EUTROPHICATION:
RESEARCH AND APPLICATION TO WATER SUPPLY

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Eutrophication and the management of planktonic algae: what Vollenweider couldn't tell us

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The "Vollenweider model" is a sophisticated mathematical statement about the long-range behaviour of (mainly temperate) lakes and their ability to support phytoplankton chlorophyll. Misapplication of the model, against which Vollenweider himself warned, has led to many misconceptions about the dynamics of plankton in lakes and reservoirs and about how best to manage systems subject to eutrophication. This contribution intends to introduce the topics addressed at this symposium on Eutrophication by framing them in context of the phosphorus-loading and phosphorus-limitation concepts. Emphasis is placed on the need to distinguish rate-limitation from capacity-limitation, to understand which is more manageable and why, to discern the mechanisms of internal recycling and their importance, and to appreciate the respective roles of physical and biotic components in local control of algal dynamics. Some general approaches to the management of water quality in lakes and reservoirs to eutrophication are outlined.

Introduction

Eutrophication is generally understood to refer to enrichment of biological systems by nutrient elements, notably nitrogen and phosphorus, and to the enhanced production of algal and higher plant biomass that the added loads stimulate. The concept has a firm factual foundation and has been understood well enough from the early days of comparative limnology (see, for instance, Thienemann 1918; Naumann 1919; Pearsall 1921). Public concern about the deterioration in recreational and drinking water quality, as a consequence of culturally accelerated eutrophication, prompted the development of a number of quantitative relationships, between selected indices of the respondent plant biomass and selected representations of the availability of nutrients to primary producers, including those of Sakamoto (1966), Lund (1970), Dillon & Rigler (1974), Oglesby & Schaffner (1975, 1978), Rast & Lee (1978). By far the best known and still the most widely applied, however, is the relationship presented by Richard Vollenweider (1968), as later extended and refined during an international collaborative project, convened by the Organisation for Economic Cooperation and Development (OECD), and ultimately published in definitive form by Vollenweider & Kerekes (1982).

These developments resolved many of the intellectual aspects of the issue and, perhaps more pertinently (Reynolds 1989a), staunched the financial support to maintain the philosophical investment in the problem. Clearly enough, the models demonstrated that the greater is the external load of phosphorus then the greater is the quantity of algal chlorophyll that will be supported. End of problem: science moves on.

Yet, no less clearly, the problem endures. Algae are still produced, pending some concerted scheme to reduce the external loading of nutrients. However, attempts to reverse the effects of eutrophication have had conspicuously variable results; not all have been so evidently successful as the Lake Washington scheme (reviewed in Edmondson 1977). In the United
Kingdom, toxic algal blooms have at last been recognised for what they are (Pearson et al. 1990) and, perhaps correctly, are popularly viewed as a symptom of eutrophication. Thus, although it is both ironic and humbling that managers and academics should return to this topic, the reasons for doing so are abundantly clear. While it is easy enough to diagnose the root causes for lake eutrophication and its consequences, it is quite another to be able to cure it or, indeed, to predict the extent and effectiveness of treatment measures. In this age of accountability, the cost-effectiveness and cost-benefit appraisals of further research have been difficult of substantiate. Who needs more models when you are already awash with blue-green algal scums?

Experimentally-verified philosophical guidance is required, however, if eutrophied systems are to be adequately managed for supply and amenity purposes and if the correct approaches are to be adopted in securing effective measures of amelioration of water-quality problems. This would presuppose there to be a consensus view of aquatic ecosystem functioning that is implicitly correct. Even cursory examination of the international literature shows this is far from being the case (see especially Carpenter 1988). It is not wholly academic to consider how given ecosystems are regulated, whether mainly internally or externally, whether from the "top down" or the "bottom up" or whether they are determined ("limited") by nutrients which arise externally or are recycled within. It is also essential to devise a strategic approach to the application of knowledge in resolving problems faced in the water-supply industry.

The objective of this paper is to identify the key issues and outstanding questions posed in the management of planktonic algal populations in eutrophied lakes and reservoirs and to contribute to a rationale for selecting the most appropriate approach to the solution of specific problems at specific sites.

What Vollenweider did tell us

I want to make it perfectly clear that the title of this article in no way implies any criticism of the Vollenweider Model or its authors. The model remains a most elegant and powerful statement about the high-level ordering of limnetic systems. After all the physical variability, chemical drives and myriad of potential biotic responses are averaged out, then the mean level of planktonic biomass (as measured by its chlorophyll content, chl\(_y\); see note 1) supported is broadly a function of the mean, in-lake availability of total phosphorus (P; \(\text{mg}\) $\text{L}^{-1}$) through the year. In this sense, the model provided empirical weight to eloquent contemporaneous argument (e.g. Schindler 1977) that a good deal of the inevitable variability among lake behaviours was attributable to their phosphorus-dependent carrying capacities. Indeed, it is perhaps remarkable that the mean annual standing-crop biomass should remain so consistently proportional to phosphorus availability, even across the spectrum of lakes where the element has been shown to be continuously or frequently limiting the production of phytoplankton. However, it is important to emphasise that the regression equation which can be fitted to the accumulated data points (Fig. 1) is an average of behaviours; it is not a slope up or down which a given lake will progress during a period of artificial enrichment or deliberate restoration.

This last point has been amply demonstrated in the IMSA analysis (Sas 1989). In several of the restoration performances considered (e.g. Wahnbach Reservoir, Fig. 2a), reduced phosphorus loadings produced an immediate and predictable response, and the year-to-year slope was closer to 1.0 than to Vollenweider’s 0.91. In other cases and to varying extents (e.g. Veluwemeer, Fig. 2b; Schlactensee, Fig. 2c) there was a noticeable lag during which mean phosphorus was sharply reduced but chlorophyll failed to respond. Later, as phosphorus was

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Usage of symbols follows, as far as possible, that of the Vollenweider/OECD and IMSA (Sas 1989) studies. In this scheme, P stands for total phosphorus.
Figure 1. The Vollenweider–OECD relationship between average chlorophyll concentrations and P-loading characteristics, with 99% confidence limits inserted. The equation of the regression is \( \log(\text{chl}_y) = 0.91(\log P_y) - 0.435 \), where \( P_y = \frac{L(P)/q_s}{[1+(z/q_s)]^{1/2}} \) and \( L(P) \) is the annual P load (in mg m\(^{-2}\)), \( q_s \) is the relative volume of water exchanged per year (m\(^3\)) and \( z \) is the mean depth of the water-body (m).

Figure 2. Stages in the restoration of three European lakes following reduction in external P loading. The heavy lines link the changing annual average chlorophyll concentration against the phosphorus available and are superimposed upon the Vollenweider–OECD regression. The bars to the right of each point represent the difference between TP (the total phosphorus) and PP, the particulate fraction. Note that this difference (equivalent to the dissolved P) is virtually exhausted before mean biomass chlorophyll declines.
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Figure 3. (a) The explanation of lake behaviour according to Sas (1990), in terms of biomass response to phosphorus reduction, moving from P-saturation and zero response to biomass reduction and compositional change. The effects of eutrophication would be approximated by reading from right to left. (b) Hypothetical P-Chl relationships from several separate lakes are represented: the Vollenweider-OECD regression is believed to fit this family of individual response curves.

still further reduced, then chlorophyll did fall, with a slope close to 1.0, against phosphorus. The shapes of the curves are generic, depending upon analogous responses, as interpreted in Sas (1989) (see Fig. 3a), but their co-ordinates are unique to individual lakes. It is not difficult to recognise that Vollenweider's regression may well describe a family of overlapping curves (Fig. 3b). Moreover, if more of the lakes in the original OECD data-set had been unresponsive to changes in P loading, it is likely that the regression coefficient would have been less than 0.91. Using a different data-set of (mainly) North American lakes, which is apparently less weighted in favour of phosphorus-deficient oligotrophic lakes, Rast & Lee (1978) were able to fit a slightly flatter regression slope (0.76).

The problems perceived with the use of the model are the same as those with any other -- its uncritical application. Vollenweider (1976) himself explained that the models were intended to be illustrative, doubted that they could be usefully developed further and cautioned against too literal an interpretation without much finer resolution and understanding (p. 78). The principal application he envisaged was the better definition of “critical loads” of phosphorus as an aid to catchment-management decisions.

Those who would extend the use of the model need to be fully aware of its conditions and limitations and also to realise that if further questions arise about managing the phosphorus-chlorophyll relationship in a particular system (as they surely must), the next steps in deductive logic must be understood to be less general and increasingly subject to stochastic error.

Capacity limitation by phosphorus

The relatively tight coupling between the quantities of algal mass eventually produced in a given system, and the amounts of phosphorus available to support them, is often assumed to attest to “limitation” of algal growth by phosphorus, as opposed to any other factor, and is even described as such. It is also becoming common to read in the literature that “lake X is phosphorus-limited”, frequently on the grounds of the elemental N:P ratio of the amounts of nutrient available (see later). Again, another implicit expectation which sometimes arises is that a given phosphorus concentration in water is necessarily accompanied by a pro rata
concentration of chlorophyll, without allowance for the time taken by algal populations
to increase to a level commensurate with the phosphorus supply. Understanding the
mechanisms of the phosphorus–chlorophyll relationship, and their application to the
management of eutrophication, is not assisted by sloppy conceptualisation.

For instance, it is important to be precise about what is limited and when. Reynolds (1992a)
has distinguished capacity-limiting factors as being those setting the eventual population
maximum: $n_{\text{max}}$ is often a function of the available nutrient pool, ($K$), and the “minimum cell
quota” ($q_o$), as conceived by Droop (1973, 1983), being the lowest amount of intracellular
nutrient upon which the cell can still function. Then,

$$n_{\text{max}} = Kq_o$$

There is no assumption that this condition is unique to phosphorus. The fact remains that, if $K$

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{figure4}
\caption{Reynolds' (1978) regression to determine maximum chlorophyll carrying capacity was solved
to show behavioural differences among Windermere North (WiN), Blelham Tarn (Ble) and Crose Mere
(Cro): the original points lie within the respective rectangles. The regression has been quite successful in
predicting the maximum biomass observed in Blelham Enclosures (A77, A78, A79, A83, B78, B80, B83, C83 are shown), Grasmere (Gra) and Rostherne Mere (Ros). The equation of the original regression is log
($\text{Chl}_{\text{max}}$) = 0.585 (log $P_{\text{max}}$) + 0.801.}
\end{figure}
is (say) silicon, $n_{\text{max}}$ could be exceeded by non-diatoms, or if $K$ is nitrogen, perhaps nitrogen-fixing cyanobacteria could expand to the limit of the phosphorus available. As no other proximal source of phosphorus is available to any phytoplankton, except the total phosphorus pool in the water, it follows that the ultimate chemical capacity is, indeed, often determined by the size of that pool (Schindler 1977).

In sub-capacity populations, the actual quota of phosphorous is likely to be rather greater than the minimum, generally falling within the range $7 - 30 \text{ mg P per g ash-free dry-cell mass}$ or, assuming 50% of the dry organic mass to be elemental carbon, $5 - 23 \times 10^{-3} \text{ mol cell P (mol cell C)}^{-1}$. As the typical chlorophyll-a content of cells has a similar range, $9 - 39 \text{ mg chl a (g dry cell mass)}^{-1}$, the ratio 1:1 is a useful guide to the phosphorus-determined carrying capacity. In reviewing the behaviour of populations raised in experimental enclosures, or “limnocorral”, Lund & Reynolds (1982) found that, though the ratio averaged nearer 1:2, the larger and more persistent maxima approached an efficiency of 1:1 at higher loads but this increased to >3:1 at low average phosphorus concentrations. These instances fit well (Fig. 4) to Reynolds’ (1978) earlier regression of chlorophyll yield upon initial phosphorus availability, which remains the only chl-a-P model that predicts the scale of the maximum (as opposed to average) phosphorus-determined yield of algal chlorophyll. The slope of the regression reflects the efficiency of utilization at chronically low phosphorus concentrations and the increasing “profligacy” of consumption at higher ones. Nevertheless, even this yield may well be unattainable if other limitations on capacity are imposed at some intermediate level of attainable yield. A hypothetical instance of this plateauing effect, with respect to the phosphorus availability, is

![Figure 5](image-url)

**Figure 5.** Conceptual figure showing the relationship of chlorophyll to phosphorus and the principle of a second capacity factor (here, light) intercepting the OECD response at higher concentrations of phosphorus. Changes in chlorophyll are not predictable to the right of this point.
same mixed layer, $\sum nR$, ($= 24 nR_{hm}$, where $n$ is the phytoplankton population expressed in terms of its chlorophyll, $R$ is the hourly respiration rate and $h_m$ is the depth of the layer), i.e., when $(\sum nP)/(24 nR_{hm}) = 1$

Evaluation of the volume-integrated photosynthesis, $\sum nP$, is scarcely simple but may be approximately derived from a model relationship, the development of which also owes, in part, to Vollenweider (e.g. 1965):

$$\sum nP = \frac{0.75 nP_{max} \Gamma}{\ln(0.7 P_{o,max}/0.5 I)}/e$$

where $P_{max}$ is the light-saturated rate of photosynthesis, $\Gamma$ is the length of day (sunrise to sunset), $P_{o,max}$ is the maximum flux density of photons passing into the water and $I$ is the intensity required to saturate photosynthesis. $e$ is the vertical coefficient of light extinction and is the sum of components attributable to water and solutes ($e_w$), the non-living particulates ($e_p$), and the absorption and scatter due to chlorophyll ($e_q = nk$, where $k$ is the area subtended per unit of chlorophyll). Whence, $n$ is solved:

$$n = \frac{1}{k} \left[ 0.75 (P_{max}R) . \Gamma/24 . \ln(0.7 P_{o,max}/0.5 I) \right] (1/h_m) - (e_w + e_p)$$

The carrying capacity can vary with season and among the factors but the capacity is not necessarily continuously filled nor even at all. The case illustrated in Figure 6 concerns Rostherne Mere, a small (0.48 km$^2$) but relatively deep ($H_{max}, 30$ m; $H$, 13.4 m) and turbid

![Figure 6. The chlorophyll content (dark silhouette) in Rostherne Mere through 1967, in relation to the capacities allowed by the available phosphorus, Chl($P$), in the trophogenic layer and the light income, Chl($I$). Chlorophyll did not come close to filling the combined capacity (heavy stipple), although there have been occasions when other populations did realise these capacities (Oscillatoria in 1978, Ceratium in 1980 and Scenedesmus in 1983). The Vollenweider-OECD prediction of average biomass is inserted for interest (right hand ordinate). Simplified from Fig. 2 of Reynolds (1992a).](image)

($e_w + e_p > 0.45$ m$^{-1}$) natural kataglacial lake near Manchester, England. It is naturally rich in phosphorus but the supply is augmented by the output of a small sewage treatment plant and an agricultural contribution. The plot of instantaneous evaluations of the phosphorus-determined chlorophyll-carrying capacity, as calculated according to the regression equation in Figure 4 from measurements made during 1967, is superimposed upon the calculated light-compensated chlorophyll-carrying capacity through the year. The actual measurements of chlorophyll in the lake through the same year imply that the carrying capacity was never close to realisation, although maxima recorded in 1978, 1980 and 1983 suggest that the phytoplankton populations are not prevented from achieving the theoretical capacity on occasions.
Each of these capacity crops is known to have become established over lengthy periods of relatively constant weather conditions (cool, windy weather with frequent mixing in 1978 provided conditions favourable to Oscillatoria growth; uninterrupted near-surface stratification in 1983 allowed the epilimnion to resemble the environment of a shallow, rich pool). Reynolds & Bellinger (1992) deduced (i) that the period over which growth of an eventual dominant species is sustained can be as relevant to the scale of the realised population as is the initial carrying capacity, and (ii) that the greater is the unfilled capacity then the more that statement (i) will apply.

**Rate limitation by phosphorus**

It is also clear that for the attainment of a capacity-filling population, an inoculum of cells requires either to be able to maintain a rapid rate of increase under optimal conditions or, if slower, to be able to sustain net increase for longer.

*In situ* species-specific increase depends upon the *in situ* rates of cell replication net of any losses through mortality. Too few reliable data on *in situ* cell division are yet available, although improving techniques for assessing mitotic separation and their wider application (e.g. Heller 1977; Braunwarth & Sommer 1985) are yielding results that generally accord with division rates reconstructed from intensive field measurements of the dynamics of individual populations (Sommer 1981; Reynolds 1982, 1986) as well as model predictions based on the behaviour of isolates in laboratory experiments (e.g. Reynolds 1989b, 1990). It is of particular interest that neither the light-saturated photosynthetic carbon fixation rates nor the maximal nutrient-uptake rates (except for certain more conservative components, such as silicate and sulphate), establish more than a resource-acquisition capability. When the supply of resources is adequate, the rates of cell replication are ultimately constrained by intracellular synthesis, translocation and assembly into new biomass. Not surprisingly, species-specific replication rates and their sensitivity to temperature and photoperiods are apparently correlated with cell morphology (Reynolds 1989c). Thus, supposing water temperatures and day-length characteristics to be those anticipated in temperate lakes (say, 20°C, 16 h d⁻¹), reported *in situ* cell replication rates (Reynolds 1982) in the order of magnitude from 1.2 d⁻¹ (for non-planktonic non-motile unicells of *Chlorella*) to 0.12 d⁻¹ (for large flagellate cells of *Ceratium*), seem to accord with respective maximal rates observed in culture, i.e. c. 21.3 x 10⁻⁶, 2.4 x 10⁻⁶ mol C fixed (mol cell C⁻¹ s⁻¹). In comparison to the 9 h or so required to complete one *Chlorella* division, the same cell could be expected to be able to fix sufficient carbon in some 5.4 h but to take up from a rate-saturating concentration sufficient phosphorus to provide for the next cell division in only 7 minutes.

Although the dependence of nutrient uptake upon external concentration conforms to Monod-type kinetics (Fig. 7), algae differ perceptibly in their rates of absorption and assimilation (see, for instance, Rhee 1982; Tilman, Kilham & Kilham 1982; Turpin 1988). It is possible to discriminate species, on the basis of the ratio between maximal rates of uptake and growth, as being (velocity-) adapted to capitalise on favourable supplies, (storage-) adapted to operate at chronically low nutrient resources (Sommer 1984; Reynolds 1987a). Nevertheless, the ultimate requirement for the cell is to obtain sufficient nutrients to supply the cell material for the next generation. In this, there are only modest deviations from the ideal (Redfield) molecular ratio of key nutrients, viz. 106C:16N:1P. Thus, whether the demand is phased over the full replication period or whether it is garnered in a shorter period of opportunity, the amount of phosphorus required to sustain the next generation is some 9.43 x 10⁻³ mol P (mol cell C⁻¹). To maintain the hypothesised growth rate of *Chlorella* (21.3 x 10⁻⁶ mol C (mol cell C⁻¹ s⁻¹)), for instance; without depleting the intracellular store, would require the assimilation of the equivalent of 0.20 x 10⁻⁶ mol P
Figure 7. Cell mass-specific phosphorus uptake by P-starved *Chlorella* cells as a function of external concentration. $K_v$ is the concentration required to half-saturate uptake. The intersection with $r_{sat}$ denotes the phosphorus concentration ($\sim 7 \times 10^{-8}$ mol P l$^{-1}$) required to balance growth rate at 20°C.

The concentration of phosphorus required to maintain this growth rate of *Chlorella* under the supposed natural conditions is marked on the curve in Figure 7; only $0.07 \times 10^{-6}$ mol P l$^{-1}$ i.e. about 2μg l$^{-1}$. When calculated in this way, moreover, the corresponding requirements of other common algae are also found to be substantially met by soluble reactive fractions of phosphorus (SRP) at concentrations in the order of $c. 10^{-7}$ mol P l$^{-1}$ or less (Reynolds 1992a).

The corollary of this deduction is that so long as the concentration of SRP exceeds $c. 0.1 \times 10^{-4}$ mol P l$^{-1}$ (i.e. $c. 3μg P l^{-1}$), it is most improbable that algal growth is phosphorus limited. Conversely, the SRP concentration must be reduced to <3μg P l$^{-1}$ before cell growth is likely to be limited by phosphorus availability. Even then, there may be a lag before the internal store ($q$) falls faster than it can be replenished towards the minimum quota ($q_o$). Other than at steady state (Bumaster 1979), the Droop formulation is likely to yield a more realistic model of the phosphorus-deficient growth kinetics than is the Monod model (see also Sommer 1991).

Three cases of vernal, generally diatom-dominated growth in northern hemisphere temperate lakes are illustrated (Fig. 8) in support of this principle. In winter, increase in chlorophyll is normally regulated by light availability – the duration, as well as the intensity, of irradiance and the interaction with vertical mixing, especially while the water remains unstratified. As the days lengthen, the light-limited capacity increases so, provided other resources are available, the spring increase gets under way accordingly. This is shown to apply in the case of an experimental enclosure (known elsewhere as "limnocorals" and "mesocosms") in Blelham Tarn, English Lake District, where dissolved phosphate, silicate, nitrate and EDTA-complexed iron were artificially replenished weekly: the chlorophyll concentration and total phosphorus increased rapidly towards a maximum in April, when the column stratified and the dominant *Asterionella* was replaced by the colonial green flagellate...
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Figure 8. Changes in vernal (mainly diatom) chlorophyll in (a) Blelham Enclosure B, in the 1978 experiment, (b) Esthwaite Water and (c) Lake Michigan. While soluble reactive phosphorus (SRP) is replenished (a), algal chlorophyll increases together with the total phosphorus (TP) in suspension; in (b) the removal of SRP to algal mass sustains an increase in chlorophyll (but not in TP) until the supply is reduced to a truly limiting concentration (<0.1 μmol P l⁻¹); in (c) phosphorus limits almost continuously.

Eudorina (for full details see Reynolds & Wiseman 1982). In the case of the natural growth in nearby Esthwaite Water, the vernal increase in chlorophyll concentration proceeds at an initially similar rate but at the clear expense of the SRP pool; its reduction to c. 1 μg P l⁻¹, i.e. some 3 x 10⁻⁴ mol l⁻¹, indicates the onset of phosphorus limitation, with a plateauing and then a decline of the chlorophyll following in close sequence. In the case of Lake Michigan, where the SRP fraction scarcely exceeds 1 μg P l⁻¹, both the rate of lake spring chlorophyll increase and the carrying capacity of the lake are arguably phosphorus-limited throughout.

Nutrient ratios

The deduction that phosphorus does not limit phytoplankton growth until it has almost all but
disappeared from solution calls into question certain other widely-held tenets concerning the supposed control of phytoplankton by nutrients, including those in the area of competitive exclusion and the selective importance of nutrient ratios. Although the requirements for (say) nitrogen and carbon are also universal among phytoplankton algae, the forms available and the optimal quantities are sufficiently dissimilar for it to be supposed that the growth of one species might become limited significantly before that of another. The deduction that, other things being equal, this would provide a competitive advantage to the latter over the former would then seem quite logical. Moreover, were the second species to be simultaneously limited by the availability of a second element, while the first was not, then they would cease to be direct competitors and thus be able to co-exist. This, indeed, is the basis of what has become known as Tilman's resource-based competition theory (Tilman 1977). Ultimately, it predicts that the greater the number of potentially limiting resources, then the greater is the number of potentially co-existing species (see also Petersen 1975).

Compelling experimental evidence has been advanced in support of this theory in the case of nitrogen-fixing cyanobacteria over, say, chlorophytes when external sources of combined nitrogen are low (Rhee 1978; Rhee & Gotham 1980), or of cyanobacteria over certain chrysophytes, and any chlorophytes that may be present, when free carbon dioxide has been exhausted and the ability to utilize bicarbonate is at a premium (Shapiro 1990a) or, again in the case of the non-diatoms, exemptions from requiring relatively large amounts of skeletal silica which allows them to supersede diatoms when soluble sources of reactive silicon (SRSi) have been exhausted (Holm & Armstrong 1981). Nor can exception be taken to the fact, ably demonstrated in the carefully controlled experiments of (e.g.) Tilman & Kilham (1976), that if the ratios of limiting resources can be maintained in some kind of steady state, the bias will inevitably bring about either the dominance of A over B, or of B over A, or the co-existence of A and B.

The real problem for the ecologist comes in detecting the relevance of this mechanism in nature. Certainly, one might predict that in a nutrient-poor lake having (say) chronically depleted levels of SRP and SRSi, some selection upon resource gradients is likely to occur. The argument is well supported among some larger lakes where the growing season is sufficient to permit long-term selections over long periods (Kilham & Kilham 1990). Indeed, this principle ought to be invoked to explain the assembly of the species associations and their typical dominant species which characterize lakes at particular points on the scale of trophy. It is perhaps more difficult to accept the argument that gradients in SRSi/SRP ratio that have been detected near fluvial inflows in Lake Michigan are either sufficiently robust or sufficiently permanent to maintain significant differences in the algal community; the challenge (Sell, Canney & Fahnenstiel 1984) that the species differences are due to the non-competitive effects of different compositional mixes introduced by the river inflows, probably has equal merit. The answer would appear to depend upon the interpretation of the dynamics of fluvial flow, limnetic dissipation and advection in relation to the doubling-times of nutrient-limited phytoplankton cells (Tilman, Kilham & Kilham 1984; see also Auer, Kieser & Canale 1986).

The explanation becomes even more implausible if the critical condition "that the cells are nutrient-limited" is ignored. For the growing cell, the only factor of relevance is whether there is enough of each of its various nutrient requirements available to sustain its next cell division. It is immaterial whether the N:P ratio is 50:1 or 3:1 if both nitrogen and phosphorus supersaturate the growth requirements for the current generation. It cannot be denied that when one or the other has been seriously depleted, the ratio may surge quite dramatically. This must be seen for what it is: a fortuitous consequence of one nutrient falling to a low availability, by which time it is the nutrient itself, not the ratio, that is critical. Moreover, if the ratio between two elements changes abruptly, as one or other is exhausted, the question must arise whether
the gradient principle has an opportunity to take effect: we cannot expect a subdominant population B to supplant a large nutrient-limited population of A when insufficient resource persists to sustain (perhaps) four or more divisions of B while A declines. In other words, the inoculum effect is the dominant criterion at such stages and sufficiently so to overwhelm a subtly altered selective bias (see Reynolds 1986 for examples). The usefulness of citing nutrient ratios relative to likely requirements of algae probably lies in determining which, if at all, is likely to become limiting during the increase phase. This may be used, for instance, in a lake with high phosphorus loading and only moderate nitrogen loading to predict a summer dominance of nitrogen-fixing blue-green algae. Even here, the ratio itself is consequential upon and not the determinant of events; thus its general application, as envisaged by Smith (1983), has proved less reliable than other criteria (Trimbee & Prepas 1987; Shapiro 1990a).

Seasonality of phosphorus availability and utilisation

If, as argued here, soluble reactive phosphorus must fall to $10^{-7}$ molar or less before phytoplankton growth is likely to be phosphorus-limited, and the quantities in which phosphorus is required are (weight for weight) generally similar amongst the algae, then it may justly be asked why the presence of bloom-forming populations of blue-green algae bear such a consistent affinity for the more eutrophic lakes and reservoirs, at least in temperate regions (Rodhe 1948; Rawson 1956; Gorham et al., 1974) and, indeed, why they respond positively to anthropogenic phosphorus enrichment (Edmondson 1977; Trimbee & Prepas 1987; Sas 1989). Even if distinction is drawn between the progressive build-up of Oscillatoria spp. (especially of the O. agardhii – O. rubescens – O. proflica sub-group) in larger, deeper lakes or the increased abundance of summer growth of Anabaena, Aphanizomenon or Microcystis spp. in smaller, physically variable basins, the organisms are generally rather slow-growing and are particularly sensitive to temperature (see Reynolds 1989c). Their growth periods thus tend to be confined to the warmer months of the year. Evidence gleaned from comparisons between years (A. E. Irish, in Harris 1986; Talling & Heaney 1988) and between lakes (Kalf & Knoechel 1978; Reynolds 1984a) strongly indicates that lake eutrophication often leads first to an “infilling” of the period between the spring and autumnal phases of algal abundance by intermediate population developments (Fig. 9). Several factors may contribute to this effect but the increased supportive capacity may often be attributable to a surplus of dissolved phosphorus in excess of the ability of the spring bloom to consume it. The opportunities to blue-green algae might then depend upon the simultaneous fulfilment of their environmental requirements for resources and for their exploitation. Other algae, of course, share these opportunities, notably the motile chrysophytes, the mucilaginous colonial species of chlorophyta and the large-celled dinoflagellates. The outcome in terms of species composition, dominance and successional changes, may well depend upon the interactions with other factors, including the subsequent spatial “segregation” of resources (Reynolds 1976, 1992b), the depletion of carbon (Shapiro 1973, 1990a) and nitrogen (Riddolls 1985), selective grazing by Cladocera-dominated zooplankton (Hrbaček 1964; Lynch 1980; Sommer et al. 1986; Sterner 1989) and the intervention of physical factors (floods, wind-mixing events; Reynolds 1987a). Particularly instructive in this context, however, is the reproducible behaviour, described in Sas (1989), of erstwhile dominant populations of blue-green algae self-regulating to greater depths in the light gradients of lakes as the summer surplus of phosphorus is reduced through restriction of external phosphorus loads.

The control of P-capacity: external sources

It is clear that in many instances, phosphorus availability sets an upper limit on algal-carrying capacity in a water-body, even though this may be achieved infrequently if at all. Where it does
Figure 9. Stages in the enrichment of the north basin of Windermere, shown by prevernal soluble phosphorus concentrations (above) and the progressive increase in algal chlorophyll during the summer period. Data from Talling & Heaney (1988) and Talling (1992).

so continuously or often, there must be a strong incentive to protect that status quo and to control the external loads of phosphorus on the system. Elsewhere, the implicit objective would seem to be to reduce the external loadings in order to lower the carrying capacity and hence to impose the rate limitation earlier in the ascendancy of phytoplankton biomass. This form of words avoids making an assumption that less phosphorus always means fewer algae. This is not, however, a matter of semantics but a recognition of the functional relationships ("subsystems"; Sas 1989) operating within the "blackbox" of the Vollenweider-OECD equation. Moreover, an adequate reduction in loading is often very difficult to achieve: some prior understanding of the relative scales of the various sources, as well as the feasibility of controlling them, is essential to determining the best options for management.

Much of the phosphorus presently perceived to contribute to the cultural eutrophication of lakes and reservoirs is not only anthropogenically derived but it is of comparatively recent origin (the last 50 years or so). The principal reason for this is the enhanced delivery of
dissolved phosphates to natural waters, following the widespread introduction of secondary treatment of domestic sewage and, more recently, detergents built on hydrolysable polyphosphates. The relative loadings due to these materials clearly differ with the scales of the sources and their dilution by the receiving waters, although estimates attributing the generation of between 0.5 and 1.0 g P per person per day seem to have a sound basis in human physiology (e.g. Best & Taylor 1958). Estimates of the fraction of limnetic loads attributable to domestic detergent range between 9 and 25% of the total (Department of Environment 1991). Industrial and non-physiological sources of phosphorus can further contribute to a per capita soluble-P generation perhaps averaging about 2.5 g d⁻¹. Secondary-treated sewage effluent may contain some 25 (± 15) mg SRP l⁻¹ and c. 40 (± 25) mg l⁻¹ inorganic N.

Sewage inputs are largely identifiable “point sources”, in the sense of being (at least, in theory) readily controllable through tertiary (P-stripping) treatment of the effluent before discharge from the sewage treatment works. An established, simple technology, relying upon coagulation and precipitation with (usually) ferric salts, has been applied at a number of sensitive sites in the UK, as indeed it has in other IWSA-member nations.

“Agricultural run-off” is often branded, though rarely with more than prejudice, as a contribution to eutrophication. There can be little doubt that certain forms of intensive animal husbandry and market-gardening are capable of generating relatively high concentrations of phosphate in drainage waters. On the other hand, the natural phosphates incorporated into bulk inorganic fertilisers are, generally, insufficiently soluble for it to be supposed that their widespread use provides a major resource of dissolved reactive phosphorus. However, the particulate flux from ploughed, arable soils, which in any case presents greatly expanded leachable surface area to run-off water and drainage, can be very greatly enhanced. Depending upon grain size, much of this material will find its way into streams and rivers and, thence, eventually enter lakes and reservoirs as part of their total phosphorus (TP) load. As such, it may add substantially to the diffuse, or non-point, natural load of particulate phosphate, derived from the weathering of phosphatic minerals (e.g. apatite) present in the catchment area. A fraction of finer particles may remain in aqueous suspension long enough to permit solution but, even though the bulk of this material may settle out of suspension, more or less quickly, it is not necessarily lost irretrievably to the pelagic system; rather, it remains potentially recyclable within it (see following section).

The impact of altering this balance between the external loads of dissolved and particulate loads of phosphorus may not have been wholly appreciated. For instance, the present external TP-load to Windermere, English Lake District (estimated to be c. 16 x 10³ kg year⁻¹; FBA unpublished data) is roughly equally divided between particulate (mainly catchment-derived) and dissolved sources (largely attributable to sewage-treatment plants, commissioned since 1960; Talling & Heaney 1988). Thus, it is deduced that while the TP-load has probably nearly doubled over the same period, the dissolved phosphorus pool in the lake, where it is readily available to phytoplankton, is now some 7- to 10-fold greater than it was four decades ago. The concomitant changes in the yield of phytoplankton biomass (Talling 1992) must reflect this ongoing elevation in “soft sources” of phosphorus rather more than the increased external load per se.

**Approaches to P-capacity reduction through control of external loading**

The example of Windermere is a good illustration of a case suitable for treatment through external-load reduction: the recent eutrophication has been brief and is still relatively mild, the natural SRP load is minimal and the major contribution is mainly processed through two substantial secondary treatment plants and half-a-dozen or so small ones (some already with tertiary P-removal). A cost-effective return on investment, in terms of an improved algal
quality, may be anticipated. Certainly, some of the more successful lake-restoration attempts include instances in which diversion or tertiary treatment has indeed brought about a greatly reduced external phosphorus load to Lake Washington (Edmondson 1977), and the several cases reviewed by Marsden (1989) and Sas (1989) furnish good examples.

The application of this philosophy to water-supply reservoirs affected by eutrophication is not always straightforward, especially where they are located in well-populated and/or intensively agricultural lowlands with dispersed or diffuse sources of phosphorus. In the case of pumped-storage schemes, where (enriched) water is abstracted from riverine source(s), it may be practicable to strip phosphorus from the proximal inflow in preference to a (probably) ineffective treatment of the individual point-sources in the catchment. Where the reservoir is an impoundment of the river, the solution may be to construct or adapt a pre-reservoir where the water may be subject to precipitation of phosphorus before entering the main store. One of the most impressively successful examples of this approach is the Wahnbach Reservoir, Germany. The enriched waters of the inflowing River Sieg are rehabilitated to the standard of a near-pristine oligotrophic source. The impact of this routine treatment of the source water upon the erastwhile character of the reservoir plankton, and the ongoing advantages in terms of the cost of treating the abstracted water for profitability have been well documented (for references and reviews, see Bernhardt 1987). By analogy, feeding nutrient and silt-laden riverine inflows through shallow reedswamp-dominated lagoons can have a similarly protective effect upon receiving lakes and reservoirs of lower trophic status (Szilágyi et al 1990).

While, in theory, it is possible to lower or to impose a constraint on phosphorus-determined phytoplankton carrying-capacity of any lake or reservoir system through control of the external loading, it is neither the only, nor the most practical, nor the most cost-effective approach in every instance, nor even is it always desirable, if others factors interfere. For instance, it is well understood in the management of fishponds that the “crop” production is enhanced by expanding the nutrient base (Korinek et al. 1987) and the deliberate addition of fertilisers (eutrophication) is, at least on site, beneficial so long as the biological yield is carefully managed to be “more of the same” (Reynolds 1987b). The same principle applies, albeit on a less intensive scale, to increasing the productivity of harvestable fish from different kinds of lake. Who is to say that the biology of some extreme base-poor, nutrient-deficient waters could not be enhanced by a modest increase in phosphorus loading? Phosphorus addition has also been shown to be positively beneficial to the restoration of acidified waters, by promoting biological production, altering the balance of carbon dioxide metabolism and invasion, generating hydroxyl ions and so raising the acid neutralizing capacity of the lake; the ambient pH may be moved positively and permanently towards neutrality (Davison et al. 1989). Davison (1987) has shown that phosphorus is 47 times more effective as a counter to acidity than the molecular equivalent of calcium carbonate. It is worth querying the policy of phosphate removal from inflows into lakes in, for example, the granitic, acid-rain sensitive areas of Adger and Telemark, southern Norway, as being inappreciative of the role played by phosphorus in maintaining the fish populations that they continue to lose through strong-acid precipitation (Henriksen, Lien & Traaen 1990).

Time-scales of P-capacity reduction: the “internal load” problem.

Supposing that restoration of a water body by the reduction of phosphorus-determined capacity is both desirable and technically feasible, some preconception of the extent and rate of recovery is desirable. While the explicit assumption of the Vollenweider–OECD regression is an output in terms of an average crop maintenance for a (continuous) supply of nutrients, there is an implicit assumption that the primary product-yield will be simultaneously eliminated, together with any unused resource, either down an outflow, or through consumption by higher
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trophic levels or, eventually, as a residual net particulate flux to the permanent (and usually chronostratigraphic) lake sediment. Several processes, both positive and negative, contribute to a net flux which, on balance over a period of time, is in the direction of sedimentary recruitment. Were this not so, it would have been more difficult than it has been to interpret past limnological environments from the contemporaneous stratigraphic variations in the chemistry of the sediment. The problem for the water manager is to anticipate the establishment of a new balance after one of the components in the current exchanges of phosphorus across the sediment–water interface is abruptly altered.

The topic is a large one with a substantial history of study (Einsele 1936, 1938; Mortimer 1941, 1942; Kamp-Nielsen 1974, 1975; Boström, Jansson & Forsberg 1982; Baccini 1985). Any attempt to emulate the recent review by Boström et al. (1988) is inappropriate here, although it is helpful to summarise the main fractions of sedimentary phosphorus, their solvency and the circumstances of their liberation into open water (see Fig. 10). Between-lake differences in behaviour reflect differences in loading, composition and retentiveness of the sedimentary phosphates and opportunities for their mobilisation. The nature of the binding to sedimentary particles is also relevant to post-restoration behaviour. The low total phosphorus content of sediments in oligotrophic lakes is dominated by refractory organic species, while the HCl-extractable (i.e calcium-bound) phosphorus of sediments in calcareous lakes provides a good buffer against subsequent internal loading. Elsewhere, in highly eutrophic lakes, the binding capacity may have been saturated, so that the pool of labile and loosely-bound (NH₄Cl-

<table>
<thead>
<tr>
<th>INPUT TO SEDIMENT</th>
<th>RELATIVE BINDING CAPACITY</th>
<th>RETURN TO WATER</th>
</tr>
</thead>
<tbody>
<tr>
<td>External phosphorus minerals</td>
<td>NH₄-extractable</td>
<td>desorption</td>
</tr>
<tr>
<td>Adsorbed/coprecipitated with Fe/Mn</td>
<td>labile and loose-bound</td>
<td>dissolution</td>
</tr>
<tr>
<td>clayoxhydride</td>
<td>NaOH-extractable</td>
<td>ligand exchange</td>
</tr>
<tr>
<td>carbonate</td>
<td>loosely-or ligand-bound</td>
<td></td>
</tr>
<tr>
<td>Biogenic particulate P</td>
<td>HCl-extractable</td>
<td>mineralisation</td>
</tr>
<tr>
<td></td>
<td>Citrate dithionate-extractable</td>
<td>hydrolysis</td>
</tr>
<tr>
<td></td>
<td>residue</td>
<td>release</td>
</tr>
<tr>
<td>Direct uptake by bottom-dwelling algae/bacteria</td>
<td>loose- or ligand bound</td>
<td>transport</td>
</tr>
<tr>
<td>Direct adsorption onto sediment</td>
<td>labile</td>
<td>dissolution</td>
</tr>
</tbody>
</table>

Figure 10. Scheme to show sources of phosphorus input to lake sediments, their internal binding (according to analytical sensitivity) and the method by which phosphorus is given up to the water. Dominant sources, binding ability and release will obviously vary from lake to lake but the table has been arranged to provide a tentative guide to the interrelationships.
extractable) phosphorus is readily mobilised. The mobility of NaOH-extractable phosphorus, supposed to correspond to redox-sensitive, ligand-exchangeable iron-, manganese- and aluminium- bound phosphorus, is sensitive to redox potential and (e.g.) the Fe\(^{2+}\) $\leftrightarrow$ Fe\(^{3+}\) transformation.

The circumstances of phosphorus "release" from the sediments can be attributable to both chemical and mechanical processes. Besides the water–sediment gradients (Kamp-Nielsen 1974), chemical mobilisation is especially influenced by microbial activity (directly and indirectly), so it is sensitive to temperature, pH and redox potential. With lowered redox (<200 mV), the use of alternative electron-acceptors in organic mineralisation leads to the presence of reduced products (such as H\(_2\)S, CH\(_4\)) affecting phosphorus cycling. The reduction of Fe\(^{3+}\) to Fe\(^{2+}\), for example, will return associated phosphorus to limnetic solution. Other limnochemical transformations influence the outcome (see Boström et al. 1988, for references); thus, although much of the phosphorus will coprecipitate with the iron re-oxidised to Fe\(^{3+}\) in the oxic part of the water column, some of the residual phosphorus may well be available to support renewed primary or microbial production (Golterman, Bakels & Jakobs-Möglín 1969).

This classical view of phosphorus recycling as a series of chemical redox reactions is widely held to be the major internal-load pathway. However, certain types of lake may rely extensively on hydromechanical factors (organism transport and sediment resuspension) to effect any kind of recycle. For instance, Boström et al. (1988) concluded that the migration into the water-column of bottom-dwelling cyanobacteria (e.g. overwintering *Microcystis*) moves significant loads of intracellular nitrogen and phosphorus out of the sediment. Additional evidence that mechanical disturbance by burrowing animals and spawning fish can return significant quantities of phosphorus to solution (Petr 1977) must be balanced against claims that simultaneously raising the redox potential and resuspending new binding capacity will enhance precipitation from the water (Davis, Thurlow & Brewster 1975). Depending upon the fluidity of the sediments, the extent to which the P-bonding capacity is saturated (and, hence, how much phosphorus is dissolved in the interstitial water) and the strength and frequency with

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**Figure 11.** Diagram to show main pathways for phosphorus in lakes, contrasting events in shallow and deep (especially low-redox) regions.
which dissipative energy is transferred, physical resuspension may lead to significant phosphorus releases from shallow margins. Wind-induced turbulent shear, dissipating energy at rates in the range $10^{-6}$ to $10^{-5}$ m$^2$s$^{-3}$, is capable of mixing perhaps the upper 30 mm (Nixon 1988), exceptionally 40 mm (data of Robbins & Edgington 1975), of the superficial sediments. In areal terms, shallow margins can be as important as deep, anoxic basins in phosphorus recycling; clearly, the relative areas may determine which is more important to the lake as a whole. In uniformly shallow waters, physical mixing of oxic sediments is the only such pathway. Certainly there is evidence that highly enriched, shallow waters (Kamp-Nielsen 1975; Osborne & Philips 1978) can develop (Fig. 11) substantial internal loads (up to 50 mg P m$^{-2}$ d$^{-1}$; Boström et al. 1982) to an extent which is sufficient to have countered the effects of external load reductions for long periods (e.g. Norrviken: Ahlgren 1980) or until such time as additional restorative steps were taken (sediment removal at Lake Trummen, Sweden: Björk 1972, 1988; flushing of Veluwemeer, Netherlands: Hosper 1984). For full restoration, the particles and interstitial water associated with the phosphorus-rich stage require to be buried, or rather progressively “diluted out” (see Guinasso & Schink 1975), by the particulate flux and interstitial water of the later, phosphorus-deficient stage. Deeper sediments play little further role in the contemporary exchanges and lake ecologies.

The point is that sediment–water exchanges of phosphorus do not exclusively follow the Einsele–Mortimer model. There is a distinct challenge to resolve a sediment typology which should both account for and predict the relative significance of the various available pathways to an abrupt shift in the overall phosphorus metabolism of a lake or reservoir. This might clarify the criteria for management and restoration objectives. In the case of the frequently disturbed lake with high, unbound nutrient resources derived from proximally diffuse sources, the control of biological capacity might be difficult to achieve by the prescription of tertiary treatment of sewage effluents; alternative approaches are then required.

**Controlling the rate of P-capacity attainment**

The alternative approaches to managing planktonic algae in eutrophic systems depend upon the imposition of a further constraint at a lower threshold which effectively prevents, or delays indefinitely, the expansion of the biomass to its phosphorus-determined capacity. In one of these, the principle is to encourage the consumption of cells faster or no slower than they are produced; the other is to slow down the rate of cell replication by depriving it of sufficient light to saturate its growth requirement.

**Biomanipulation**

Biomanipulation is a term introduced by Shapiro, Lamarra & Lynch (1975). It is increasingly restricted to mean the control of organisms by deliberate adjustment of the abundance of the next trophic level of consuming organisms. A large literature and a great deal of debate have been directed towards this topic. It is inappropriate here to review the relative merits of the “top–down” trophic cascades theory (Carpenter, Kitchell & Hodgson 1985) as opposed to the “bottom–up” resource regulation, implicit in the Vollenweider–OECD model. It is not a case of which theory is correct – there is plenty of good evidence for either mechanism being effective at particular times. On the one hand, the initiation of active populations of secondary-produced herbivore populations cannot occur independently of primary production; on the other hand, the late vernal “clear-water” phase observed in many mesotrophic and eutrophic temperate lakes is often wholly, or in part, attributable to pelagic grazing which proceeds more rapidly than the rate at which food plants replace themselves (Carpenter 1988). Reynolds (1991) suggests that, at equilibrium “top–down” and “bottom–up” effects collapse into one another and become indistinguishable; thus, if one or other process is clearly dominant, it is
symptomatic of a persistent non-steady state. Thus "biomanipulation" is a real and reasonable
objective for controlling certain kinds of (edible) phytoplankton biomass. How to "make it
stable" (Shapiro 1990b) may be illusory compared to "how often" the biology of the latter may
be modified sufficiently to effect long-term practical benefits.

The most convincing demonstrations of lasting control of phytoplankton biomass have come
from small, shallow waters (e.g. Shapiro et al. 1983; Moss 1990 and in this volume). Whereas
in larger, deeper systems, where the zooplankton is more strictly pelagic and extremely
responsive to the abundance and dynamics of the dominant food source (planktonic algae and
bacteria: Ferguson, Thompson & Reynolds 1982; Sommer et al. 1986), the macrophytic
vegetation and the benthic accumulation of organic detritus in the smaller or shallower water-
bodies offer more refuges from predators and alternative food resources. In this way, a stock of
herbivores adequate to control potential algal outbursts may be more plausibly maintained.
Confirmation is required for the developing appreciation that the potential for management of
planktonic algae by biomanipulative techniques may be greater among shallow lakes
(McQueen 1990; Reynolds 1991), especially where nutrient limitation of the algae and tight
regulation of the food chain are demonstrable (Elser & Goldman 1991). It is of interest that the
fish ponds studied by Hrbacek et al. (1961), whose work inspired much of the subsequent
interest in biomanipulation of pelagic systems as a means of managing phytoplankton, actually
conform well to this generic description. At the other extreme, deep, weakly-flushed, enriched
lakes are least likely to succumb to biomanipulative techniques, without (say) a simultaneous
reduction in nutrient loading (Benndorf 1990). More zooplankton grazing only seems likely to
drive the pelagic community towards dominance by self-regulating, grazing-resistant
populations of algae, including cyanobacteria, assuming that their other environmental
requirements are satisfied (Reynolds 1986, 1987c; Sterner 1989).

Physical manipulation

The remaining practical approaches to the control of algal biomass yields, species composition,
and the rate of capacity attainment, have invoked the artificial enhancement of physical
limitations. Methods for extending the period of full isothermal mixing in lakes deep enough to
stratify, either by artificial destratification or by preventing stratification from occurring at all,
have been available for over thirty years (see Irwin, Symons & Roebeck 1969; Dunst et al.
1974; Tolland 1977). The early experiences were perhaps founded upon observations that
naturally-mediated variations in the extent of mixing generally have beneficial effects on the
mass and species composition maintained in the phytoplankton, and a concomitant benefit in
terms of stored water quality (Ridley 1970). Several authors, notably Steel (1972, 1975), have
successfully modelled the quantitative responses and their effects upon maximum carrying
capacity. The species-selection mechanisms have proved more difficult to explain, though
broadly these seem to result in species associations similar to those in equivalent conditions
promoted by natural mechanisms (see Reynolds et al. 1983; Reynolds & Reynolds 1985).
Several of these responses have been imitated, on a pilot-scale, in the mesocosmic enclosures
in Blelham Tarn (Reynolds, Wiseman & Clarke 1984; Reynolds 1986) and analysed in detail
(Reynolds 1983a, b, 1984b, 1989c). Moreover, the responses appear to have plausible
physiological explanations, in terms of strategic adaptations (Reynolds 1989c, 1992a; Dauta et
al. 1990).

The arguments in favour of exploiting the dominance of physical factors in the dynamic
behaviour of phytoplankton, as a practical management tool, have again been advocated by
Reynolds (1992a): provided sufficiently abrupt alternatives in the physical environment can be
effected and then maintained, a water column can be managed in a way which might favour the
smaller, nanoplanktonic and edible species, of the desmid-diatom-Oscillatoria associations of
well-mixed but increasingly light-deficient columns, and resisting for as long as possible the development of large nuisance populations of (e.g.) bloom-forming blue-green algae.

There is a danger of embracing any advocated method as a catch-all solution to the problem of eutrophication management. Artificial mixing is no more a panacea than is biomanipulation; it will not be successful in every circumstance. There is little to be gained, for instance, from destratifying a 5-m lake which habitually stratified at about 4m. If it were 10 m deep, destratification need not produce much change if the water column is generally clear. Moreover, constant mixing of even a deep reservoir may well successfully exclude (say) Microcystis but it may nevertheless promote large populations of diatoms, to the capacity predicted by Steel (1972). This need not be a problem if the diatom crops are preferred to the blue-green algae but it must be understood that artificial mixing does not obviate algae per se! Further, prolonged mixing would be expected to lead ultimately to Oscillatoria dominance (Reynolds 1989b): that it has not done so in the case of the routinely destratified Thames Valley reservoirs (Toms 1987) may be a function of their short retention times (Reynolds 1992c); a combination of destratification with 10 – 30 day retention times may be decisive.

In cases of excessive build-up of (say) diatoms and Oscillatoria it might be possible to consider one further technique, which is to destratify intermittently. Stopping artificial mixing might permit rapid stabilization of the water column, loss of diatoms from suspension and selection, initially, in favour of small, fast-growing nanoplankton. Conversely, mixing should be reimposed only after sufficient time had been allowed for a reduction of the earlier mixing-tolerant population to take place, but at the same time allowing the production of only a generation or two of the bloom-forming species. A cycle based on 2–3 in situ generation times (probably 7–14 days) would seem to be, in theory, an optimum period for a UK reservoir (see also data of Trimbee & Harris 1983).

Discussion

The ability to manage the quality of water in lakes and reservoirs depends upon an understanding of the underlying processes. By adopting a regression equation describing large-scale behaviour and using it as a basis for intervention with, essentially, large-scale counter-measures, the present attitudes to quality management tend to be correspondingly coarse and stochastic in their effects. This review is critical of three such attitudes, implicit in recent approaches to the eutrophication question.

1. That phosphorus is regarded as a pollutant when it is a non-toxic life-supporting but scarce element which happens to be typically in chronically short supply. Cultural eutrophication is the oversupply of the element, the biological over-growth that may be promoted and which is prejudicial to the structure and health of the aquatic ecosystems so affected.

2. That supported biomass responds smoothly and proportionately to increase or decrease in phosphorus loading when it manifestly acts in stepwise fashion; since phosphorus “limits” only when it is exhausted, a change may or may not alter the actual carrying capacity. While the biomass is within capacity, there is no ecological dependence upon the rate of phosphorus uptake, nor upon the ratio of phosphorus to another saturating element.

3. That the reduction of phosphorus will have an immediate result on abundance or species composition, unless phosphorus is already continuously limiting. Phosphorus reduction, if feasible imposes a lowered capacity and, if appropriate, one which will act before the present crop sizes are achieved and do so for longer. On the other hand, if reduction is difficult to achieve, is inadequate or is offset by internal resilience, other management techniques may be needed.
Assiduous students of the literature will recognise that these points have been made before (Björk 1973; Harris 1980). There is no reason to believe that these strictures will be any more readily embraced this time. The suggestion may be made that a new scheme for lake management is required which recognises the individuality of lakes and their particular sensitivities. The diagram in Figure 12 is intended as a qualitative word model or decision tree, which might form the basis of a quantitative and deterministic approach to lake management. In a sense, this sort of scheme is already achievable, through the application of general behaviour models (e.g. of P-determined or light-determined carrying capacity) to operate the option switches. The outcome, however, would prescribe the “probable best approach” rather than entreat on “how much phosphorus must be removed”. The further contributions in this symposium volume will assist in bringing the necessary quantitative resolution to Figure 12 and, in any case, give an enhanced understanding for the future management of freshwater ecosystems.

Figure 12. Provisional “decision tree” for lake restoration and management. Each of the boxes requires to be quantified and no option is exclusive. Future research might usefully concentrate upon the refinement of this approach and its application.

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