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Modelling phytoplankton dynamics and its application to lake management

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Abstract

Conceptual models assist the understanding of complex, multivariate problems. Management models should offer reliable predictions of the outcome of alternative approaches to problems which assist the manager to decide the optimal course of action. It is rare for one model to fulfil both purposes. Excessive phytoplankton production in lakes, reservoirs and rivers presents, at best, a potentially conspicuous detraction from water quality or, at worst, a lethal cocktail which must be excluded from recreational waters and potable supplies. Thus, the difficulties may relate as much to the type of organisms present and to the problems they may cause as they do to the biomass that may be achieved. Examples will be cited of some particular problems of lake and reservoir management that have been confronted in recent years. The range of model solutions available to plankton biologists is reviewed. The philosophies of these are unsympathetic to specific management problems; the models are shown to be unhelpful and potentially misleading in the context of the questions usually asked. Even when quite general questions are submitted to generalised models, imprecision can lead to erroneous judgements. Approaches to making much more process-based models and expert systems are advocated. The ability to identify and quantify the principal regulatory processes in operation, including the effects of light, turbidity and physical mixing and those relating to the trophic structure, is highlighted. Dynamic simulations, based upon the population ecology of several selected species simultaneously can give reasonable fits to observable phenomena. Applying altered model components to simulate viable options can be tested for their likely comparative impacts. A yet more recent approach to modelling lake metabolism is introduced for its potential as a guide to determining management impacts and priorities at particular sites. The objective of the paper is to encourage the development of site-specific functional models which are oriented to both conceptual and management issues. We have to overcome the widespread but naive "my lake is phosphorus-limited" syndrome if we are to learn how to better manage our standing waters.

Introduction

There can have been few periods in the past when public interest in the United Kingdom over the management of the nation's water resources was more acute. Popular concern over health-related aspects of recreational water and the quality of product delivered to the tap is expressed frequently. In the past, quality of water was a matter for the engineers – to design and operate purification plants to the capacity of the water to be supplied and against the magnitiude of the defilement of the raw resource that nature might throw at them. Meanwhile, the academics continued to bolster their applications for grant-aid with the justification that their research 'would benefit the water industry', even if nobody was quite sure how or, if it were true, how the technology could be passed on. Then water became a matter for the accountants, who identified 'efficiency savings' if they could reduce the scale of treatment problems, and for the public relations representatives whose job is to assure the wider public that the toxic cyanobacterial scums that kill their dogs cannot possibly affect the water drawn from the kitchen tap, even if both come from the same reservoir. Over the last 5 years or so, there has been an explosion of interest in the causes of poor quality of raw source waters in lakes and reservoirs and how these might be overcome or avoided in the first place. At the very time that ecology was set to figure more prominently in management, the corresponding efficiency drive within the academic community had, by then, depleted its knowledge base and eroded its core capability so far that qualified advice has been in short supply and even that is perceived to be expensive.

It is against this background that the urgent need for managers and academics to evolve ecologically based strategies for the management of lakes and reservoirs should be approached. They need to understand each other's problems and they have to talk in the same language (This is so self-evident to need saying!). The widespread availability and power of the personal computer provide the vital bridge between those who think they know what happens and those who wish to monitor and regulate it appropriately: 'can we make a model of that?'. A well-developed artificial intelligence is surely the best assistance to the manager on a day-to-day basis, provided that it is robustly based and the extent of its reliability is clearly known. Not only is it uncertain whether these provisions are always met, there is also a further difficulty in applying models if the author's objectives differ significantly from those of the user or if the variance inherent in biological systems is not accommodated.

This paper begins by comparing the probable perceptions about models of their authors and their users, with special reference to phytoplankton growth in source waters. The nature of the specificity of the problems encountered by managers is briefly illustrated by some summarised case histories, while the generalised nature of familiar models are shown to provide little guidance to managers about how the problems might be overcome. The paper goes on to advocate models which are dynamically based and driven by components whose worth is strongly site-sensitive. Some recent models which have adopted this approach are reviewed and are suggested to hold great promise for managers in the near future.

What do we want from models?

The ability to make a mathematical model which simulates a natural system or process is a measure of the modeller's understanding of that system. Nowadays, however, models are popularly equated with computer outputs. Certainly, the power of the modern PC allows models to be quickly assembled, run and rejected. The last is important, for the power of a modern PC also exceeds, often considerably, the wisdom of the operator, to the extent that the simulation of any but the simplest responses of selected aquatic biota to a single stimulus can scarcely represent the almost infinite and stochastic variability of the fluid, three-dimensional environment. How this issue is resolved is greatly influenced by what is wanted from the model. Among reservoir managers, for instance, there is a strong desire for site-specific models which will process relevant information about the condition of the system and a few key inputs to yield a probabilistic prediction of events. The black box of internal processes is acknowledged to be complicated and to be within the province of the physiological ecologist. In order to be able to generate the appropriate algorithms, however, the ecologist may follow one of two further approaches: either to probe exhaustively the relevant internal workings, component by component, and then build simulations of component functions; or to predict the broad function of the box by analysis of the outputs of a statistically significant number of such boxes in other systems. These limitations are quite familiar to modellers, as the three approaches correspond to Levins' (1966) classification of model-building strategies. The first is a Type-I model, that simulates so far as it can the precise inputs and responses, but loses general applicability. The second has the Type-II attribute of limited inputs to isolated processes which do not yield real-world solutions. Providing its generalism through breadth rather than precision, the third is a Type-III approach.

While there is no fundamental reason why approaches should not be combined, case studies tend not to have done so: there is still a hiatus between the requirements of the manager and the instinctive guardedness of the scientist's predictions. The latter's desire to support concepts and hypotheses is culturally different from the manager's desire for precision and reliability. In the next two sections, an overview of the types of problem with which managers and regulators have to deal is contrasted with the range of main-stream, empiricised conceptual models on offer. To protect commercial confidentialities, however, real names have largely been omitted.

Problems with phytoplankton

Planktonic autotrophs are essential to the function of pelagic (open water) ecosystems. Their production sustains the base of the pelagic food webs, usually culminating in fish; and, in contributing a net oxygen flux into the system, the photosynthetic gas exchanges normally aerate the surface waters. It is also wellunderstood that the production is often seasonally regulated, mostly through the interaction of temperature and the aggregate underwater photoperiod (as modelled by Reynolds, 1989). Its biomass accumulates accordingly, up to limits broadly related to the supply of inorganic nutrients and to the extent of consumption by planktonic animals.

Most (but by no means all) of the problems associated with phytoplankton arise from the biomass it is or may be able to achieve. As hinted above, the planktonic biomass that forms in storage reservoirs has to be removed in treatment for potability, at a cost representing a substantial (25–35%) fraction of the price of the delivered product (OFWAT, 1994). Elsewhere, public reaction to green-coloured amenity waters ranges from disquiet to hostility, fuelling demands for corrective action. The decomposition of accreting algal products in the deep waters of lakes not only leads to anoxia and low redox dissolution of metal–phosphate complexes but simultaneously reduces habitat tenability to cold-water demersal salmonid fish (Baroudy & Elliott, 1994), as has been infamously demonstrated in the case of the Windermere charr (see Elliott & Reynolds, 1996). Where progressive nutrient enrichment appears to be the cause of the consequentially additional plant production (together the qualification for the term ‘eutrophication’ (Rohlich, 1969; Vollenweider, 1968)), managers need to know whether proposed corrective action is likely to be effective. Other frequent questions relate to waters already enriched and known to be supportive of potentially high phytoplankton crops: ‘what feasible alternative methods for retarding plankton production would be most cost-effective?; ‘were I to modify an existing impoundment or create a new one, what problems can I anticipate and could I design out?’. Models have also been sought in respect of proposed coastal barrages and for which the statutory impact assessments must include: ‘what kind of problems will phytoplankton cause us, and how might we mitigate them?’.

As often as not, the questions relate to likely species composition, for it is increasingly acknowledged that all planktonic algae do not equal all other planktonic algae and certainly not so in the extent of the nuisance they may create. Odour-, flavour-, slime- and foam-production are traits which vary specifically. In water-treatment processes assembled around flocculation and upward-flow filtration, instances of penetration by planktonic cyanobacteria are a familiar headache; large populations in the raw water may well lead to very serious filtration difficulties and plant shut-down, if their intake into the works cannot be reduced. Not surprisingly, the industry seeks scientific guidance when it asks ‘how can we avoid having these species?’. Since the summer of 1989, when the capacity of certain species of cyanobacteria to form surface scums and to produce acutely toxic microcystins and anatoxins was at last taken seriously in the UK (NRA, 1990), the question has become more pressing. Both suppliers and regulators are anxious to have models that will identify waters that are or will become susceptible to phases of cyanobacterial abundance, that will predict the onset of bloom conditions and that can evaluate alternative control strategies.

Current model availability

If the expectations of models are so clear, is it not then a simple matter for science to satisfy them? Well, no. So far as scientists are concerned, they might be dubbed ‘the wrong kind of questions’. The tried and tested models currently used by plankton scientists are generalised, based on the mathematical fit (or conformity to an empirical behaviour) of collected data to a long-range behaviour. They come up either with Type-III probabilistic solutions with predictable margins of variability (which those used to dealing with precision judge to be ‘chaos’) or with Type-II outcomes that are insensitive to other attributes. Both are fundamentally inappropriate to the Type-I problems rehearsed above. Even where the problem raised is a general one: ‘at what kinds of site will we be liable to problems with plankton algae?’ – the solutions are reluctant and wrapped in so many caveats that they cannot be proved wrong under any circumstance. Indeed, a weakness in the conceptual basis of some of these models is often exposed.

It was not within the scope of my brief to review the structure and predictive reliability of all the models available. Besides, such a thankless and rapidly outdatable exercise has recently been undertaken by Jørgensen (1995) and it would be difficult to surpass the authority of either his overview or his critiques. It is interesting that he should comment that models which seek generality in application and precision in prediction are so complex that they cannot be supplied with all the data to drive them and that anything approaching an attestable simulation of a particular site requires complete re-evaluation of the interaction of the variables at the next site. I take this to mean that our systems models are too inflexible to accommodate the fact that no two sites function in the same way. So far as this essay is concerned, I take a few, central model tenets and question the validity of their application to the main issues of management issues. Later, I shall seek to show how they might yet contribute through new approaches to common management problems.

The principal general models relating to the ecology and dynamics of phytoplankton are directed towards describing (note, not necessarily predicting) how much plankton biomasss lakes support, how quickly they can furnish it and what kinds of algae are present. There is no great mismatch there with the manager's questions: why should it then be inappropriate to apply the one to the other? Let us look at each of these approaches, beginning with the question, how much will be produced?

Capacity models

Plants of the plankton need light and carbon dioxide to photosynthesise every bit as much as do plants on land. Moreover, photosynthetic rate *(P)* is relatively easy to measure by gas-exchange and, between 1950 and 1965, a great many data relating to the photosynthetic productivity of phytoplankton were amassed. It was very clear that the productivity of the biomass *(P/B)* related first to the availability of underwater downwelling light energy (*I*). There has been great interest in the solution of the *P/I* relationship and thus to the calculation of the maximum light-supportable biomass, $B(I)_{\mathrm{max}}$. Solutions of Talling (1957) and Vollenweider (1965) are just as valid 30 years on but experience has shown that, although pelagic plant biomass scarcely exceeds the predicted capacity, it is also rarely attained – other factors intervene. Even when the physical conditions allow, the production reaches a ceiling imposed by the supply of carbon or the availability of nutrients. By coincidence, concerns about the impacts of eutrophication were then running high: during the next decade and a half (1965–1980), attention switched quickly to the biomass yields of available nutrients. The work of Vollenweider (1968; 1976), especially, established the statistically robust linkage between the average phytoplankton biomass supported in lakes, $B(P)_{\mathrm{mean}}$ and the morphometry- and flow-weighted phosphorus loads, $\Delta(P)$ (Vollenweider & Kerekes, 1980). Because few other elements in lakes exercise this critical control or because shortages of other elements are inexclusive in their biological limitation (e.g., nitrogen, silicon), phosphorus has tended to be regarded as the critical factor in the level of biomass supported. Among lakes where all the free phosphate is consumed, the maximum biomass, $B(P)_{\mathrm{max}}$, has been shown to be a predictable function of the soluble fraction of the element supplied (Reynolds, 1992).

By itself, neither approach has much relevance to the manager. Either will confirm what he knows already – the capacity to produce too much phytoplankton is there – but can give him no more than the imprecise idea that if he could reduce substantially the light dose or the phosphorus load he should have less biomass on average, but he still does not know when or how often it will be troublesome. Neither will the regression tell him by how much the loading should be reduced. His position is analogous to the student of social trends who is trying to forecast the number of houses that will be built in a year from the number of bricks that are supplied to the builders. One may assume that builders do not stockpile reserves of bricks indefinitely and that, realistically, such a rough, Type-III correlation exists but it makes no allowance for land availability, labour, weather – all of which could influence the outcome and, at times, be more critical to production than the number of bricks. How much must the brick supply be reduced before the number of houses built is a continuous function of the brick supply?

Rate models

The question of how quickly plankton biomass can be recruited to and lost from the open water has been addressed in a variety of modelling approaches, each based on aspects of the investigations into the population dynamics of phytoplankton, which became fashionable in the mid- to late-seventies. Topics explored experimentally and resolved by mathematical equations included: the relationship between *in-situ* growth rates and photosynthesis (see Forsberg, 1984; Peterson, 1978); that between the rates of nutrient uptake by plankton and the concentrations available, founded essentially on the insights of Dugdale (1967) and of Droop (1973); and the rates at which plankton is lost to settlement and to grazers (Reynolds et al., 1982). The difficulty here is that the controlling conditions are not faithfully reproduced by those who wish to apply the models or for how long the relationships might apply. It can be easily demonstrated that the capacities for photosynthetic carbon fixation and nutrient uptake far exceed the rates of cell replication, unless substantially reduced to the point where it can be shown that the cell replication rate depends exclusively upon the flux of one or other of the resources (Reynolds, 1994). Without the satisfaction of this condition, none of the widely embraced concepts about the growth of populations being either light- or nutrient-limited actually hold. Something else, usually the time that is required to assemble the raw materials at that temperature, determines the rate of growth. In this way Type-II models of single processes do not assist the manager until he knows that the control is operative. To return to the house-building analogy, we are trying to gauge the rate of completions from the number of bricks actually on site. The Dugdale/Droop formulation recognises that deliveries of bricks determine that the number of bricks on site fluctuates with time but the prudent builder ensures a frequency of supply that maintains a sufficient stock to meet his anticipated needs. Burmaster's (1979) theory that the completion of houses and the supply of bricks achieve equivalence is also honoured. However, the rate of completion is not determined by the number of bricks on site (as suggested by the Droop model), until the supply to the site is slower than they are being incorporated into new houses. Neither is their erection halted until the stockpile is exhausted.

Composition models

There is, as yet, no tradition underpinning the philosophy of species selection: Shapiro (1990) was still able to argue the relative merits of a dozen factors claimed to be crucial to the dominance of plankton assemblages by just one group of cyanobacterial genera. The most prominent assumption is the Darwinian one of continuous competition among species and the selection of the best adapted. Within this context, Tilman's (e.g. 1982) resource-based competition model is the most influential and is founded on data from experiments with planktonic algae (Tilman & Kilham, 1976). In essence, this showed that the supply of nutrients that would impose the control of growth rate was not the same for all species and, thus, it was possible to nominate concentrations at which one species was nutrient-limited and another not. He further showed that this applied to algal growth against other nutrients and he contrived experiments with two algae at different concentrations of two resources. There were combinations at which one would grow faster than the other but others where the relative growth rates were reversed. Most interesting of all, he could generate combinations wherein the species co-existed because one was limited by the first resource and the other was simultaneously limited by the second. Hence, adjustment of the ratio between the two resources allows one to escape its constraint and, thus, to select for its dominance.

One popular deduction is that the ratio between nutrient resources (N:P is a great favourite) determines the outcome of 'competition' between different types of phytoplankton, (for instance, cyanobacteria versus other, eukaryotic genera), though rarely with any regard for the Tilman–Kilham condition that both elements are simultaneously limiting or with any recognition of the rates of replication achieved by either. The spuriousness of models embracing resource ratios as determinants of competitive outcome can be shown up by returning, yet again to the house-building analogy. What we are now saying is that there are two kinds of house, both using bricks and cement but one design uses a greater percentage of bricks than the other, this latter one using relatively more cement than the first (this is an analogy to 'seventies' thinking!). If one is short of cement, one should build the first kind; if bricks are the problem, go for the cement jobs. If both are in short or erratic supply, one can probably manage to build a few of each. But if neither material is limiting the rate of house building, one retains the ability to build both. Moreover, if brick ones can be completed more quickly than cement ones, the probability is that more brick ones than cement ones will have been built, unless cement ones happen to sell faster. The point is that none of these outcomes is ratio driven. Absolute quantities or other factors are always responsible for the differences in completion rates.

The lesson is important – even where the between-species differentiation is more sharply defined than their respective capabilities for uptake of nitrogen and phosphorus (for instance, losses to selective grazing) – species ascendancy and dominance must be modelled on empirical inputs. Many who apply Tilman's resource ratio model forget that it holds only for limiting supplies – growth rate is dependent upon the nutrients concerned. We still need to know how fast one can build houses.

Descriptive models

The fourth kind of model is a complex development of the curve-fitting exercise of Type-I models, essentially based on multiple regression analysis and the identification of the sources of variation. To formulate these, a first-class mathematical modeller is often required. The approach has been used to great and elegant effect: I have great admiration for the mathematical description of the seasonal fluctuations in the concentration of phytoplankton in the River Thames (Whitehead & Hornberger, 1984). Such models are research tools, inso far as they assist investigators to determine the key variables driving a highly variable system. Principal components analysis does this too, while canonical co-variance analysis assists the researcher to compare a number of sites. Without the experience and intuition to interpret the apparent relative influence of the quantified vectors, we are in danger of misunderstanding how they might be applied to management or just how much of what is found out even describes other systems. The model still lacks the generality that the manager requires but the site-to-site adaptation of the methodology would overcome its inflexibility.

Some recent modelling approaches

Lest this account be taken as too critical about models or too despondent about what they can contribute to management, I want to draw attention to some promising results from process-based simulations. Common to these modelling approaches is their initiation with the organismic capability. If it is known what the organism requires to sustain a given performance and it is known quantitatively what the contribution is of each of the various factors in sustaining that performance, then it is possible both to determine which factor is critical and to decide by how much it should be altered to better manage the output. Resorting once more to the problem confronting the social analyst – 'how many houses can be built in the year?' – the basic unit is the time it takes to build one house under the optimal conditions we can contrive. The number of persons engaged in the building is important but there is a point when they restrict each other's activities or when one task awaits the completion of a precursor task, or when they all have to wait for the paint to dry. Let us say that twenty men in fine weather could finish a house in 2 weeks. Then a labour force of one million could build 25000 houses per week. A smaller or larger workforce could build fewer or more, but let us stay with the 25000. Can land be released and prepared at the rate of 1000 ha per week? Do we have the capacity to make enough bricks, quarry enough sand, supply enough of every component to be able to match the production? If not, which is the limiting factor?

In order to determine how sensitive lakes are to cyanobacterial bloom formation and to which standard form of control they might readily respond, the Environment Agency is using a model called PACGAP (Prediction and Assessment of Cyanobacterial Growth and Production). PACGAP has by analogy exactly the above logic. On the basis of its morphometry, thermal structuring, flushing time and nutrient loads, it calculates the supportive capacity of each factor, $B(I)_{\max}$ $B(P)_{\max}$ in turn and finds the lowest. It also requires to know something about the carbon relations and the present levels of algal chlorophyll produced, from which it characterises the habitat as being either often, seasonally or rarely likely to meet the requirements of bloom-forming cyanobacteria.

So far as I am aware, it is tantalisingly accurate in stating what is provable – what the lake supports now. Its predictive powers have not, as yet, been generally verifiable. The routine can be used to experiment with management approaches: running the programme with altered nutrient loads, faster flushing rates, deeper or more frequent mixings allows the operator to judge which strategies for avoiding or eradicating bloom populations might be more successful.

The operating instructions with PACGAP insist that it is a guide and not suitable as the basis for strategic decision making. Yet much the same philosophy lies in the coding of the day-by-day simulations of phytoplankton growth constructed by the PROTECH-family of models. The original PROTEC (Phytoplankton Responses to Environmental Controls) was developed jointly by the Freshwater Biological Association and the former Welsh Water Authority to demonstrate the predictions of the scale and composition of phytoplankton in the proposed Cardiff Bay Barrage. The management questions posed to the modellers were clear enough – 'will we have algal growth?' 'how much?' 'when?' 'will they form blooms?' The programme, like the long-hand predictions, considered how fast different species would grow in situ, for given light and nutrient inputs at given temperatures. The model could recalculate the biomass for each of eight species as many as 15 times per hour given the day of the year, the temperature and the rate of riverine input. It was set for the 'worst-case' scenario, everything grew at its fastest sustainable rate, all nutrients from grazed species were instantaneously regenerated, and being eaten or washed into the Bristol Channel were the only mortalities. The high flushing rate in fact kept the algal population down to the few micrograms of chlorophyll per liter that occur in the Taff and Ely rivers but in dry weather, the nutrient richness would favour the very rapid growth of small green algae, which would increase biomass sharply to the light capacity until a growing zooplankton, responding to the food resource, caught up sufficiently to clear algae faster than they could be recruited. Prolonged low flows were predicted to lead to *Oscillatoria* dominance at populations of over 100 μg chlorophyll 1^{-1} which flushing but not grazers could remove. However, not even the prediction that *Microcystis* was unlikely ever to grow in the lake, even were it the only species, would cheer up the sponsors: ‘how do we know we can believe it?’. In fact, the model’s authenticity was handsomely displayed when tested on a dataset for the periodically well-flushed, shallow coastal lagoon, Slapton Ley: it was substantially correct in the scale of biomass supported, its periodicity and in its summer dominance of *Peridinium* and *Anabaena* (FBA, 1989).

PROTEC P was a direct and rather more sophisticated development of the flushed lagoon. It concentrated on better descriptions of in-lake properties, and included more variables, which extended its suitability to lakes and reservoirs whose retention times are in the order of months rather than days. The structure of this model and its operation were described by Hilton *et al.* (1992).

Two lessons about real lakes with longer retention times were reinforced: settling becomes a dominant process and internal nutrient recycling assumes major metabolic importance. The next variant to be developed became known as PROTECH2 to acknowledge that ‘C’ now meant ‘CHange’ and ‘2’ refers to a second, vertical dimension. For this is a multi-layered model, inspired by the physical model DYRESM (Imberger & Patterson, 1981), which not only allows integration and separation of water mixing or stratifying according to the interaction of wind-forcing and buoyancy but also lets algae sink, float or swim according to their specific abilities. The model is used exclusively by the EA to predict the onset of bloom conditions in lakes and reservoirs. Finally, some preliminary work has been undertaken which simulates the accumulation and diagenesis of sedimentary material and under appropriate shear conditions will resuspend and redisperse the sedimented material and the nutrients leached therefrom. It is possible that these two additional features will bring still greater authenticity to these simulation models and greater confidence in their sensitivity to alterations in basin management.

Other bottom-up process models of phytoplankton have been in use for some time. That of Jiménez Montealegre et al. (1995) simulates the growth of one cyanobacterium in a shallow lake system. Steel’s dynamic simulations have been evolved carefully and in their latest form (Steel, 1995; Steel & Duncan, 1999) tackle complex issues like light-adaptation of populations. Like the *Oscillatoria* model and many other previous modelling attempts, Steel begins further still towards the bottom with algal photosynthesis and nutrient uptake. Selection is incorporated by reference to typical properties of phylogenetic representatives. The model is easy to use and apply and produces its predictions as plots developing before the operator’s eyes. It also makes it easy to vary inputs and re-run with altered scenarios.

Lastly, I draw attention to a first water-quality management model for Windermere. This is not directly concerned with what will grow so much as when the growth of certain organisms (or the consequences thereof) will become, or cease to be, a nuisance in the lake. The villain here is sewage-derived phosphorus and, over 30 years, it has led to a steady eutrophication of the lake’s South Basin. From a careful analysis of 50 years’ data on the lake, the phosphorus supply was computed. The fate of this load has been reconstructed from the database. It is then assumed that all the residual, assimilable phosphorus generates phytoplankton carbon in strict stoichiometric ratio, this carbon being then allocated to sediment and outflow. That which sediments consumes hypolimnetic oxygen in the stoichiometric ratio. Thus, a given phosphorus load will generate a prediction of the degree of hypolimnetic oxygen tension, the effect on fish survival and breeding success, and the potential to support bloom-forming cyanobacteria. This model is fully authenticated by the historical data which confirm where in the eutrophication of the lake, each of these symptoms developed. Happily, as the restoration proceeds, the symptoms are disappearing pretty well as the model provides (unpublished reports to North West Water Ltd and the NRA North West Region).

Conclusion

This brief tour of the types of models of phytoplankton dynamics that have been developed by ecologists finds that they have not proved to be astonishingly helpful to managers with specific problems. This owes most to the philosophy of generalisation of the models and the natural reluctance of scientists to sacrifice accuracy of prediction in responding to a problem of precision. However, the power of computers opens the way to more elaborate process models which build up scenarios in the same way that natural phytoplankton populations develop in the waters we seek to manage: from modest inocula and within the constraints set by the capacities of the environmental factors. Similar models will be useful in helping all of us to improve our perception of the dynamic structure of lake ecosystems on a site-by-site basis. This is essential to proper management of lakes and reservoirs. We simply have to overcome the naive and erroneous 'my-lake-is-phosphorus-limited' syndrome which has so distracted our progress in phytoplankton ecology.

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