free nutrient pool stays constant. When the steady-state biomass of species A1 increases to the minimum (\(A_{\text{min}}^\text{g}\), µM P) where a grazer is capable of balancing its loss (\(E = [P]_{min} + A_{\text{min}}^\text{g}\) of A1), a second trophic level is established. With increasing \(E\), the growth rate of species

\[157\]
A1 continues to increase. This does not result in a higher biomass, however, since the predator removes the product to increase its own growth rate and biomass. Thus, grazing controls the algal biomass at a constant level, $A^*_\text{min}$, and through recycling, increases the pool of free nutrients.

Thingstad & Sakshaug (1990) showed that with increasing $E$, a long linear food chain might build up on species A1 before its growth becomes saturated. Establishment of an odd number of trophic levels in a linear chain increases the steady-state biomass of phytoplankton and keeps the steady-state level of free nutrients constant. An even number of trophic levels has the opposite effect (constant biomass and increasing free nutrient). When growth of the small alga reaches P saturation, increasing $E$ will only increase the concentration of free nutrient. Depending on its $[P]_{\text{min}}$ criterion, a larger alga (A2) may invade at some level of $E$ either before or after the growth of species A1 has reached saturation.

Armstrong (1994) used allometric relationships to model grazer-controlled coexistence of various algal size classes, the nominal size of which increased logarithmically from $4^0 \mu m$ to $4^4 \mu m$. Depending on the parameter values, a nitrogen enrichment of $E = 10 \mu M$ allowed the coexistence of 5 to 6 size classes (1 to $4^4 = 256$ and $4^5 = 1024 \mu m$, respectively) while $[P]_{\text{min}}$ for the smallest to the largest successfully invading class increased from 1 nM to a mere 10 nM – 100 nM. Similarly, Thingstad & Sakshaug (1990) showed that invasions might occur at undetectable increases in $[P]$. As seen from Equation 4, lower affinity for growth and higher background loss increases the concentration of phosphate where transitions occur.

In agreement with the observations, these models predict the dominance of small algae and intense grazing–nutrient recycling in oligotrophic conditions. With increasing eutrophication, successively larger algae enter the community, while the growth of smaller species may no longer be limited by P availability. Establishment of large cells rapidly increases the rate of sedimentation, which scales with $r^2$ (Stoke’s law) and is inversely related to mixing depth. This substantially elevates the $[P]_{\text{min}}$ required for the invasion of large phytoplankton (Equation 4). Annual succession, however, is directed towards the dominance of large algae developing in a rarefied environment (Reynolds, 1997). Once again, success here relies on additional adaptations such as the greater capacity of faster sedimenting large algae to achieve higher rates of ascendency by either buoyancy regulation or active motion (Reynolds, 1997), exploitation of spatial and temporal variability of resources, and/or utilising alternative forms of resources (organic forms, mixotrophy).

Concluding this section, the coarse pattern is that oligotrophic environments favour small microorganisms, while P enrichment and enhanced spatio-temporal variability in P supply select for larger phytoplankton. Current views on plankton dynamics and food web interactions serve as a suitable theoretical framework to analyse the pelagic P cycle and offer a broad set of testable hypotheses for experimental work. Competition experiments are very useful particularly when they consider the P acquisition and assimilation strategies of the species involved. More studies are needed that look at the P-related adaptations of key species as part of their complex life history. Conspicuously less progress has been made in clarifying P-dependent interactions among various size classes of planktonic microorganisms in shallow lakes compared to deep ones. This may indirectly reflect higher variability in the interactions among biota (and abiotic processes) in shallow systems.

### 4. What are the consequences of grazing on a P-deficient diet?

Sedimentation of mainly the inedible algae and grazing on the edible ones are the two key processes that determine the fate of primary production in aquatic ecosystems (Section 3). As shown in the extremely oversimplified scheme in Fig. 5, these processes have clearly distinct consequences for the cycle of P (as well as that of other nutrients). Even though a fraction of the sinking detritus may be recycled through autolysis and other processes, sedimentation represents a net, and often considerable, loss of nutrients from the photic zone. This loss must be replenished from external and internal sources to maintain a quasi-constant production. In contrast to this, grazers mostly recycle...
inorganic P in the photic zone making it immediately available for use by bacteria and primary producers. Fast sinking of faecal pellets of large zooplankton adds to the loss of P by sedimentation (Turner & Ferrante, 1979) thereby decreasing the amount of nutrient recycled in the water.

Studying the N cycle in the sea, Dugdale & Goering (1967) formalised the contrasting effect of grazing and sedimentation on the mass balance of the epilimnion by dividing primary production into two categories: ‘recycled’ and ‘new’. The latter is fuelled by nutrients that replenish sedimentation loss. Since N is mainly recycled in reduced forms (ammonium and urea) while most of the import comes as nitrate in stratified systems, the concept offered a constructive framework in studies of the N cycle. Phosphorus is both recycled and replenished mainly as ortho-P, making a similar distinction methodologically less tractable and conceptually less useful (Caraco et al., 1992, argued for the opposite). Influenced by Vollenweider’s (1969) mass balance approach, P-cycle studies have adopted the nutrient load concept. ‘New production’ and ‘total (internal + external) loading’ can be perceived as the two sides of the coin.

On a long time-scale (a year or longer), sedimentation is intrinsically coupled to the trophic dynamics of lakes. On a shorter scale, frequent shifts occur in the balance between sedimentation and grazing (recycling). Fully neglecting both long-term coupling and short-term dynamics, we focus on the effect of consumer-driven nutrient recycling with respect to P.

Inverse allometric scaling of nutrient regeneration to the body size of grazers has long been recognised (Johannes, 1964). If, however, the stoichiometry of the food does not match the nutritional requirements of the grazer as determined by its physiological status, and the grazer is capable of maintaining a relative metabolic homeostasis, inorganic nutrients will be regenerated differentially. This, in turn, modifies the nutrient supply ratios experienced by bacteria and algae. Strongly motivated by the biomanipulation theory (Shapiro et al., 1975; Scheffer et al., 1993), current research centres on the mechanisms and consequences of differential recycling in the nutrient–food

Fig. 5. Schematic presentation of sedimentation and recycling. Arrows of various thickness represent a rough qualitative weighting of the relative importance of various processes.
organism–grazer system. Since protist grazers feeding on P-rich bacteria are at low risk of being P deficient, protist grazers are considered to recycle inorganic nutrients with reasonable efficiency. Nevertheless, the efficiency of regeneration was shown to decrease when the diet was P deficient or the grazer grew exponentially (Andersen et al., 1986; Jürgens & Güde, 1990). In rotifers, somatic growth and reproduction are suppressed when feeding on an N- or P-deficient diet (Jensen & Verschoor, 2004), but differential recycling of nutrients has not been studied. This may be addressed in the future since small rotifers are often responsible for recycling a considerable fraction of P (Gaedke et al., 2002; Ejsmont-Karabin et al., 2004).

Significant intraspecific variability has been found in C:N:P ratios among crustacean zooplankton. Andersen & Hessen (1991) found that cladocerans were much richer in P and needed somewhat less N than calanoid copepods. Daphnia longispina (Cladocera) and Acanthodiaptomus denticornis (Copepoda) represented the two extremes with mean C:N:P molar ratios of 85:14:1 and 212:39:1, respectively. The stoichiometry of crustaceans was relatively constant from spring to autumn in spite of the seasonal variability in the elemental composition of the seston. Both experimental starvation and P-rich extra food failed to significantly alter the ratios of body nutrients. These observations suggested that crustaceans maintained their homeostasis rather efficiently.

Enclosure experiments have indicated that the amount of P released by Daphnia pulex decreases linearly with the decreasing P quota of the diet (Olsen et al., 1986). The authors proposed that the specific rate of regeneration ($R$, μmol P [mmol body C]¹ h⁻¹) is determined by the balance between P ingestion ($I_p$, μmol P [mmol body C]¹ h⁻¹) and the demand for P for growth and reproduction ($G_p$, μmol P [mmol body C]¹ h⁻¹):

$$R = I_p - G_p$$

Assuming perfect homeostasis, $G_p$ equals the product of the specific growth rate ($\mu$, h⁻¹) and the specific P content of the animals ($Q_{p,a}$, μmol P [mmol C]¹). At a threshold dietary C:P ratio in the region of 320:1 to 430:1, P regeneration is predicted to drop to zero. At C:P ratios above the threshold ($G_p < I_p$), the growth of animals becomes P-limited.

Subsequent experiments have indicated that the homeostatic regulation is not as rigid as previously thought and P release is not a simple linear function of the P quota. DeMott and co-workers (1998) performed a particularly instructive growth and feeding experiment with Daphnia magna along a wide gradient of dietary C:P ratios (Fig. 6). Firstly, the specific growth rate of animals was lower by a mean factor of 2.5 when grown on a P-deficient Scenedesmus acutus diet as compared to a P-sufficient diet. By the end of the experiment, well nourished Daphnia were much bigger, contained more P and produced more eggs than their P-starved counterparts (Fig. 6). Secondly, the specific growth rate increased linearly with the P content of the animals. This in itself introduces nonlinearity into Equation 5 (the $G_p = \mu Q_{p,a}$ equation transforms to $G_p = aQ_{p,a} + bQ_{p,a}^2$, where $a$ and $b$ are constants). Thirdly, the gross growth efficiency (growth/ingestion) for C decreased monotonically along the gradient of increasing P deficiency of the diet (Fig. 6). Since the specific rate of C ingestion ($I_c$, mmol C [mmol body C]¹ h⁻¹) was nearly constant, this decrease reflected the reduced assimilation efficiency of C. Possible mechanisms of coping with the excess C relative to P might include increased respiration and enhanced excretion of DOC. At the same time, the gross growth efficiency for P peaked at intermediate levels of dietary C:P ratios (Fig. 6). On a P-rich diet, the excess P was released both by excretion and egestion. On the extremely P-deficient diet, P egestion decreased to nearly zero since Daphnia was able to assimilate only a small fraction of P, possibly due to some metabolic disorder. This resulted in both a dramatic drop in the gross growth efficiency for P and a steady excretion of this nutrient. Thus, Daphnia was a sink for P at moderate levels of dietary P deficiency and a net source of P at each extreme. Considering that the P demand of juveniles exceeded that of the adults, the threshold C:P ratio for P-limited growth was estimated as 90:1 in this experiment. This value was low compared to C:P molar ratios of the seston in most lakes and suggested that P availability might often limit the growth of large cladocerans in nature.

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Fig. 6. Growth, metabolism and P recycling in *Daphnia magna* along a gradient of dietary C:P ratios. (a) *D. magna* grew poorly and contained less P on a P-deficient (P-; molar C:P ratio ~80) as compared to a P-sufficient (P+; C:P ratio ~900) *Scenedesmus acutus* diet. Dry mass difference between animals fed on P+ and P- alga is shown. (b) Gross growth efficiency for C decreased monotonically with the increasing P deficiency of the diet while gross growth efficiency for P peaked at an intermediate value. C:P ratio of healthy animals was ~80. Percentage change in the C:P ratio of seston after 2 days of grazing mirrored the changes in gross growth efficiency for P. (Redrawn from DeMott et al., 1998.)
The coupling between the herbivore and its food cannot be understood by assuming a rigid homeostasis in the grazer (Elser & Urabe, 1999). If the P demand of the grazer exceeds the P content of the diet, recycling steadily reduces P availability and thereby intensifies the P deficiency of the phytoplankton. This could be seen in the experiment of DeMott and co-workers (1998) at intermediate levels of dietary C:P ratios (Fig. 6). The single long-term outcome is then the extinction of the grazer. The small but persistent P release by *Daphnia* growing on an extremely P-deficient diet broke this positive feedback (Fig. 6) but ultimately would lead to the exclusion of the grazer. Thus, to explain the stable coexistence of a P-deficient prey and a homeostatic grazer we need an additional dimension.

This dimension was added by Andersen (1997) who considered that food was a source of both energy (C) and the essential nutrient, P. To grow maximally, the grazer must match the requirements for both of these simultaneously. As the biomass of edible algae increases, zooplankton feeding, and thus P recycling, eventually saturates. As the rate of recycling relative to the P demand of algae declines, the food organism becomes more P deficient. According to the Droop model (Droop, 1973), this results in slower growth of algae. The declining energy supply reduces zooplankton growth, biomass and P demand leaving more nutrients for algal growth. In this way grazers convert a high but P-poor algal biomass to a smaller but P-richer biomass. This system shows a complex dynamic behaviour depending on parameter values and external P inputs. Possible outcomes include internal equilibrium, stable cycles and grazer extinction.

Experimental evidence has supported the contention that quality (=specific P content) and quantity (=energy) of food differentially influences the population dynamics of the grazer. Andersen et al. (2007) have found that the green alga *Selenastrum capricornutum* had a high biomass yield and a low P quota at saturating light intensity, compared to the alga grown at reduced light. As expected, *Daphnia magna* grew initially faster on the low-light, P-rich alga. However, the steady-state biomass of the grazer was dependent on the food quantity (carrying capacity) and the growth rate determined only the time needed to fill this capacity. The distinct effect of food quality and quantity was due to the reduced P demand of maintenance metabolism during the stationary phase as compared to the initial growth phase (cf. DeMott et al., 1998; Klausmeier et al., 2004).

Field studies have indicated that growth of *Daphnia* can be P-limited in nature but frequent transitions between shortages of energy and P are more likely than persistent P limitation (DeMott et al., 2001). Gaedke and co-workers (2002) showed in their particularly careful analysis of long time-series from Lake Constance that consumers covered their C demand by grazing mainly on algae whereas P was mostly obtained from bacteria and their protist predators. Increasing P deficiency during the summer selected for omnivores that minimised their P deficiency at the cost of enhanced energy limitation. In this season, herbivores maintained high biomass but contributed to P recycling only by 30% because of their high P need. Elemental composition of bacterivorous flagellates, carnivorous crustaceans and fish was similar to that of their food. Thus, these organisms dominated recycling. Energy- and P-limitation of various groups of zooplankton fluctuated rapidly during the season and in various years.

Grazers maintain homeostasis with respect to other nutrients, too. This results in a differential recycling of, for example, N and P as a function of the difference in the N:P stoichiometry of the food and the grazer (Sterner, 1990). Provided that the phytoplankton is supplied with the two nutrients in a near-optimal ratio, and thus a relatively small increase in the supply of the limiting nutrient causes the other nutrient to become limiting too, differential N to P recycling may cause a transition from P- to N-limited algal growth. Elser and co-workers (1988) demonstrated in a few lakes that *Daphnia* dominance resulted in P deficiency of the phytoplankton while the dominance of calanoid copepods associated with a change in fish predation resulted in the algae being N deficient. The reason was that large cladocerans with N:P molar ratios of about 14:1 differentially retained P and recycled N, while copepods with larger N:P ratios (30:1 to 50:1) did the opposite (Elser & Urabe, 1999).

In conclusion, theoretical, experimental and field studies unequivocally indicate that the nutrient–food organism–homeostatic grazer system is closely coupled...
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through a series of reciprocal interactions that generate complex dynamic behaviour. The stoichiometric theory that analyses the constraints and consequences of mass balance of multiple elements provides an efficient theoretical framework to capture a wide range of these interactions (Elser & Urabe, 1999). From the perspective of ecosystem structure and function, the question remains: to what degree does differential nutrient regeneration by various grazer groups (including rotifers, small cladocerans and copepods that have not been studied so intensely) modify the simple allometric scaling of recycling? Although the recent ‘metabolic theory of ecology’ (Brown et al., 2004) has successfully unified allometric scaling and biochemical kinetics (temperature dependence), the third component, biochemical stoichiometry, has not yet been satisfactorily integrated. More comparative studies are needed that highlight the mutual dependence of energy and nutrient depletion of various consumer groups in real food webs.

5. How much can we simplify the P cycle to predict eutrophication-related changes in lakes?

Predicting the efficiency of eutrophication management strategies represents a major challenge for many freshwater scientists who study one or other aspect of aquatic P cycling. The simple practical question typically concerns the critical external load that will not support a higher phytoplankton biomass than targeted and that will suppress cyanobacterial dominance. In the majority of cases, two divergent classes of models are used to plan management measures:

1. simple empirical relationships and
2. sophisticated dynamic models.

In the first class, the elegant set of OECD (Vollenweider-type) models is predominant (Vollenweider & Kerekes, 1982). These models provide a useful, though risky, tool to approximate the potential behaviour of a given lake (Somlyódy & van Straten, 1986). The risk is hidden in the fact that the OECD model does not reflect the trajectory of eutrophication in individual lakes but roughly characterises the ‘average’ behaviour of lakes in which the biomass capacity is P-determined (Reynolds, 1992). This average behaviour is governed by regular changes in population responses across a range of trophic states from nutrient recycling systems towards poorly grazed phytoplankton (Harris, 1994). Studies that have used the OECD approach to compare the same lake before and after load reduction have revealed important similarities and differences in the path of recovery in shallow and deep lakes (Sas, 1989; Istvánovics & Somlyódy, 2001). When, however, the lake fails to recover after load reduction, the OECD model with its single aggregate parameter, apparent sedimentation, does not help to clarify the causes of failure.

Predictive, ‘process-oriented’ dynamic models aim at synthesising our knowledge on ecosystem functioning with respect to some problem, in this case, eutrophication (Somlyódy & van Straten, 1986). Jørgensen (1999) identified three major difficulties when using these models:

1. insufficient data availability,
2. uncertainty in parameter estimation and
3. fixed model structure that contrasts the most fundamental property of real ecosystems, their adaptive response to external forcing.

The last deficiency led Jørgensen to develop his structural dynamic models in which a system-level property, exergy (biomass and information expressed in units of energy) is used as a measure of the distance of the system from thermodynamic equilibrium. Exergy serves as a ‘goal function’ that allows for structural changes in the model through directional changes in parameter values. Changes are directed towards maximising the exergy of the system in a variable environment. Irrespective of this conceptually very important difference between the traditional ‘rigid’ and structural dynamic models, both types share the ambition of tracking the fate of various compartments (state variables) from instant to instant by explicitly describing resource acquisition, resource-limited growth and various loss processes of populations that are considered to play important roles in the given lake. Although this ambition seems to be self-explanatory, this may not be the case in shallow, polymictic lakes where growth-limiting factors alternate frequently. I illustrate this point with the case of Basin 1 of shallow Lake Balaton (Fig. 7).
The lake suffered rapid eutrophication in the 1970s (Herodek, 1986). Management measures taken during the 1980s resulted in some 50% reduction in the external P load. After some delay, the annual mean biomass of phytoplankton decreased faster than previously expected (Istvánovics & Somlyódy, 2001). The composition of summer phytoplankton progressed from assemblages dominated by Ceratium hirundinella and large diatoms through the ascendancy of N₂-fixing Cyanobacteria (Anabaena and Aphanizomenon spp.) to a virtual monoculture of invasive Cylindrospermopsis raciborskii and then to the first signs of a move back towards ‘pristine’ assemblages (Padisák & Reynolds, 1998, Fig. 7). The composition and biomass of consumers (zoobenthos and to a lesser degree, zooplankton) followed the changes in phytoplankton (Specziár & Vörös, 2001; Istvánovics et al., 2007).

Light, phosphorus and nitrogen were identified as factors that may limit phytoplankton growth in Lake Balaton. Wind-induced sediment resuspension and slow sedimentation of the precipitating carbonates (mean 1.7 g CaCO₃ m⁻² d⁻¹) result in rapid light attenuation (mean $K_d$ ~3 m⁻¹) throughout the vegetation period. The generally low light availability selects for shade tolerant species. Randomly occurring storms often interrupt phytoplankton succession and result in a transient energy limitation of growth, usually lasting no longer than one to two days. Cyanobacteria gain dominance under longer periods (two to three weeks) of relative quiescence (Padisák, 1993; Honti et al., 2007). Considering the low light requirement of C. raciborskii (Dokulil & Mayer, 1996; Shafik et al., 2001), improving light availability during these periods may be less effective than rapid warming and diminishing P availability.

Sediment resuspension and subsequent desorption is a major source of P supply to the water during the summer (Istvánovics & Herodek, 1995; Istvánovics et al., 2004). According to rather indirect estimates, 50% to 60% of P can be recycled through the microbial loop (Vörös et al., 1996) and less than 10% to 20% by zooplankton grazing (G.-Tóth & Drits, 1991). External load peaks in the Spring when the algal demand is relatively low and growth may often be P-saturated. The SRP concentration was remarkably constant during both eutrophication and recovery (< 100 nM P to 150 nM P) and the ortho-P concentration hardly exceeded 5 nM to 10 nM after the Spring (Istvánovics & Herodek, 1995). Close coupling between P replenishment and amplifying energy deficit from late spring onwards restricts the opportunities of invasive ‘C species’ sensu Reynolds (1997) and progressively increases the advantage of P storage. The latter is one of the factors that selects for stress tolerant ‘S species’ during phytoplankton succession.

The concentration of nitrate is high in early Spring (>7 µM N) and decreases rapidly after the spring floods. The causes of the collapse of the spring diatom bloom remains uncertain but in many years it was associated with the decrease in the external N load (Fig. 8; Présing et al., 2001). Uptake ratios of C to N were usually close to the Redfield ratio (Présing et al., 1996, 2008). Strongly temperature dependent ammonium inputs from the sediments more-or-less balance the N loss caused by sedimentation. C. raciborskii had high affinity for ammonium uptake and preferentially covered its N needs by acquiring ammonium. N₂ fixation contributed no more than between 5% and 30% to the demand of even large blooms. The significant reduction in growth rate when grown in laboratory culture in a N-free medium (a reduction of between 25% and 30% relative to ammonium-supplied cultures; Shafik et al., 2001) suggested that N₂ fixation was a costly ‘emergency tool’ of meeting the N demand of growth.

Thus, in Lake Balaton resuspension-related random variability is superimposed on the smooth seasonal transitions from growth-limitation by the one resource to the other. Too frequent shifts relative to growth rates prevent each of the ‘players’ gaining dominance over the others. Dominance patterns change in an unpredictable way and communal biomass remains very much below the carrying capacity for up to 80% of the vegetation period (Honti et al., 2007). Consequently, modelling the rate of resource acquisition and growth appears to be a futile attempt. Moreover, errors in estimating the dynamically changing growth conditions (resuspension-related light availability, inputs of nutrients from external and internal loads and recycling) will quickly propagate when growth rates are modelled since the biomass gain of a species depends as much on its initial biomass and the length of the favourable
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Fig. 7. Lake Balaton and its catchment; mean P load ($L_p$) in Basin 1 (from daily data of the West-Transdanubian Water Authority) and annual mean biomass of the phytoplankton (weekly to fortnightly data from the National Water Quality Data Base). The main factors that contributed to load reduction and compositional changes in the phytoplankton are indicated, these include the construction of two reservoirs in the catchment.
period as on the actual growth rate. The conclusion is that, unlike theoretical models of plankton dynamics (Reynolds, 1997, 2002, Section 4), predictive models for eutrophication management in dynamically changing shallow lakes should consider capacity limitation instead of growth limitation.

In Basin 1 of Lake Balaton, the light-supported biomass capacity (about 200 mg chl a m$^{-3}$ during the summer) was not filled, with the exception of a few summers which were particularly favourable (warm, calm) for *C. raciborskii*. Nitrogen might determine the biomass capacity only during the Spring. The P-limited capacity could best be determined from the mass balance model of Lijklema et al. (1986) and the mean phytoplankton biomass in August. Large and small symbols indicate years when capacity was filled and not filled, respectively. (c) Linear regression between P capacity and August biomass in years when the capacity was filled ($r^2 = 0.90$). (d) Mean spring biomass of chironomids and mean phytoplankton biomass during the previous July to September in various areas of Lake Balaton and in various years, in order of increasing phytoplankton biomass. (b to d are redrawn from Istvánovics et al., 2007.)

Fig. 8. Observations used to develop the threshold model for Basin 1 of Lake Balaton. (a) External load of nitrate ($L_N$) and phytoplankton biomass during spring 2004. (b) Mobile P content of the surface sediments (a proxy for P-capacity) as determined from the mass balance model of Lijklema et al. (1986) and the mean phytoplankton biomass in August. Large and small symbols indicate years when capacity was filled and not filled, respectively. (c) Linear regression between P capacity and August biomass in years when the capacity was filled ($r^2 = 0.90$). (d) Mean spring biomass of chironomids and mean phytoplankton biomass during the previous July to September in various areas of Lake Balaton and in various years, in order of increasing phytoplankton biomass. (b to d are redrawn from Istvánovics et al., 2007.)

being reached. More interestingly, a two-year pattern was nearly always observed in the population dynamics of *C. raciborskii*, in which high and low biomass years alternated for no easily observable reason. In the latter years, the P-determined capacity was not filled. Unlike in many other lakes, zooplankton grazing is too low to control the biomass of phytoplankton (G.-Tóth & Drits, 1991). This is due to the low biomass of energy-limited large cladocerans that ingest 4 and 100 inorganic particles to obtain a single bacterium and alga, respectively, at the mean concentration of suspended solids (G.-Tóth et al., 1987; G.-Tóth, 1992). Capacities can be filled only when growth of species is sustained for a sufficiently long period of time (Reynolds 1992, 1997). Threshold models represent one of the solutions to simultaneously omit growth rates as determined by the actual limitations and still account for the time needed to fill the capacity (Honti et al., 2007;
We have developed a dynamic threshold model to follow long-term changes in phytoplankton biomass and composition in Basin 1 (Honti & Istvánovics, in prep.; Fig. 9). The model considers four species/functional groups of phytoplankton: spring diatoms, *Ceratium hirundinella*, *Cylindrospermopsis raciborskii* and other N$_2$-fixing Cyanobacteria. In this model, thresholds and capacities set the length of the opportunity windows for the various species. When a threshold is passed, the appropriate species is assumed to grow at the maximal temperature-dependent growth rate unless the capacity is filled. Thus, in the threshold model the opportunity window is a sort of ‘black box’ that averages out fluctuations in limiting factors and growth rates. Below thresholds and beyond capacities, the biomass of the species decreases.

In the absence of other hypotheses, the two-year ‘cycle’ of *C. raciborskii* in Lake Balaton is assumed to have resulted from the action of an unidentified ‘enemy’ on

**Fig. 9.** Scheme of the threshold model (a, b) and model results in Basin 1 of Lake Balaton (c). (a) Driving forces (curved arrow) make their path in the $n$ dimensional environmental space. From time to time, the path enters a subspace (opportunity window) in which one or the other species has the opportunity to grow. (b) Temporal representation of the process.
the inoculum size of Cyanobacteria. The enemy might be the host-specific, virus-like cyanophage Cr-LS that was found to decrease the biomass of a cultured strain of the cyanobacterium by 86% (Young & Pollard, 2005). In the present version of the model, chironomid larvae are assumed to be the enemy. This hypothesis is based on two lines of observations. First, *C. raciborskii* invested 25 to 45 times more biomass in akinete production (Padisák & Istvánovics, 1997) and maintained a larger akinete pool in the sediments of Basin 1 than did other N$_2$-fixing Cyanobacteria (Kovács et al., 2003; Padisák, 1997, 2003). Viable akinetes were found at a depth of 30 cm below the sediment surface (Gorzó, 1985) but only akinetes close to the sediment/water interface had a chance to germinate. Increased bioturbation, for example by chironomid larvae in the spring, may disperse the akinetes more evenly in the sediments and reduce the inoculum size of *C. raciborskii* (and other Cyanobacteria) available for growth later in the year. Second, chironomids also showed a two-year oscillation in biomass, with large blooms of *C. raciborskii* followed by large chironomid peaks the following spring. High chironomid biomass (>1 g m$^{-2}$) was associated with compositional changes, being attained only when *Chironomus balatonicus* dominated the zoobenthos. This occurred in those years when the mean concentration of chlorophyll $a$ had reached above a threshold of about 20 mg m$^{-3}$ during the previous July to September (Specziár & Vörös, 2001; Istvánovics et al., 2007; Fig. 8).

Contrary to its simple and transparent structure, the model better reproduces the biomass of phytoplankton in Basin 1 over the past 30 years than do dynamic models (Somlyódy & van Straten, 1986; Koncsos, personal communication; Fig. 9).

In summary, we are forced to simplify both phytoplankton dynamics and P cycling almost to the extreme to predict eutrophication-related changes in real aquatic systems. The simplification, however, requires detailed data on interacting physical, chemical and biological processes in the particular lake, and must be based on theories of plankton dynamics. One should keep in mind that to understand the motivations of human beings we are better to consult, say, Dostoevsky. However, to predict the behaviour of John Smith in the war and back home, we should carefully watch him acting over a sufficiently long period of time and use the keys from Dostoevsky to decipher J.S.’s motivations. Without a wealth of information, we are better making order-of-magnitude predictions using statistical models (Vollenweider & Kerekes, 1982; Somlyódy & van Straten, 1986; Sas, 1989).

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