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From algal culture to ecosystem; from information to culture

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Introduction

Presidential addresses pose problems. Should one review some area or report a new piece of research; or should one be less predictable? I have chosen the latter, inspired by a BBC radio talk given by Sir Peter Medawar (1964). The talk, 'Is the scientific paper a fraud?', introduced a series about how scientific work is really done. Medawar, a biologist and Nobel Laureate, concluded that the scientific paper *is* a fraud because it misleads the reader, indeed generally lies about the making of scientific discoveries, which are usually presented as well-planned, objective, logical and dispassionate. Scientists, he wrote 'should not be ashamed to admit, as many of them apparently *are* ashamed to admit, that hypotheses appear in their minds along uncharted byways of thought; that they are imaginative and inspirational in character; that they are indeed adventures of the mind.'

There followed a series of talks by the likes of Otto Frisch, Edward Bullard, Tom Cottrell and R. V. Jones which amply demonstrated Medawar's conclusions. Finally there was a summary by a historian and philosopher, J. W. N. Watkins (1964), which commented on the conventional style ('didactic dead-pan') of scientific papers: 'if natural scientists … took to writing in a candid, uncensored, autobiographical way, setting out their ideas in their natural order, didactic dead-pan would gradually fall into discredit outside science too. A gratuitous barrier to mutual comprehensibility would have faded away.' We should heed these words at a time when science has never been so successful in developing understanding of natural phenomena; but a time also when it has abysmally failed to retain public confidence, partly through alienation with its jargon, partly through the arrogance of some of its practitioners, and partly through the suspicion which harnessing of science for exploitative interests naturally brings.

I have a story to tell about how ideas have developed in understanding the role of algae in shallow freshwater ecosystems and I shall tell it in a way that Medawar and Watkins would have approved of. Recently I received a questionnaire asking me which of several things determined what research I do. It had much of the standard terminology of bureaucrat-driven management: Foresight exercise; Competitiveness; Research assessment exercise; Patents; Grant income. It was redolent with the terminology of money, power and influence, none of which have much relevance to the research I do or why I do it. I think that for me, at least, doing research is one way of understanding myself, and my needs, and therefore, possibly, the needs of others. What I do, how I do it, and how I interpret the data are functions of my past experience and of lucky opportunities that have arisen. They have little to do with forward planning and I do not believe that I am unusual in any of this.

First steps

I came from a background that at first looks unpromising for a budding biologist. There was some rural interest on my mother's side; my grandfather used to take me to agricultural shows and I have been fond of farm stock ever since. My father was a confirmed townsman, with a belief that the insects crawling from the various samples that I brought home would burrow into the furniture he had acquired, from a small wage and with great difficulty, in the austere post-war period of the late 1940s and 1950s. It took me several decades to explain the principle of the ecological niche to him, and even then I am not certain he was fully convinced. But he had a quality, whose example for what I would like to be I have only just appreciated: a concern for others that manifested itself in a helpful personality, a willingness to take on chores, and a penchant for writing frequent letters to newspapers deriding what he saw as abuses of privilege and wealth.

There was an element of chance in my deciding to work with algae and freshwaters, rather than with higher plants and soils. In my sixth form days I had been fascinated with plant ecology through courses with the Field Studies Council, and although one of these had been on the meres and mosses of Shropshire, it had not displaced a preoccupation with higher plants. For an undergraduate, however, it is the personalities of those who teach that are far more important than what they teach or even how they teach it. Perhaps it was a certain attractive devil-may-

care approach on the part of Frank Round, but this was my introduction to the algae and limnology and a fortunate flexibility on his part allowed me to become a happy ecologist rather than the miserable electron microscopist I was otherwise destined to become.

Field monitoring and measurement versus laboratory culture

Algal ecology in the 1960s was largely a descriptive occupation, not greatly fettered by statistical analysis. There was experimentation but the great preoccupation was measurement of productivity, biomass, and community structure and attempts to relate spatial distribution to water chemistry. The many data gathered, in the hands of experienced people, could be made to reveal important patterns. Pearsall's (1921) work on the Cumbrian lakes was an inspiration; Lund's (1964) studies on the seasonal cycles of diatoms unfolded a drama of enormous fascination set in the changing sets of thermal stratification, nutrient availability and daylength. Thienemann (1909) and Naumann (1917) had conceived their lake types and the model of oligotrophic and eutrophic lakes provided a framework on which to hang lots of otherwise disparate information. Round (1979) put together the first real synthesis of algal biology and ecology. All these people displayed powerful synthetic powers; their approach would now be called holistic or environmental; they saw whole systems. Some of their ideas have been discarded but that is inconsequential. Their approach to thinking about ecology was the appropriate one.

But university biology departments can be peculiarly intolerant places. Fashions reign and some approaches gain at least temporary ascendancy. In the Botany Department at Bristol in the 1960s you were clearly a lesser being unless you were an experimentalist with a pet cultured organism and preferably working at the enzyme level. Postgraduates are influenced by the prejudices around them and so it was that when I arrived in 1968 as a new appointee to an American university and was asked what research I was going to do, more or less as my feet touched the airport tarmac, I automatically said that it was going to be experimental and involve cultures of algae. The linkages that Thienemann and Naumann had made in creating their 'types' of eutrophic and oligotrophic lakes provided the hypothesis a few weeks later!

What physiological properties of different algae led to their occurring in one or other type of lake? It was a good question, well defined, or so it appeared, and would allow me to emulate my apparent betters in orchestrating an array of cultures. However, it is those strains best adapted to glass or plastic tubes, and high nutrient concentrations, that survive the culture collection and I thought that some of these might give misleading information. I decided that I must work with several species to find the common denominators, and tried to isolate some myself from lakes whose chemistry I knew. That was when I discovered that isolation of interesting algae – the ones that occur characteristically in plankton, as opposed to the 'weeds' that occur everywhere – is difficult and I was glad of the culture collection from which I could buy the labours of others, even if the algae might be somewhat deviant from their wild forebears. No-one at the time seemed concerned with desmid ecology; desmids were attractive to look at ('real' algae, not like *Chlorella*, which I associated with the prejudiced views of laboratory physiologists), so I concentrated on them.

My insurance policy was that if I worked with many strains, any common patterns of physiology would still emerge and I made sure that the nutrient media really did resemble natural lake waters and not nutritious soups. Chu-10 medium (Chu, 1942) was my starting point; it grieves me that it seems to have disappeared from the kitchens of the culture collections. I had determined from the literature that distinct 'eutrophic' and 'oligotrophic' groups did not occur but that there was one group widespread in waters of a great range of chemistry, including both oligotrophic and eutrophic ones, and one that was confined to oligotrophic ones. The only criterion of lake trophy, for which data were widely enough available in the literature linking algal occurrence to water chemistry, was alkalinity, the concentration of weak acid salts, largely bicarbonate. Fortunately bicarbonate is well correlated with other major ions and, with the exception of marl lakes, with availability of nutrients such as nitrogen and phosphorus. 'Oligotrophic' desmids were only recorded at alkalinities lower than $1 \cdot 5$ mequiv l^{-1}; 'eutrophic' algae, including some desmids of the genera *Cosmarium* and *Closterium*, grew also at much higher concentrations.

The results were interesting. Despite a literature replete with the supposed importance of calcium and other major cations as determinants of algal distribution, such ions showed no differential effects on growth of a group of oligotrophic desmids, compared with green algae common in eutrophic lakes. Perhaps there was an element of circularity when the only experimental alteration to water chemistry that showed differential influences on the growth of my cultures was pH, which is intimately linked with bicarbonate concentrations and alkalinity.

However, the eventual conclusions, crafted together (Moss, 1972*a*, 1973*a–c*) in the cold and conventional way that Watkins (1964) had derided as 'didactic dead-pan', earned me an extra salary increment that year, and were the results of respectable experimental laboratory science! Certainly pH, alkalinity and the relative abilities of different species to take up bicarbonate for photosynthesis were important in determining algal distribution and have been echoed elsewhere in work on macrophytes (Sand-Jensen *et al.*, 1992), but there was no real relevance of the value of alkalinity of $2 \cdot 5$ mequiv l^{-1} that had differentiated growth of the 'eutrophic' and 'oligotrophic' groups in my laboratory.

It was far too high, even with my attempts to reconcile it, through calculations of associated free CO_2 concentrations, with the $1 \cdot 5$ mequiv l^{-1} that seemed to dif-

ferentiate distributions in the field. Talling showed soon afterwards (1976), with elegant work on natural communities, that it was availability of CO_2 that was of key importance – some species could absorb it at much lower concentrations than others and there was a continuum of such abilities. My results were broadly indicative but the classification into groups was an artefact of the medium and a culture approach. Nonetheless, the work had served a different, perhaps more important, purpose. I could do, had done, such laboratory-orientated work. I could now move on to what I really thought was useful and was more predisposed to (not necessarily the same thing) with more confidence.

Experimental ponds

In the USA I had not only done culture work. I had also monitored a large lake, which gave me experience of deep-water limnology (and opportunities to hand-draw depth-time diagrams (Moss, 1972*a*), which I find peculiarly pleasurable), eutrophication problems, and the local politics of nutrient control. I had also analysed epiphyte and macrophyte samples from an experiment carried out in twenty 0·07-ha ponds at Cornell University (Hall *et al.*, 1970; Moss, 1976) and there were key lessons from this. First, the designers of this experiment, W. C. Cooper and D. J. Hall, were zoologists, secondly the experiment was ambitious in scope and thirdly it involved whole systems – chemistry, plants, algae, invertebrates and fish.

Cooper and Hall, on completing doctorates in animal population dynamics, had decided that they wanted to investigate the interaction of what they saw as the two key features of all ecosystems in a particular climate regime – nutrient availability and predation – which, 30 years later, with the convenient amnesia that attributes novelty to mere neologism, we have rechristened bottom-up and top-down control. It impressed me that, with the versatility that comes from an American training, they had contemplated either a terrestrial old-field system to carry out the experiment or a pond system, and that they were quite happy to embrace both plants and animals despite the fact that they were zoologically trained. This might seem less significant now than it did then, but in the Britain of the 1960s the University fiefdoms of separate botany and zoology departments strongly undermined even the mildest of multidisciplinary approaches.

The Broads

When I returned to the UK, ultimately to a post at the University of East Anglia in Norfolk, it was thus with a much broader background than I had left it and to a new multidisciplinary environment. The School of Environmental Sciences at UEA was a revelation to me. It had none of the hierarchies that prevail in biology departments. It was, at first, a bit like Noah's ark: two geophysicists, two oceanographers, two ecologists, two human geographers, two social scientists, so no particular group was big enough to develop any pretence of intellectual superiority. The Norfolk Broadland, a system of riverine lakes, was an obvious place to carry out research and was clearly eutrophicated; it was a big system with important conflicts between man's activities and nature conservation. Others in the School were interested in geomorphological, historical and social aspects of the system. The sense of history that the Broads conveyed was attractive to me – the lakes had been formed by the excavation of peat from the ninth to the thirteenth centuries – and I was impressed by the collaborative work of a group consisting of a botanist, a geomorphologist, an engineer and a historian who had worked this out only a few years before (Lambert *et al.*, 1960).

Remarkably, and happily for me, there had been only a little detailed attention to water quality (Mason & Bryant, 1975) and none since the 1920s (Griffiths, 1927) to the algal communities. There were only hints that the volumes of sewage effluent being discharged to the Broads were of any relevance. Boats, not those of the local residents, of course, but those hired to the tourists, were the then current *bête noire* (Broads Consortium Committee, 1971), perceived to underlie all the problems.

In the 1970s we amassed a wealth of evidence (Moss, 1983) that phosphorus inputs, largely from sewage effluent, together with nitrogen inputs from the land, were a major problem. They were associated with change from a former clear-water marl lake system, with a well-known collection of unusual charophytes as well as vascular macrophytes, to turbid water with abundant diatoms in spring and autumn, and combinations of these with cyanophytes in summer. The submerged macrophytes and water lilies had disappeared from most of the system. The evidence came from correlation analysis (Moss, 1977), nutrient budgets (Moss *et al.*, 1988), palaeolimnology (Osborne & Moss, 1977; Moss, 1979, 1980, 1988) and some tank experiments with epiphytes and macrophytes (Eminson & Phillips, 1978), but in the early stages lacked field experimentation. A simple linear model (Fig. 1) seemed to explain the situation. The changes had been driven by eutrophication; restoration of the plants and clear water would surely follow if the nutrient input was reduced.

The palaeolimnological evidence was convincing enough for the then Anglian Water Authority to be persuaded that it should instal phosphorus removal treatment at one main sewage works discharging to one of the best-known Broads, Barton Broad, and divert the effluent from another. We were convinced that this would lead to a rapid improvement in the Broad, the phytoplankton crops would decline, and the macrophytes, perhaps even the charophytes, would return. There were dramatic precedents for lake restoration by phosphorus control at Lake Washington in the USA (Edmondson, 1991), in the Swiss alpine lakes (Fricker, 1980; Schanz & Thomas, 1981) and in the North American Great Lakes (Vallentyne & Thomas, 1978).

Restoration of clear water and macrophytes by reduction in phosphorus loading
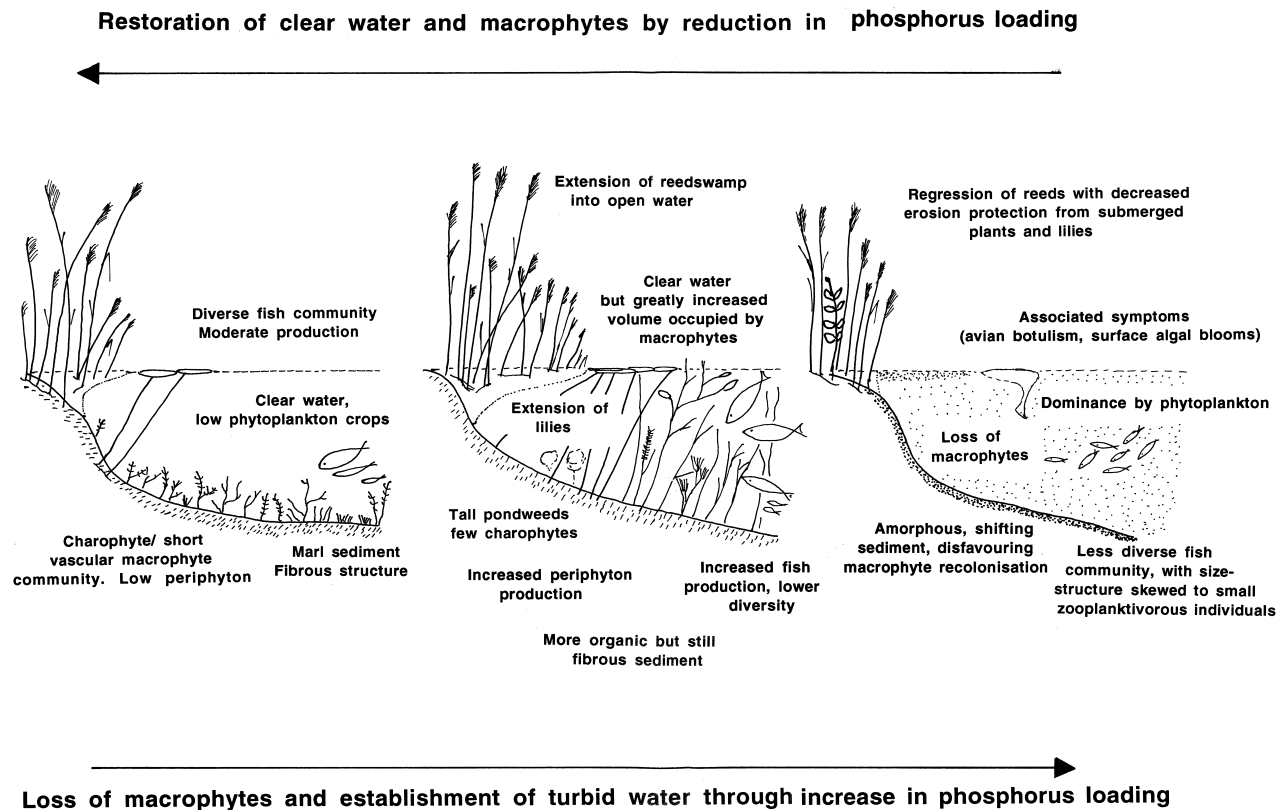

Fig. 1. Linear model of changes with eutrophication in shallow lakes.

The phosphorus was removed, we waited year by year in the early 1980s for a successful restoration, but very little happened. The algae continued to form crops, measured as chlorophyll *a* concentration, annually averaging over 100 μg l^{-1}, no plants grew and my biologist colleague, Geoffrey Phillips, in the Water Authority made the best he could of some small decline in the proportions of cyanophytes to his managers (Phillips, 1984). Release of phosphate from the sediment was blamed. It was certainly rife and removal of sediment was advocated but was too expensive.

Subsequently we have learned that phosphate probably emerged from the sediments of most shallow lakes in quantities sufficient to support substantial phytoplankton crops (Marsden, 1989; Stephen *et al.*, 1997), and dredging exercises have proved futile (Moss *et al.*, 1996a). The real problem was biological. Yet again my 1960s British training that ecological problems were either botanical or zoological and that to understand plant and algal distribution one need only consider growth and the chemical milieu, was surfacing. My American experience with experimental ponds was overwhelmed by the earlier conditioning. The eventual solution to the Broads restoration problem was to involve all sorts of other elements, many of them zoological.

There were two turning points, both serendipitous, in the Medawarian (1964) analysis of science. In monitoring one lake, Hoveton Great Broad (Timms & Moss, 1984), rich in nutrients fed from the River Bure into its two connected basins, we found that one basin, still with

substantial beds of water lilies, retained clear water in summer. In the other basin, lacking lilies or any submerged plants, the water was turbid with *Aulacoseira*, *Oscillatoria* and other diatoms and cyanophytes. Two nights of hourly monitoring, and experiments in large polyethylene bags suspended in the basins, showed that the lilies supported large communities of herbivorous Cladocera which appeared in the open water at night and grazed down the phytoplankton. Where lilies were absent, zooplanktivorous fish prevented any substantial population of Cladocera from accumulating and the algae took advantage of the copious nutrient supply to maintain large populations.

The second turning point came in an experiment carried out in ponds we had made by serially damming along a dyke (a ditch constructed in the wetlands some hundreds of years previously for the passage of wide boats bringing out marsh produce such as hay, sedges and reed). The dyke had a rich macrophyte community and we attempted to displace the plants by fertilizing with nitrogen and phosphorus. The original design was intended to determine the critical threshold at which the plants would disappear. But they did not, despite huge nutrient loadings. They grew even better. Only when we had previously raked out the plants did the phytoplankton grow in response to the nutrient loads we were giving (Balls *et al.*, 1989; Irvine *et al.*, 1989).

There was more evidence from elsewhere. Our Danish colleagues had collected much information from a large number of lakes and shown that over a wide range of
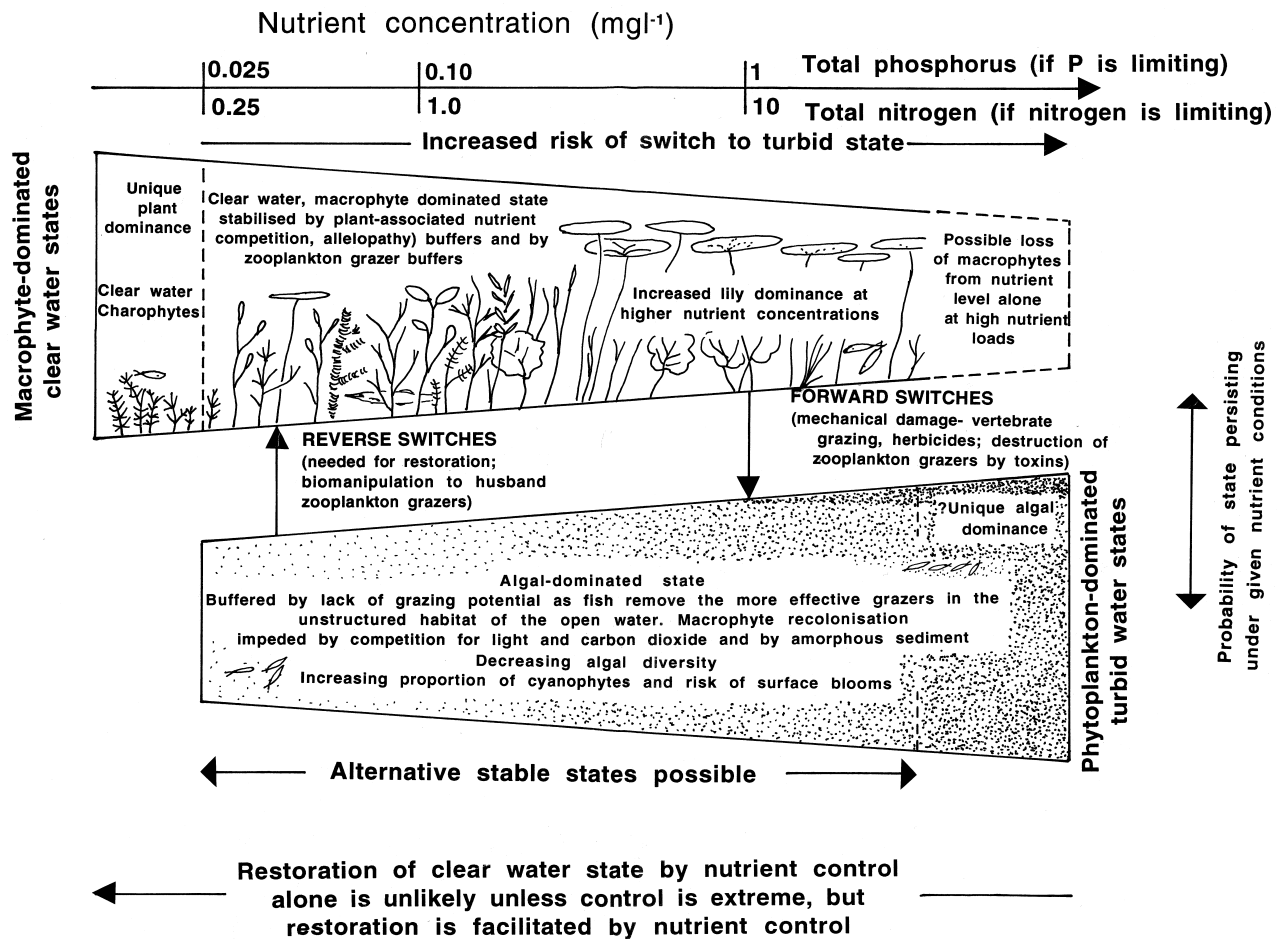
Nutrient concentration (mgl⁻¹)

Fig. 2. Alternative stable states model of changes with eutrophication in shallow lakes.

phosphorus concentrations, some lakes had clear water and others had turbid (Jeppesen *et al.*, 1994), independently of the phosphorus concentration. Later, several groups in Holland, Denmark and Germany, as well as ourselves, adopted the approach of biomanipulation from Shapiro *et al.*'s (1975) experiments in the USA and showed that an algal-dominated water could be cleared, and macrophytes restored, by the expedient of removing fish for a time. This husbanded the cladoceran population and kept the water clear for long enough for plants to re-establish. Our original simple linear concept (Fig. 1) that nutrient increase had stimulated algal growth, which had shaded out the plants, and that reversal of the nutrient loading would linearly restore the system, had to be abandoned. I must add that this was not without resistance, so humanly dependent are we on the security of familiar structures. It was replaced by an alternative stable states model (Irvine *et al.*, 1989; Scheffer *et al.*, 1993) (Fig. 2).

The alternative stable states model of shallow lake ecology

Like all models the alternative states model is still evolving. It currently has three main features – states, buffers and switches – set in a background of nutrient loads or concentrations. Ultimately, however, it reflects

the balance of importance of the terms in an equation for development of algal populations:

$$\mathrm{d}B/\mathrm{d}t = \mu B - (gB + sB + wB)$$

where B is biomass, t is time, μ is growth rate, g is grazing rate, s is sinking rate (or burial rate for benthic algae) and w is washout rate.

The model has two general states: clear water and plant dominance; or turbid water and phytoplankton, and sometimes filamentous algal, dominance. These can be seen as outcomes of the growth equation in which either the loss rates of algae predominate, or the growth rates. At very low nutrient supply, whatever the algal growth rate and crop accumulation, algal growth is too small seriously to limit aquatic plant growth. This might be, in shallow waters, at less than about 25 μg P l⁻¹ or 250 μg N l⁻¹, dependent on whether phosphorus or nitrogen is driving the system (this is still not clear) and based on experience of available sites.

At very high nutrient concentrations there might be a unique algal-dominated state, where algae grow so well that they cannot be controlled by any of the loss factors in the equation, but there is uncertainty about this because of examples of lakes with huge nutrient levels where algae are controlled by grazers, the water is clear and aquatic plants persist (Carvalho, 1994). Cyanophytes complicate

the picture because they are often abundant at high nutrient concentrations and are often less edible to zooplankters than other algae (de Bernardi & Giussani, 1990; Moss *et al.*, 1991). However, there are instances where they have been controlled by grazing (Annadotter *et al.*, 1999) and at the highest nutrient levels in shallow lakes they are often replaced by more edible green algae (Jensen *et al.*, 1994).

Over the main range of nutrient concentrations found in shallow waters, however, it seems possible to have either plant or algal dominance. Each state is stabilized, once it is established, by buffer mechanisms, which either promote algal growth or prevent it; and to move between states, switches must be applied.

The buffers of the plant-dominated state include those which decrease algal growth rates or increase death rates. The former include allelopathy (Blindow, 1992; Gross & Sutfield, 1994) and nitrogen limitation created by plant uptake (Ozimek *et al.*, 1990), or dentrification by bacteria deep in the plant beds, where redox conditions can be low and can fluctuate diurnally. The latter include enhanced grazing by zooplankters (Timms & Moss, 1984; Lauridsen & Buenk, 1996) and plant-associated crustaceans, whose populations are able to build up among the physical and chemical refuges the plant beds provide against fish predators of these grazers. The buffers of the algal-dominated state are the converse of these. Absence of plants removes any possibility of allelopathy and competition for nitrogen, whilst the open water leaves the larger and more effective crustacean grazers vulnerable to fish predation.

Because of the existence of the buffers, it is unlikely that the system will change from one state to the other simply by change in nutrient status. One or more forward switches must be present to move the plant community to the algal-dominated state. Forward switches either damage the plants directly (severe cutting (Balls *et al.*, 1989) or boat propeller damage, major increase in water level (Blindow *et al.*, 1993), herbicides (Van Donk *et al.*, 1989), intense grazing by waterfowl or common carp (Crivelli, 1983; Carvalho & Moss, 1995)) or undermine the grazing of algae by Cladocera (pesticide run-off (Stansfield *et al.*, 1989), markedly rising salinity (Bales *et al.*, 1993) or increased zooplanktivory caused by differential kills of piscivorous fish by deoxygenation under ice or on still summer nights (Bronmark & Weisner, 1992)).

Spontaneous reverse switches, which convert algal-dominated communities back to plant dominance, are unusual but may include lowering of water level, which may improve the light climate for the plants (Blindow *et al.*, 1993). More usually the reverse switch is achieved by deliberate alteration of the fish community (biomanipulation) to reduce predation on the Cladocera and reinstate grazing pressure on the algae.

Nutrient availability still has a role in the alternative states model in that the thresholds for operation of forward switches seem to be depressed at increasing nutrient concentrations and, similarly, biomanipulation is more effective if nutrient loads are reduced (Jeppesen *et al.*, 1999). There are still many uncertainties, however, not least the relative importance of nitrogen and phosphorus. The traditional emphasis on phosphorus control may be less appropriate in shallow lakes. There may have been normally high internal loads of phosphorus from the sediment under plant-dominated conditions and available nitrogen is very scarce, often undetectable in summer, in plant-dominated shallow lakes. These suggest that increases in nitrogen loading, rather than phosphorus loading, may have been most important in creating conditions for forward switches to operate.

Relevance to warm-water lakes?

Despite the uncertainties, the model has been valuable in directing attempts at shallow lake restoration and a general strategy can be defined (Moss *et al.*, 1996a). This strategy has seven steps: (1) determine the target for restoration; (2) remove any existing or potential forward switches; (3) reduce nutrient loads as much as possible; (4) biomanipulate; (5) introduce macrophytes if necessary and protect them from damage as they develop; (6) reintroduce an appropriate fish community; (7) monitor and reflect on the results.

The danger, however, arises that the appeal of an internally consistent model and a range of successful applications (Moss *et al.*, 1996a,b) might lead to over-extrapolation of the strategy. For example, Lake Naivasha in Kenya (Harper *et al.*, 1990; Harper, 1992) provides a good example of a switch from a plant-dominated state to one of turbidity with large algal crops. It was well known, for much of this century, for its submerged macrophyte communities and associated bird populations. But, following invasion and expansion of the coverage of *Salvinia molesta*, a floating fern, and removal of substantial areas of fringing papyrus swamp by farmers during a period of low water level in the 1980s, it finally lost its macrophytes in the 1990s from all but a semi-isolated basin set in a volcanic crater in the south of the main basin. Nutrient loads may have increased as dairy-farming has expanded on the Kinangop plateau from which much of its water is supplied to the lake. In 1997 the lake had turbid water, and in the main basin only a thin fringe of introduced water hyacinth (*Eichhornia crassipes*) to replace a once-rich plant community.

There are three potential forward switches that might have operated, including run-off of pesticides from intense flower cultivation close to the lake, but available analyses have yet to provide good evidence of this. A greater possibility is that over-fishing and poaching have removed all large fish, including predators on small invertebrate feeders, introduced to control mosquitoes, and left an intensely zooplanktivorous community. The likely most important forward switch, however, has been the introduced American red-spotted crayfish, *Procambrus clarkii*, which, although an omnivore, feeds preferentially on submerged plants. Decline of the plants coincided with

burgeoning of the population of the crayfish, whose feeding preferences can readily be demonstrated experimentally (Harper, 1992).

It is tempting, therefore, to recommend that the clear water and macrophytes, together with the bird communities which have been markedly reduced in this Ramsar site lake, might be restored by application of the restoration strategy outlined above. Papyrus could be allowed to recolonize the areas from which it has been removed, so as to form as wide a nutrient-absorbing buffer as possible, the fishery might be controlled to a much greater extent than at present and poaching reduced by application of existing legislation, and the crayfish might be eliminated. This, however, would be far from easy and might not be possible until the lake level falls substantially (there is a history of marked fluctuation in level), allowing treatment of residual pools of water with crustacicide.

There is a possibility, however, that application of the restoration strategy worked out in temperate lakes, in such a lake may be a complete failure. Temperatures are high and although control of algae by zooplankton grazing is usual in colder, north temperate shallow lakes, the algal growth rates at greater temperatures may be so high that the zooplankters cannot cope with large algal crops established in response to increased nutrient loads. This might mean that biomanipulation by removal of zooplanktivorous fish from warm lakes, or crayfish in Lake Naivasha, will be ineffective and that a strategy of intense nutrient control (to achieve the low nutrient, unique plant-dominance, referred to above) will be needed. Frequently also, small tropical fish reproduce so rapidly (Lowe-McConnell, 1966), sometimes every few days in the case of cyprinodonts, that biomanipulation is effectively impossible.

If this is so, the emphasis in the algal growth equation, having shifted from μ to g in development of the alternative states model, may have to be reversed in modifying the model for tropical lakes. A conceptual wheel may have fully turned!

The alternative stable states model and the human situation

The example of Lake Naivasha brings me back to why I do research. Although the loss of aquatic plants from a Norfolk Broad may be regrettable on conservation grounds, it seems far less important than the changes in a lake like Naivasha, where the human population has been directly dependent on the protein resources obtainable from the lake and where a decline in income from ornithological tourism could further impoverish an already poor area.

More importantly, if there are general lessons to be learned from this story, which inform our understanding of ourselves and our society, then it becomes of much greater significance. The alternative states model may illuminate some aspects of how we have handled the global and local environmental trends which have affected

Table 1. Buffers of the diverse state, compared among macrophyte-dominated shallow lake systems and traditional human cultures

Shallow lakes	Traditional cultures
Intricate physical structure	Heterogeneity of surroundings and customs
System stability increased by low nutrient supply	Parsimonious resource use
Allelopathy	Communal controls on disruptive behaviour
Importance of grazing by zooplankters; provision of refuges	Sustainable management of resources for continued use

human societies. It may be helpful in diagnosing some of the solutions to what are manifest problems of excessive use of non-renewable resources, destruction of natural habitats and unfortunate changes in the felicity of our social structures.

I have drawn elsewhere (Moss, 1995*a,b*, 1998) an analogy between the clear-water, diverse stage of shallow lakes and a sustainable society and the less diverse, turbid, algal-dominated state and the society which increasingly dominates the planet – our western technological system. The latter has replaced a large number of alternative human systems, none of which most of us would wish to adopt in their entirety but from which, collectively, many lessons concerning sensible use of resources might be learned. My presumption is that western society will have to change and move towards applying some of these lessons if it is to achieve the sustainability trumpeted as its desirable goal at the Rio (Earth Summit) conference in 1992.

Comparatively recently, biologists tended to see the problems largely as those of conflict between humans and other species. Greater reflection now shows them to be closely interlinked with how humans treat each other; conservation, resource use, human rights, poverty and war are all manifestations of how we organize our societies and how we perceive one another (Harrison, 1992; Guha & Martinez-Alier, 1997). Most of us, pondering our current environmental and social problems, would doubtless agree that change must occur. The problems *inter alia* include global warming and extreme weather patterns, ozone depletion in the stratosphere, wrecking of large tracts of the world's heritage of biodiversity, an inordinate number of small wars, increasing refugee numbers and needs, penetration of toxic industrial and agricultural chemicals to even the remoter reaches of Earth, increasing populations of extremely poor people, increasing uncertainty in even our own personal security as economic systems favour globalization and competition, increased rates of stress-related diseases and reduced opportunities to influence events and social structures.

The key underlying problem, however, is that although there is wide recognition of these problems we seem

Table 2. Buffers of the less diverse state compared among shallow, algal-dominated lake systems and western technological cultures

Shallow lakes	Technological cultures
Lack of structure	International uniformity 'Macdonaldization'
Presence of exotic pest species	
Large pools of available nutrients	Unrestricted resource use
Nocturnal deoxygenation	Large volumes of waste pollutants
Highly competitive algal species (high growth rates, resistance to grazing, toxin production)	Market economics, dependent on global competition
Dominance by limited biotic group (microalgae of a few Divisions)	Dominance by relatively few powerful interests (states, transnational corporations)
Stability increased with large supplies of available nutrients	System depends on unsustainable use of resources ('economic growth')

Table 3. Forward switches compared for the transitions from plant-dominated shallow lake systems to turbid, algal-dominated shallow lake systems and for the replacement of traditional cultures by western technological systems

Shallow lakes	Human cultures
Destruction of plant structure (mechanical, boats, exotic vertebrate grazers, herbicides)	Habitat destruction (forest, food animals) by economics or war
Removal of plant-associated buffers (e.g. allelopathy, nutrient competition)	Replacement of traditional systems of governance (often by colonial invaders)
Removal of ancillary buffers (zooplankton grazing) by toxins or superabundant small fish	Replacement of locally appropriate, sustainable economies by global markets and large, hard currency loans

Table 4. Mechanisms compared for restoration of plant dominance in shallow lake systems and potentially for an orderly transition to sustainability in human cultures

Shallow lakes	Human cultures
1. Agree target	1. Agree target
2. Remove forward switches	2. Curb hawkish institutions
3. Control nutrients	3. Reduce resource use, recycle
4. Biomanipulate	4. Replace market forces by locally appropriate economics
5. Replace plant community	5. Restore heterogeneity of institutions by restricting hawkish influence
6. Reintroduce appropriate fish community	6. Reward co-operation and sharing rather than competition and acquisition
7. Monitor and reflect	7. Eternal vigilance is the price of freedom[a]

[a] The original form of this, which comes from a speech given by John Philpot Curran (1750–1817) on the Right of Election of the Lord Mayor of Dublin, on 10 July 1790, is 'The condition upon which God hath given liberty to man is eternal vigilance; which condition if he break, servitude is at once the consequence of his crime, and the punishment of his guilt'.

in their region have cultural and survival significance (Table 1). Conversely, algal-dominated systems and technological society (Table 2) are characterized by uniformity and dominance by very few groups. Nutrients, especially nitrogen, are scarce in plant-dominated systems, generally liberally available in algal-dominated systems; in parallel, natural resources are profligately used in western technological societies, rather carefully conserved in traditional cultures.

Current technological systems are stabilized by market economics and competition, and dominated by a very few countries and transnational corporations; traditional cultures have existed in glorious variety, stabilized by a variety of local economical systems and cooperation. Similarly, it is the competitiveness of microalgae in capturing light, nutrients and carbon dioxide that ensures continued algal dominance; the co-functioning of macrophytes, periphyton, plant-associated invertebrates and zooplankton which stabilizes the plant-dominated state. The algal-dominated state and the increasing uniformity and emphasis on high productivity of western societies have many of the characteristics of the algal culture vessel.

Forward switches (Table 3) can also be compared. Destruction of plants is paralleled by destruction of the habitats on which many traditional cultures have depended. Destruction of buffer mechanisms, like zooplankton grazing, by toxins like pesticides or rising salinity, has been paralleled by destruction, often by colonial powers, of locally appropriate judicial and governance systems and economies by imposition of those of western cultures.

Perhaps the key table, however, is Table 4, which suggests parallels in restoration strategies between the two sorts of systems, These comparisons are arranged in the order of the shallow lake restoration strategy, outlined

powerless to move significantly towards solving them. Progress towards sustainability, following the Rio conference, has been minimal, perhaps even negative (Flavin, 1997). Application of the alternative states model with its components of resource use, buffers and switches might help thinking about why this has been so.

In Tables 1 to 4 I have drawn comparisons of buffer mechanisms and forward switches for the shallow lake system and the systems of human societies. The latter are based on an analysis of anthropological works, ably summarized in Reader (1988), Kemf (1993) and Turnbull (1961, 1972, 1985), and my own experience of our current western society. The systems are alternatively more diverse (plant-dominated shallow lakes; traditional cultures and a desirable sustainable society) and less diverse (phytoplankton-dominated shallow lakes, unsustainable western systems) and I have drawn parallels between the buffer mechanisms which seem to me to be analogues in each sort of system.

Thus, heterogeneity and structural complexity are characteristics of plant-dominated systems and sustainable cultures. In traditional cultures, numerous natural features

earlier. I equate the activity of hawkish institutions with forward switches, for it seems to me that the exercise of power in the interests of acquisition of wealth has probably been the most destructive of all human institutions and is currently ultimately responsible for most of the world's significant problems. The counteracting of these hawkish tendencies by the replacement of global dominance by locally appropriate economics and the decentralization of decision-making is the equivalent of biomanipulation.

I believe the existence of powerful forward switches is why, despite wide acceptance of the existence of global environmental problems, relatively little major progress has been made towards solving them. What is more sinister, however, is that there is deliberate obstruction to their solution. Itself a buffering mechanism stabilizing western technological society, the use of manipulative advertising, in effect propaganda, is rife. A recent article (Beder, 1998) surveyed the many examples where corporations and industry associations worldwide are sponsoring and producing educational materials for schools. These materials give a corporate view of environmental problems, cast doubt on the scientific basis for environmental regulation and tend to promote superficial solutions that will have minimum impact on the operations of the promoting companies. Not surprisingly it is the larger and more hawkish institutions that invest most in this propaganda. One American professor of education (Molnar, 1995) suggests that 'by the end of the century, the link between public education and schools' ability to deliver corporate profits may be impossible to sever. And if that happens, the substitution of market values for democratic values in public education will largely be accomplished.'

We, in the universities, will naturally deprecate this, but our own house is far from ordered. We too have allowed ourselves and the nature of our institutions to be betrayed by our own hawks and have become a greater part of the problem than we might be of its solution. Consider again the terminology of modern research: 'Foresight exercise, Competitiveness, Research assessment exercise, Peer reviews, Science management audits, Patents, Grant income, Prestige, Increasing the nation's wealth'. Though some of these have merit, they are, I believe, being used as manipulative tools that are ultimately destructive. There can be no other reason for the existence of a university (Newman, 1852) than that it should continually question the *status quo* – whether they be of ideas about algal community composition, of human ethics and morality or of systems of organization of society. And although this has ever been at risk (Cornford, 1908), the more universities are beholden to support from specific interests rather than from society as a whole, the less they are able to question and the less valuable they become.

Coda

My father never entirely gave up writing letters of protest to newspapers, but, as he aged, they became increasingly concerned with local trivia. He was, I realized later than I should, a good man who really did care for others. He died 10 years ago, the ideals of his twenties, when he emerged from the army into a post-war world full of hope that the inequities of the early decades of this century would be removed, crushed by a system that he knew to be defective. Deep down, he gave up on the really important issues, as many of us do. But we must not and that is one of the reasons why I have drawn the parallels that I have. For me research has meaning when it explores the questions of 'why' rather than the easy and innocuous questions of 'what'. If this is considered by some to be outside a scientist's province, let me refer again to Medawar, and suggest that science will promote little confidence unless its human presence is acknowledged and it climbs down from its current arrogance and manipulation by its hawks. And if I have not articulated this sufficiently convincingly, let me have recourse, in my frustration, to those who can use words to greater effect, to W. B. Yeats' love poem:

> Had I the heavens' embroidered cloths,
> Enwrought with golden and silver light,
> The blue and the dim and the dark cloths
> Of night and light and the half-light,
> I would spread the cloths under your feet:
> But I, being poor, have only my dreams;
> I have spread my dreams under your feet;
> Tread softly because you tread on my dreams.

Acknowledgements

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