

## MODELLING THE DYNAMICS OF PHYTOPLANKTON WITH THE NEEDS OF THE END USER IN MIND

COLIN REYNOLDS, ALEX ELLIOTT  
AND TONY IRISH

<sup>1</sup>Prof. C.S. Reynolds, <sup>2</sup>Dr J.A. Elliott and Dr A.E. Irish,  
Algal Modelling Unit, Centre for Ecology and Hydrology Windermere,  
Far Sawrey, Ambleside, Cumbria, LA22 0LP, UK

### Introduction

Phytoplankton plays an important role in the primary biological production and the flow of energy and matter in open-water systems and increases in relative importance with the depth and size of the water body. However, in many waters, the excessive production and sustainable biomass of planktic algae is seen as undesirable. To those responsible for managing reservoirs, from the standpoint of being able to deliver abundant high-quality water to consumers, phytoplankton is simply an impurity that must be removed from the final product, at the lowest economic cost. It has, for a long time, been implicit that this task is eased if the plankton biomass is small. Storage reservoirs in upland areas of high rainfall are generally poor in the nutrients that support producer biomass. This is just one of several reasons why water suppliers prize their upland water sources. However, in lowland areas, wherein demand is usually great and where rivers represent the main exploitable resource, the proximal water is generally rather richer in dissolved nutrients and, once impounded in a reservoir, has the potential to support very large populations of phytoplankton. Such problems were experienced and catalogued by the scientists of the former Metropolitan Water Board (Ridley 1970; Steel 1976). This was the statutory supplier of drinking water to London and its surrounding area – around one fifth of the residents of the United Kingdom – but whose principal sources of raw water were the Thames and Lea rivers, both hugely enriched by the treated wastes of upstream towns. How to regulate phytoplankton growth in a series of London reservoirs has continued to occupy managers and strategists for some fifty years or so, now, and mathematical models have always featured in their design and operational constraints (see Steel 1972; Steel & Duncan 1999). In recent years, rather more sophisticated simulation models have begun to be available and these, ideally, purport to

---

Current address: 1. 18 Applerigg, Kendal, Cumbria LA9 6EA, UK. Email: csr@ceh.ac.uk  
2. Centre for Ecology and Hydrology Lancaster, Lancaster Environment Centre, Library Avenue, Bailrigg, Lancaster LA1 4AP, UK. Email: alexe@ceh.ac.uk

provide the manager with improved forecasting of plankton blooms, the likely species and the sort of decision support that might permit management choices to be selected with increased confidence.

This account describes the adaptation and application of one such model, PROTECH (Phytoplankton Responses To Environmental CHange) to the problems of plankton growth in reservoirs. The model itself has been described in detail elsewhere (Reynolds et al. 2001), and the verification, validation and sensitivity testing have also been presented already (Elliott et al. 1999a, b, 2000). This article also supposes no background knowledge of the main algal types; neither does it attempt to catalogue the problems that their abundance may cause in lakes and reservoirs. For further information, the reader is referred to Ridley (1970), Steel (1972) or to Reynolds (1984, 1999).

### The biological basis of PROTECH

Like other models, PROTECH is based on the belief that it is possible to make realistic estimates of the rates of change of phytoplankton populations in the water, provided that sufficient information about the controlling conditions is furnished. PROTECH differs from all other models (so far as we know) in adopting the idea that planktic algae will grow as fast as they can within the defined conditions and that, thus, the exercise is to model the subtractions from a maximum performance, rather than the synthetic assembly of reconstructed rate-limited growth. Hitherto, many workers have pointed out, correctly, that they cannot measure how fast most algae can grow in their natural environments. PROTECH makes the assumption that they do not exceed the maximal performances under controlled laboratory conditions where the temperature-specific growth rates and their sensitivity to light intensity, photoperiod and resource supply are readily and consistently measurable for species after species. Using data sets assembled at Windermere, Reynolds (1989) was able to fit robust equations to describe (i) the growth rates of phytoplankton at 20 °C under conditions of continuous saturating irradiance and nutrient supply, (ii) the sensitivity of growth rate to altered temperature, and (iii) the sensitivity of growth rate to altered light intensity, each as a function of the size and shape of the algae (surface area, volume, maximum linear dimension). In combination, these equations yield simulated in-situ growth rates that were verifiable against data on natural populations raised in the large limnetic enclosures that were maintained and operated in Blelham Tarn for many years (see Lund & Reynolds 1982). The same three equations remain at the heart of PROTECH, generating instantaneous values of the potential of algae to increase their mass under the physical conditions obtaining.

In nature, this growth potential is not realised because natural populations are subject to displacement in water exchanges, or through settlement, or they are consumed by herbivorous zooplankton. PROTECH adopts terms, also assembled from the experimental investigation of species-specific loss rates in the Blelham Enclosures (Reynolds et al. 1982). The dependence of species-specific loss rates on the interaction of sinking rates and mixing depth, and on algal size in relation to the ingestion rates of finite populations of zooplankton filtering predictable quantities of water, are similarly incorporated into the biomass-removal modules of PROTECH simulation runs.

Running through a sequence of subroutines, in respect of each spatial unit (a whole lake, an upper mixed layer or a single 10-cm slice of the lake) for each time-step set (usually one day but smaller timesteps are available), PROTECH will calculate the potential rate of increase of each of up to eight (one version of PROTECH can handle 99 species at once) preselected species. It will also calculate the corresponding rate as limited by each of the introduced environmental constraints. It picks the lowest of these as the nominated maximum increase in specific mass that is sustainable on the basis of the contemporaneous empirical description of the environment. The standing biomass of each species originally introduced is recalculated over the appropriate time step, while the resource depleted and the additional light-absorptive capacity are worked out for the next iteration. However, before that is executed, the biomass of each species is adjusted for losses of formed cells, with respect to the rate of settlement to a deeper layer (or of gains by upward migration) and to rate of removal by the standing crop of filter feeders. Realistically, filtration increases or decreases according to the ability of the food supply to sustain the demands of the grazer to achieve its maximum growth rate or meet its minimum survival demand.

The routines are, in reality, driven by complex limits and conditions (for details, see Reynolds et al. 2001). However, it will be plain that, following a series of time steps, the growth increment and the net recruitment to each species can be tracked as a changing specific standing crop, much in the way that monitoring observations are plotted and with which they are directly comparable. Visual comparison of the simulated changes in standing crop and the original observations make a ready and often convincing validation of the model's ability to model the critical events in the development of phytoplankton populations.

### **The physical background for PROTECH simulations**

The first applications of PROTECH were confined to uniformly mixed, unstratified environments (FBA 1989; Hilton et al. 1992) but most of the

lake and reservoir environments for which simulations are required will be thermally stratified for part or all of the time. As this major segregation of the growth environment influences the distribution and mutual matching of the resources and light energy, it was soon clear that any universally useful model of plankton dynamics would have to accommodate the effects of water movements and their inherent variability.

It had been supposed that it would a relatively simple piece of programming to have taken one of the elegant physical models then emerging and simply write into it the biological provisions of the earlier PROTECH routines. Our experiences were less encouraging, for the physical models were especially hungry for environmental inputs that we and, certainly, most biological monitoring programmes do not measure or retain, including solar energy inputs at the relevant frequency, wind speed and direction, saturation vapour pressure and relative humidity. It became clear that we would have to devise our own, simpler approach to the physical environment but which would still carry sufficient realism and sensitivity to be able to drive the PROTECH model.

PROTECH2 (prepared for the then National Rivers Authority) and PROTECH-C (a rebuilt model with the option of trading in species-specific carbon instead of chlorophyll, though retaining the original dynamic equations) were each assembled around a one-dimensional view of the water column, divided, upwards from the lake bed, into 10-cm slices. Instead of retaining averages for the entire water body at the end of each iteration – the temperature, the insolation, the concentrations of nutrients and how much of which alga is retained – the stratifying models store the information about each slice. The contents of each layer may then be integrated with those of adjacent layers, compensated for the diminution of slice area and volume with increasing depth, to simulate the entire surface-mixed layer. Else, they may be left intact, when the simulated mixing fails to entrain the layer. The eventuality or resistance to entrainment is determined by two original subroutines. One, based on the Monin-Obukhov equation (see Spigel & Imberger 1987), compares the mechanical energy transferred to the water by wind stress on the surface with the buoyant resistance to penetrative mixing provided by the solar heat flux. These quantities provide an instantaneous estimate of the depth of wind mixing in an otherwise uniform water column. The second subroutine invokes the Wedderburn formulation (Imberger & Hamblin 1982) to refer the estimate to a memory of past events, essentially to determine whether the accumulated resistance of past heating or the residual resistance of a cooling surface layer is sufficient to restrict entrainment. When the energy is sufficient or the resistance too feeble, the subroutine is re-iterated, integrating a layer at a time until stability is once again achieved.

This model has been calibrated in smaller water bodies and has been found to simulate actual observations on the duration and depth of seasonal stratification, intermediate phases of intensification of stratification and episodes of deeper mixing, and the sequence of autumnal destratification. Its practical feature is that it needs no more than the heat income and the wind speed as driving variables. It is even written to calculate the heat income for each day of the year at the given latitude, corrected for cloud cover.

It would be extremely remarkable if this were all that was required to gain valid simulations. Certain relevant assumptions have to be written in to the model that compensate for the fact that it carries no formal terms to calculate evaporative heat loss. That their impact is to keep the water close to the maximum air temperature translates well into a model rule. Nevertheless, it is always necessary to verify the predictions of temperature structure of a water body against observed data in order to determine the basin correction to the Wedderburn calculation.

Predictions of temperature structure based on the above were found to be poorer in large bodies of water, where residual momentum prolongs the exchange of heat in the water column and eddy diffusivity plays a relatively larger role in mixing and entrainment. Relevant equations were devised by Elliott (2000) to simulate tidal mixing in a sea-loch (where salinity and not temperature is the predominant agent of density structure) and these are superimposed in the physical models for PROTECH-M and PROTECH-D (see Table 1). The latter is also most suited to reservoirs subject to deep-water inflows and abstraction points, where jetting and mixing by helixors or by bubble aeration can be simulated (see Lewis et al. 2002; Reynolds et al. 2005, this volume).

### Application of PROTECH models

Although founded upon important experimental work and observations on the dynamics of natural populations of phytoplankton (albeit in carefully managed limnetic enclosures), the original impetus for PROTECH modelling was a commercial requirement to predict the impact on phytoplankton and water quality of the lake to be created by the Cardiff Bay Barrage in south Wales. As with all our applications, commercial confidences are respected and our findings cannot be given in any detail. The purpose of this section is to give a flavour of the sorts of practical problems to which PROTECH has been applied.

The most usual application has been to model impacts of structural (expanding or deepening) or operational (supplemental supplies, destratification strategies) changes to the capacity of reservoirs to support nuisance levels of phytoplankton. Both types of question quickly exposed

Table 1. The PROTECH model family.

PROTEC (H)	Original 0-D phytoplankton simulation, described and validated in FBA (1989); published examples of predictions, Hilton et al. (1992), May et al. (2001). Numerous commercial applications.
PROTECH2	First 1-D translation of PROTECH to accommodate thermal stratification and vertical movements of phytoplankton, commissioned by the National Rivers Authority (1991–93) and now the property of the Environment Agency for internal use.
PROTECH-C	Reconstruction of PROTECH in 1-D, using Monin-Obukhov equation and Wedderburn testing. Has options to work in carbon; also has sediment 'memory', BOD generation and nutrient recycling. Extensively used commercially; but verification, validation, sensitivity and several sets of results are published in the literature (Elliott et al. 1999a, b, 2000, 2001, 2002; Reynolds et al. 2001).
PROTECH-M	Similar to PROTECH-C but designed specifically for estuaries and sealochs where density stratification is influenced as much by salinity as temperature (Elliott 2000; Elliott et al. in review).
PROTECH-D	Being developed as the current standard; as PROTECH-C but with physical environment described by eddy diffusivity. Used commercially, results in preparation for publication.
PROTECH99	A version of PROTECH-D devised to investigate dominance and Shannon diversity in the plankton, with 99 species instead of 8. Successfully executed, paper in preparation.
PROTECH-Z	A version of PROTECH-D devised to differentiate the interactions of several kinds of zooplankton with the food resource – under development.
RIVERPROTECH	PROTECH equations written into a simulation of flowing-water in the River Thames. Specific commercial use only.

the requirement to include the vertical dimension and the depth of mixing that PROTECH-C was able to simulate. The model was particularly successful in assisting the (then) Essex Water Co. to select and specify the operational requirements of intermittent destratifiers to manage water quality in the Hanningfield Reservoir and especially of the production of bloom-forming Cyanobacteria in drier summers (see Simmons 1998). PROTECH-C was used to show the reduction in the phosphorus loads to a series of Anglia Water reservoirs necessary to effect a reduction in the

scale of cyanobacterial blooms experienced. This was shown to be very substantial, given the extent of phosphorus saturation in local riverine raw-water sources. Though facing enrichment problems at the other end of the spectrum, United Utilities or its forebears have supported several investigations of the impact of abstraction and sewage disposal on a series of Cumbrian lakes, notably Ullswater, Hawes Water, Coniston Water, Grasmere and Bassenthwaite Lake.

Other commissions requiring PROTECH-C have been to explain the impacts of reservoir draw-down during dry summers (for Thames Water) and to predict the longer-term impacts of altered climatic conditions on the same reservoir (for the United Kingdom Water Industry Research, UKWIR).

At the time of writing, the applicability of PROTECH-D is still being established. It was first used in the REFLECT<sup>1</sup> project (part of the first EU-sponsored LIFE programme) to provide authentic simulations of plankton variability in Esthwaite Water, England, and in the Swedish Sjön Erken during a sequence of model-projected climate scenarios. Since then, the version has been used in an application to an Australian reservoir and the optimisation of destratification. The most recent use has been to address the challenge provided by the LIFE98 project described in this volume, and to demonstrate how fundamental knowledge and understanding of pelagic processes can be brought to the amelioration of operational problems in the water industry (see Reynolds et al. 2005, this volume).

Although most of the applications have been sponsored commercially for outside clients and agencies, the power of PROTECH models has been exploited to investigate particular research questions. PROTECH99 was written to work with a much expanded 'flora' of seeded species (up to 99, instead of the usual maximum of 8). It is in use to test current ideas about the role and mechanisms of high species diversity against the tendency for competition to exclude the majority at an early stage of community assembly. PROTECH-M was devised by Elliott (2000) to see if the simulations work adequately in the sea. To do this required the incorporation of the effect of salinity into the density calculations and submitting the description of the more robust mixing by wind and tide to calculations of diffusivity. Remarkably, the growth rates of marine phytoplankton are still satisfactorily reconstructed by the original PROTECH equations. Only the thresholds of limitation, by phosphorus, nitrogen and silicon and of the grazing effects of calanoids instead of *Daphnia*, needed adjustment to achieve verifiable simulations of successional sequences. PROTECH-Z is a first attempt to examine the

<sup>1</sup> REFLECT – Response of European Freshwater Lakes to Environmental and Climate Change.

simultaneous responses of different types of freshwater zooplankton to fluctuations in the abundance and composition of the algal foods available.

Finally, RIVERPROTECH has been under development for about four years with the intent of simulating the dynamics of river plankton as it moves downstream. Progress was made only by visualising the passage of a block of water moving downstream but superimposing upon it the effects of variable discharge, turbidity and travel times, as corrected for 'dead-zone' retentivity (see Reynolds 2000). So far, no general model has been created but one specific to the middle-to-lower Thames has been developed, which yields realistic and verifiable simulations of bloom events. The model describes well the growth and downstream recruitment of phytoplankton and their sensitivity to discharge. However, biomass losses in rivers are not well-predicted by the limnetic model, placing serious challenges to our assumptions about the fate of plankton in rivers. We suspect that the most significant sinks are the huge populations of large, filter-feeding bivalves in the bottom mud and to the burrowing larvae of chironomids, although this may be verified only by a formal field and laboratory investigation. Not for the first time, mathematical modelling forces us to review our prejudices and persuades us of the need to look more closely at processes in the real world. Too much of our present understanding is underpinned by unverified and possibly flawed assumptions.

## Conclusions

We trust that this account will have given a general overview of the PROTECH philosophy, of its scientific basis and its potential value to managers and aquatic scientists addressing issues of the behaviour of phytoplankton in environments where they can cause serious or expensive problems. A reliable and responsive simulation is a valuable support to strategic decision making. Getting predictions wrong is of little consequence at the model scale but it becomes extremely costly when you are engineering lakes, reservoirs or river basins. A companion article (Reynolds et al. 2005, this volume) provides a helpful demonstration of the application of a model to a persistent but misinterpreted problem caused by phytoplankton.

We believe PROTECH has many academic as well as commercial applications. It took us almost fifteen years to gain confidence in the quality of the simulations. Now that we feel that this is a confidence that can be shared, we hope that this article may arouse the interest of the reader to delve further into our papers and reports.

### Acknowledgement

This work was part-funded by the European Union LIFE Programme (Project number LIFE98 ENV/UK/000607). We thank Dr Glen George for his encouragement to write this overview and for his supreme confidence in inviting our participation in the LIFE98 programme.

### References

- Elliott, J.A. (2000). *Investigating the assembly of phytoplankton communities with PROTECH*. Ph.D. thesis, Napier University. (unpublished)
- Elliott, J.A., Irish, A.E., Reynolds, C.S. & Tett, P. (1999a). Sensitivity analysis of PROTECH, a new approach to phytoplankton modelling. *Hydrobiologia* **414**, 45-51.
- Elliott, J.A., Reynolds, C.S., Irish, A.E. & Tett, P. (1999b). Exploring the potential of the PROTECH model to investigate phytoplankton community theory. *Hydrobiologia* **414**, 37-43.
- Elliott, J.A., Irish, A.E., Reynolds, C.S. & Tett, P. (2000). Modelling freshwater phytoplankton communities; an exercise in validation. *Ecological Modelling* **128**, 19-26.
- Elliott, J.A., Irish, A.E. & Reynolds, C.S. (2001). The effects of vertical mixing on a phytoplankton community: a modelling approach to the intermediate disturbance hypothesis. *Freshwater Biology* **46**, 1291-1297.
- Elliott, J.A., Irish, A.E. & Reynolds, C.S. (2002). Predicting the spatial dominance of phytoplankton in a light-limited and incompletely mixed water column using the PROTECH model. *Freshwater Biology* **47**, 433-440.
- FBA (1989). *The FBA-Welsh Water simulation of phytoplankton dynamics in flushed systems; authentication in a coastal lagoon*. Freshwater Biological Association, Ambleside (Cyclostyled).
- Hilton, J., Irish, A.E. & Reynolds, C.S. (1992). Active reservoir management: a model solution. In: *Eutrophication: research and application to water supply* (eds D. W. Sutcliffe & J. G. Jones), pp. 185-196. Freshwater Biological Association, Ambleside.
- Imberger, J. & Hamblin, P.F. (1982). Dynamics of lakes, reservoirs and cooling ponds. *Annual Review of Fluid Mechanics* **14**, 153-187.
- Lewis, D.M., Elliott, J.A., Lambert, M.F. & Reynolds, C.S. (2002). The simulation of an Australian reservoir using a phytoplankton community model: PROTECH. *Ecological Modelling* **150**, 107-116.
- Lund, J.W.G. & Reynolds, C.S. (1982). The development and operation of large limnetic enclosures in Blelham Tarn, English Lake District, and their contribution to phytoplankton ecology. In: *Progress in*

- phycological research, Vol. 1* (eds F.E. Round & D.J. Chapman), pp. 1-65. Elsevier, Amsterdam.
- May, L., Bailey-Watts, A.E. & Hilton, J. (2001). An assessment of the likely effects of phosphorus load reduction on phytoplankton biomass in Bassenthwaite Lake, Cumbria, England. *Verhandlungen der internationale Vereinigung für theoretische und angewandte Limnologie* **27**, 4009-4012.
- Reynolds, C.S. (1984). *The ecology of freshwater phytoplankton*. Cambridge University Press, Cambridge. 384 pp.
- Reynolds, C.S. (1989). Physical determinants of phytoplankton succession. In *Plankton ecology; succession in plankton communities* (ed. U. Sommer), pp. 9-56. Brock-Springer, Madison.
- Reynolds, C.S. (1999). Phytoplankton assemblages in reservoirs. In *Theoretical reservoir ecology and its applications* (eds J.G. Tundisi & M. Straškraba), pp. 439-456.
- Reynolds, C.S. (2000). Hydroecology of river plankton: the role of variability in channel flow. *Hydrological Processes* **14**, 3119-3132.
- Reynolds, C.S., Thompson, J.M., Ferguson, A.J.D. & Wiseman, S.W. (1982). Loss processes in the population dynamics of phytoplankton maintained in closed systems. *Journal of Plankton Research* **4**, 561-600.
- Reynolds, C.S., Irish, A.E. & Elliott, J.A. (2001). The ecological basis for simulating phytoplankton responses to environmental change (PROTECH). *Ecological Modelling* **141**, 271-291.
- Reynolds, C.S., Irish, A.E. & Elliott, J.A. (2005). A modelling approach to the development of an active management strategy for the Queen Elizabeth II Reservoir. *Freshwater Forum* **23**, 105-125.
- Ridley, J.E. (1970). The biology and management of eutrophic reservoirs. *Water Treatment and Examination* **19**, 374-399.
- Simmons, J. (1998). Algal control and destratification at Hanningfield Reservoir. *Water Science and Technology* **37**(2), 309-316.
- Spigel, R.H. & Imberger, J. (1987). Mixing processes relevant to phytoplankton in lakes. *New Zealand Journal of Marine and Freshwater Research* **21**, 361-377.
- Steel, J.A. (1972). The application of fundamental limnological research in water supply system design and management. *Symposia of the Zoological Society of London* **29**, 41-67.
- Steel, J.A. (1976). Eutrophication and the operational management of reservoirs of the Thames Water Authority, Metropolitan Water Division. In: *Eutrophication of lakes and reservoirs*, pp. J1-J12. Institute of Public Health Engineers, London.
- Steel, J.A. & Duncan, A. (1999). Modelling the ecological aspects of bankside reservoirs and implications for management. *Hydrobiologia* **395/396**, 133-147.