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Nutrient loadings and algal blooms in Australian waters - a discussion paper

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Summary

The recent outbreaks of toxic algal blooms in water bodies in SE Australia necessitate a close look at the relationships between nutrient loadings, algal blooms and the species composition of those blooms. Management actions to reduce or prevent blooms must be based on a secure knowledge of ecosystem function and predictable ecological relationships. This paper reviews the international literature on these subjects and provides a critical look at the present state of knowledge in Australia.

Increased nutrient loadings to water bodies drive a sequence of events within the ecological structure of the system. Blooms arise when external nutrient loadings exceed the capacity of the grazing food chain to assimilate and recycle nutrients. Once this capacity is exceeded, nutrient concentrations in the water begin to rise, larger celled species (or colonial forms) begin to predominate, phytoplankton biomass increases, grazing efficiency decreases and the nutrient regeneration mechanisms become predominantly benthic. A large number of other changes in food chain and ecosystem structure accompany these changes in food chain dynamics. Many features of ecosystem structure can therefore be predicted from a knowledge of nutrient loadings, water residence times and morphometry. It is argued that control of nutrient loadings (in particular, phosphorus) to water bodies can control ecosystem structure and function.

Nuisance algal blooms are seen to arise from the alterations in ecosystem structure and function which result from increased nutrient loadings. In Australia, nutrient loadings are dominated by storm events so this requires a good knowledge of flow and load relationships for Australian catchments. It can be predicted that reductions in the external load of nutrients will cause a reversion of system state to oligotrophic conditions and a reduction in the severity of nuisance blooms. Phosphorus loading reductions are the key control factor although nitrogen availability (which may be reduced by denitrification in eutrophic systems) is a further factor influencing the species composition of blooms. The cycling of nitrogen and phosphorus within aquatic ecosystems is a function of trophic state. Physical processes (mixing and flow) are identified as critical determinants of both biological and chemical processes in water bodies.

At present, few predictions can be made about the growth of phytoplankton in rivers. Growth of phytoplankton in rivers is paradoxical - the residence time of water in unregulated rivers is often theoretically too short to allow blooms to occur. The fact that plankton do grow in rivers means that back eddies and pools must provide a mechanism for retention of plankton and regions where growth can occur. Regulation of river flow and extraction of water increases the residence time of water in the system so that it comes to equal that in small lakes. Phytoplankton production dominates the system dynamics in the lower reaches of regulated rivers. Knowledge of phytoplankton growth in lakes and storages therefore has a direct application to growth in weir pools and regulated rivers. Management actions may be planned accordingly. Nutrient control strategies and maintenance of flow are both important ways to control algal biomass.

Predictions of the species composition of algal blooms are much less secure than predictions of biomass and are based on a number of contingent factors: the vagaries of immigration, biogeography, climate variability and ecological interaction to name but a few. Because of the complex non-linear interactions between components of the aquatic ecosystems, predictions of the occurrence of particular species are fraught with uncertainty and probably always will be. The contingent variability of aquatic ecosystems at the level of species is driven by a variety of processes which fluctuate at a range of temporal and spatial scales. Manipulation of species composition may be possible by means of alterations in the frequency components of environmental fluctuations.

The paper concludes with a list of knowledge gaps and research opportunities. Priorities for future work are identified.

1.1 Preamble - an historical introduction.

Given the recent widespread outbreaks of toxic algal blooms in Australian waters there is a need for the development of some predictable relationships between nutrient loadings, phytoplankton biomass and species composition which are suitable for local conditions. Management action must be based on the best available knowledge and on practical schemes which will have predictable outcomes. We therefore need to develop some ecological relationships which have predictive power under Australian conditions. Unfortunately, the Australian track record in this area has always been rather thin; when compared to countries like Canada the limnology community in Australia is small and scattered. The phytoplankton ecology community in Australia is even smaller. The net result is that relatively little work has been done here in this area. Ganf et al (1982) made precisely this point in a paper 12 years ago. Not much appears to have been done to rectify the situation in the intervening years. It is to be hoped that the newly-formed CRC for Freshwater Ecology can begin to redress the shortage of qualified people in this area.

It is possible to argue that Australia, for very good reasons, concentrated more on the management of water quantity risks than on water quality risks over the last twenty years. Only recently has the issue of water quality risk become a major issue. Fortunately for Australian water quality managers the scientific fundamentals of this problem were worked out nearly twenty years ago in North America and Europe. While there are some surprising gaps in Australian knowledge we are now in the excellent position of being able to take advantage of the twenty five years of accumulated limnological research and management experience which is documented in the international literature. Many of the most newsworthy (and toxic) blooms have occurred in Australian river systems in recent years although there have been many equally problematic blooms in storages and weir pools. Compared to lakes, the literature about algal growth in rivers is small and the understanding similarly lacking. Nevertheless I will attempt to show where limnological insights may be transferred from lakes and storages to rivers and estuaries.

In the twenty-five years since Vollenweider first published empirical relationships between phosphorus loadings, concentrations of phosphorus in the water of lakes and storages and algal biomass we have learned much about the structure and function of aquatic systems. Broadly speaking, in Canada and Europe the decade of the 1970s saw the development of a sophisticated understanding of the relationships between nutrient loadings, in-water nutrient concentrations and algal biomass in lakes and impoundments. A broader understanding of the impact of altered nutrient loadings on zooplankton, fish, macrophytes and other components of the pelagic food chain was developed during the 1980s. In particular, a series of summary papers by members of the McGill limnology group have brought together more than twenty years of global work and greatly extended the range of known empirical relationships between nutrient loadings and the structure of aquatic systems. These papers bring together large amounts of data from many water bodies around the world to display general relationships. Systematic work on rivers is relatively recent as the attention of managers has switched from storages to flowing water systems.

Broadly speaking, if we are to understand the dynamics of phytoplankton blooms in lakes, storages and rivers we will have to consider both "top down" factors (factors which arise "higher" in the food chain, such as grazing pressure from zooplankton) and "bottom up" factors (factors which influence phytoplankton growth from "below" such as light, temperature, nutrients etc., see Agusti et al 1992). Vollenweider's models concentrate on "bottom up" factors of nutrient loadings and availability. This was the approach of the 1960s and 1970s. Exceptions to the standard nutrient loading relationships soon appeared and encouraged workers to look at "top down" factors which might modify the average response. Biomanipulation, as it is called, became popular.

Biomanipulation began as an attempt to manipulate phytoplankton crops by changing the grazing pressure from zooplankton. Basically the idea of biomanipulation came from the "size efficiency hypothesis" of Brooks and Dodson (1965) but this hypothesis did not stand up to scrutiny in the long term (Harris 1986). Changing the fish community was the topic of choice in the early days (Gophen 1990 - see also the papers in Hydrobiologia 200/201, 1990) but it rapidly became clear that the results of such manipulations were very complex and frequently gave surprising and unexpected results. By the late 1980s it became possible to summarise the results of numerous biomanipulation experiments. Review papers and summaries of experimental manipulations of food chains by McQueen and others have contributed much to our knowledge of the way aquatic food chains work. Gophen (1990) credits Harris (1986) with the first realisation that "biomanipulation" really meant "complex interaction" but this idea was in wide circulation at the time. Carpenter (1988) edited a volume of this subject a couple of years later.

Biomanipulation has now come to mean manipulation of all kinds of interactions including riparian vegetation, lacustrine macrophytes, sediments, fish etc. and the challenge has become how to stabilise the results of experimental manipulations (Shapiro 1990). What has happened over the last twenty-five years is the slow realisation that the world is much more complex than we think and that simple concepts such as the "size efficiency hypothesis" will no longer suffice (Peters 1992). As with other ecological ideas simplicity has been replaced by complexity (Slobodkin 1992).

This paper chronicles the acceptance of "complex interactions" as a fact of life and tries to explain how in the 1990s, if we are to attempt to manage both the biomass and the species composition of algal blooms, we will have to cope with some very complex ideas and some complex dynamics. A whole system view is required so both "top down" and "bottom up "factors (and the interaction between them) will need to be considered. We have moved from an era of loading models to statistical, empirical models and now to models of complex dynamics which trace the fate of individual organisms and their interactions with others. We have begun to realise that manipulation of both the flow and the nutrient load can produce desirable results. We have begun to understand that only a view of the entire system will suffice if we are to understand the full complexity of real world problems. Thus water quality in lakes, storages and rivers cannot be divorced from land use and events in the drainage basins - Total Catchment Management is the order of the day.

A recent paper by Harris (1994) has attempted to bring many of these ideas together into an overall conceptual framework which relates changes in trophic state to the predictable changes in algal biomass, food chains, community structure and species composition. If we are to develop this work further to include an understanding of the factors which influence the species composition of phytoplankton blooms then the decade of the 1990s will need to see further advances in both ecological concept and management practice. It is worth noting, perhaps, that in many respects conceptual knowledge of system behaviour in freshwater ecology leads the general ecological literature. For a number of reasons freshwater ecology is at the leading edge of ecological understanding (Harris 1985, 1986, 1994, Harris and Griffiths 1987).

It is worth noting at the outset that the ideas and concepts presented in this paper apply equally well to coastal waters and blooms of organisms such as the toxic marine "red tides" as well as to freshwater blooms of toxic cyanobacteria (blue-green algae[1]). There is little difference between marine and freshwater systems (Harris 1986) and many of the same concepts can be applied. It is too simplistic to say that while freshwater systems are phosphorus limited, marine ecosystems are nitrogen limited (see below) and therefore they must be treated differently. Paerl (1988) has reviewed the factors which lead to nuisance blooms in coastal, estuarine and inland waters and has shown that there are many similarities. Both need increased nutrient loads and stable water columns.

An increase in the frequency of the occurrence of blooms of cyanobacteria in inland waters is largely the result of nutrient enrichment by human activity although some blooms may be entirely natural in origin. The same may be said of dinoflagellate blooms in coastal waters. Hallegraeff (1993) has recently shown that coastal blooms of toxic species have become much more common in recent years as a result of coastal eutrophication. Physical processes of water column stratification play an important role as well as nutrient enrichment. Algal blooms in rivers result from similar processes - the key parameters are nutrient loadings and flow rate or residence time.

One thing this paper attempts to do is to derive an understanding of the general functioning of freshwater ecosystems. There is much concern at present with the "health" of aquatic systems all around the world. "Health" may be measured in many ways, but clearly one way is to look at the essential features of system function and to look for perturbations from the pristine state. System function may be a more or less useful indicator of "health" depending on the response times and scales of the processes involved.

There are few cross-system comparisons of ecosystem function in the literature which have sufficient resolution to be able to examine changes in the functioning of

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[1] Cyanobacteria (otherwise known as blue-green algae) are correctly classified as photosynthetic bacteria. They are structurally identical to prokaryotic bacteria and, in many ways, quite different from the rest of algae which are eukaryotes.

ecosystems with human impact. One significant exception is the review paper by Kelly and Levin (1986). Kelly and Levin examined the relationship between external and internal nutrient loadings for over 200 natural ecosystems and were able to show trends which revealed important changes in ecosystem state in response to altered loadings. Biodiversity is presently popular as a measure of ecosystem "health" but it will be susceptible to a lot of short term variation in population and community dynamics. Measures of system function may be a better way to examine changes due to human impact over longer time scales in cases where biodiversity is not obviously changing or where there is much short term "noise" in the abundances of species. I will return to this point at the end of the paper.

If we are to understand the underlying causes of the recent spate of algal blooms in Australian waters (be they due to nutrient enrichment, river regulation or climate variability) and if we are to manage the threat to public health, then we face a number of tasks. There is a need to review the existing international literature on the relationships between phosphorus and nitrogen loadings, algal biomass and community structure in rivers, lakes and storages. There is then a need to place the existing Australian knowledge in the context of the world wide information and to identify gaps in our present knowledge. This is a first step to the formulation of priorities for further Australian research in this area. This discussion paper attempts to provide a framework for these tasks. Much of this discussion paper is taken directly from Harris (1994) but additions and deletions have been made to suit this particular task.

This paper therefore assembles a review of recent world-wide literature and places it in an Australian context. Much emphasis is placed on using the international literature to understand the general condition. It must be remembered that conditions in Australian freshwater and coastal marine systems are frequently said to be quite different from those in Northern Hemisphere systems where much of the theoretical development of this work was carried out. Australian freshwater systems are rarely cool, clear, deep and mono- or dimictic. On the contrary they are usually warm, shallow, turbid, saline and either polymictic or meromictic. The Australian climate, hydrology, geology, geomorphology and biology are, in some very important respects, quite different from the rest of the world (Williams 1982).

The question is: to what extent these apparent differences lead to different ecosystem behaviour and call for different management responses? General relationships may be discerned, so science is possible; but significant differences exist, so science is necessary. World-wide best practice may need to be modified in the light of local conditions.

This paper is structured as follows: first I review the development and theoretical underpinnings of Vollenweider's models which relate nutrient (particularly phosphorus, P) loadings to the concentrations of P in the water of lakes and storages. Having determined the amount of nutrient in the water it is then possible to apply a number of empirical relationships which connect the concentration of P in its various forms to the algal biomass which develops (as chlorophyll concentration in the water). Having discussed the potential of a water body to develop algal blooms of a given size, I then turn to factors which are likely to modify the general patterns of system behaviour. Finally I discuss food chain interactions, the question of the species composition of that bloom and the potential to predict the species composition from a relatively simple subset of additional ecological parameters. In all cases the relationships developed are based on large sets of limnological data published in the international limnological literature. In each case it will be necessary to decide if the general relationships found elsewhere are applicable to local conditions. I have biased this review in favour of papers which contribute to a general understanding of system behaviour. I have therefore tended to ignore descriptive studies of individual systems in favour of syntheses and data compilations encompassing large numbers of studies.

Many not fully familiar with the limnological and ecological literature and with the nuances of ecological theory will find this paper complex and difficult. I make no apology for this. The question raised - precisely what is predictable about aquatic ecosystems and why? - is at the cutting edge of ecological theory and practice. This question is "complex interactions" and system behaviour writ large. Big and complicated questions require big and complicated replies until a sophisticated understanding is achieved. Only then may we attempt to simplify. We have discovered time and time again in ecology that simplification of a complex problem (usually in ignorance) leads to unexpected and surprising (even tragic) results. I have therefore included sections on the history and philosophy of ecology. There are no "magic bullets" in ecology at present and there probably never will be. In the early 1990s ecology is undergoing a reappraisal and there are a number of new conceptual ideas being tested. In my opinion this is not before time. As the years have gone by we have slowly begun to realise that the ecological world is much more complex than we think and that simplistic models and simplistic prescriptions for research topics do not realistically describe what common sense tells us is happening. We sorely lack good practical recipes for many severe environmental problems.

1.2 Ecology as a social construct.

The conceptual basis of science is not free from the biases of the society in general and many questions can only be addressed in particular ways depending on the philosophical climate of the day. Concepts and vocabulary determine what can be discussed and how. Ecology is no exception and has a strong foundation in social and, even, economic theory (McIntosh 1985, Kingsland 1985). It comes as no surprise to find, therefore, that in this so-called "postmodern" era (Jameson 1991) at "the end of history" (Fukuyama 1992) when a belief in certainty has evaporated, science itself is being called into question (Appleyard 1992) and ecology is going through a period of reassessment also. Peters (1991, 1992) has criticized the widely accepted theoretical bases of ecology and has criticized ecologists for their adherence to "elusive and ethereal goals". He has called for the formulation of more testable hypotheses and their validation by comparison with data from the field. Like Peters, I see too much theoretical bias (Harris 1986) too much descriptive work, too many simple approaches to complex problems, too many "band wagon phenomena" and too little critical analysis. Too little ecology seeks syntheses and general relationships (Allen and Hoekstra 1992).

Peters (1991) has criticized the standard equilibrium ecological theory and has argued for a kind of "instrumentalism" or "phenomenalism", an approach that has a good measure of reliance on "use what works" rather than a heavy reliance on particular theoretical frameworks. I believe that we do need a new conceptual framework for much of ecological theory and that we need to spend a lot more time trying to understand how the world works before adopting a particular theoretical framework or management approach. To this end I applaud the effort of Allen and Hoekstra (1992), Pimm (1991) and Peters (1991, 1992) who have not only provided a critique of traditional theory but have tried to use data from field observations to test hypotheses and to look for patterns that can be explained in realistic terms. Limnology can provide a unique test of theory because of the wealth of data now available on system function.

The challenge is to find a conceptual basis and quantitative ecological relationships which have predictive power. A predictive ecological capability is an essential goal in a world beset with severe environmental problems. A predictive capability can only be predicated upon robust knowledge of ecological structure and function, pattern and process. Even if prediction turns out to be very difficult we need to know what is possible and why. After periods in the development of the science of ecology when equilibrium community models and systems analysis were popular but produced little of practical value (at least according to Berlinski 1976 and Peters 1991, 1992) we are left with few useful predictive models. Water quality managers need to appreciate that demanding simple answers to simple questions will no longer suffice.

The sheer complexity of the real world and the fact that species and processes interact over such a wide range of scales (Harris 1980, 1986, Allen and Hoekstra 1992) makes it very hard to do good (scientific) ecology. By scientific I mean the application of traditional scientific techniques based on algorithmic compression. Algorithmic compression is the use of simple and elegant sets of simple mathematical equations to describe complex real-world events. This was very much the "modern" approach. It is the basis of Newtonian physics, engineering and much of the technological development of the modern world. But algorithmic compression simply does not work well in ecology because there are too many complex, interwoven interactions at a range of scales (Harris 1980, 1986). As Slobodkin (1992) has noted, ecology is the least tractable science. Ecology has entered into a new phase of sceptical realism - what do we know and why? What works and why?

So we embark on a difficult and complex journey - bear with me. I will keep the language as simple as possible and the arguments as clear as possible. I hope the reader will agree with me that the end point is well worth the effort.

2. Nutrient loadings and the biomass of phytoplankton and other components of the pelagic ecosystem.

When Vollenweider first began collating data from a wide range of water bodies under the auspices of the OECD eutrophication study, his express intention was to seek relationships which transcended the contingent variability inherent in each site. He did not want to have to come to grips with the complexity of each and every body of water. Vollenweider produced a series of ground breaking papers which described the relationships between nutrient loadings, concentrations of nutrients in the water and phytoplankton biomass in a set of predominantly northern temperate lakes. The basis of this work was an analysis of the mass balances of substances in lakes treated essentially as "black boxes" with inputs, internal transformations and outputs. The concepts originally outlined by Vollenweider were then developed and extended by a series of authors so that a significant body of knowledge was developed.

Twenty five years of hindsight gives a perspective not available to those doing the work at the time. Vollenweider's models are a special case of a more general set of "plankton models" which describe the relationships between input and output of nutrients in water bodies and processes within the food chains (see section 2.4 below). Phytoplankton biomass is indeed controlled both by "bottom up" processes such as temperature and the availability of light and nutrients, and by "top down" interactions such as zooplankton grazing. Vollenweider clearly realised this and the following diagram appears in many of his papers

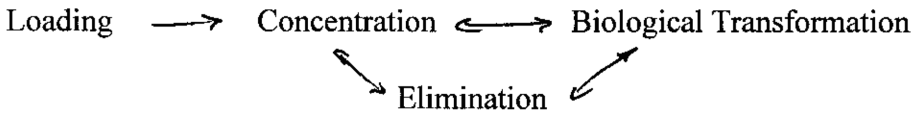

Figure 1 is a more complete diagram of some of the more significant interactions and transformations in these systems. Nutrient sources can be broadly divided into external loadings and those fluxes of nutrients originating from internal processes such as sediment release and nutrient regeneration from zooplankton grazing. Losses from the system can be broadly divided into washout and permanent incorporation in the sediments. As will become clear one of the most important factors in the interaction between loadings and the expression of the phytoplankton response is the relative magnitude of loadings derived from external sources of nutrients and those derived from internal regeneration (Gachter 1987).

As Thomann (1977) pointed out, these models are a subset of a broader class of "plankton models" which describe the interactions and transformations of materials and energy in aquatic ecosystems (See Fig 1). Large scale ecological modelling of this type - which broadly may be called system simulation - was very popular in the 1960s and early 1970s and was (ironically) derived from models of war games derived by the Rand Corporation (Berlinski 1976). Some of the largest early plankton models were those constructed for Lake Ontario as part of the International Field Year of the Great Lakes in 1972-3 (Thomann et al 1975, 1981, Scavia 1980). Many of these models were over parameterised and lacking in proper validation. Berlinski described this approach as "grand theories.... brought low by insufficient means".

Inflow, outflow, water residence time and sedimentation may be modelled by physically and mathematically rigorous equations. The residence time of water in the system is a key parameter which controls the balance of sedimentation and outflow of nutrients. {Even though the terminology is different in rivers and lakes ("nutrient spiralling" in rivers, "internal loadings" in lakes) the fundamental principles are the same. Nutrient loaded into the system are, to a varying extent, exchanged with the sediment.] Biological interactions within the food chain such as grazing are less amenable to rigorous mathematical description and are usually treated by statistical and empirical models. Vollenweider's models may therefore be treated as two essentially separate subsets; loading models which have a sound basis in physical theory, and empirical statistical models which relate the yield of algal biomass (usually expressed as chlorophyll) to nutrient concentrations in the water (Chapra 1980, Ahlgren et al 1988).

2.1 Loading models.

Although this work has a long history (Sawyer 1947), the theoretical development of these models was primarily done by Vollenweider and his co-workers in Canada (Vollenweider 1968, 1969, 1975, 1976, Vollenweider et al 1980, Vollenweider and Kerekes 1980, Janus and Vollenweider 1981, 1984) during the 1970s. An excellent summary is given in Vollenweider and Kerekes (1980) and a brief outline of the major parts of the theory will be reiterated below (see also Ahlgren et al (1988) and references therein). It is necessary to understand the basic assumptions used so that elaborations of the theory into inappropriate situations may be avoided.

If a lake is assumed to be an open system then the mass balance equation may be written as

$$dM/dt = I - O - (S - R) \qquad (1)$$

where dM/dt is the gain or loss of substance M over time dt and where I is the external load, O is outflow loss, S is loss to sediments and R is sediment regeneration (internal load).

Following Vollenweider et al (1980), at any given time the instantaneous change of phosphorus (P) in a lake can be calculated as follows:

$$dP\,,t\,/\,dt \;=\; Q_{j,t}\,[P]_{j,t} - Q_{w,t}\,[P]_{w,t} - A_eF_e(P) + A_sF_s(P) \qquad (2)$$

where $Q_{j,t}$ = volume of jth inflow at time t ($m^3\ s^{-1}$)
$[P]_{j,t}$ = concentration of the jth inflow at time t ($mg\ P\ m^{-3}$)
$Q_{w,t}$ = outflow at time t ($m^3\ s^{-1}$)
$[P]_{w,t}$ = concentration of outflow at time t ($mg\ P\ m^{-3}$)
A_e = area of epilimnion (m^2)
A_s = area of sediments (m^2)
$F_e(P)$ = flux through base of epilimnion ($mg\ P\ m^{-2}\ s^{-1}$)
$F_s(P)$ = flux through sediment surface ($mg\ P\ m^{-2}\ s^{-1}$)

Equation 2 is a more complete form of (1). Vollenweider used annual averages to sum inputs and derive average concentrations of P in the water. He also approximated $A_eF_e(P)$ by assuming:

$$A_e\,F_e\,(P) = A_e\,V\,[P]_L$$

where V is an apparent annual average settling rate for P in $m.y^{-1}$(not the same as the instantaneous sedimentation velocity) and $[P]_L$ is the average lake concentration. By summing inputs and outputs, and by using annual average concentrations (2) becomes:

$$\Delta P / \Delta t = Q [P]_j - Q [P]_L - A_e V [P]_L + A_s F_s (P) \qquad (3)$$

where Q $[P]_j$ is the product of the annual average inflow and the mean inflow concentration, Q $[P]_L$ is the product of annual average outflow (assumed equal to inflow) and mean lake concentration, A_e V $[P]_L$ is defined above.

If both sides of (3) are divided by lake volume V_o and steady state conditions are assumed then $[P]_L$ may be approximated by:

$$[P]_L = (Q/V_o) [P]_j + (A_s/V_o) F_s (P) / Q/V_o + (A_e/V_o) V \qquad (4)$$

which shows that the average epilimnetic concentration of P is increased by external loading and sediment release (numerator) and decreased by outflow and sedimentation (denominator). This model assumes that annual outflows equal annual inflows and that rainfall exceeds evaporation. It is also necessary to assume that the annual average loading is a valid parameter. In sub-tropical and tropical storages these assumptions may not be valid (Harris 1986). Many sub-tropical Australian storages fill in a few days once a decade. Between times there may be little or no inflow or outflow and evaporation exceeds rainfall.

Further models were developed by making some particular assumptions as follows. V_o/Q_o is the filling time or water residence time T_w, A_e and A_s may be approximated by lake surface area A_o and V_o/A_e and V_o/A_s both are approximately equal to the mean depth of the lake (Z). Further definitions included:

$Q/A_o = q_a$	the hydraulic load ($m\ y^{-1}$)
$[P]_j\ q_a = L(P)$	areal load of material to the lake ($mg\ P\ m^{-2}\ y^{-1}$)
$L(P)/Z = l(P)$	volumnar load of material to the lake ($mg\ P\ m^{-3}\ y^{-1}$)
T_w	reciprocal of flushing rate y^{-1}, hydraulic residence time
q_s	mean depth / hydraulic residence time, Z/T_w ($m\ y^{-1}$)

The above terms are to some extent interchangeable so a variety of equations can be derived from equation (4). Vollenweider generalised equation (4) to:

$$[P]_L = [P]_j + F_s (P) f_1 (T_w, Z) / 1 + V f_2 (T_w, Z) \qquad (4a)$$

If the internal loading is assumed to be zero this reduces to an important limiting case where:

$$[P]_L = [P]_j \ / \ 1 + V f(T_W, Z)$$

Vollenweider obtained $V f(T_W, Z)$ by a regression analysis of $[P]_L$ against $[P]j$.

The basic OECD relationship postulated by Vollenweider (1968) was a classification of lakes based on the relationship between the phosphorus loading L(P) and the mean depth divided by the hydraulic residence time (Z/T_W). This framework allowed managers to separate eutrophic lakes from oligotrophic lakes, to define "excessive" loadings and to set "permissible" P loads.

Vollenweider (1969, 1975, 1976), Vollenweider and Dillon (1974) and Dillon and Rigler (1974a) applied this set of constructs to lake phosphorus models. Vollenweider (1969) originally obtained:

$$[P]_L = L(P) \ / \ Z\,(1/T_W + s) \qquad (4b)$$

where $[P]_L$ is the average lake concentration of P, L(P) is the annual average P load and s is a phosphorus sedimentation coefficient. If this equation is expressed in the same form as (4a) assuming a zero internal load Vollenweider achieved

$$[P]_L = [P]_j \ / (1 + \sqrt{T_W}) \qquad (5)$$

Vollenweider assumed s to be a function of V/Z with V having a value of 10-20 m y^{-1}. With most northern hemisphere lakes having a mean depth in the region of 10 - 20 m then V/Z is approximately 1 y^{-1} - equal in magnitude to the averaging time of the models. Dillon and Kirchner (1975) found that the apparent values of V varied between 1.4 and 51.6 m y^{-1} for a set of individual lakes, so V cannot really be regarded as constant.

It is quite possible to calculate the nutrient loadings to rivers (and hence the nutrient concentrations in them) as long as the hydrology of the system is known and some assumptions are made about such things as settling velocities and nutrient spiralling. In situations where the nutrient loading to rivers and storages is driven by storm events (a common pattern in this country) particulate loadings may increase dramatically during storm events. Thus much of the particulate nutrient loading may enter and sink quite rapidly over a period of days to weeks. Settling velocities are therefore a function of the magnitude of individual events and cannot be regarded as constant. Settling is significant even in flowing waters and is dependant on velocity. The sediments of regulated rivers will act as nutrient sinks during periods of low flows but dramatically increased flows during storm events will scour out previously sedimented material. Australia has the full spectrum of water bodies from freely flowing rivers, through regulated rivers to weir pools, storages of various sizes and finally lakes. In all cases water residence time (and its variability through time) is a key determinant of events in the system.

The apparent settling velocity of P in lakes and rivers is a function of a number of features of physics, chemistry and biology including loading factors (see above), alkalinity, pH, ionic strength, iron, calcium, dissolved humic substances, suspended solids, algal biomass and species composition, food web structure, physical stratification, hypolimnial anoxia, turbulence, lake surface area and mean depth (Ahlgren et al 1988). Vollenweider (1976) recognised the complexity of the factors underlying s and adopted some "more or less defensible shortcuts". The best correlation for large storages and lakes was between s and $1/\sqrt{T_W}$.

Dillon and Rigler (1974a), Kirchner and Dillon (1975), Larsen and Mercier (1976) and Ostrofsky (1978) examined variants of equation (4) that defined a P retention coefficient R_c, which represented the portion of the P load retained by the lake. This is usually equal to that portion of the load which ultimately sediments to the bottom. After a statistical analysis of lake data Larsen and Mercier (1976) found that the best expression was

$$R_c = 1 / 1 + \sqrt{(1/ T_W})$$

which is equivalent to the Vollenweider model.

Lazenby (1975) measured the AHODs in 14 Ontario lakes and looked for correlations between AHOD and other water quality variables. A significant correlation existed between summer secchi depths and AHOD but not between AHOD and mean seston dry weights. Canfield and Bachmann (1981) carried out an extensive analysis of data from 626 northern hemisphere lakes (many based on the US EPA surveys) and showed that they also could predict in-water P concentration from L(P), Z, T_W and s. Furthermore they showed a significant correlation between total P (TP) in 301 US rivers and the concentration of suspended sediments. They showed poor correlations between chlorophyll and s.

P loading models work reasonably well for a "population" of lakes but can be quite imprecise when applied to individual water bodies (Ahlgren et al 1988). Janus and Vollenweider (1981) compared the standard OECD relationships to data from 130 Canadian lakes and identified a number of situations where the usual relationships between flow, load and biomass did not hold. The statistical comparison of the OECD with the Canadian data identified the following problem areas:

euphotic zone depth/mixing depth ratios $>> 1$
high or irregular hydraulic load - rapid flushing
high mineral turbidity
N/P ratios < 5 and or TP > 100 mg.m^{-3}
P relatively inert or high internal load
dynamic equilibrium between load and lake concentration not attained

The basic assumptions of the limiting case Vollenweider model are annually averaged loads and in-water concentrations of P, a zero internal load and a sedimentation velocity, mean depth relationship of approximately unity. In other words the model assumes that the water body is a net sink for P and achieves a steady state at a scale of one year (Harris 1986). This also effectively assumes that water residence times are of an equivalent magnitude. These models work well for the usually cool, oligotrophic, clear, deep and mono- to dimictic Northern Temperate lakes. *Many of these limiting* *assumptions are violated by Australian lakes, storages and rivers. More effort needs to be put into developing models for the estimation of P concentrations in Australian rivers and storages.*

2.2 Loadings from land use etc.

Nutrient loadings arise from a number of both point and diffuse sources. Point sources of P (usually waste water treatment plants) are fairly easy to quantify but variations in flow and load require careful attention to ensure that the actual time-averaged loading is accurately measured. Diffuse sources of nutrients arise from surface runoff, streamflow and groundwater discharge and are much more difficult to quantify. There is a large body of international work which attempts to quantify diffuse loadings from various land uses as a function of vegetation type and cover, slope, rainfall intensity etc. In particular a large amount of work was done in the Great Lakes region of Canada and the USA in the 1970s under the auspices of the International Joint Commission, Pollution from Land Use and Related Activities Research Group (PLUARG 1978). Dillon and Kirchner (1975) examined the export of P from 34 catchments in Southern Ontario and provided a literature review.

Diffuse loads of total P (TP) vary from about 0.1 kg $P.ha^{-1}.y^{-1}$ in undisturbed forests and vegetated terrestrial ecosystems to in excess of 20 $kg.ha^{-1}.y^{-1}$ in areas of disturbed ground under urban development or intensive horticulture on slopes (Ahl 1988). Total N (TN) loads range from about 1 to 50 $kg.ha^{-1}.y^{-1}$. Generally speaking, P predominantly exists in insoluble forms in soil and is therefore transported in particulate forms, whereas N loads are usually in the form of nitrate which is soluble in both surface runoff and groundwater. In Australia, Cullen, Rosich and Smalls have, amongst others, been active in estimating diffuse loads from local catchments (see e.g. Cullen et al 1978, Rosich and Cullen 1982, Cullen 1991).

Kira (1991) summarised data from 145 lakes world-wide and showed that a number of water quality parameters were directly related to land use in the basin. Transparency was greatest in large lakes and decreased with decreasing lake volume. The concentration of suspended solids in the water decreased as the amount of forest cover in the drainage basins increased. Suspended solids concentrations increased exponentially as the proportion of agricultural land increased in relation to lake volume. TN and TP concentrations were directly related to the human population in the drainage basins when this was expressed as a function of population per unit water volume. The broad relationships between events in lakes and conditions in their drainage basins led to the development of the Morphoedaphic Index (MEI) in the 1960s and 1970s as a broad predictor of fish yield (Ryder et al 1974). The use of MEI is not precise because of the large number of variables but it does reflect the dependence of water quality on processes in drainage basins.

More recently the CSIRO Division of Water Resources has developed a Catchment Management Support System (CMSS) which attempts to provide estimates for nutrient export based on land use, rainfall, soil type, slope and location. As part of the CMSS project Marston et al (1993) have carried out a literature survey of work published both in Australia and overseas in the last twenty years and a dossier of references and nutrient export data has been developed. Australian catchments, being largely subtropical, are characterised by more intermittent streams and are much more prone to flash floods than North American or European catchments (see below). Soils are susceptible to erosion, particularly when damaged by overgrazing or changes in land use. Large amounts of fine particulate material can be washed off Australian drainage basins subject to human intervention (Cullen and O'Loughlin 1982, Olive and Walker 1982).

Cosser (1989) examined the relationship between rainfall and nutrient export coefficients in South Pine catchment in Southeast Queensland. What he found was that the use of coefficients simply based on units of kg ha^{-1} was not sufficient to describe the observed patterns of nutrient export from the catchment. He found that it was necessary to take rainfall intensity into account as well so, that the best units were those of $kg.ha^{-1}.mm^{-1}$ of rainfall. The proportion of stormflow was the major determinant of nutrient export and 75-89% of the P loads to the river were carried in 2.8% of the time. Significantly, even in P deficient soils, storm erosion and runoff was sufficient to produce P concentrations of up to 2.48 mg l^{-1} in the runoff. Concentrations as high as this are sufficient to produce significant phytoplankton blooms in receiving waters as long as the runoff is a significant fraction of the water in the system after storms and as long as the particulate P is available for phytoplankton uptake and growth. This is certainly true in parts of this country - especially South-eastern Queensland.

Nutrient export regimes from Australian catchments are therefore likely to be quite different from overseas conditions. Given the long history of interest and the importance of diffuse loads in determining water quality in rivers and water bodies, *I find it surprising that no-one has seen fit to do more measurements of export from Australian catchments or do a detailed, up to date review of the Australian literature and a critical comparison with international biogeochemistry and management experience. This needs to be done.*

2.3 Seasonality and short term variation in loadings

The subtropical climate of much of Australia ensures that rainfall rates are very high on occasion (rainfalls of >500 mm per storm event are frequent) and that many rivers and streams are ephemeral, drying up completely during drought. Rain rates are in any case lognormally distributed with a statistically predictable top end tail in the distribution (Kedem and Chiu 1987). Australian rivers and streams show the most variable stream flow patterns in the world (Body 1979) and the discharge is very "flashy" (Stevens and Smith 1978). Ephemeral desert rivers have recently been shown to have sediment transport characteristics quite unlike those in perennial rivers (Laronne and Reid 1993). Sediment transport is frequently one million times greater than in perennial rivers and bed scouring is extensive. *New predictive sediment transport equations will need to be developed for such rivers.* Given the high variability in rainfall rates in Australia and the impact of flash floods on otherwise dry creek beds, loadings to lakes and storages are therefore likely to be dominated by storm runoff events. Storages (such as those in SE Queensland) may receive up to 50% of their storage volume in one day - and then nothing for many years! What, we are entitled to ask, can be done to mitigate the effects of cubic kilometres of water wandering around the landscape, scouring particulate nutrients from catchments and depositing them in downstream pools, storages and channels? If concentrations of particulate P reach the mg l^{-1} range, algal blooms will inevitable follow in storages and river sections where the water residence time is sufficiently long.

High variability in flow, and uncertain relationships between flow and load, lead to great uncertainties in the estimated loadings from Australian rivers. This is, however, a matter of degree. Despite the use by Vollenweider of annual averaged loads the calculations of nutrient loadings from most rivers is problematical - perhaps more so than is usually admitted. As Bailey-Watts and Kirika (1987) noted, there are relatively few water bodies for which detailed loadings measurements have been made at time scales capable of resolving storm events. The studies of Bailey-Watts and Kirika (1987) and Stevens and Smith (1978) in the northern hemisphere are exceptions and show that even in these more "typical" climates situations arose where in Loch Leven, for example, 60% of the P load from one stream occurred in six days. In County Antrim, N. Ireland the River Main showed "flashy" flow regimes. and was studied in detail by Stevens and Smith (1978). Sampling at eight day intervals overestimated the soluble N and P loads by 18% and 12% respectively but underestimated the total P load by 43%. High flow periods diluted the soluble N and P load but dramatically increased the particulate P load. High flow periods were generally missed by the regularly spaced sampling regime.

The calculation of loads from flow data is fraught with uncertainty. There is a non stationary correlation between flow and nutrient concentration. Concentrations often increase sharply as the flow increases during a storm, followed by dilution as the runoff continues. Hysteresis effects are widespread (Olive and Walker 1982). Particulate P and N concentrations increase sharply with flow due to erosion of the catchment and the bed, whereas soluble nutrient concentrations decrease due to dilution. Plots of flow vs. concentration are often widely scattered so that statistical correlations between flow and concentration are very poor. Flow is measured much more often than concentration so that concentration data are usually sparse and data interpolation routines produce uncertain results. There is a tendency to produce plots of load (flow x concentration) against flow and, because flow varies much more than concentration by orders of magnitude, the correlations are improved. Obfuscation does not, however, improve the basic data or the uncertainty of the relationship.

Cullen and Smalls (1981) summarised a number of results of detailed loading measurements from, amongst others, Lake Burley Griffin (Cullen et al 1978, Cullen and Rosich 1979, Cullen and O'Loughlin 1982). Loads to the lake were dominated by flood periods which lasted at most a month. P retention was inversely related to the hydraulic loading, ranging from 91% during drought to 12% during floods. Cullen (1991) quotes data from Monkey Creek (NSW) which showed that 61% of the total P and 41% of the water moved down the Creek in 1% of the time. During periods of low flow, creeks and rivers become sinks for nutrients when organic material settles in the bed. During periods of high flow, this material is mobilised as well as material from the river bed itself (Cullen and Smalls 1981). *Automatic sampling of the entire flow regime at frequent intervals (at least daily) is required in order to fully document the* *load/flow relationship for any given stream.* Given the long time periods between floods this may require many years of intense monitoring before the full relationship is known. Automatic equipment capable of remote operation for long periods is now becoming available. *This will be the only way to accurately measure loadings from Australian rivers and streams.*

Rainfall, runoff and river flow are strongly linked to interannual climate variability in Australia through mechanisms such as the El Nino - Southern Oscillation (Simpson et al 1993). ENSO events have a hemispheric dimension and are associated with fluctuations in sea surface temperature in the Pacific Ocean and large scale changes in the position of the continental high over Australia. ENSO events have a characteristic time scale of the order of seven to ten years and have a strong influence on rainfall, runoff and crop production in Australia (Nicholls 1985). Australian rainfall is highly irregular and intense and is linked to ENSO events throughout NSW and SE Queensland and the entire Murray-Darling Basin (Simpson et al 1993). In addition, Harris et al (1988) documented an eleven year cycle in the Zonal Westerly Winds over Tasmania which was linked to ENSO and which had impacts on a number of processes in both coastal marine and freshwater ecosystems. As nutrient loadings to Australian storages are predominantly driven by storm events, they are, in effect, part of a climate variability problem which has hemispheric and interannual dimensions.

River regulation will totally alter the flow vs. load relationships of Australian rivers and storages. Flood flows will be trapped along with the suspended particulates and nutrients. Weir pools will act as sinks until the extreme floods which will flush out the system and transport materials downstream, only to deposit them again at some point. Water extraction from river systems will influence the transport of nutrients down river system by slowing the flow and trapping nutrients. Thus river regulation will have significant implications for large river systems like the Murray-Darling - flow regulation will be nutrient transport regulation and phytoplankton growth regulation all in one! (see below also).

Fire is another feature of the Australian landscape which is influenced by climate and ENSO events through the incidence of drought. Climate variability has a great effect on the severity and timing of bush fires - as does human forest management practice (Clark 1988). Not only does runoff increase after fire, so also does the concentration of nutrients in that runoff. Cullen and Smalls (1981) and Cullen and O'Loughlin (1982) gave some data for runoff from the Little River catchment (NSW) after fire which showed a tenfold increase in total P concentration in the river after the catchment was burnt. Smalls (pers. comm.) has noted that events in Lake Burragorang (NSW) were driven by infrequent storm and fire events which had impacts on the phytoplankton dynamics in the lake for years afterwards (Ferris and Tyler 1985, 1992).

Climate variability will have a major impact on the population dynamics of phytoplankton in storages through the effect of periodic nutrient loadings after storm or fire. Not only will the loadings determine the overall trophic state of water bodies for up to a decade after the event, but the timing of the event during any given year will have significant "downstream" ecological consequences on the seasonal succession of species. This can be seen in the weekly data from North Pine storage in Brisbane (Baxter, unpublished) where individual storm events had consequences for years afterwards. Washout of particular successional stages can lead to long term consequences for the expression of particular ecological states. Storm flows tend to bring in significant inputs of silica from soil erosion, so that the growth of diatoms tends to be favoured by the high flows after storms. River flow itself, through its effect on turbulence, also has a direct effect on the growth of certain types of phytoplankton blooms (see below). Cyanobacterial blooms are more prevalent in low flow conditions and tend to be favoured by the silica depleted conditions which exist after the diatoms have exhausted the silica supply and ceased growth (Talling 1986). There are, therefore, at least two mechanisms by which climate variability will have a major impact on the occurrence of nuisance algal blooms.

In general it seems that, in Australia, phytoplankton dynamics are dominated by irregular and infrequent extreme events - a situation which is not infrequent in tropical and subtropical lakes and storages (Talling 1986), but which is quite different from that found in the more completely studied northern hemisphere catchments (Talling 1993). There is, as yet, little Australian data to support this assertion - some of the (very few) longer term studies that do exist must be published without delay so that both researchers and managers may appreciate more fully that "nature of the beast". Unfortunately the strong link between climate variability and algal bloom dynamics will almost certainly mean that the present concern over the high incidence of blooms will abate as rainfall returns to parts of this country. Support for research will abate also. *There is a real need for work to be done on the interannual variability in climate and the incidence of toxic algal blooms - including an analysis of anecdotal historical data (even such data as newspaper reports).*

So while there are large gaps in our knowledge of Australian systems in terms of nutrient loadings - and the situation is not helped by the fact that we suffer badly from systems driven by brief storm events which are widely scattered over long time scales - there is no practical or conceptual reason why these gaps cannot be filled. The understanding of the problem exists and the equipment which can provide the data also now exists. Automatic remote sampling systems can now provide hourly or daily data for years on end. Flow regimes can be (and are) similarly monitored.

2.4 Availability of various forms of P

Having determined the concentration of total P in the water body from the loadings, water residence time etc. it is also necessary to decide whether there are factors at work which affect the conversion of total P to algal biomass and hence the "expression" of the nutrient loading. The primary from of P used by phytoplankton for growth is inorganic phosphate (PO_4 - P) although some organic forms of P may be used, particularly when phosphate is scarce in oligotrophic lakes. Clearly, if the majority of the P loading is in a form which is rapidly available for algal growth (such as sewage effluent) then the resulting biomass will be greater than if much of the P is in particulate or organic forms which are not readily available to the algae. It has been estimated that 70% of the P in sewage is available for phytoplankton growth (Holtan et al 1988). Other sources of P input which include more refractory forms of organic P are less available in the short term (see below).

There is, in fact, a spectrum of forms of P in all waters from inorganic, particulate (unavailable) P, through various forms of organic P in particulate, colloidal and soluble forms, through a range of molecular weights to inorganic phosphate (Holtan et al 1988). Not all analysis techniques give the same answers because of differences in methodology and the effectiveness of various digestion techniques. Thus "soluble reactive P" (SRP) is that P which yields to acid treatment during the normal phosphate analysis method - and thus includes both phosphate and various low molecular weight, labile organic forms of P. Most of these species of P are assumed to be available for algal growth. SRP is not a measure of the true phosphate - P in the water. Rigler (1964, 1966) demonstrated this thirty years ago by means of isotope dilution techniques using ^{32}P - PO_4. The phytoplankton respond to depletion of SRP pools by producing phosphatases which are capable of hydrolysing certain low molecular weight organic forms of phosphorus. These enzymes are inhibited by SRP in the water so one measure of SRP depletion is phosphatase activity in the water (Jansson et al 1988). "Total P" includes those soluble and particulate, organic and inorganic forms of P that are rendered to phosphate by either acid or alkaline persulphate digestion. Certainly these species of P are not all available for algal growth.

Even these essentially chemical definitions are by no means sufficient. In living ecosystems P is tied up in a wide spectrum of living and abiotic pools (Harris 1986, see also Fig 1). These pools have turnover times ranging from seconds to years (Harris and Griffiths 1987). Some of the P is tied up in living pools (phytoplankton, zooplankton, fish, macrophytes) and a water sample from the surface will only include some of these pools. Storage of the water sample will lead to the death of many organisms and the release of their labile P pools into the water. Hence it is important to analyse samples without delay and the precise sampling and analysis protocol must be designed to answer some precise questions with a clear knowledge of the purpose in mind. Filtering water samples will exclude particulate and living forms of P but include colloidal forms. Water samples (filtered or not) do not include macrophyte and sedimentary pools of P which will, in most cases, be significant (Figure 1). Great care must be exercised when analysing historical data because the original sampling design and the analytical techniques used at the time will affect the results obtained. Unfortunately not much of the old data is very reliable. *Data from samples collected for one purpose rarely yields useful information when interrogated for another, later purpose. Uncritical analysis of piles of old data rarely yields "great truths".*

There have been claims that Australian waters differ from those overseas because more of the total P here is said to be unavailable for algal growth (Geddes 1984). This has arisen partly, I suspect, because some comparisons between Australian data and the standard OECD relationships has shown lower algal biomass in Australian storages than would be predicted by Vollenweider's relationships (refs here). There does not yet appear to be sufficient published data to fully support this conclusion. In my opinion there is a great lack of good nutrient and water quality data from Australian rivers and storages. Even now the precision and accuracy of many analyses is insufficient. Many laboratories quote P concentration data to the nearest 10 ug l^{-1} when a precision of <2 ug l^{-1} is required. After all, 10 ug l^{-1} total P is the break point between oligotrophic and mesotrophic conditions in the OECD models. Much historical data is unreliable and, while severe logistical problems in sampling remote sites are admitted, there is a general lack of good nutrient data from many crucial sites. Given the climate variability, how can we really determine if water quality has deteriorated over recent years without good long term data sets?

The question of P availability in Australian waters is complicated by terminology and deciding what is a "limiting" nutrient (see Section 6 and Harris 1986). Because of the wide variety of processes in operation in natural waters (growth, grazing, microbial metabolism, sedimentation) and the rapid turnover of some P pools, it is possible to argue that over sufficient time almost all the P in the system will be available for the accumulation of phytoplankton biomass. What will determine the biomass produced will be the exchange coefficients between all the chemical and biological forms of P in the system and the final distribution of pool sizes. The phytoplankton pool of P is but one pool of many. What controls the rate of growth of the phytoplankton is the *flux* of P which links the uptake of P by the algae to the turnover and depletion of the other pools. Thus nutrients may limit growth but not biomass and vice versa.

I cannot find sufficient data to unequivocally determine if Australian waters really are different in terms of total P availability from other parts of the world. Certainly Australian waters are more turbid than many in other parts of the world. Particles in Australian waters are coated with organic material (they have the same absorption spectrum as dissolved organic carbon in the water - Kirk 1983) which can exchange P with the soluble and colloidal forms in the water. Oliver et al (1993) have recently published details of an Fe stripping method which effectively acts as an infinite sink for P and measures the P which can be stripped from particulate and other organic sources over a period of up to two hours. Oliver et al (1993) have reported an excellent comparison between this method and measures of available P using algal culture experiments. Shan et al (1994) have also recently perfected a flow injection analysis method using immobilised phosphatase enzymes to measure the total "available" P. Neither method has yet been fully tested against other, more traditional, methods of P analysis.

In an analysis of the P in suspended particulate, colloidal and dissolved fractions, Oliver et al (1993) showed that different waters displayed quite different proportions of P in the various fractions. There was great variability in the proportions of P in the dissolved and colloidal fractions as well as variability in the fraction of total P that was desorbable by the Fe strip method. "Available" total P was at least 80% of total P in all cases. *There is, as yet, insufficient data from a range of natural waters to show whether or not Australian waters really do have a different distribution of P between available and non available pools from that which would be expected.*

3. Relationships between $[P]_L$ and algal biomass.

The next step from an ability to predict mean in-water P concentrations from L(P), Z, T_W and s and the fraction of that P which is available, is the assessment of the impact of that P on the trophic state of the lake or storage. Predictions of the mean annual algal biomass (usually expressed as chlorophyll a, mg m^{-3}, Chl) from the annual mean in-water TP require a knowledge of the Chl:TP ratio for natural water bodies. This work has a separate pedigree from loading models. Vollenweider's genius was to bring the two approaches together to predict trophic state from P loadings.

Sakamoto (1966) was the first to report Chl:TP data from a range of Japanese lakes and this, together with the full realisation that P was the key element limiting algal biomass in freshwaters (Schindler et al 1971), led to the rapid development of further work. Vollenweider, in the OECD (1968) data compendium, showed that there was a statistically reliable relationship between TP and mean annual Chl concentration in the surface waters of lakes and storages and this formed the basis of management prescriptions relating TP loadings to algal biomass. Dillon and Rigler (1974b) produced data from 19 Ontario lakes and showed a strong correlation between mean summer Chl and TP at spring overturn. Schindler (1978) brought together a large set of data from IBP studies in many countries and showed that there was a significant correlation between mean summer Chl and both measured TP and TP estimated (as above) from loadings.

Canfield and Bachmann (1981) split their extensive data base into natural and artificial lakes. While it was possible to predict in-water TP concentrations with some precision in both categories, the regressions describing the relationship between TP and Chl, and that between Chl and secchi depth were significantly poorer for artificial lakes. The conclusion drawn was that artificial lakes were less predictable by Vollenweider type relationships relating L(P) through T_W, Z and s to Chl. The natural lakes in north America are predominantly in glaciated regions and tend to be cool, deep and clear. The artificial lakes, on the other hand, lie mostly in older geological formations and are shallower, more turbid and warmer; particularly in the hypolimnion. Non biological, allochthonous turbidity was a particular problem in artificial lakes because it interfered with the underwater light climate and because it was a form of particulate bound P which was, possibly, biologically unavailable. This is the common Australian situation.

A number of syntheses of large data sets showed that Chl yields per unit TP were proportionally lower in eutrophic lakes (Rast and Lee 1978, Janus and Vollenweider 1981, Canfield and Bachmann 1981). The relationship between TP and Chl in a large set of north American and European lakes is clearly non linear with Chl yields proportional to TP falling at high P loadings. Chl:TP ratios decline from about 1.0 $mg.mg^{-1}$ in oligotrophic lakes to 0.2 to 0.3 in eutrophic lakes (Harris 1986). Basically this indicates that as P loads increase more P turns up in other forms than phytoplankton. For example the OECD data of Vollenweider shows that as TP increases dissolved nutrient pools build up and more of it is in the form of soluble reactive P.

Hern et al (1981) looked at these relationships in a number of lakes in the US EPA data set and in lakes off the Laurentian Shield on the Canadian Prairies - shallow turbid lakes are common in both data sets. They found that a number of factors may prevent algal biomass reaching the usual Chl:TP ratios in shallow turbid lakes: these include light availability, limitation by N and other factors rather than P, domination of the lake system by vascular plants rather than by phytoplankton, short hydraulic retention times and the presence of toxic substances. Light attenuation by particulates not associated with Chl had a dramatic effect on the total algal biomass found in turbid lakes. Prepas and Trew (1983) looked at Chl:TP ratios in Canadian Prairie lakes and came to similar conclusions. They also showed that salinities in excess of 500 mg l^{-1} caused reductions in the total algal biomass found in the lakes. Pace (1984) showed that changes to the zooplankton community structure (but not biomass) had a significant impact on the Chl:TP ratio in lakes (see below).

Stauffer (1991) reviewed an extensive set of Chl:TP data and showed that there was a degree of complexity involved not appreciated by previous workers. In fact the relationship between Chl and TP is not linear throughout the entire range of TP. At low TP concentrations the Chl tends to be constant but a threshold TP concentration is reached at which the Chl rises steeply only to plateau again at high biomass. The explanation of this behaviour lies in the relationships between phytoplankton and "higher level" interactions in the food chain. In oligotrophic to mesotrophic water bodies grazing can control the biomass of phytoplankton up to a threshold where the algae escape grazing control and blooms form. Stauffer's (1991) data review reveals a great deal about system function which needs to be better appreciated. There are complexities in the relationship between TP and Chl which can be explained in terms of changes in system function as the trophic state is changed. These include changes in the relative importance of external and internal nutrient loadings and changes in the rates of grazing and sedimentation.

De Angelis (1992) has extensively reviewed the development of mathematical models of the processes of phytoplankton growth, nutrient regeneration, grazing and sedimentation. Ever since the seminal paper of Rosenzweig (1971) it has been known that plankton models like Figure 1, incorporating nutrient uptake, growth and grazing, can have some very complex properties. As the nutrient status of a water body is increased the sequence of events is as follows: in oligotrophic and mesotrophic waters phytoplankton biomass remains relatively constant as P loads are increased. Grazing controls the algal biomass (DeAngelis 1992) and P regeneration by grazing is an important process. As eutrophication proceeds, however, sufficient nutrient builds up in the water so that large, ungrazed phytoplankton may bloom and escape control by the grazers. At this point the system begins to oscillate wildly with blooms and crashes of phytoplankton and large oscillations in the populations of zooplankton. Sedimentation and decomposition on the bottom become the major loss process for the phytoplankton. Internal loadings from sediment P release under anoxia begin to dominate the nutrient regeneration mechanisms. The mean annual biomass of phytoplankton rises until light becomes limiting and the Chl:TP ratio is influenced by self shading in the algal community. Chl:TP ratios decline accordingly.

Close examination of some of Vollenweider's Canadian OECD data relating TP to Chl shows the non linearity of the result quite clearly (Janus and Vollenweider 1981). There is a steep rise in Chl as TP is increased above 10 ug l^{-1} and the rate of increase of Chl with TP decreases above 50-100 ug l^{-1} as light limitation sets in. Chl:TP ratios decline from 1.0 to 0.3. The Canadian OECD data did not give many points below 10 ug P l^{-1} so the highly oligotrophic region of Stauffer's (1991) data was not well represented. Nevertheless it is clearly visible.

Vollenweider's (1968) OECD data shows a complementary trend of increases in the proportion of TP which is PO_4 - P as eutrophication proceeds (Janus and Vollenweider 1981). In oligotrophic waters PO_4 - P is scarce and DOP is an important source of P for algal growth. As eutrophication proceeds and TP concentrations increase there is an increase in the proportion of TP which is soluble inorganic PO_4 - P and significant concentrations of PO_4 - P may be found free in the water. Much of this P may be entrained into surface waters from hypolimnetic sources of P released from sediments under anoxia. *One important result of the build up of significant concentrations of soluble inorganic P in surface waters is the fact that it allows large, slow growing phytoplankton with high half saturation concentrations for nutrient uptake (K_s) to survive and bloom. Thus the changes in biogeochemistry which occur in eutrophic surface waters favour the growth of large bloom forming species (or colonies) which have high nutrient requirements and are free from grazing pressure. Similar events seem to occur in both lakes and rivers. These changes in system function need to be better appreciated by Australian managers because they are the underlying reason for the appearance of algal blooms when nutrient loadings are increased.*

3.1 Modification of Chl:P relationships by turbidity

While self shading undoubtedly affects the Chl:TP ratio in eutrophic waters there is also a significant impact from competition for light between phytoplankton and particulate material. Availability of P may be reduced in systems loaded with particulates. Particles in the water adsorb P and can compete with the phytoplankton for SRP, or at least they form one more pool for P amongst the particulate, soluble, living and abiotic pools in the system. There are therefore some complex interactions between altered P availability and light availability. Harris (1978, 1986) summarised the relationship between maximum biomass and light limitation underwater in the form of an equation first derived by Vollenweider (1965, 1970) in a paper on one dimensional integral photosynthesis models. This work was later developed by Bannister (1974a,b, 1979) and Wofsy (1983).

The maximum biomass in the photic zone (if limited by light and self shading rather than nutrients) is given by

$$\gamma_{max} = 1/k_c\ [1/r\ 1/Z_m \ln (2I_oP_e/P_{max}) - k_b]$$

where γ_{max} is the maximum biomass possible in the photic zone (mg Chl m^{-2}), k_c is the specific absorption coefficient of chlorophyll (m^2 mg^{-1}), r is the respiration rate as a fraction of the maximum photosynthetic rate (dimensionless), Z_m is the depth of the mixed layer (m), I_o is the surface irradiance (E m^{-2} s^{-1}), P_e is the photosynthetic efficiency (mgC mg Chl^{-1} E^{-1} m^2), P_{max} is the photosynthetic capacity (mgC mg Chl^{-1} s^{-1}), and k_b is the background attenuation due to water and other substances (m^{-1}).

Basically this relationship looks at the balance of self shading, photosynthetic adaptation and background light attenuation in natural waters. If the background attenuation is small then biomass will increase until all the light in the euphotic zone is absorbed by the phytoplankton. Using well known approximate values for the photosynthetic parameters, k_c and r (Harris 1978, Harris et al 1980) and some realistic values of Z_m, it is possible to show that biomass levels of up to about 500 mg Chl m^{-2} can be achieved if nutrients are not limiting. (See above and Section 6 for what is meant by limiting.) If the background attenuation is increased to values of the order of 2 - 4 m^{-1} (realistic values for turbid Australian waters, Kirk 1983) then the maximum biomass can be reduced by at least 50% compared to clear water.

Light attenuation by organic material and particles is therefore just as important a modifier of the usual Vollenweider - type loading relationships as is the availability of P in the system. Indeed it is probably the major reason why turbid Australian waters do not always achieve the biomass levels predicted.

3.2 Calculation of Areal Hypolimnetic Oxygen Deficits (AHODs) and light penetration (Secchi depths)

Eutrophic waters frequently become anoxic at the bottom due to the sedimentation and decomposition of organic material produced in surface waters. This can happen in both storages and in the deeper pools of slowly flowing rivers. Martinova (1993) has recently reviewed the mechanisms of accumulation, transformation and release of N and P and organic matter in bottom waters. He showed that in Russian lakes more than 70% of the organic matter which accumulated in sediments accumulated as a result of autochthonous production in the water column. In most cases the source of this organic matter was phytoplankton production in the water column, but in certain shallow lakes macrophyte production exceed phytoplankton production and became the major source of organic carbon accumulation. Anoxia results when the rate of decomposition of organic matter and total amount of oxygen demand exceeds the diffusion of oxygen into bottom waters and the stock of oxygen dissolved in the hypolimnion. Hypolimnial anoxia is therefore unlikely in deep oligotrophic lakes but frequently severe in eutrophic lakes, weir pools and poorly mixed stagnant rivers with shallow hypolimnia.

Phytoplankton biomass and production can be estimated from P loading models so it is possible to extend the Vollenweider approach beyond the phosphorus:chlorophyll ratio in surface waters to sedimentation of the plant biomass and to hypolimnial anoxia. Cornett and Rigler (1979) extended the work of Dillon and Rigler (1974a) to include the calculation and prediction of areal hypolimnetic oxygen deficits (AHODs). Hutchinson (1938) had proposed that the oxygen deficit in eutrophic lakes should be expressed on an areal basis. Cornett and Rigler (1979) found a good relationship between R_c and AHOD for a set of lakes described in the literature. The major driving variables were the P retention coefficient (a function of T_w), the thickness of the hypolimnion and hypolimnetic temperature. Charlton (1980) introduced the idea of modifying the value of AHOD depending on the relative thicknesses of the epilimnion and the hypolimnion and on hypolimnetic temperature. For any given level of productivity, lakes with shallow hypolimnia will experience greater oxygen depletion than those with deep hypolimnia where the stock of oxygen in bottom waters is larger. Hypolimnetic temperatures will control the rate of the bacterial metabolism which is the mechanism of oxygen depletion.

Rast and Lee (1978) used the extensive US OECD data base to test many of the Vollenweider relationships on a large set of US lakes. Jones and Lee (1982) used the Vollenweider relationship for the normalised annual areal P loading, $(L(P)/q_S)(1 + \sqrt{T_W})$, to predict AHODs in a set of N American lakes quite successfully. They also showed good correlations between normalised annual P loads and the secchi depth in lakes. Increased P loads lead to increased algal biomass and hence a reduction in light penetration. Mean summer secchi depths decreased from over 10m to less than 1m in eutrophic lakes. Rast et al (1983) discussed the use of these relationships by water quality managers. Vollenweider and Janus (1982) used a number of models of AHOD in an attempt to come up with a more satisfactory model than Charlton (1980). By including biological parameters such as primary productivity, algal biomass and the depth of the euphotic zone they were able to improve the predictability of the relationships.

3.3 Sediment P release rates - internal loadings

Hypolimnial anoxia leads to a number of chemical and biochemical changes in the surficial sediments at the bottom of water bodies. Anoxia leads to drastic changes in the redox potential (Eh) in the surface layers of the sediment and influences a number of chemical reactions. Reducing conditions lead to the formation, amongst other things, of nitrogen gas, methane, ammonia and sulphides, all of which build up in bottom waters or are released as gas to the atmosphere. All this has been known since the early classic work of Einsele (1936) and Mortimer (1941-42). Bacterial populations change to those species capable of exploiting reducing conditions. The elimination of the macroinvertebrates which are responsible for bioturbation (or the biological stirring and reworking of surface sediments) leads to reduced infiltration of bottom waters into the surface sediment layers and exchange processes which are dominated by diffusion across the sediment water interface. Exchange of nutrients and other chemicals between the sediment and the bottom water is controlled by the gradient between the concentration in bottom waters and the concentration in the pore waters of the surface sediments. Martinova (1993) has shown that exchange rates between sediment and bottom waters increase in rivers where the bottom waters are moving over the sediment. The basic principles are, however, the same.

The source of the C, N and P either incorporated into the sediment or recycled under anoxia is predominantly primary production in the water column (Martinova 1993). In lowland rivers most of the production is autochthonous so similar relationships are to be expected. C,N and P are taken up in surface waters in proportions which approximate the Redfield ratio of 105C: 15N: 1P (Redfield 1958). Phytoplankton growing in surface waters deplete nutrient concentrations in approximately these ratios (Harris 1986) and release these elements again when they sink to the bottom and decompose in the sediment. Oxygen is taken up by bacterial decomposition of reduced C compounds such as carbohydrates and proteins. Organic C,N and P accumulate on the bottom in proportion to phytoplankton production (Martinova 1993).

The proportion of primary production reaching the bottom varies from about one tenth in oligotrophic lakes to one half in eutrophic lakes. In undisturbed oligotrophic water bodies the relationship is non linear with sedimentation remaining low and constant until primary production exceeds about 100 g C m^{-2} y^{-1} (Martinova 1993). Both N and P show this non linearity. Organic matter accumulation on the bottom reaches a maximum at depths equal to the euphotic zone. At greater depths some of the organic matter is reprocessed and decomposed in the water column before it reaches the bottom. In this respect inland water bodies are just like shallow oceans (Harris et al 1987).

From the point of view of the cycling of phosphorus and nitrogen within water bodies the onset of anoxia in the surface layers of sediment is especially important (Martinova 1993). In oligotrophic lakes the oxygenated surface layers of sediment act as a net sink for nutrients which are buried and incorporated permanently into the bottom sediments. Release of P from oxic sediments is small but can nevertheless be significant. P release from oxic sediments can be stimulated by scouring by water flow in rivers or resuspension of sediments by fish such as Carp (Gehrke and Harris 1994).

Once anoxia sets in N and P behave differently (Martinova 1993). The external loading of N from the drainage basin and internal loading of N from exchange with algal material decomposing in the sediment are linearly related. Organic N sedimenting from the water column is decomposed by bacterial action and the ammonia produced is nitrified to nitrate under oxic conditions. N compounds tend to be soluble whereas P tends to be bound to particulate material. The relationship between the external and internal loadings of P is non linear. Under oxic conditions P release from sediments is small At low external P loadings (<1 gP m^{-2} y^{-1}) and low phytoplankton productivity (< 100 gC m^{-2} y^{-1}) internal loadings of P are very small. Once anoxia sets in internal loads of P increase rapidly and may far exceed the external load in eutrophic water bodies.

In eutrophic water bodies, once anoxia occurs, N is released from the sediments as dinitrogen gas and P is released as phosphate from organic P and other less available P sources. The N and P are derived from material sedimented from the water column. In eutrophic systems N and P are cycled in quite different ways and the onset of anoxia leads to major changes in the N:P ratio within the system. Anoxia leads to the cessation of nitrification (nitrate production) and a build up of ammonia in the hypolimnion. N and P are recycled into surface waters through the internal loadings from sediment release and the entrainment of hypolimnial water into surface waters once more by wind mixing. As eutrophication proceeds, internal loadings of P may rise faster than internal loadings of N. Highly eutrophic water bodies tend to become enriched with P in relation to N because of the loss of N from the system by denitrification. Denitrification appears to be more rapid in warm bottom waters (Martinova 1993) so N losses are more rapid in tropical and subtropical systems than in temperate systems. This may influence the availability of N and P in eutrophic subtropical waters and may have important ecological consequences. Bioturbation of the anoxic sediments by the release of gas bubbles increases the internal release of P by increasing the exchange rate between water and sediment.

Eutrophic waters therefore have both an external loading of N and P from the drainage basin and an internal loading of N and P from the sediment. Vollenweider's original models were never built to cope with this situation although developments and modifications to the basic framework extend the realm of their application. Thirty years of limnology has assembled enough data to provide a broader range of models. Luckily the ways in which aquatic systems operate seem to follow some fairly simple statistical and allometric rules so that empirical models of system function provide insights about what is going on. We can now see how the system responds to changed loadings of nutrients.

In eutrophic lakes the internal nutrient load may dominate the external load so that the water body continues to be eutrophic (Kilham and Kilham 1990) - fed by internal nutrient recycling through the sedimentation and release of N and P - even when the external loading is decreased. In most cases the total stock of P in the sediments exceeds the annual external load by a factor of ten or one hundred. This is an important factor to be taken into account when lake restoration is being considered. Chemical transformations in the sediment under anoxia may also change various less available forms of P which arise in the drainage basin to phosphate and thus make them potentially available. The internal load recycles less available portions of the external load and makes them available for phytoplankton growth.

It was classically believed that the major result of anoxia was the altered chemistry (Mortimer 1941-42). It is now believed that the changes to the bacterial populations are as important as the changes to the chemistry and that bacteria play a vital role in the cycling of oxygen, energy and materials between the sediments and the water column (Gachter and Meyer 1993, Martinova 1993, see also other papers in Hydrobiologia 252:(1) 1993 and 253:(1-3) 1993). Bacteria are responsible for the various biochemical and redox transformations of N from protein to nitrate or nitrogen gas. Various organic P transformations controlled by bacteria are critical determinants of the internal P load. Organic P is converted between various forms, poly-phosphates, and inorganic P. Bacteria play a vital role in all these processes depending on the redox potential in surface sediments (Gachter and Meyer 1993). In oligotrophic sediments there may be more P tied up in bacterial biomass than the amount deposited yearly by production in surface waters. In oligotrophic sediments also more refractory P is formed than in eutrophic lakes. Sulphate metabolism and sulphate bacteria are an important component because of the role played by sulphate as a source of oxygen for bacterially mediated reduction reactions. Caraco et al (1989) found a positive relationship between P release from sediments and the sulphate concentration of natural waters. Anoxia also leads to the reduction of iron oxides, the formation of sulphides and the release of phosphate from forms of P bound to iron.

Nurnberg (1984, 1988) and Nurnberg et al (1986) have collated a large number of sets of data and have reviewed the relationships between external and internal P loads, sedimentary and hypolimnetic P concentrations. The point of departure for Nurnberg (1984) was the observation that the P retention coefficients of lakes (R_c - section 2.1) with anoxic hypolimnia were much lower than those for oligotrophic water bodies. Two approaches were taken. The first was to predict the internal P load from the difference between the observed P retention coefficient and a model of P retention based on that for oligotrophic lakes (i.e. with no internal load). This approach worked well. The second approach was the predict the internal load from known rates of P release from sediments, the surface area of the sediments and the period of anoxia. This did not work so well, more data was required. Nurnberg et al (1986) therefore looked at the relationship between in-water TP concentrations and the rate of release of P from sediments with data derived from observations on cores and the rate of increase of P in the hypolimnion. Increases in TP in the water column led to significant increases in the rate of internal release of P from the sediments through uptake, phytoplankton growth, sedimentation, decomposition and subsequent release.

Nurnberg (1988) looked at empirical relationships between sedimentary TP concentrations (derived from autochthonous production in the water column) and P release rates. She found a significant relationship between P concentrations in the sediment and internal loadings. This is sensible because the rate of P release from sediments is driven by the concentration gradient between sedimentary pore water and the overlying water in the hypolimnion. Martinova (1993) found a correlation between the concentration of organic matter in sediments and the concentration of inorganic P in the pore water of the sediments. Sedimentary TP concentrations ranged from less than 1 to about 10 mg.g dry weight^{-1} and release rates varied with trophic state from less than 1 to over 50 mg TP m^{-2} d^{-1}. In particular reductant soluble P (which estimated the Fe-bound fraction of TP) seemed to play an important role in the exchange process under anoxic conditions. As might be expected sediment release rates are low and rather constant in oliogtrophic lakes with low sedimentary concentrations of organic matter and TP (Martinova 1993). N release rates vary from less than 1 to over 200 mg N m^{-2} d^{-1} and are similar in marine and freshwater systems (Martinova 1993).

Thus the links between external loadings, phytoplankton growth, sedimentation and (eventually) anoxia and internal P loadings are clear. In oligotrophic lakes much P is regenerated within surface waters by grazing and the P which does reach the sediment is permanently buried. P retention coefficients are high. With the onset of eutrophic conditions, sedimentation becomes more important than grazing, decomposition in bottom waters becomes more rapid and, eventually, anoxia sets in. Internal loadings dramatically reduce P retention coefficients. Oligotrophic systems are dependant on external sources of nutrients and on sources of nutrients regenerated entirely within surface waters. Eutrophic waters depend on a balance of external loadings and on internal loadings of P recycled through large, long cycles involving the water column, the hypolimnion and the sediments. In both cases macrophytes play significant but differing roles. Macrophytes in oligotrophic systems are nutrient sinks whereas they may in some shallow eutrophic systems contribute more particulate organic C, N and P to the sediments that the phytoplankton in the water column. *Having looked in broad terms at the changes in biogeochemistry brought about by altered nutrient loadings I shall now examine the changes in the food chain structure and the rest of the ecosystem which are brought about by eutrophication and which contribute to these changes in system function.*

4. The effect of P loadings on the structure of aquatic food chains.

Why do Chl:TP models work at all? To answer this question we have to examine the more recent work which looks at changes in the rest of the aquatic food chain at increased P loadings. As Vollenweider showed, increasing the phosphorus loading or increasing the nutrient status of a body of water causes the biomass of phytoplankton to rise and hypolimnial anoxia to appear. Simultaneously a number of other changes occur throughout the food chain of the ecosystem. These trends have been documented by Peters (1986), Seip and Ibrekk (1988), Cushing (1989), Carney (1990) and Harris (1994). There is a clear pattern of changing structure and function with changing trophic state. Only Carney (1990) seems to have realised that these patterns run across marine and freshwater systems. The features of interest are the allometric changes in the proportions of components in the food chains as the nutrient status is increased. Remember, these data were obtained from regression lines that summarise the relationships between data sets averaged over large (generally annual) temporal and spatial scales.

Fundamentally the pelagic ecosystems of water bodies change from those dominated by bacteria and picoplankton (when nutrients are present in low concentrations) to those dominated by large netplankton and colonial forms (when the nutrients are in abundant supply). This trend runs right across the marine/freshwater divide so that an overall pattern is discernible from the most oligotrophic pelagic marine systems to the most eutrophic freshwater systems. As the mean cell (or colony) size of the phytoplankton increases with nutrient status, grazing pressure decreases until it can almost be neglected in the case of large colonial cyanobacteria and dinoflagellates (Watson et al 1992). Vollenweider's models would not work if grazing pressure did not decline in this way. Both models (De Angelis 1992) and observations back up this assertion. Table 1 lists the published empirical relationships between P loadings and various parameters of the aquatic food chain, macrophytes and other measures of ecosystem function.

This pattern of allometric trends in the structure of pelagic food chains has been postulated before by both Cushing (1989) and Carney (1990) and, when coupled with estimates of the impact of grazing, are entirely consistent with the syntheses of data arising from biomanipulation experiments (McQueen et al 1986). *What the data shows is that there are trophically induced changes in the strength of "top down" control on phytoplankton biomass with the effect weakening as overall production and algal biomass increases.* This means that previously postulated ideas about the role of competition and grazing in food chains (Hairston et al 1960, Murdoch 1966, Oksanen et al 1981) are all partially correct and the effects are altered both by overall ecosystem productivity (Oksanen et al 1981) and by physical disturbance (Connell 1978). (See Pimm 1991 for an extended discussion of this.)

The impact of grazing (by microheterotrophs and ciliates) is greatest in ultra-oligotrophic waters and marine systems where the microbial loop dominates the recycling of nutrients, energy and materials (Azam et al 1983, Banse 1992). These are systems dominated by bacteria and picoplankton, by regenerated production and by low "f" numbers ("f" numbers relate the rate of "new" production based on newly supplied nutrients from outside the system to total production, Eppley and Peterson 1979). Overall production is low and there is little "new" production, so little energy flows to larger organisms at higher trophic levels. While the biomass of bacteria increases as trophic state increases, the ratio of bacterial to phytoplankton biomass declines exponentially as trophic state is increased (Simon et al 1992). Coupling between bacterial abundance and the abundance of heterotrophic nanoflagellates is complex (Gasol and Vaque 1993) being influenced by nutrient supply and grazing pressure and also by complex trophic interactions with numerous feedbacks.

Del Giorgio and Peters (1993) have recently looked at the balance of production and respiration in surface waters of lakes with a wide range of trophic state and algal biomass. At low biomass and total production (oligotrophy) the Photosynthesis: Respiration of pelagic communities is less than unity indicating that all the primary production is recycled within surface waters. Small pelagic heterotrophs are very active. (Indeed it appears that energy subsidies are required to support the pelagic food chain - from dissolved organic carbon sources perhaps?) Oligotrophic systems dominated by "regenerated" production are largely dependent on biological interactions within the food chain (such as grazing) to return nutrients to a form suitable for primary production. P:R ratios only become greater than unity in surface waters as algal biomass rises. Bacterial metabolism shifts predominantly to the sediments in eutrophic systems.

More productive (and coastal) marine food chains and less oligotrophic waters are dominated by nanoplankton, small diatoms, flagellates and copepods which can provide significant energy flows to higher trophic levels (Cushing 1989). Such systems require some "new" nutrients to support the primary production.

The impact of grazing by crustacean zooplankton reaches a maximum in mesotrophic lakes where Cladocerans in particular can have a major impact on the biomass of phytoplankton and can produce clear water phases in late spring (Carney 1990). Mazumder (1994a,b,c) has recently shown that cladocerans can have a significant impact on the biomass of phytoplankton in lakes if present in sufficient numbers. These systems show great seasonality as nutrients regenerated from bottom waters in winter are depleted by spring and summer production. These are also systems in which the impact of piscivorous fish can be clearly seen (McQueen et al 1986). "Top down" control within the food chain may be strong at times (Mazumder 1994a,b,c). Cladocerans do not, however, appear to be as frequent a component of Australian ecosystems as expected from northern hemisphere systems. The presence of high turbidities (as occurs frequently in Australian waters) also appears to have a direct suppressive effect on grazing by interfering with the grazing activity of cladocerans, copepods and rotifers (Jack et al 1993). Other than an effect on light availability, Jack et al's experiments could detect no direct effect of suspended clays on the phytoplankton.

In eutrophic waters with higher phytoplankton biomass and larger cells, the impact of grazing on the phytoplankton biomass declines therefore to the point where there is little effect of "top down" control by food chains (McQueen 1990). Under these circumstances biomanipulation through zooplankton and fish is rarely effective and the abundance and growth forms of phytoplankton are largely controlled by "bottom up" factors such as nutrient availability, light limitation and hydrodynamics. This conclusion is bolstered by the syntheses of McQueen et al (1986) who have analysed data on biomanipulation experiments. Highly eutrophic systems require continuous nutrient inputs to support the growth of large blooms of algae. These nutrients must come from external inputs or sedimentary pools.

At high phytoplankton biomass and production levels P:R ratios exceed unity and the "excess" production is recycled via sedimentation and benthic decomposition. Grazing can frequently be ignored in eutrophic waters because cell and colony size increases to the point that the units are larger than the zooplankton. Grazing is more important to oceanographers than to those working in freshwater systems, but is frequently neglected there too (Banse 1992). Gutelmakher and Makartseva (1990) have shown that while the biomass of zooplankton increases as trophic state is increased, the contribution of zooplankton to overall P cycling declined. More eutrophic systems depend on decomposition and regeneration of nutrients at sites removed from the site of primary production and therefore depend on physical processes (such as entrainment, winter overturn, inflow or upwelling) to make nutrients available. One important signal of eutrophication is the sharp rise in the biomass and productivity of epibenthic microalgae as nutrient cycling shifts from the water column to the sediments(Brown and Davies 1991).

As the time and space scales of nutrient regeneration increase and concentrations rise, the impact of physical processes becomes more important so that they come to dominate much of the picture in highly eutrophic systems. Physical processes of sedimentation, turbulence and vertical mixing control the diffusion of nutrients from surface waters to sediments and vice versa. In eutrophic systems algal biomass increases and sedimentation takes precedence over grazing. Deep water and benthic pools become more significant and exchanges between these and surface waters may take days to months. In lakes, rivers and estuaries exchange rates depend on the physics of turbulence and stratification. Growth and loss rates are lower, nutrient turnover times are extended and so resilience is reduced. Pools of particulate C, N and P may be regenerated through bacterial and chemical interactions in different places and at different time scales so the variability of the seston C:N:P ratios in eutrophic systems expands into "high dynamic" behaviour (Harris 1986, Vollenweider 1990). The physiological Redfield ratios become end members of a large range of ratios and are only encountered when algal blooms dominate the seston. At other times fluxes between detrital and various soluble organic and inorganic pools are frequently controlled by biogeochemical and physical processes that can temporarily distort the stoichiometry. Janus and Vollenweider (1984) showed that there are allometric trends in the cycling of P in lakes of varying trophic state.

As the scales of recycling expand to include bottom waters and sediments the coupling between pools becomes looser and variances increase. Oligotrophic, mesotrophic and eutrophic ecosystems show quite different patterns of temporal behaviour in algal biomass (Marshall and Peters 1989) as well as soluble and particulate nutrient pools (Harris 1986, Harris and Griffiths 1987, Vollenweider

1990). Phytoplankton in eutrophic systems become less susceptible to "top down" controls because of the size of the phytoplankton cells and colonies (Vanni 1987, Watson et al 1992). Also, the greater temporal variability indicates that the processes of growth and loss are uncoupled leading to the formation of blooms. The lower resilience and greater degree of variance in epilimnetic pools and populations are brought about by slower turnover of nutrient and biomass pools and by stronger interference at lower levels in the food chain by larger, slower pools of nutrients affected by fish, macrophytes, bottom waters and bacteria and chemical processes in sediments.

Vollenweider's models work because of the trend towards larger (poorly grazed) cells and colonies in eutrophic waters (Watson et al 1992) and because of regular statistical relationships between all the components of the pelagic food chains. i.e. there is a proportioning of the pools of C, N and P (and micronutrients) between a variety of living and dead, organic and inorganic, particulate and soluble pools. Over the long term and when annually averaged, there are regular statistical properties that show trophically related patterns. *Vollenweider's models work because of an assumption of equilibrium between pools at annual scales. Equilibrium certainly does not exist over shorter time periods.*

The annual and seasonal averaging involved in the production of the total phosphorus and biomass data takes into account the various assumptions about the turnover times of nutrient and biomass pools, and scales of sedimentation and nutrient regeneration (i.e. the averaging time is as long as, or longer than, the longest time scale of biomass or nutrient turnover). It also averages out all the temporal dynamics of the various biomass and nutrient pools in the pelagic system. These models work because annual scales are much longer than the growth rates of pelagic organisms and the turnover times of most nutrient pools, even in the largest loops. Sedimentary pools of phosphorus may, however, have much longer turnover times and this is one reason why reductions in loadings to eutrophic lakes often produce the expected effects only after considerable time lags.

The restoration of water bodies (and rivers) by the removal of P is both feasible and has been demonstrated. Cullen and Forsberg (1988) brought together the results of many lake restoration experiments which had been carried out in the previous 25 years. The results demonstrated many instances where the trophic status of the water body had been altered from eutrophic to oligo- or mesotrophic by P reduction, removal or diversion. Perhaps the most famous example of P lake restoration by P removal is that of Lake Washington (Edmondson and Lehman 1981).

Predictive relationships in ecology only work if the scales of the cause and effect are commensurate and are not influenced by larger, longer term effects (Allen and Hoekstra 1992). *We should not therefore expect to use Vollenweider type relationships in rivers or weir pools, or other storages where the water residence times are the order of days. On the other hand reaches in regulated rivers where residence times may be significant (>100 days) may be treated as long thin lakes and modeled accordingly. Storages which have residence times of decades with intermittent flushes and nutrient replenishment must also be treated with caution.*

What is the meaning of annual averages made up from data from storages and regulated river reaches which have residence times varying intermittently between a few days and (effectively) infinity? Further work is required here.

5. What do biomanipulation experiments tell us about the functioning of aquatic food chains?

A considerable effort has been put into biomanipulation experiments in the last decade. Much has been claimed despite much inherent variability (Carpenter et al 1987). Only now, after more than a decade of experimental manipulations and when the mass of available data has been fully assessed, has it become possible to get a realistic picture. The picture is much more complex than was originally assumed (Gophen 1990). The synthesis has finally come from statistical relationships and other correlations that separate the effects of uncontrolled variances from the effects of the treatments. The pattern revealed is consistent with that outlined above (McQueen 1990, McQueen et al 1986, 1989, 1992a,b, De Melo et al 1992).

People began with just manipulating fish and zooplankton populations but the results were frequently inconsistent. Statistical analyses of many sets of data, however, revealed consistent patterns of behaviour. Relationships between planktivores and zooplankton are usually negative, relationships between zooplankton and phytoplankton are unpredictable, relationships between total phosphorus and various measures of phytoplankton abundance are always positive (Kerfoot and DeAngelis 1989, McQueen 1990, McQueen et al 1986, 1992a, b - see Mazumder 1994a, b, c however). Grazing controls on phytoplankton biomass are strongest in oligotrophic and mesotrophic ecosystems. Over short periods there are strong negative relationships between zooplankton (especially large *Daphnia*) and phytoplankton but these events are unpredictable and are seldom related to piscivore abundance (McQueen et al 1992a,b). Food chain manipulations can change the species composition of the phytoplankton by removing the smaller, grazed, species and leaving the larger species and the cyanobacteria (Vanni 1987). In eutrophic ecosystems the phytoplankton may frequently escape grazing and blooms of large celled species are formed. *Control of phytoplankton biomass by food chain manipulations is therefore less successful in eutrophic waters and in any case is unpredictable in timing or effect (Shapiro 1990).*

While many experiments have been done by manipulating the fish and zooplankton populations in lakes, inevitably none have been able to control for or manipulate all the other natural interactions and periodicities in the system (Benndorf 1988, Gophen 1990). There have been many occasions when there has been interference from larger, slower, nutrient fluxes and pools leading to an inability to control the experiments, poor replication and low predictive power. This is a common ecological problem (Allen and Hoekstra 1992). Asking messy questions gives messy answers. Let us look on the bright side, however, far from being a failure, the biomanipulation experiments have told us much about the functioning of aquatic ecosystems. It is possible to seek general relationships in the results from assemblages of specific, applied, experiments (Slobodkin 1988). *The technique should not, however, be sold to managers as a panacea.*

Part of the mess arises from the presence of internally generated sources of variance and non-equilibrium at a wide range of scales. Non-linear interactions will ensure that the whole system displays complex dynamic behaviour and is moving on a chaotic "strange attractor" (Schaffer and Kot 1985). Ecological experiments will be almost impossible to replicate from year to year. As aquatic macrophytes, riparian vegetation, fish populations and sediments are all involved in the recycling of nutrients within water bodies (as well as the phytoplankton and zooplankton) there may be some quite surprising and long lasting effects of storm events, fires, changing fish recruitment and macrophyte growth on planktonic populations (McQueen 1990). Even at the presumed time scales of the trophic cascade - years to decades - (Carpenter 1989) the results of biomanipulation experiments are by no means clear (Evans 1992). Confounding effects may be seen in grazing effects and the turnover of large, slow pools of nutrients which therefore come to influence phytoplankton in surprising ways. Havens (1993b) has showed that both benthic nutrient cycling and cascading trophic interactions are regulators of algal biomass, but that the former effect was by far the more important, accounting for more than 60% of the overall effect. In contrast to oligotrophic water bodies, eutrophic systems are predominantly driven by benthic interactions.

Problems arise because the fish, zooplankton and phytoplankton populations respond to quite different time scales of variance which range from hours to months and years (Harris and Griffiths 1987). There are always indirect effects at a variety of scales (Vanni 1987). Further, indirect effects may arise from the influence of fish populations and macrophyte growth on turbidity and sedimentation that interact strongly with the underwater light climate (McQueen 1990). Indirect effects which come from higher, slower, levels make it very difficult to control and repeat experiments where manipulation of the food chain structure is involved (De Melo et al 1992). *In the framework of complex dynamics it must be remembered that the same perturbation may, on different occasions, produce a spectrum of possible responses, frequently similar but occasionally quite different. This is a fundamental limitation on predictive capacity in food chains except in a statistical sense. This must be more widely appreciated.*

6. TN:TP ratios and the relative turnover times of N and P - nutrient fluxes and models

Many factors may limit the total expressed biomass of phytoplankton and hence the apparent Chl:TP ratio. It must be remembered that the apparent Chl:TP ratio is a combination of a whole series of events in the food chain and the proportioning of N and P between a number of pools of various sizes and turnover times. N and P limitation is not just a limitation of phytoplankton growth - it represents changes in the pools of N and P throughout the system. The primary determining factors of algal growth rate and the final biomass reached are nutrients, light, temperature, micronutrients, sedimentation rate and grazing pressure from zooplankton. Each may, on occasion, be limiting singly or in combination. The accepted wisdom is that P limits rate processes and total biomass in freshwater and N does the same in marine waters, that light sets an upper limit on biomass when self shading sets in, that temperature may limit rate processes in winter and that micronutrients may be ignored. (Micronutrients are usually assumed to be unimportant in aquatic systems although Fe limitation has become popular in the oceans lately because of evidence that it may stimulate phytoplankton growth in the open oceans away from land.) As we have seen the balance between growth, sedimentation and grazing is an important feature in all aquatic systems.

There is good reason to attend to the question of both N and P limitation in water bodies because it has been suggested that nuisance blooms of nitrogen fixing cyanobacteria can be reduced if N limitation is avoided (Smith 1983, 1985, 1986). Smith and others (reviewed in Pick and Lean 1987) have suggested that manipulation of the TN:TP ratio can be exploited as a means to avoid nuisance blooms of cyanobacteria. There is some debate about whether this is always the case (Pick and Lean 1987). What therefore do we know about the fluxes of N and P in aquatic systems and is this argument supported?

Much has been written about nutrient limitation and the debate is far from over. P is clearly the dominant limiting factor at a variety of scales in freshwater systems (Hecky and Kilham 1988). Elser et al (1990) recently examined the evidence for N limitation as a secondary factor in freshwater systems. They found that, in general, the experimental protocols used were not sufficiently rigorous to decide if this conjecture was true (see also Pick and Lean 1987). N may be the more important limiting nutrient in marine systems but both N and P may be limiting on occasion (Howarth 1988). Given the small scale variability in aquatic systems and the general lack of equilibrium at scales of a few days it is probably not surprising that measurements of N and P limitation have not produced conclusive results (Fong et al 1993). It is necessary to look at the way the entire system functions in order to see if N or P limitation is an important factor.

There is confusion as to what "limiting" means: i.e. what is limiting what (Harris 1986) and over what time scale? For example: do nutrients limit growth or biomass? Or both? Are the processes which limit growth the same as those which limit biomass? What is the relationship between nutrient concentrations and fluxes? Can a simple measure of total nutrient concentration (TP or TN) give a true measure of limitation when it is the flux of nutrients that is important for rate processes? If so what is the relationship between concentrations and fluxes? Nutrient pools and phytoplankton biomass are continually replenished and depleted by a variety of processes. An extensive discussion of the concept of limiting nutrients can be found in Chapter 7 of Harris (1986) where it was shown that the assumption of steady state at a variety of scales is essentially wrong and that the debate must be couched in terms of fluxes, rate processes and growth and loss terms. The correct questions have to be carefully defined.

For many years nutrient limitation was discussed in terms of nutrient concentrations because of early observations of an apparently simple relationship between nutrient concentration and phytoplankton biomass in the ocean (Hentschel and Wattenberg 1931) and the apparent inverse relationship between nutrients and biomass in the northern spring. Early classic work by E. Harris (1959) in Long Island Sound began to define the important processes of nutrient uptake and grazing. A number of papers were written in the 1970s and 1980s describing work which attempted to examine nutrient limitation in lakes and coastal waters. Most were inconclusive. In North America in the 70s and 80s a major debate broke out in oceanographic circles over the rate of processes in the ultra oligotrophic Central North Pacific Gyre region. Some (Eppley) stated that the practically unmeasureable N concentration must indicate N limitation of growth by phytoplankton in this system whereas others (Goldman) placed more emphasis on nutrient recycling mechanisms and rapid growth and grazing (Harris 1986). On balance the evidence now seems to favour rapid growth and loss and high fluxes of N at low concentrations. Much new work was stimulated by the debate.

It has always been assumed that P limits growth in freshwaters (Hecky and Kilham 1988) and that nutrient limitation can lead to competition between the phytoplankton for nutrients in the manner classically described by Tilman (1982). Tilman (Titman 1976, Tilman 1977, Tilman et al 1981) developed the resource ratio theory of competition based on concentration ratios and Michaelis Menton kinetics based on work by Monod (1942). The key parameter for phytoplankton is the half saturation constant for nutrient uptake, K_S. K_S is the concentration of nutrients at which we observe a 50% reduction in the maximum growth rate. Species with high K_S values require high concentrations of nutrients to sustain high growth rates. As two species deplete nutrients by growing together, the species with the lower K_S will always win because it will grow faster at lower nutrient concentrations. Droop (1974) worked out a relationship between minimum cell quotas of nutrients and growth rate in culture which is formally equivalent to the Tilman approach at steady state (Goldman 1977, Burmaster 1979, DiToro 1980). The development of the theory may be found in Harris (1986). This conceptual framework has more recently been developed by Sommer (1989) who has produced both field and laboratory demonstrations of the theory and of the existence of competition between species.

Competitive exclusion of one species by another does not take place instantaneously, it takes time, up to 30 days or so. Non steady state conditions in the field may disrupt the course of competitive exclusion and lead to higher diversity in the plankton community by "moving the goal posts" before one species beats the other (Harris 1986, Sommer et al 1993). Perturbations in the environment at scales of 10 - 20 days have an important effect on the outcome of competition (Harris and Trimbee 1986) because the environment is changed before competitive exclusion can occur. Intermediate disturbances "work" because the scales of perturbation and response are closely matched and the interference from processes "higher" in the system at longer scales is not strong over these time periods.

Tilman's approach uses nutrient concentrations as determinants of resource availability and competition between phytoplankton species. The key question therefore is; what is the relationship between concentrations of TN and TP and the fluxes of N and P in aquatic systems? Tilman's resource limitation approach has some validity (Sommer 1990) so there must be some kind of monotonic relationship between nutrient flux ratios and concentration ratios. Is there any evidence for this? As Figure 1 indicates there are essentially three dominant fluxes of N and P in aquatic systems - the external nutrient flux or loading (estimated by Vollenweider's loading models), the regenerated flux of nutrients from zooplankton grazing and the net internal flux or loading from sediments, lacustrine and riverine margins, macrophytes etc. The first and second are usually positive influences on phytoplankton growth while the third may be negative (sediments and macrophytes act as a sink in oligotrophic systems) or positive (internal loadings are significant in eutrophic systems).

While there are many measurements of nutrient concentrations in aquatic systems little is known about nutrient flux ratios. Some approaches have been tried but are not generally well known. One, based on Vollenweider's models, attempts to measure whole basin fluxes of N and P in relation to T_W and trophic state. A much more recent development by Sterner, Hessen and Elser, uses stoichiometric models of zooplankton grazing to estimate the internal loadings of N and P from grazing in lakes and the ocean. In both cases we are looking at system function rather than short term measures of nutrient flux.

6.1 Whole lake budgets of N and P

Vollenweider (1975) developed the theory of input/output models to include the velocities of movement of substances through lakes and storages. In the early 1980s Lorraine Janus (a student of Vollenweider's) further developed the theory of the turnover times of N and P in lakes and storages because it became clear that there was not a simple relationship between TN and TP and the relative fluxes of N and P. A knowledge of the inputs and outputs of N and P to and from lakes enabled Janus to calculate the whole basin turnover times of N and P in relation to the water residence times (Janus and Vollenweider 1984).

Using the Vollenweider approach the continuity equation for P is:

$$d[P]_L/dt + dP_j/dt + dP_W/dt + dP_S/dt = 0$$

where $[P]_L$ is the in-water concentration of P, P_j are the summed products of flow and concentration in the inputs, P_W the product of flow and concentration in the outputs and P_S losses due to sedimentation. The reference value is the residence time of the water T_W and the extent of reaction ε_m for N or P can be defined as:

$$\varepsilon_m = l(P)/[P]_L \quad y^{-1}$$

which can be thought of as similar to the water residence time. A conservative substance would give a result equal to $1/T_W$. The velocity of movement E_m is:

$$E_m = L(P)/[P]_L \qquad m.y^{-1}$$

which can be thought of as the velocity of a substance moving though the water body with both vertical and horizontal components. It should be remembered that Vollenweider assumed mixed reactors and the residence time is assumed to be the time it takes to replace all the molecules in the pool given a continuous flux. If these measures of whole lake metabolism are expressed as ratios i.e. $\varepsilon_n/\varepsilon_p$ or E_n/E_p then such expressions largely eliminate uncertainties and inhomogeneities in the distributions of N and P in the system because it can be assumed that advection and stratification act similarly on both substances. The ratios of the turnover times are the inverse of the ratios of extent of reaction and velocity of movement.

When the values of the ratios for N and P were compared for a range of lakes which varied in trophic state it became clear that N and P behaved differently. There appeared to be a rough proportionality between T_w and τ_n whereas τ_p showed a decidedly non linear relationship. τ_n/τ_p varied between 0.5 and nearly 10 with high values in oligotrophic waters and low values in eutrophic situations. These conclusions appear to indicate that in oligotrophic waters metabolism is dominated by the flow velocities of P so that the τ_n/τ_p is >1. As the trophic state of the whole system is increased by external loadings then the P remains in the system longer. Vollenweider's OECD data clearly shows that as TP increases the proportion of P in the form of soluble reactive P increases. In the final phase of eutrophication N may become limiting and the ratio of τ_n/τ_p may drop below unity. Note that it is the non linear relationship between T_w and τ_p which dominates the ratios of the turnover times of N and P. τ_n is linearly related to T_w. Martinova (1993) developed a similar scheme of relative turnover times for N and P in sediments. The result were very similar.

This leads us to the conclusion that it is the metabolism of P which is the dominant feature of freshwater (and possibly some coastal marine!) systems. This conclusion is borne out by the work of Trimbee and Prepas (1987) who found that despite the assertions of Smith's (1986) paper, that TN and TN:TP ratios were good predictors of cyanobacterial biomass in eutrophic lakes, TP alone was a better predictor of the abundance of these organisms. Molot and Dillon (1991) looked at the response of average chlorophyll levels in 15 Ontario lakes to changes in mean epilimnetic P concentrations and TN:TP ratios. They showed that TN:TP was of little or no use as a second independent variable in regression analysis of Chl data in P limited lakes. This corroborates the results of whole lake fertilization experiments and the addition of N to P limited enclosures by Prepas and Trimbee (1988).

Harris (1986) also calculated τ_n/τ_p ratios from a range of lakes sampled in the USEPA survey and showed a weak trend towards ratios less than unity at low TN:TP ratios. Evidence therefore supports the statement that N may become limiting relative to P in eutrophic lakes and that there is a weak monotonic relationship between TN:TP ratios and τ_n/τ_p ratios. Concentration ratios are some guide to flux ratios but the N limitation effect is, however, not strong. Certainly the biogeochemical cycling of N is quite different from that of P and the mechanisms which control the availability of P in eutrophic systems (sediment P release) are quite different from that of N (ammonification and (some) denitrification). Harris (1986) summarized phytoplankton data from 435 lakes in the USEPA reports and showed that N fixing cyanobacteria were more frequently observed as blooms in lakes where the TN:TP ratio was < 25-30. This was also the TN:TP ratio at which the ratio of turnover times became less than unity. This supports the evidence for an interaction of P sufficiency and N limitation in eutrophic waters. *Efforts should be made to estimate the relative fluxes of N and P in Australian waters and their impact on phytoplankton dynamics.*

In short, while there is evidence of N limitation which may give N fixing cyanobacteria a competitive edge in highly eutrophic lakes, the effects are rather weak and difficult to prove because of the effects of changing P fluxes. These conclusions are supported by data from Thomas (1955, 1956) which formed the basis of the nutrient depletion ratios calculated by Vollenweider (1975, 1990) and quoted by Harris (1986). High C:P depletion ratios (>2000) are frequently observed, as are high N:P ratios (200) - both indicate rapid recycling of P in oligotrophic systems. N:P ratios lower than the standard Redfield ratio (about 7 by weight) are rarely observed in eutrophic waters so the effect of N limitation must be weak. *All the evidence points to the fact that by far the best course is to reduce external P loadings (and increase the TN:TP ratio by that means) rather than to attempt to change N loadings to achieve "balanced" effluents* (see also Gachter 1987).

6.2 Nutrient regeneration from grazing by zooplankton.

Zooplankton grazing of phytoplankton biomass reduces the abundance of the phytoplankton (particularly in mesotrophic waters) and regenerates nutrients within the water column. N and P are not, however, necessarily regenerated at equal rates and the stoichiometry of the regeneration rates may lead to N or P limitation of phytoplankton growth (or both simultaneously). Zooplankton growth may also become N or P limited depending on the concentration ratios in the food supply. Based on data assembled by Le Borgne, Sterner (1990) attempted to model the interaction of phytoplankton growth, grazing, zooplankton growth and nutrient regeneration. This is just like having two versions of Figure 1, one each for N and P, coupled together by the necessary N:P stoichiometry for algal and zooplankton growth. The results of this, and more recent work, are quite striking.

The basic conclusion is that the key variables are the TN:TP ratio in the food, the TN:TP ratio in the zooplankton pool and the N:P ratio in the soluble nutrients regenerated by zooplankton excretion (Sterner 1990). Available data indicate that there is a proportionality between the TN:TP concentration ratios in the zooplankton food and the N:P ratio of their excreta. TN:TP concentration ratios are thus a reasonable surrogate for N and P flux ratios. The proportionality is, however, slightly non linear. It appears that zooplankton try to maintain homeostasis in their internal N:P ratio. This means that they will sequester N or P in their tissues if either N or P is in short supply in their food (Sterner 1990, Urabe 1993). The outcome of this behaviour is to cause the N:P ratios in the phytoplankton to diverge further from the "balanced" Redfield ratio of 7 by weight if N or P limitation in the food supply sets in. Thus the zooplankton will tend to accentuate N or P limitation of phytoplankton growth.

While there is a good general relationship between TP loadings and zooplankton biomass (Table 1, also Hessen 1992) not all zooplankton have similar minimum nutrient quotas for growth. Some become more easily P limited than others. Copepods have higher C:P ratios than cladocerans and can tolerate more P limitation. Cladocerans have high P requirements and are more easily P limited. Cladocerans may therefore drive up seston C:P ratios if P becomes limiting for growth by sequestering P within their bodies. Similarly copepods may drive pelagic systems towards N limitation. (Curiously cladocerans are a freshwater group, copepods are predominantly marine.) This adds an extra wrinkle to the biomanipulation story. Altering the species composition of the zooplankton by predation may have a large impact on the phytoplankton through changes to nutrient recycling rates (Elser et al 1988). Significantly Pace (1984) showed that the greater impact on the Chl:TP ratio came from changes in zooplankton community structure not changes in biomass. Cladocerans (such as large *Daphnia*) will funnel P out of the algal pool and will tend to reduce the growth rates of phytoplankton through P limitation as well as reducing the biomass directly by grazing. N limitation through zooplankton grazing is a different story because N content is less variable across taxa than is P content. *Nevertheless the stoichiometry of nutrient recycling rates is a function of the zooplankton species composition and shifts in the species composition of the zooplankton can have strong effects on the recycling rates of N and P in pelagic systems (Elser et al 1988, Sterner et al 1992). This requires further study.*

6.3 Nutrient stoichiometries

Both Vollenweider and I (Harris 1986, Vollenweider 1990, Harris et al 1992) have shown that the apparently chaotic temporal dynamics of the various particulate and dissolved nutrient pools follow regular stoichiometric patterns. There are fundamental ratios of C:N:P for both algae and zooplankton such as the Redfield ratio (Redfield 1958) which have evolved similarly in both marine and freshwater systems. The available data were summarized in Harris (1986) and Hecky et al (1993). (Incidentally the situation is not helped by the limnologists' tendency to measure Particulate Organic Carbon, (POC) and TP but not TN, whereas the oceanographers have a tendency to measure POC and TN but not TP. We have C:P data from freshwaters and C:N data from marine systems but there is little data on C:N:P ratios in both types of system.) The stoichiometries of C:N:P cycling through organisms and other particulate and soluble pools at the range of scales typical of the trophic status of the system determine the dynamic range of ratios observed (Harris 1986, Vollenweider 1990). The physiological requirements of the various organisms determine the stoichiometries of nutrient uptake and regeneration and control the cycling of energy and materials (Hessen 1992). Physiological constraints limit the scope of ecological variability.

Rates of production and grazing are tightly coupled in oligotrophic systems and nutrients are regenerated by grazing in surface waters, so that the C:N:P ratios of particulate material from such systems show what Vollenweider has called "low dynamic" behaviour. C:N:P ratios in the seston cluster closely around the physiological ratios of the Redfield ratio (Harris 1986). The resilience of such systems is a function of the rapidity of growth and grazing (Harris 1986). De Angelis has shown that there is a very important link between resilience, nutrient turnover times and high growth and grazing rates in such systems (De Angelis et al 1989, De Angelis

1992, Carpenter et al 1992). C:N ratios in the seston are more consistent than either C:P or N:P ratios or other ratios involving chlorophyll as a measure of biomass (C:Chlorophyll, N:Chl or P:Chl) reflecting the dominant role of P limitation and infrequent severe N limitation. There is good evidence from data on the depletion of C:N:P from soluble pools in surface waters to show that N and P are recycled more rapidly than C in oligotrophic surface waters and that the Redfield ratio is an "end member" of these depletion ratios (Harris 1986).

In more eutrophic systems algal biomass increases and sedimentation takes precedence over grazing. Deep water and benthic pools become more significant and exchanges between these and surface waters may take days to months. Growth and loss rates are lower, nutrient turnover times are extended and so resilience is reduced. Pools of particulate C, N and P may be regenerated through bacterial and chemical interactions in different places and at different time scales so the variability of the seston C:N:P ratios in eutrophic systems expands into "high dynamic" behaviour (Harris 1986, Vollenweider 1990). The physiological ratios become end members of a large range of ratios and are only encountered when algal blooms dominate the seston. C:N:P ratios in the zooplankton food supply vary greatly in eutrophic systems and the activities of the zooplankton will tend to exaggerate the fluctuations in N and P availability. Thus incipient N or P limitation will tend to be reinforced by the activities of the animals. In addition to grazing fluxes between detrital and various soluble organic and inorganic pools are frequently controlled by biogeochemical and physical processes that can temporarily distort the stoichiometry.

Even though the temporal dynamics appear to be chaotic the stoichiometric patterns are statistically quite regular (Harris 1986, Janus and Vollenweider 1984, Vollenweider 1990) revealing a pattern of exchanges between pools controlled by the stoichiometry and biological rate processes of the organisms involved (Hessen 1992). The physiology and ecology of the component species are interwoven with the changed environment. Some of the species respond to changes in the environment at various temporal and spatial sales and some themselves cause changes in the environment. Contingency and natural history are important. Susceptibility to grazing and sedimentation are two very important feed back mechanisms which work in different ways.

Harris and Griffiths (1987) called attention to the importance of variances in pelagic ecosystems and their role in an understanding of ecosystem function. This opinion has been supported by more recent work and, as a result of both empirical and experimental ecology, variances in soluble and particulate pools can now be seen to be a vital aspect of ecosystem function. High level models of parameters such as total phosphorus and annual average phytoplankton biomass can average out small scale variances and temporal dynamics in most cases, but models of processes and components of the biomass at shorter time scales and smaller spatial scales (such as those concerned with the interaction of species) cannot do so and must contend with a spectrum of possibilities arising from a number of levels in the food chain. Fundamentally as we move away from annual averages of high level variables such as TP and Chl (the Vollenweider approach) towards species abundance and population dynamics, then we are driven more and more towards the consideration of the kind of contingent variability which Vollenweider sought to avoid. At this level of organisation the "noise" in the system is the signal of interest and structure, function and fluctuation are inextricably intertwined (Harris 1986, 1994). System dynamics become "noisier" the "lower" we go and predictions can only be couched in statistical terms.

A system view of storages and water bodies leads us to believe that indeed N *can* become limiting to phytoplankton growth in highly eutrophic water bodies. It does appear that the mechanisms of nutrient cycling in eutrophic water bodies lead to the loss of N relative to P and that this may indeed favour N fixing organisms such as cyanobacteria in these waters. Coastal marine environments (such as Port Phillip Bay) which are undergoing nutrient enrichment can become N limited for similar reasons. *The management implications of this statement need to be explored.* The effects are however complex and highly variable in time and space. *The pattern therefore seems to emerge best not from short term nutrient limitation experiments but from an examination of average system behaviour.* Given the difficulty of demonstrating the effect of N limitation it still appears that limiting P loadings to eutrophic systems is a better way of controlling the growth of cyanobacterial blooms than changing the N:P ratio. *Studies of nutrient fluxes and whole ecosystem behaviour need to initiated.*

7. Macrophytes, nutrient cycling and the "two states" of lake systems.

Shallow lakes tend to characterised by two major steady state conditions. In very general terms oligotrophic lakes tend to be clear and dominated by macrophytes, whereas eutrophic lakes may frequently be turbid and dominated by phytoplankton. At intermediate nutrient levels the lakes may be in either state, or more interestingly may switch from one to the other (Blindow et al 1993). If high biomass of submerged macrophytes is not likely to cause a problem (for recreational fishing for example) then the clear, macrophyte dominated state is obviously more aesthetically pleasing than the turbid, phytoplankton dominated state. If toxic algal blooms can be avoided by this switch in state then there will be public health benefits as well. This raises all sorts of interesting questions? What causes the two states? Can they be manipulated in any way? Is this a possible management option?

We already know that in Australia it is possible to encourage the switch from clear to turbid. Lake Mokoan was, at one time, clear and dominated by macrophytes but draw down of water levels killed the macrophytes. On refilling the lake became turbid and dominated by *Microcystis*. So there are local precedents for this international experience.

The existence of two stable states and the possibility of switching from one to the other has important ecological implications. The existence of multiple stable states has been a matter of some controversy. Very few long term studies have been carried out which might reveal the existence of such states (Benndorf 1988, 1990). Blindow et al (1993) presented a set of data from two lakes in Sweden which showed transitions between the two states over a period of 40 years. They suggested that the two states were stabilised by negative feedback mechanisms. It has been suggested that the macrophyte dominated state is stabilised by reductions in turbidity (brought about by reductions in water movement and wave scouring, Lohammar 1966), by oxidation of bottom sediments and a consequent reductions in P release rates (Carpenter et al 1983, Meijer et al 1990, van Donk et al 1990a), allelopathic interactions between macrophytes and phytoplankton (Hasler and Jones 1949) and changes in grazing interactions and fish populations (Timms and Moss 1984, Irvine et al 1989, Bronmark and Weisner 1992). The turbid state is apparently stabilised by turbulence which resuspends particulate material, reduces light availability (Moss 1990), reduces grazing pressure (Hanson and Butler 1990, van Donk et al 1990b, Jack et al 1993) and prevents establishment of macrophytes (Schiemer and Prosser 1976).

Changes in fish communities may have also an impact (Johansson and Persson 1986, Diehl 1988). Predation on cyprinids by fish such as pike is reduced in turbid water so that cyprinids become abundant in the turbid state and may uproot plants by their feeding behaviour and increase the turbidity (Lammens et al 1990, ten Winkel and Meulemans 1984). Both processes increase nutrients in the water and reduce light availability (Andersson 1981, Andersson et al 1988, Meijer et al 1990). Macrophytes may cause changes in fish community structure by preventing bottom feeding fish from gaining access to the lake bottom and by providing habitat complexity thus favouring predation (Diehl 1988, Eklov and Hamrin 1989).

Whatever the precise negative feedback mechanism (or group of mechanisms) causing stability the two states appear to be quite stable and persistent for a number of years. A large perturbation is required to cause the switch from one state to another. Fluctuations in water level can cause both a switch to and from both states and changes in fish populations have also been implicated (Wallsten and Forsgren 1989, Gulati 1990, Hanson and Butler 1990, Sondergaard et al 1990). In accord with the conclusions reached above (Section 5) Blindow et al (1993) were not able to unequivocally decide whether the perturbations which caused the shifts were "top down" or "bottom up" in origin. The Swedish data did not provide unequivocal support for the "trophic cascade hypothesis" (Carpenter et al 1985) and strong "top down" control. If anything, the data showed that the causes of the shifts between clear and turbid states lay in factors such as changes in water level and nutrient reductions which favoured macrophyte growth or reduced macrophyte abundance. Changes in macrophyte abundance led changes in food chain structure rather than lagging them as predicted by the trophic cascade hypothesis. Blindow et al (1993) concluded that macrophytes, once established, have a strong structuring and stabilising effect on aquatic ecosystem structure and function. One important role may be the provision of refuges from predation for large cladoceran grazers (Moss 1990, Shapiro 1990).

More work needs to be done in Australia on the possibilities and mechanisms of switching lakes and storages from turbid to clear states. This is not yet a tested management option but it should be studied. What is required is manipulation of the nutrient fluxes in some of the larger, longer loops in eutrophic storages so that the flux of nutrients to the pelagic zone is reduced. This can be achieved either by reducing or stopping the internal loading of nutrients (by stopping sediment regeneration of P during anoxia) or by sequestering large amounts of nutrients in large, slow pools such as macrophyte beds. Experimental sites should be established where macrophyte growth is encouraged. Nutrient loading and flow (storage level) control may be required as well as artificial establishment of the required plant species. Artificial destratification may be a possible means to reduce hypolimnial anoxia and the regeneration of sedimentary P. The turbidity of inflow streams should also be reduced by control of "flash" runoff, conservation of wetlands and the establishment of artificial wetlands, and by re-establishment of riparian vegetation in farm drains.

8. Potamoplankton - phytoplankton in rivers.

Our knowledge of phytoplankton growth in rivers is not large when compared to knowledge of phytoplankton growth standing water bodies. This undoubtedly reflects the bias of the development of the science. There is no reason, however, to suppose that the factors which control phytoplankton growth in rivers are fundamentally different from those in standing waters. Light, nutrients and turbulence are still the dominant factors. The question is: to what extent the system is different in terms of fluxes of energy and material through the various biotic and abiotic pools?

The differences between rivers and standing waters are therefore differences of degree - particularly in regulated rivers where some sections may be stationary. Reynolds (1988) summarised the what is known about the ecology of the potamoplankton found in rivers. In free flowing rivers the turbulence regime is quite different from that in standing waters. Increased flow rates in rivers tended to decrease the growth rates of potamoplankton through a direct effect of turbulence on the organisms, a reduction in the time spent in the light (increased turbulent mixing) and an increase in turbidity. Phytoplankton in rivers (the potamoplankton) therefore cannot buoyancy regulate. There is usually a strong correlation between flow and turbidity in rivers (see the section on flow and particulate loads above) so the underwater light climate deteriorates as a direct function of flow. Residence times in freely flowing rivers tend to be of the order of days so potamoplankton tend to be washed out. Therefore periods of strong flow therefore lead to a reduction in phytoplankton biomass as a result of poor light availability, high turbulence, low growth rates and washout.

Reynolds (1988) also showed that the residence times of water and phytoplankton in rivers were such that back eddies and regions of reverse flow were essential to the maintenance of populations of cells in the rivers (Reynolds et al 1991). This is one of the paradoxes. How do potamoplankton maintain themselves in rivers when theoretically they should get washed out? The answer must lie in the fact that average residence times are not valid numbers. Populations at the centre of the stream are rapidly washed downstream and out of the system whereas populations in weir pools, back eddies and river margins (even countercurrents) have much longer residence times. It is this region that cells may divide and grow so that populations in the centre of the river are continually seeded in from the margins. Bilabongs and other off river storages serve a similar function. *The relationships between physical processes and the survival of plankton in rivers and weir pools need to be better understood.*

Despite the differences in the hydrologic flow regime and the interaction of flow and turbulence, as long as nutrients are available and the residence time is long enough for cells to grow then there is no reason to assume that the Chl:TP ratio will be any different from that observed in storages. Calculation of the TP concentration in rivers is not conceptually difficult - there may be practical difficulties to do with storm flows and sampling problems but fundamentally the task can be done. Therefore the expected Chl concentration in stretches of river should be predictable from TP given that the Chl yield per unit TP will be reduced by turbulence, turbidity and residence times. In fact managers should not expect to have problems with algal growth during periods of high flow for the reasons given above. Problems may be expected in eutrophic rivers when flows decrease, turbidity drops and residence times increase - these are precisely the times when the relationships will be closest to those normally found in storages, so accepted relationships may be employed.

The bulk of the productivity in the lower stretches of rivers is autochthonous - that is primary productivity by phytoplankton makes up a very large proportion of the total flow of energy and materials (Admiraal et al 1992). Certainly, in the more eutrophic rivers, the input of material from the catchment is strongly modified and supplemented by the *in situ* growth of phytoplankton. As much as two thirds of the particulate C and three quarters of the particulate N can be attributed to phytoplankton in the lower reaches of eutrophic rivers such as the Rhine (Admiraal et al 1992). This effect will be increased in regulated river reaches with long residence times. Knowledge from lakes and storages is therefore directly relevant to rivers.

Talling (1986) reviewed the seasonality of phytoplankton in African lakes and rivers and showed that the inverse pattern of abundance of *Melosira* and cyanobacteria such as *Microcystis* was a common feature of tropical and subtropical lakes, storages and rivers. In all cases the two species occupied different hydrographic regimes. There is a similar, well known interaction between flow and the species composition in Australian rivers and storages. Diatoms such as *Melosira granulata* are favoured by increased flow whereas buoyant cyanobacteria such as *Microcystis* and *Anabaena* do better under low flow conditions. Diatoms have relatively high sedimentation rates and are physiologically suited to growth under deeply mixed, low light conditions (Harris 1978) when silica is available. Diatoms therefore respond to increased flows. Very high flows will, of course, result in washout. We might therefore expect and inverted "U" shaped response from diatoms with respect to increases in flow.

Cyanobacteria which show buoyancy regulation are able to position themselves at a particular depth through a mechanism of gas vacuoles and ballast accumulation which is linked to photosynthesis and the underwater light climate (Reynolds et al 1987). This buoyancy regulation mechanism is necessarily rather slow so rapid fluctuations in turbulence and the underwater light climate do not favour this growth strategy. Only in quiet waters can cyanobacteria grow sufficiently to accumulate in surface scums and cause management problems. Cyanobacteria therefore tend to have an inverse response to flow compared to diatoms, blooming when flow reduces to low levels.

Jones (1993) has presented data which shows a negative relationship between cyanobacteria and flow in storages in the Murray-Darling system and has advocated flow control as the prime blue-green control mechanism. Jones has suggested that because background nutrient levels in parts of the Murray-Darling system are quite high, and because even a small biomass of cyanobacteria can cause severe problems in calm storages, flow control is probably a better strategy than nutrient control. I believe that this is only a partial answer. *Flow control is undoubtedly very important in determining the species composition of blooms but strategies which reduce the flux of nutrients to surface waters should also be investigated.* Total catchment management can deliver both control strategies. The timing of the pulses of water flowing down regulated rivers will be as important as their magnitude. Each event will have a profound effect on the nutrient availability and cycling in the system as well as the growth rates of the individual species. The timing of pulses during the seasonal development of the phytoplankton community in the river will determine the outcome.

9. Predictions of species composition

I have shown that at least within bounds it is possible to predict the expected biomass of phytoplankton from P loads and a Chl:P ratio, and I have discussed some of the features of system behaviour which are likely to modify the standard relationships. Biomass control is a well tried and tested management tool. But Jones has raised a very important question. Biomass control is one thing, but if the biomass is low and it all appears as a single toxic species we still have a management and a public health problem. So biomass is not the only thing we need to know. We need some guide as to when certain nuisance species are likely to appear and whether it is possible to manage the species composition of the phytoplankton community. I now turn to this topic.

9.1 Seasonal successions

Eutrophic systems are inherently more variable than oligotrophic systems. The species composition is also different. This begs an important question. If we try to predict the species composition of algal blooms, how important are the internally generated (non linear) population and community interactions and the nutrient cycling effects generated "higher" in the system? Is it possible to predict the presence of individual species on the basis of physiology and environment alone? What is the role of predation, competition for nutrients and other internally generated sources of variance? In short, can we predict the occurrence of species without taking the higher level interactions into account?

Data presented by Harris (1986) showed that plots of the presence of blooms of individual species against physical and chemical variables were capable of having some predictive capacity. In a large sample of US lakes, blooms were found to occur in any given combination of conditions up to 50-60% of the time. The patterns that resulted made intuitive sense with buoyant species of cyanobacteria responding to physical mixing conditions and nitrogen fixing species responding to low N:P ratios. Given the multiplicity of interacting factors a 50% prediction of bloom occurrence is remarkable. This would appear to suggest that "bottom up" predictions might work.

Others however, (Drake et al 1993), have shown that (at least in culture) there are marked species assemblage rules where competitive interactions control the order of species invasions (see Wilson 1992). There is evidence for some non linear patterns in assemblage rules of the "you can't get there from here" variety (Lewin 1993). Certainly there are some events in the seasonal succession of species which control the further development of the phytoplankton community (Harris 1988) but in a complex non linear system it will be difficult to predict outcomes from year to year. Some interactions are due to competition between phytoplankton species and may be termed "horizontal" interactions, whereas others are more "vertical" in that they involve interactions with higher trophic levels and other factors that influence nutrient availability over large space scales and long time periods. Drake et al's (1993) species assemblage rules are both "horizontal" and "vertical" interactions in that they involve both competition and grazing in an experimental set of "ponds". To what extent are competition and "vertical" interactions important in nature? What is predictable? To what extent is it necessary to have detailed information about the natural history of the system in question (Wilson 1992)?

One answer to this question lies in the extensive body of work done by Margalef (1963, 1978, 1980) and Reynolds (1980, 1982, 1984a,b, 1987) on the predictability of successions of species of phytoplankton in northern temperate lakes. A knowledge of the factors underlying seasonal species successions may make it possible to predict the occurrence of particular species. Harris (1986) also discussed this topic. Even though northern hemisphere lakes are clearer, cooler and more seasonal that Australian waters the basic principles which determine species composition are the same. In some respects, Australian conditions may be likened to "permanent summer" in the northern hemisphere (Kilham and Kilham 1990). There are structural factors in natural environments that influence the sequence of events in succession (Harris 1988). For example, Heaney (1987) showed that the size distribution of species in English lakes in spring has a marked effect on subsequent events in the seasonal succession and the removal of *Ceratium* from Esthwaite Water by fungal parasites totally changed the biogeochemistry of the system (Heaney et al 1988, 1992). Sedimentation and removal of nutrients from surface waters by large celled species have quite different effects from regeneration of nutrients in situ by grazing on small celled species. Precisely the same effects can be seen in marine coastal waters (Harris et al 1992).

Successions of species show "memory effects" which, like biomanipulation, are due as much to direct interactions between species as to indirect effects from higher trophic levels, larger, slower nutrient pools, decomposition, sediments, macrophytes, fish and other components in the system. These effects become more important in eutrophic systems. *We need to explore how we might manipulate "memory effects" in eutrophic systems.* Directional change in temperate successions results from directional changes in turbulence, progressive nutrient limitation in surface waters and a seasonal change in zooplankton populations. The so-called PEG model - developed by the international Plankton Ecology Group - is the most complete description of this sequence of events (Sommer et al 1986). Margalef (1963, 1978) pointed out that as turbulence declined and stratification became more pronounced, competitive interactions became more likely in stable environments and dominance by one species became more likely.

Processes which lead to diversity in the phytoplankton community are not necessarily those which lead to structured, directional change. When one species of phytoplankton comes to dominate the entire phytoplankton community (such as in a cyanobacterial or dinoflagellate bloom) then diversity is reduced. Stability is also reduced (Tilman and Downing 1994) and resilience decreases because of the reduced growth rates of the organisms (DeAngelis 1992).

From the water quality manager's point of view the desirable state is a diverse plankton community without dominance by one or two species. Reynolds (1980, 1982, 1984a,b) and Harris (1986) showed how disturbances in the physical structure of the water column led to increases in diversity by first favouring the growth of one species, then another. The seasonal succession of species can undergo "reversions" to earlier states as a result of injections of new nutrients (entrainment, floods etc.) or jump to later states as a result of washout. Harris and Piccinin (1980) and Harris (1983) showed that rates of community change were closely coupled with changes in the depth of the mixed layer in Hamilton Harbour, a eutrophic embayment in the Great Lakes. Time lags between changes in environmental turbulence and community structure ensured that non steady state conditions existed at a scale of 10-20 days (Sephton and Harris 1984, Trimbee and Harris 1984a, Harris and Trimbee 1986). Even though the environmental fluctuations ensure non equilibrium conditions and high diversity in perturbed environments at a scale of days (Sommer et al 1993), there is a longer term predictable set of interactions between environmental conditions and the species composition of the phytoplankton community.

Margalef (1978) and Reynolds (1980, 1982, 1984a,b) produced "mandalas" - diagrams which summarised a whole series of observations about the relationships between physical and chemical parameters and the occurrence of phytoplankton species. Reynolds' "mandala" indicated the domain of each of a number of groups of dominant species relation to water column stability and to nutrient stress. These diagrams can be used to broadly predict when certain species, or groups of species, are likely to occur. *There is therefore a degree of predictability in the occurrence of freshwater phytoplankton.* The species themselves influence the nature of the succession and hence the probability of their replacement by influencing the balance of sedimentation and grazing. Sedimentation reduces nutrient concentrations in surface waters whereas grazing regenerates nutrients in situ. Biology influences biogeochemistry.

One of the most potent "memory effects" in seasonal successions and a dominant factor in the occurrence of species from year to year is the evolution of cysts, akinetes and other resting stages by phytoplankton. By leaving cysts, autospores and akinetes on the sediment surface after each bloom, nuisance species like cyanobacteria and dinoflagellates plant the seeds of next year's bloom or blooms for many years afterwards. Cysts and autospores may survive for many years and may be transported around the world with traces of sediment in ballast water (Hallegraeff 1993). Many of these species have evolved strategies to make their establishment in the plankton of the following year or years more likely, such as responding to periods of overturn (dinoflagellates such as *Ceratium*, Harris 1983), light and anoxia (cyanobacteria). Trimbee and Harris (1984b) were able to watch the recruitment of cyanobacteria in a small Ontario lake (by trapping them in upside-down sediment traps as they floated upwards) and showed that the akinetes on the sediment responded to periods of increased light availability and anoxia. Growth of akinetes on the sediment surface led afterwards to blooms in the water column as the cells became buoyant. *Once a nuisance bloom of many species has occurred it is much more likely to reoccur each year thereafter and may be very difficult to eliminate. Studies of the resting stages of nuisance species should be carried out in Australian waters.*

9.2 The role of competition and grazing

Competition between phytoplankton, if it occurs over a long enough time periods (> 20-30 days) can lead to domination by one, or a few species. How often does this occur? Well, views about this vary. I have, for many years, been an advocate of the "competition isn't very important" school (Harris 1986). Not everyone agrees. Sommer (1989, 1990, 1991) has criticised my conclusion that because C:N:P ratios of natural phytoplankton populations are frequently close to the Redfield ratio, (and growth rates are therefore close to maximal most of the time) there is little evidence for nutrient limitation of growth rates and competition between species. Whilst my conclusion remains true much of the time, it certainly *is* possible to find distorted C:N:P ratios and competition in natural phytoplankton populations. Particularly good examples of distorted C:N:P ratios can be found in populations like *Ceratium* that grow in stable metalimnia for weeks at a time (Harris 1983, Heaney et al 1987, Sommer 1989).

There is, perhaps, less difference between the views of Sommer and myself than some would have us believe (e.g. Sommer 1985). In many environments perturbations disrupt the progress towards competitive exclusion. Harris (1986) discussed the importance of the intermediate disturbance hypothesis as an explanation for phytoplankton diversity and pointed out that competition and nutrient limitation of growth was possible in physically stable environments. Padisak et al (1993) have recently published a symposium volume on this topic. It really isn't a debate about whether competition occurs but how often it is an important determinant of events.

Physiological measures such as the half saturation constant for nutrient limited growth, K_S, have great significance in determining the outcomes of competition in waters of fluctuating nutrient concentrations. *It is difficult to find good physiological data for some of the more common nuisance algal species in Australian waters (e.g. Melosira) - autecological studies on the physiology and growth rates of the more common bloom forming species should be carried out.*

Some data (Sommer 1989, 1990, 1991) point to many cases where it is difficult to identify nutrient limitation of growth and competition in epilimnetic populations. There is a counter intuitive link with trophic state. Competition for nutrients may be expected to occur most frequently (like the *Ceratium* example) in stable, nutrient rich waters where grazing and the consequent biological nutrient regeneration mechanisms are not effective. Physical mechanisms such as diffusion control the rate of nutrient supply to metalimnia in such cases. Regeneration by grazing is unimportant. (This is growth limitation by *nutrient flux* rates.) Conversely, in oligotrophic waters where nutrient concentrations may be quite low, grazing by small zooplankton and microheterotrophs is sufficient to maintain a high flux of recycled nutrients and sustain high growth rates. Thus nutrient limitation of *growth* and competition for nutrients may be found most frequently and severely in the most eutrophic waters. This situation will be reinforced by what zooplankton grazing there is as N or P limitation will be reinforced by the habit of zooplankton to sequester scarce nutrients. The stoichiometries of the nutrient data presented in Harris (1986) and Vollenweider (1990) support this conclusion. *Physical perturbations applied to such waters might be expected to have strong ecological effects through influences on nutrient regeneration and a reduction in competition. This warrants further study as a possible management tool.*

Competition for nutrients may well be an important factor in determining the presence of species in some circumstances but it is modified by other factors. Tilman et al (1986) have shown that the outcomes of competition experiments between diatoms and cyanobacteria are temperature dependent. Cyanobacteria tended to dominate at 24°C over a wide range of N:P ratios less than about 20 whereas they were never dominant at any N:P ratio at temperatures less than about 17°C. McQueen and Lean (1987) showed no correlation between the TN:TP ratio and the occurrence of cyanobacteria in Lake St. George over a 13 yr period. The percentage abundance of cyanobacteria was, however, positively influenced by temperature and inversely related to the concentration of nitrate in surface waters (see also Royle and King 1992). Cyanobacteria became more common at temperatures above 21°C. The presence of nitrate in the water will have a strong effect on the metabolism of nitrogen within phytoplankton cells because it is one of the regulators of enzyme activity and a strong determinant of which form of nitrogen is metabolised. TN:TP ratios are therefore not the sole determinant of competitive interactions involving cyanobacteria. One further supporting factor is the observation by Suttle and Harrison (1988) that N fixing cyanobacteria are not good competitors for P. This would explain the reduction in relative biomass of cyanobacteria at low P concentrations.

Carbon availability is also an important feature of some freshwater systems and may be a factor which influences the course of the succession of species. When photosynthesis is rapid a rise in the pH of surface waters may occur because of the removal of CO_2 from the CO_2-bicarbonate-carbonate system which is the main pH buffering system in freshwaters (Talling 1976). Talling (1985) has also shown that cyanobacteria are capable of photosynthesis at higher pH values than many other phytoplankton so that they may have a competitive advantage under these conditions. Phytoplankton which are capable of photosynthesis at high pH are able to do so because they can utilise bicarbonate rather than dissolved CO_2.

The outcome of competition between diatoms and cyanobacteria is also modified by the depletion of Silica which occurs when diatoms bloom in freshwater systems (Horn and Horn 1990). As Si is depleted in surface waters, diatom growth is suppressed and other species may come to the fore. This may cause large changes in the entire biogeochemistry of the system (Conley et al 1993) as diatoms which sink rapidly are replaced by cyanobacteria which control their buoyancy. Sedimentation rates decrease sharply. It is also possible that Si depletion may contribute to some recent cases of amnesic poisoning caused by diatoms because production of the toxin appears to increase during the stationary phase of growth (Bates et al 1991).

Varis (1993) has recently reviewed the factors which can lead to blooms of cyanobacteria. He listed the following hypotheses: elevated water temperatures, nutrient enrichment, low N:P ratios, low light conditions, high pH or low CO_2 availability, ineffective grazing by filter feeding zooplankton, competition with other phytoplankton, low loss rates as a result of buoyancy regulation in stratified water columns. Each of these factors may play a role and it is difficult to determine which is the most important. Varis' model of a 15 year data set from Finland was unable to unequivocally identify the dominant factor. Whatever the dominant factor in any particular case it is easy to see that this combination of factors is frequently encountered in warm, turbid, eutrophic Australian water bodies. *Physiological and autecological information needs to be collected for Australian species so that the particular combination of factors prevalent here may be identified.*

Evidence points to a strong interaction between ecological structures (community diversity, size distributions and food chain structure) and the periodicities in, and structural components of, the physical environment (Holling 1992). This may be seen in the data from measurements of the size structure of phytoplankton communities. Measurements of the size distributions of phytoplankton communities show more peaks and higher variances in eutrophic waters than in oligotrophic waters (Harris 1986, Harris et al 1987). Variances around the mean values of the slopes of the particle size distributions are also higher in eutrophic waters (Sprules and Munawar 1986). Which is cause and which is effect is unclear as there are higher spatial and temporal variances in eutrophic systems as compared to oligotrophic systems both in the chemistry and in the biology. Physical processes of entrainment and mixing couple the chemistry to the biology. With feedbacks from the biology to the chemistry also driven by physical processes such as sedimentation it is difficult to decide which is responsible for what. *Environmental variability and its impact on competitive interactions and community structure needs to be systematically examined in Australian waters.*

Connectedness in ecological food chains has been studied for some time using a variety of data sets (Cohen 1978, Pimm 1982, 1991), many of them from freshwater systems. In general, increased connectedness between an increased number of species reduces stability, but the relationships between connectedness and the number of species and between stability and complexity are not straightforward (Pimm 1982, 1991). There is some debate at present about the relationships between a number of food chain properties and species number (Pimm et al 1991, Martinez 1993) with the recent debate centered around the interpretation of data from a large number of Adirondack lakes (Havens 1993a) and acidified lakes (Havens 1993c).

Carney (1990) presented evidence to show that connectedness was a function of trophic state. This is to be expected given the relationships between system variance and resilience. Carney's data showed that connectedness rose to a maximum in mesotrophic systems. Oligotrophic to mesotrophic food chains are heavily dependent on "vertical" grazing links for nutrient regeneration. Resilience appears to be high

(DeAngelis 1992). Such systems are dependent on nutrient regeneration within the food chain and, based on nutrient stoichiometries, seem to show little nutrient limitation of phytoplankton growth and little competition because of high fluxes of nutrients at low concentration. Eutrophic food chains, on the other hand, seem to be less resilient and much more connected to nutrient pools external to the food chain. Nutrient regeneration is slower and perhaps less efficient because of the involvement of the sediments. Physiological and hydrodynamic explanations therefore work better in the eutrophic than in the oligotrophic case. It is possible to demonstrate competition more frequently (using nutrient stoichiometries) so the evidence for intermittent "horizontal" connections is stronger. These explanations are, in reality, an extension of the Hairston et al (1960) model and are consistent with the Oksanen et al (1981) and Murdoch (1966) models. Aquatic ecosystems vary between the "yellow", "green" and "prickly and tastes bad" states (Pimm 1991). Kaufmann's (1993) models predict that connectedness is regulated by system function and should, therefore, be a function of trophic state. *Other than Carney (1990) I can find no data to test this hypothesis. More work needs to be done in this area.*

9.3 Diversity and stability - measures of ecosystem "health".

A recent paper by Tilman and Downing (1994) has reopened the old debate about the relationship between community diversity and ecosystem stability. The basic thesis is that more diverse ecosystems are more stable than ones which contain fewer species. Before we go on we need to define both diversity and stability. This, in itself, is no mean feat! Biodiversity can be defined both by the total number of species in the community and by the relative abundances of species. Diverse communities are usually defined to be those which have both a large number of species and a relatively even distribution of abundances. There is a standard information theory statistic to measure this (Harris 1986). There are various definitions of stability, but most would agree that stability is measured by resistance to change (how difficult is it to get a community to change in response to an external perturbation?) and by resilience (how fast does the community recover after perturbation?). See Pimm (1991) for a full discussion of stability concepts.

The diversity/stability concept was suggested by people such as Elton (1958) and many others accepted the basic idea that the two concepts were inextricably linked in natural ecosystems. The conservation movement makes much use of this concept to justify conservation of high biodiversity. *There has been much uncritical use of the idea and rigorous examination of the concept has been generally lacking.* Perhaps the most complete examination of the concept was the theoretical modeling carried out by May (1973). The box models of species interactions in ecosystems which were developed by May basically showed that the more species there were, the less stable the overall system was. Too much interconnection caused the model communities to fall apart. This result caused many to question the overall validity of the relationship.

Tilman and Downing (1994) have studied the relationship between species diversity and both resistance and resilience in 207 grassland plots exposed to drought and have shown that a significant relationship exists. The relationship is not linear and appears to saturate - i.e. addition of species past a certain point does not cause a significant improvement in stability. The freshwater data discussed in this review appears to agree with Tilman and Downing's result. Increasing nutrient loadings to aquatic systems increases overall productivity, alters cell size distributions and reduces diversity (Table 1). The main effect is on evenness (Lazerte and Watson 1981, Harris 1986) - eutrophic systems tend to be dominated by one or a few species, especially cyanobacteria.

I have already shown that eutrophic systems appear to be more variable than oligotrophic systems in terms of biomass, nutrient stoichiometry and other factors. Resilience is reduced - recovery times are longer because growth rates are slower and grazing pressure is reduced (Table 1). Species diversity is also reduced (Table 1). Thus eutrophic ecosystems appear to confirm the trend suggested by Tilman and Downing's data. Nutrient loadings push aquatic ecosystems from a diverse, stable state dominated by recycling of energy and materials within the water column towards a state which is less diverse, less stable and in which benthic recycling mechanisms predominate.

If there is indeed a positive relationship between diversity and stability (as there appears to be) then there is merit in the measurement of diversity because, apart from the aesthetic aspects of diverse ecosystems, there is a synergy between high biodiversity, resilience and resistance. The feedbacks between biodiversity and ecosystem function mean that stability and diversity will, to some extent, be reinforcing. *Management actions which increase diversity should have a beneficial effect on ecosystem function.* Biodiversity will, however, always be dependent on the vagaries of contingent variability, on biogeography and on accidents of immigration (Talling 1950), whereas measures of ecosystem "health" derived from spatially and temporally averaged measures of ecosystem function can be expected to be more robust. *Measures of ecosystem health based on ecosystem function as well as biodiversity need to be developed for Australian waters.*

Nutrient loadings interact with climate fluctuations to produce an aquatic ecosystem which has a given stability and functional attributes. Increased nutrient loadings lead to reduced diversity and stability; increasing climatological fluctuations lead to first an increase in diversity, then a decrease (Harris 1986). Intermediate disturbances lead to the highest diversity - too few disturbances lead to competitive exclusion, too many disturbances lead to too much turbulence or washout (Sommer et al 1993). *We might therefore predict that water bodies undergoing high nutrient loadings in rather stable climates would be dominated one or a very few species and that blooms of nuisance species might be prevalent. Nutrient loadings and interannual climatological variability interact to produce undesirable results. River regulation will exacerbate this effect.* Ecosystems in eutrophic storages dominated by undesirable blooms are "unhealthy" for displaying both low diversity and displaced metabolism. *With the feedback between diversity and biogeochemistry dependent on the sedimentation (or otherwise) of carbon and nutrients fixed in surface waters, actions to modify the species composition by means other than a reduction in nutrient loadings can be expected to produce changes in ecosystem function and "health". These techniques should be explored.*

10. Manipulation of species composition.

Artificial manipulation of the species composition of the phytoplankton community by means other than a reduction in nutrient loadings has been attempted. Biomanipulation is one such effort, though there are other techniques available. Controlled biomanipulation experiments will always be difficult, if not impossible, to perform because it is very difficult to replicate lakes or control the climate (Magnusson et al 1990) and dynamic systems are inherently unpredictable (Shapiro 1990). But why not turn the argument around and instead of complaining about the effects of contingent variability, why not try to control or exploit it? It is possible to manipulate or augment the physical perturbations experienced by the system and thereby influence the internally generated dynamics from the "bottom" as it were. Intermittent artificial destratification is one such strategy - an attempt to improve ecosystem "health" by increasing phytoplankton diversity without reducing external loadings.

Fortunately it appears that many of the larger nuisance or toxic species of phytoplankton may be particularly susceptible to physical perturbations because they are less connected to events higher in the food chain. Changing the physical mixing regime, particularly when such a mixing regime interacts strongly with important ecological and biogeochemical time scales, can have major ecological consequences for phytoplankton populations and the structure of food chains. Two examples come to mind, one concerning the manipulation of the species composition of phytoplankton and one concerning food chain structure. It will take some work and some new approaches to the management of biological structures before we see if this aspect of aquatic ecosystems can be controlled in a fashion that gives some predictive and statistical power. *It is not yet a proven technique but it shows considerable promise.*

The first example is well known and is the use of artificial destratification to control the species composition of algal blooms and to deter the growth of cyanobacteria. This has been known since the early work of Reynolds (Reynolds et al 1983, Reynolds 1986) and has been developed and reviewed by others (Trimbee and Harris 1984a, Steinberg and Zimmermann 1988, Steinberg and Hartmann 1988). The key aspect of this management tool is the use of periodic partial overturns to disrupt the buoyancy regulation mechanisms and growth of the cyanobacteria. The periodicity of the physical perturbations must be chosen to interact strongly with the mechanisms (such as nutrient regeneration and competition) which control the diversity of the phytoplankton community in surface waters (Harris 1986). The optimum periodicity appears to be of the order of 10 days. This is a temporal scale which occurs frequently in natural ecosystems and which represents the periodicity of fluctuations in wind stress due to the passage of highs and lows in temperate latitudes (Trimbee and Harris 1984a, Harris and Trimbee 1986). Intermediate disturbances are a powerful way to influence the diversity and species composition of phytoplankton in eutrophic waters because of the predominant influences of hydrodynamics and nutrients. Even though the community is a messy concept because of a confusion of scales (Allen and Hoekstra 1992) imposition of a strong 10 day perturbation has a significant effect on epilimnetic populations.

Given the susceptibility of cyanobacteria to the hydrodynamic regime and the underwater light climate, periodic artificial destratification by mixing the water column of selected storages (or increasing river flow) at a scale of 10 days or so should be a good management strategy. Basically what we are trying to do is to impose a set of external perturbations on the system which should lead to environmental fluctuations, a reduction in competition, higher diversity and reduced dominance by a small number of species. Slower growing species should be at a disadvantage compared to species which can grow more quickly and exploit the fluctuating conditions. This should lead to suppression of blue-green growth to the point where washout by flow control should be possible. Artificial destratification will also reduce anoxia and regeneration of sedimentary P and reduce the internal loading of nutrients to surface waters. (Care will be needed here because artificial destratification without reducing anoxia and sedimentary P release will actually *increase* entrainment of hypolimnial P in the epilimnion!) Some careful physical modeling will be required to ensure the correct outcome. A combination of reductions in the external loading of P and artificial destratification should produce the required result.

The second example is the interaction of the 40 day oscillation in the wind over the Tasman Sea with the biology of the food chain in those waters. Harris et al (1992) described how the strength of the 40 day oscillation in westerly wind strength changed from year to year in Tasmanian coastal waters. The reason for the interannual changes in wind strength lay in changes in the position of the continental high pressure ridge over the Australian continent and the presence of a strong pressure gradient between the highs over the continent and lows over the Southern Ocean. There is also an as yet unexplained interaction with El Nino Southern Oscillation (ENSO) events (Harris et al 1988). Changing wind stress at this frequency (40 days) did not affect the mean wind stress from year to year (Clementson et al 1989). The variations of the wind stress at a period of 40 days led to periodic overturns in coastal waters that caused nutrients regenerated in bottom waters by decomposition to be returned to surface waters. Periodic overturns increased the nutrient loading to surface waters in this case.

Climatic variability at a scale of 40 days had a dramatic effect on the biomass of various groups of zooplankton and the structure of the food chain. Pulses of "new" production and blooms of diatoms occurred after each wind event. Years in which the 40 day oscillation was strong led to strong vertical mixing, pronounced production pulses dominated by diatoms and enormous blooms of salps. Years of weak oscillations in wind stress led to infrequent overturns, oligotrophic surface waters, domination by small flagellates and copepods and predominantly "regenerated" production. In intermediate years the zooplankton community was dominated by euphausiids (Harris et al 1992). A commercial jack mackerel fishery in the area was dependent on a high abundance of euphausiids to cause the fish to form commercially viable schools that could be fished with purse seine nets. The fishery failed in calm years (Harris et al 1992).

The natural spectrum of external perturbations changes weekly, seasonally and interannually, and is influenced by human activity. There are many examples of the effects on phytoplankton of processes acting at a range of time scales (Harris 1980, 1986, Sommer 1989, Reynolds 1990). The phytoplankton community is a complex entity because of the confounding of scales and interactions (Allen and Hoekstra 1992). This may be expected to produce a range of ecological states in response. Trophic state influences the biological response (Marshall and Peters 1989). Principal component analyses of phytoplankton population data (Harris 1983, 1986) shows tracking of seasonal changes in water column stability and nutrient availability by epilimnetic populations. Time series analysis (Trimbee and Harris 1984a, Harris and Trimbee 1986) reveals the time lags and transfer functions. Magnusson et al (1990) found poor coherence between biological parameters in seven lakes in Northern Wisconsin but did not attempt to compare lakes of similar trophic state.

Anthropogenic influences on the external perturbations may be subtle but nonetheless important. For example, the spectrum of perturbations experienced by potamoplankton in regulated rivers is quite unlike that experienced by plankton in rivers left to run free (Reynolds 1988). Because of the highly irregular and “flashy” flows in Australian rivers any attempt at regulation is likely to have a proportionally grater impact on the river ecosystems. Flow control therefore has had a major impact on the ecology of rivers in this country. Manipulation of the spectrum of perturbations experienced by aquatic ecosystems may lead to insights into ecosystem function, but only if confounding scales can be separated and internally generated interactions reduced. This may be the case in eutrophic regulated rivers as it is in some eutrophic lakes but we must beware making up general stories from specific examples. We do not yet have any general rules on which to base management advice.

A recent review article (Shinbrot et al 1993) has shown that it is possible to control the behaviour of chaotic non-linear systems by the imposition of small periodic perturbations. Small periodic perturbations can have a disproportionately large effect in non-linear dynamic systems - much larger than would be expected from a linear system. In linear systems small influences have small effects. The important realisation for ecological systems is the discovery that periodic perturbations cause chaotic systems to settle down into a simple subset of all possible states - even to apparent steady states (Shinbrot et al 1993). The ability to influence species composition by the imposition of periodic perturbations appears to be proven. *Much research will be needed however to discover how to exploit this property of aquatic ecosystems in a predictable way. Even in the best cases "predictable" will only be interpretable in statistical terms.*

11. Individual models and prediction in complex, logically deep ecosystems.

With the "postmodern" age comes a new conceptual basis and a new vocabulary based on the theories of chaos (Gleick 1987) and of complex dynamic systems (Kaufmann 1993). We have to live with the realisation that the world is much more complex than we think. Statistical, empirical models only describe some aspects of reality and (at least according to some) do not contribute to a real understanding of function and process. In the 1990s ecologists now build models which explicitly describe processes and which attempt to describe the functioning of ecosystems. As computer power has grown, so has the complexity of models so that now supercomputers can be used to trace the paths and fates of individual phytoplankton cells in the mixed layer. Models have become very complex "individual" models (Judson 1993) with some very complex dynamics, chaotic properties and unpredictable outcomes. The problem with non linear models of complex dynamics is that they are highly dependent of the initial state (Gleick 1987) and cannot ever be expected to produce anything other than a statistical distribution of outcomes. While, at the level of biomass, means are sufficient and patterns emerge; at the level of individual species we shall have to make do with probabilities.

Network models of the type displayed in Fig 1 can be turned into sets of mathematical equations but they are only simplistic cartoons of the real world. They do, however, describe real processes even if there are problems with aggregation errors (Bartell et al 1988, Logofet and Svirezhev 1986, Luckyanov 1983/84, Luckyanov et al 1983). For example, we cannot describe all the interactions in this form of model and we do not know how to assign species to "boxes" which represent trophic levels. Some models are highly complex others less so. Costanza and Sklar (1985) reviewed the properties of 87 models of freshwater systems and wetlands and concluded that there was an optimum degree of complexity which produced maximum effectiveness. There was a happy medium between models which "said much about little" and those which "said little about much".

Even very simple ecological models of population dynamics can, for certain choices of parameters, generate chaotic solutions. May (1974a, 1976) was one of the pioneers of a now burgeoning field. There have been problems deciding if ecological (population) data is formally chaotic, usually because of the rather short data sets involved. Schaffer and Kot (1985) have, however, shown that large variations in population statistics may have their origins in simple deterministic mechanisms. They showed that "strange" multidimensional attractors, the chaotic counterparts in non-linear dynamics of equilibria and limit cycles in linear dynamics, can be identified in ecological data and may play an important role in ecological systems.

The discovery of "strange" attractors forces us to consider the implications of extending our equilibrium assumptions about population and community dynamics. Simple effects competitive effects of one species on another can no longer be found. Both the signs and the magnitudes of the interaction coefficients change with time as the system moves around the attractor. Equilibrium rarely occurs. "Field experiments, designed to estimate the interactions, remain valid only if one knows at the outset where the system happens to be in phase space" (Schaffer and Kot 1985). "For the same reason, it becomes difficult to argue for (consistent) rules of community assembly ..... and such unarguable constructs as food webs and trophic pyramids acquire a certain evanescence. For imagine trying to keep track of energy flow in a system on a strange attractor: this year's major conduit may well be next year's insignificant path" (Schaffer and Kot 1985).

Other "postmodern" theoretical constructs may also be useful in ecology. Many aspects of populations and communities in ecological systems can be represented by models which are logically deep; that is models which are simple in concept but intricate in execution (Rucker 1988, Lewin 1993, Kaufmann 1993). The very simple

"Game of life" is one example (Rucker 1988). The observable properties of such systems are statistical in nature rather than deterministic and it is not possible to use logically shallow mathematical models to say very much that is meaningful about a logically deep world. Simple sets of mathematical equations simply do not describe what is going on. If the world really has reached great complexity from simple beginnings through intricate execution then unfortunately there is "no quick and dirty way to predict things about it" (Rucker 1988). In that case there probably never will be a simple ecological Theory of Everything. Techniques such as simulation modeling become "great ambitions without great theories" (Berlinski 1976).

Models of dynamical complexity (which show an evolution of properties and process with time and some extraordinarily complex dynamics) are certainly in vogue at present (Rucker 1988, Waldrop 1992, Lewin 1993, Kaufmann 1993) and are a new way of looking at the world. Such models stress the importance of history, of contingency and of things evolving great complexity over the passage of time. We have seen the rise of individual models in ecology - models which keep track of all the species and all the interactions in ecosystems (Judson 1993). Such models have some extremely complex properties and are probably only explicable in statistical terms. Kaufmann's (1993) models apply equally well to a large number of biological systems showing complex dynamics, including the expression and regulation of genotypes, metabolic control and development. Recent conceptual models of the function of the brain are similar (Dennett 1993). All these models depend on a concept of adaptive parallel processing of information, materials and energy. This is a totally different approach from that of traditional equilibrium ecological theory (McIntosh 1985, Kingsland 1985). These models make some statistical predictions about the dynamical properties of populations and communities in ecosystems that can be compared to the real world (Kaufmann 1993).

Models of complex dynamics (Kaufmann 1993) indicate a fine balance between structure, function and fluctuation. The fluctuations are an integral part of the functioning of the system. Not only is there predicted to be a spectrum of pool sizes (some large with slow turnover, some small with rapid turnover) but there should also be a spectrum of temporal dynamics as well (Harris and Griffiths 1987). Kaufmann's (1993) models predict a particular kind of structure and temporal behaviour that is consistent with observations of aquatic food chains. Simple Boolean models of complex systems show a spectrum of temporal behaviour and a particular statistical distribution of components that is highly skewed - more so than the lognormal (Kaufmann 1993). Data from aquatic food chains shows that most components are at least lognormal in distribution (Harris 1987, Harris and Griffiths 1987). Many data are frequently even more skewed, being made up from a number of underlying lognormal distributions (Harris 1983, 1987, Harris et al 1993). Lognormal distributions are not however, by themselves, evidence of a great underlying organising principle they may simply arise from central limit phenomena (May 1974b).

The predictions of models of dynamical complexity (Kaufmann 1993): namely a spectrum of organisms of differing size operating at a range of temporal scales is also entirely consistent with observations. As has been documented by Rodriguez and Mullin (1986), Sprules et al (1983), Sprules and Munawar (1986) and Harris et al

(1992, 1993) there are regular patterns in the slopes of the regression lines that relate the logarithms of organism size to the logarithms of abundance in each size class in pelagic marine and freshwater food chains. In such a relationship a slope of -1.0 means equal biomass in all size classes. Oligotrophic systems show characteristic slopes of about -1.2, indicating that the pelagic food chains are dominated by small organisms, whereas eutrophic system show slopes of about -0.8, indicating dominance by larger organisms.

Into this framework of complex, non-linear, contingent models of ecosystem structure and function we must place the impact of periodic, infrequent, extreme events such as floods and fire. We can now see why the impacts of these events are unpredictable in nature and extent. According to the models, external perturbations produce many small internal readjustments and a few very large changes. The same perturbation, if repeated, produces a spectrum of results. The outcome is contingent on previous events. The precise timing of events is critical as is the magnitude. The outcomes will be a range of possibilities from huge impacts to small ones. This places inherent limits on prediction, except in annually averaged or statistical terms. Statistics must be used with care because of the nature of the ecological data. Ecological and water quality data usually violates most of the assumptions required by statistical techniques. The data is rarely normally distributed and of stable mean and variance over time (Harris 1986, 1987). However the statistical "noise" that many try to remove by averaging (Harris 1987) *is* the signal of interest (Harris and Griffiths 1987).

The annual and seasonal averaging involved in the production of the total phosphorus and biomass data takes into account the various assumptions about the turnover times of nutrient and biomass pools, and scales of sedimentation and nutrient regeneration (i.e. the averaging time is as long as, or longer than, the longest time scale of biomass or nutrient turnover). It also averages out all the temporal dynamics of the various biomass and nutrient pools in the pelagic system. These models work because annual scales are much longer than the growth rates of pelagic organisms and the turnover times of most nutrient pools, even in the largest loops. Sedimentary pools of phosphorus may, however, have much longer turnover times and this is one reason why reductions in loadings to eutrophic lakes often produce the expected effects after considerable time lags (Cullen and Forsberg 1988). Predictive relationships in ecology only work if the scales of the cause and effect are commensurate and are not influenced by larger, longer term effects (Allen and Hoekstra 1992).

There are numerous statistical properties of aquatic food chains that I have already discussed (Table 1, Peters 1986, Seip and Ibrekk 1988, Carney 1990, Harris 1994). Vollenweider's models work because of the trend towards larger (poorly grazed) cells and colonies in eutrophic waters (Watson et al 1992) and because of regular statistical relationships between all the components of the pelagic food chains. i.e. there is a proportioning of the pools of C, N and P (and micronutrients) between a variety of organic and inorganic, particulate and soluble pools. Many other structural trends can be observed which must have a basis in function. Over the long term and when annually averaged, there are regular statistical properties that show trophically related patterns. Vollenweider's models work because of an assumption of equilibrium between pools at annual scales.

Model of the flows of energy and materials in such systems show that the flows are dominated by flows around small loops in oligotrophic systems and around larger loops in eutrophic systems (Pahl-Wostl 1992). Size dependent relationships, such as the ratios of the size of predators and prey (Cohen et al 1993), are commonly found in aquatic food chains and are a powerful way of classifying ecosystem function (Dickie et al 1987). The basic allometric scaling rules of metabolism and resource use provide a basis of these patterns (Peters 1983). There are, however, considerable variances around the mean trends (Harris and Griffiths 1987) which can be interpreted in terms of system dynamics (Boudreau and Dickie 1992).

I have shown that there are a number of regular properties of aquatic ecosystem structure and function which respond in statistically repeatable ways to changes in nutrient loadings. As such I have identified a number of properties of ecosystem function which can be used as a measure of system "health". Indeed, I have argued that because of the short term (day to day) variability in processes, population abundances and community structure (which are essential attributes of system function) and the impact of flood, fire and storm it will be difficult to determine whether longer term trends exist. The fluctuations in the system - the periodic "crunches" - are the events which control the species composition and the overall system function. Cyanobacterial blooms may be indicator species of disturbances to the oligotrophic state and of what Vollenweider has called "displaced metabolism" - the shift of recycling mechanisms from the water column to the sediments. Due to the evanescent nature of algal blooms however the presence or absence of individual species is not as good an indicator of system health as measures of system metabolism.

Population and community data may be chaotic and driven by extreme events. For example, it is very difficult to determine from short term incubations if N or P is the limiting factor in aquatic ecosystems. Taking a system view does however indicate a clear trend towards N limitation in highly eutrophic systems - a view consistent with the increased abundance of cyanobacteria in such systems. Stable equilibrium states and average relationships are not fundamental properties of ecological systems but are properties that emerge asymptotically from extrapolation to sufficiently large spatial and temporal scales (DeAngelis and Waterhouse 1987). In order to sort out the "wood for the trees" it is necessary to take a larger system view of the problem. I suggest that the present preoccupation with the measurement of species abundances and biodiversity in natural ecosystems may suffer from the same problems. It may indeed be difficult to "see the wood for the trees" in population census data. Measures of ecosystem "health" derived from system level properties may be better indicators.

So what limits our ability to predict the abundance and occurrence of species in a complex non linear system? The question can only be answered in terms of a balance between the interaction between environment and physiology ("bottom up" controls, assuming no connections) and the influence of "vertical" and "horizontal" connections and interactions in the food chain. Models of complex dynamics assume the supremacy of coevolution, information flows, communication and the flow of energy and materials in the food chain (Kaufmann 1993). Such models clearly mimic many aspects of real systems. Autecological models, on the other hand, assume the primacy of climate and nutrient forcing and physiological responses by the individual species. Some (Wilson 1992) advocate explanations based on natural history alone. Certainly the presence or absence of certain "keystone" species can bias the entire result. Climate does influence both the growth form of higher plants (Box 1981, Prentice et al 1992) and the gross morphology of some phytoplankton (Harris 1986). Environmental parameters may be used to give some predictions about which species might occur. Which explanation dominates? As usual the answer probably lies somewhere between the two and may be a function of trophic state. Happily for the managers, autecological predictions will probably work better in eutrophic waters where toxic blooms are a problem. *New models need to be developed using the new ecological vocabulary to see if these new approaches provide better insights into the factors which determine the species composition of algal blooms. The development of a predictive capability is a desirable outcome.*

Intermediate disturbances are a powerful influence on community structure (Harris 1986, Sommer et al 1993) and "memory effects" involve a number of external nutrient pools whose availability may be controlled by hydrodynamics. Intermediate disturbances can determine the abundance of particular species and may disrupt the competitive interactions which occur in stable environments. Depending on the scales of intervention and interaction, disturbance effects may propagate throughout the food chain. Only in those cases where it is possible to avoid the confounding effects of interactions at a variety of scales will it be possible to give an unequivocal answer as to which process dominates (Allen and Hoekstra 1992). These cases will be rare. We must beware of generalisations based on specific cases.

12. Testing the predictions in the Australian context.

So we are left with a confusing and complex situation. We now know that we can only predict events at a fairly high level in the ecosystem (at the level of biomass or other system level properties for example) and that lower level predictions of population dynamics and species composition are fraught with contingency and complexity. There are clearly no "magic bullets" but, nevertheless, we do know a surprising amount. Empirical models (Vollenweider 1968) work at the higher levels if the averaging period is long enough and statistical relationships (Harris 1986, 1994) work at the population level if enough instances (lakes) are examined. Neither works well in specific cases (Cullen and Forsberg 1988). Exceptions always occur. How do we go about predicting what might happen in particular cases? What models might we use and how do we test them?

We can begin with loading models and empirical models of the response at the level of biomass. *There is little good data on P loadings to Australian water bodies and rivers. More data should not be difficult to obtain and the models are straightforward provided that hydraulic loadings, water residence times, and morphometry are known.* Storm events dominate the hydraulic loading in this country. The consequences of this must be appreciated and action taken to understand the true nature of the problem. *Good data from storm events will be required, but again there is no conceptual problem - the problem is the will, funding and manpower. Automatic* *samplers now exist which can render this problem tractable. Data on P availability is being gathered, we need more of it.* There is, as yet, little evidence that Australian P loadings differ in anything other than degree from overseas experience. *The precision and accuracy of the chemical analysis of samples needs attention, as do the protocols which relate to sampling methods and transportation.* Again the knowledge exists, it merely must be put into practice. Education is required. We can easily test that Australian Chl:P relationships are similar to internationally accepted values. *There may be modification of the relationship arising from high turbidity and suspended solids, salinity levels and unavailable, particulate P. This can be tested and we now understand the relationships well enough in water bodies of the world to know if the Australian relationships are, indeed, different.*

In short, at the level of the biomass response and system function, progress can be made fairly easily. At the level of the population and community response the situation is very different. At present we cannot reliably predict when cyanobacteria or dinoflagellates will occur or what the species composition of the phytoplankton community will be. Surprises will always occur. Some of these surprises will be a danger to public health. In any case we need *system* level approaches - we must acknowledge the complexity of what we are trying to do and develop approaches that incorporate this level of organisation. System level approaches take into account the properties of the entire ecosystem - drainage basin, soils, land use, flow regimes, nutrient loadings and biology. *This requires a new generation of models which combine Geographic Information Systems and spatial data with ecosystem models of sufficient realism.*

We have a range of models at our disposal which might, if developed further, reduce the ecological risks. We can develop "plankton models" of the kind shown in Fig 1 in the clear knowledge that they can be seriously flawed by aggregation errors and problems associated with the depiction of complex interactions by more simple equations (Luckyanov 1983/84, Luckyanov et al 1983, Bartell et al 1988). These models can be analysed to show where the critical points are and where errors in knowledge are going to be most serious. In particular great care must be paid to the representation and modelling of processes at different time and space scales. There is a hierarchy of events and processes at a wide range of time and space scales (Harris 1980, 1985, 1986) and the representation of these by models is not a simple matter (Allen and Starr 1982). *Nevertheless, I have shown that the considered use of plankton models can reveal much of interest about system behaviour. Research in this area should be supported.*

In the realm of "individual models" and models of complex dynamics there is much to be done. This is a new area of ecological theory that is still is its infancy (Judson 1993). All in all we need a whole suite of models of different kinds that each represent some different kind or aspect of reality. Modelling for modelling sake is not uncommon - what we need are tests of theories and concepts. When models are all put together with empirical data (which after all describes what *really* happens - I think! - an interesting philosophical question this) then we can begin to test whether what we know has any bearing on reality (Pimm 1991, Peters 1991, 1992).

A considered program of modelling is therefore warranted as long as it is clearly stated what aspect of the system is being modelled and what the overall purpose is. A compilation and analysis of empirical data sets for Australian conditions, and a comparison of the data with overseas experience, will allow us to obtain a clearer picture of those factors which are peculiarly Australian. It will also define which aspects of Australian work are inadequate and which require further effort. *Interannual variability in climate must be recognised and the relevant data assembled and analysed.*

Most importantly it will be essential to test mathematical and empirical models to see "what works" in practice. These models can only be tested by reference to the real world; either in an empirical sense or by experimental manipulations and management actions. This will require the comparison of model results with bottle experiments, mesocosms, experimental "tubes" or the manipulation of whole ecosystems. Science works - we need a combination of theory, hypothesis and test. *What is required are testable ecological hypotheses (Peters 1991) and experimental verifications or falsifications of predictions. If we do not do this we are wasting time and money.* Experimental manipulations can be deliberate variations in flow in regulated rivers, additions of nutrients to large scale enclosures, nutrient removal experiments, manipulations of turbidity, mixing, oxygen concentrations, food chain structures or macrophyte populations. The possibilities are enormous but the precise protocols must be chosen with great care so that testable results are obtained. We must stop making up stories from particular cases.

A recent issues of the Australian Journal of Ecology addresses the issue of predictable management interventions and the reduction of ecological risk for managers. The contributors showed that the uncertainties of management interventions are such that experimental manipulations are required to check that the outcome of the management intervention is what is intended. Because of the natural variability in the system due to contingent variation and climate variability, statistical techniques are required to detect whether or not an effect has been induced. *The issue of what is termed adequate "statistical power" is a real one which must be addressed.*

Perhaps most importantly what is required is the political recognition that large scale experimental facilities are required to test some of these hypotheses. Canada established the Experimental Lakes Area in the 1960s and the UK established the Blelham Tarn "Lund Tubes" at about the same time (Lund and Reynolds 1982). Both were large scale facilities for whole ecosystem manipulation. The ELA still exists and has been used to examine a number of whole ecosystem responses to stresses such as eutrophication and acidification. The Lund Tubes were sunk in the early 1980s for a number of reasons (some of them aesthetic - they were in a National Trust site!) but while in operation they contributed greatly to knowledge of eutrophication in the English Lakes (Lund and Reynolds 1982). They are the basis of Reynolds' significant contributions to algal ecology. Both facilities contributed to a wealth of understanding that we are all able to derive benefit from. *Without a similar Australian facility we are never going to be able to test Australian models of phytoplankton dynamics and see if the peculiar set of environmental conditions that pertain here really do demand singular ecological responses by Australian managers.*

Not only do we require experimental facilities but they must be operated for a number of years. I have shown how climate variability has a dramatic impact on the occurrence of blue-green algal blooms in Australia and that such variability has time scales of at least seven to ten years. Any experimental facility must encompass such time scales if it is to provide statistically reliable data. Therefore long term data sets are a vital adjunct to any such study. None of these things are conceptually difficult - it requires political will and the granting of adequate resources over sufficient time periods. What *is* conceptually difficult is the ecological understanding which must define the manipulations and the science. That is a real challenge for the future. *What I suggest as a high priority is the education of water quality managers to the international best practice level. The fragmentation of the Australian limnological community over the years has meant that there is a general lack of knowledge about the factors which influence the dynamics of algal blooms in Australian waters. This can, and must, be remedied quickly.*

13. Australian research priorities

The following points may be made:

- When compared to countries like Canada the limnology community in Australia is small and scattered. The phytoplankton ecology community in Australia is even smaller. The net result is that relatively little work has been done here in this area. Ganf et al (1982) made precisely this point in a paper 12 years ago. Not much appears to have been done to rectify the situation in the intervening years.

- If we are to understand the dynamics of phytoplankton blooms in lakes, storages and rivers we will have to consider both "top down" factors (factors which arise "higher" in the food chain, such as grazing pressure from zooplankton) and "bottom up" factors (factors which influence phytoplankton growth from "below" such as light, temperature, nutrients etc.)

- We have begun to understand that only a view of the entire system will suffice if we are to understand the full complexity of real world problems. Thus water quality in lakes, storages and rivers cannot be divorced from land use and events in the drainage basins - Total Catchment Management is the order of the day.

- One of the most important factors in the interaction between loadings and the expression of the phytoplankton response is the relative magnitude of loadings derived from external sources of nutrients and those derived from internal regeneration.

- The basic assumptions of the limiting case Vollenweider model are annually averaged loads and in-water concentrations of P, a zero internal load and a sedimentation velocity, mean depth relationship of approximately unity. In other words the model assumes that the water body is a net sink for P and achieves a steady state at a scale of one year (Harris 1986). This also effectively assumes that water residence times are of an equivalent magnitude. These models work well for the usually cool, oligotrophic, clear, deep and mono- to dimictic Northern Temperate lakes. Many of these limiting assumptions are violated by Australian lakes, storages and rivers.

- More effort needs to be put into developing models for the estimation of P concentrations in Australian rivers and storages.

- Many sub-tropical Australian storages fill in a few days once a decade. Between times there may be little or no inflow or outflow and evaporation exceeds rainfall.

- Automatic sampling of the entire flow regime at frequent intervals (at least daily) is required in order to fully document the load/flow relationship for Australian streams. Given the long time periods between floods this may require many years of intense monitoring before the full relationship is known. Automatic equipment capable of remote operation for long periods is now becoming available. This will be the only way to accurately measure loadings from Australian rivers and streams.

- Because of storm flows, nutrient export regimes from Australian catchments are quite different from overseas conditions. Given the long history of interest and the importance of diffuse loads in determining water quality in rivers and water bodies, I find it surprising that no-one has seen fit to do more measurements of export from Australian catchments or do a detailed, up to date review of the Australian literature and a critical comparison with international biogeochemistry and management experience. This needs to be done.

- Infrequent events, such as storms and fire in the drainage basin, has long term consequences for the phytoplankton in rivers and storages - sometimes lasting for decades. As nutrient loadings to Australian storages are predominantly driven by storm events and fires, they are, in effect, part of a climate variability problem which has hemispheric and interannual dimensions. Rainfall, runoff and river flow are strongly linked to interannual climate variability in Australia through mechanisms such as the El Nino - Southern Oscillation (Simpson et al 1993). There is a real need for work to be done on the interannual variability in climate and the incidence of toxic algal blooms - including an analysis of anecdotal data.

- River regulation will have significant implications for large river systems like the Murray-Darling - flow regulation will be both nutrient transport regulation and phytoplankton growth regulation. This effect needs to be studied.

- There are large gaps in our knowledge of Australian systems in terms of nutrient loadings - and the situation is not helped by the fact that we suffer badly from systems driven by brief storm events which are widely scattered over long time scales - there is no practical or conceptual reason why these gaps cannot be filled.

- Much historical water quality data is unreliable and, while severe logistical problems in sampling remote sites are admitted, there is a general lack of good nutrient data from many crucial sites. Given the climate variability, how can we really determine if water quality has deteriorated over recent years without good long term data sets?

- There have been claims that Australian waters differ from those overseas because more of the total P here is said to be unavailable for algal growth. There is, as yet, insufficient data from a range of natural waters to show whether or not Australian waters really do have a different distribution of P between available and non available pools from that which would be expected. None of the new methods has been adequately tested.

- At least within bounds it is possible to predict the expected biomass of phytoplankton from P loads and a Chl:P ratio. There is no evidence that the Chl:P ratios of Australian rivers and storages differ from those found elsewhere.

- One important result of the build up of significant concentrations of soluble inorganic P in surface waters is the fact that it allows large, slow growing phytoplankton with high half saturation concentrations for nutrient uptake (K_S) to survive and bloom. Thus the changes in biogeochemistry which occur in eutrophic surface waters favour the growth of large bloom forming species (or colonies) which have high nutrient requirements and are free from grazing pressure. Similar events seem to occur in both lakes and rivers. These changes in system function need to be better appreciated by Australian managers because they are the underlying reason for the appearance of algal blooms when nutrient loadings are increased.

- Light attenuation by organic material and particles is just as important a modifier of the usual Vollenweider - type loading relationships as is the availability of P in the system. Indeed it is probably the major reason why turbid Australian waters do not always achieve the biomass levels predicted.

- With the onset of eutrophic conditions, sedimentation becomes more important than grazing, decomposition in bottom waters becomes more rapid and, eventually, anoxia sets in. Hypolimnial anoxia is unlikely in deep oligotrophic lakes but is frequently severe in eutrophic lakes, weir pools and poorly mixed stagnant rivers with shallow hypolimnia.

- In eutrophic water bodies, once anoxia occurs, N is released from the sediments as dinitrogen gas and P is released as phosphate from organic P and other less available P sources. The N and P are derived from material sedimented from the water column. In eutrophic systems N and P are cycled in quite different ways and the onset of anoxia leads to major changes in the N:P ratio within the system.

- In most cases the total stock of P in the sediments exceeds the annual external load by a factor of ten or one hundred. Anoxia leads to the reduction of iron oxides, the formation of sulphides and the release of phosphate from forms of P bound to iron. Once anoxia sets in internal loads of P increase rapidly and may far exceed the external load in eutrophic water bodies.

- There is a clear pattern of changing structure and function with changing trophic state. The features of interest are the allometric changes in the proportions of components in the food chains as the nutrient status is increased. Fundamentally the pelagic ecosystems of water bodies change from those dominated by bacteria and picoplankton (when nutrients are present in low concentrations) to those dominated by large netplankton and colonial forms (when the nutrients are in abundant supply). This trend runs right across the marine/freshwater divide so that an overall pattern is discernible from the most oligotrophic pelagic marine systems to the most eutrophic freshwater systems.

- Highly eutrophic systems require continuous nutrient inputs to support the growth of large blooms of algae. These nutrients must come from external inputs or sedimentary pools. Reduction in nutrient loadings reduces the frequency of blooms and causes changes in system structure and function which favours stability and diversity.

- Oligotrophic, mesotrophic and eutrophic ecosystems show quite different patterns of temporal behaviour in algal biomass as well as soluble and particulate nutrient pools. Vollenweider's models work because of the trend towards larger (poorly grazed) cells and colonies in eutrophic waters and because of regular statistical relationships between all the components of the pelagic food chains. i.e. there is a proportioning of the pools of C, N and P (and micronutrients) between a variety of living and dead, organic and inorganic, particulate and soluble pools. Over the long term and when annually averaged, there are regular statistical properties that show trophically related patterns. Vollenweider's models work because of an assumption of equilibrium between pools at annual scales. Equilibrium certainly does not exist over shorter time periods.

- We should not expect to use Vollenweider type relationships in rivers or weir pools, or other storages where the water residence times are the order of days. On the other hand reaches in regulated rivers where residence times may be significant (>100 days) may be treated as long thin lakes and modeled accordingly. Storages which have residence times of decades with intermittent flushes and nutrient replenishment must also be treated with caution. What is the meaning of annual averages made up from data from storages and regulated river reaches which have residence times varying intermittently between a few days and (effectively) infinity? Further work is required. New models should be developed for Australian conditions- there is no conceptual reason why this cannot be done.

- Biomanipulation experiments have given very variable results, however, far from being a failure, the biomanipulation experiments have told us much about the functioning of aquatic ecosystems. It is possible to seek general relationships in the results from assemblages of specific, applied, experiments. The technique should not, however, be sold to managers as a panacea.

- While there is evidence of N limitation which may give N fixing cyanobacteria a competitive edge in highly eutrophic lakes, the effects are rather weak and difficult to prove because of the effects of changing P fluxes. All the evidence points to the fact that by far the best course for controlling cyanobacteria is to reduce external P loadings (and increase the TN:TP ratio by that means) rather than to attempt to change N loadings to achieve "balanced" effluents.

- The stoichiometry of nutrient recycling rates is a function of the zooplankton species composition and shifts in the species composition of the zooplankton can have strong effects on the recycling rates of N and P in pelagic systems (Elser et al 1988, Sterner et al 1992). This requires further study.

- A system view of storages and water bodies leads us to believe that indeed N *can* become limiting to phytoplankton growth in highly eutrophic water bodies. It does appear that the mechanisms of nutrient cycling in eutrophic water bodies lead to the loss of N relative to P and that this may indeed favour N fixing organisms such as cyanobacteria in these waters. Efforts should be made to estimate the relative fluxes of N and P in Australian waters and their impact on phytoplankton dynamics.

- The pattern of N and P limitation therefore seems to emerge best not from short term nutrient limitation experiments but from an examination of average system behaviour. The effects are however complex and highly variable in time and space. The management implications of this statement need to be explored.

- More work needs to be done in Australia on the possibilities and mechanisms of switching lakes and storages from turbid to clear states dominated by macrophytes. This is not yet a tested management option but it should be studied.

- Our knowledge of phytoplankton growth in rivers is not large when compared to knowledge of phytoplankton growth standing water bodies. This undoubtedly reflects the bias of the development of the science both in Australia and overseas. There is no reason to suppose that the factors which control phytoplankton growth in rivers are fundamentally different from those in standing waters. Knowledge from lakes and storages can be applied to the lower reaches of rivers where phytoplankton production dominates the biogeochemistry.

- Flow control is undoubtedly very important in determining the species composition of blooms in rivers but strategies which reduce the flux of nutrients to surface waters should also be investigated. Total catchment management can deliver both control strategies. The timing of the pulses of water flowing down regulated rivers will be as important as their magnitude. The relationships between physical processes and the survival of plankton in rivers and weir pools need to be better understood.

- Reynolds and Margalef have related water column stability to nutrient stress and indicated the domain of each of a number of groups of dominant species. These diagrams can be used to broadly predict when certain species, or groups of species, are likely to occur. There is therefore a degree of predictability in the occurrence of freshwater phytoplankton.

- By leaving cysts, autospores and akinetes on the sediment surface after each bloom, nuisance species like cyanobacteria and dinoflagellates plant the seeds of next year's bloom or blooms for many years afterwards. Once a nuisance bloom of many species has occurred it is much more likely to reoccur each year thereafter and may be very difficult to eliminate. Studies of the resting stages of nuisance species should be carried out in Australian waters.

- It is difficult to find good physiological data for some of the more common nuisance algal species in Australian waters (e.g. Melosira) - autecological studies on the physiology and growth rates of the more common bloom forming species should be carried out.

- Physical processes dominate the redistribution of nutrients in eutrophic waters. Physical perturbations applied to such waters might be expected to have strong ecological effects through influences on nutrient regeneration and a reduction in competition. This warrants further study as a possible management tool.

- Changing the physical mixing regime, particularly when such a mixing regime interacts strongly with important ecological and biogeochemical time scales, can have major ecological consequences for phytoplankton populations and the structure of food chains. Environmental variability and its impact on competitive interactions and community structure needs to be systematically examined in Australian waters. Physiological and autecological information needs to be collected for Australian species so that the particular combination of factors prevalent here may be identified.

- The ability to influence species composition by the imposition of periodic perturbations appears to be proven. Much research will be needed however to discover how to exploit this property of aquatic ecosystems in a predictable way. Even in the best cases "predictable" will only be interpretable in statistical terms.

- Competition for nutrients may well be an important factor in determining the presence of species in some circumstances but it is modified by other factors. Cyanobacteria became more common at temperatures above 21°C. TN:TP ratios are not the sole determinant of competitive interactions involving cyanobacteria.

- Connectedness in food chains should be a function of trophic state. If so, this will have important management implications. Other than Carney (1990) I can find no data to test this hypothesis. More work needs to be done in this area.

- Biodiversity will always be dependent on the vagaries of contingent variability, on biogeography and on accidents of immigration, whereas measures of ecosystem "health" derived from spatially and temporally averaged measures of ecosystem function can be expected to be more robust. There has been much uncritical use of the term biodiversity and rigorous examination of the concept has been generally lacking. Management actions which increase diversity should, nevertheless, have a beneficial effect on ecosystem function. Measures of ecosystem health based on ecosystem function as well as biodiversity need to be developed for Australian waters.

- At the level of the biomass response and system function, progress can be made fairly easily. At the level of the population and community response the situation is very different. At present we cannot reliably predict when cyanobacteria or dinoflagellates will occur or what the species composition of the phytoplankton community will be. Surprises will always occur. Some of these surprises will be a danger to public health.

- With the feedback between diversity and biogeochemistry dependent on the sedimentation (or otherwise) of carbon and nutrients fixed in surface waters, actions to modify the species composition by means other than a reduction in nutrient loadings can be expected to produce changes in ecosystem function and "health". These techniques should be explored.

- Applied ecosystem management requires a new generation of models which combine Geographic Information Systems and spatial data with ecosystem models of sufficient realism.

- What I suggest as a high priority is the education of water quality managers to the international best practice level. The fragmentation of the Australian limnological community over the years has meant that there is a general lack of knowledge about the factors which influence the dynamics of algal blooms in Australian waters. This can, and must, be remedied quickly.

I suggest the following priorities:

1. A close examination of the relationships between rainfall intensity, runoff, land use, nutrient concentrations, storm flows and P concentrations is required. A comparison with international experience must be compiled. Accurate models to calculate P concentrations in Australian rivers and storages are required.

2. Comparative studies of oligotrophic and eutrophic ecosystems are required to validate the arguments presented above. Are these allometric changes in food chain structures occurring in Australian waters? Are the Chl:TP ratios what we might expect? Are these system level insights correct for Australian conditions? Can we switch from one state to the other by reducing N and P loads to rivers and storages?

3. System level studies of N and P cycling in systems of varying residence times are required to study the varying degrees of N and P limitation in oligotrophic and eutrophic systems. Both means and variances in concentration ratios and fluxes should be studied and their effects on phytoplankton community structure assessed.

4. The possibilities of switching water bodies between the "turbid and cyanobacteria" and "clear and macrophytes" states should be examined as a means of suppressing cyanobacterial blooms. Both river systems and storages should be studied in this regard.

5. Artificial destratification and other physical perturbation techniques (such as flow regulation) should be used in experiments to suppress cyanobacterial growth.

Manipulation of the frequency components of the environment should be attempted as a control measure for cyanobacteria.

6. Measures of aquatic ecosystem "health" based on fluxes and ecosystem processes rather than biodiversity should be developed. These should be used as a guide for management practice and successful manipulation.

7. A new generation of ecosystem models should be developed based on the new ecological concepts and their validity should be tested against experimental manipulation of whole ecosystems. Experimental ecosystems suitable for testing hypotheses about Australian conditions need to be developed. Management protocols should be examined and tested by modeling and experimental manipulation.

8. Studies of the interaction of climate variability, storm intensity, rainfall, runoff, stream flow, drought, fire and phytoplankton community structure are required. Those long term data sets which exist should be sought out and published.

References

Adams, S.M., B.L. Kimmel and G.R. Ploskey (1983) Sources of organic matter for reservoir fish production: a trophic dynamics analysis. Canadian Journal of Fisheries and Aquatic Sciences. 40: 1480-1495

Admiraal, W., D.M.L.H.A. Jacobs, P. Breugem and E.D. de Reuter van Steveninck (1992) Effects of phytoplankton on the elemental composition (C,N,P) of suspended particulate material in the lower River Rhine. Hydrobiologia 235/236: 479-489

Agusti, S., C.M. Duarte and D.E. Canfield (1992) Self regulation, bottom-up and top-down control of phytoplankton communities: a reply to the comment by Kamenir. Limnology and Oceanography. 37: 683-687

Agusti, S., C.M. Duarte and D.E. Canfield (1990) Phytoplankton abundance in Florida lakes: evidence for frequent lack of nutrient limitation. Limnology and Oceanography 35: 181-188

Agusti, S., C.M. Duarte and J. Kalff (1987) Algal cell size and the maximum density and biomass of phytoplankton. Limnology and Oceanography. 32: 983-986

Agusti, S. and J. Kalff (1989) The influence of growth conditions on the size dependence of maximal algal density and biomass. Limnology and Oceanography. 34: 1104-1108

Ahl, T. (1988) background yield of phosphorus from drainage area and atmosphere. Hydrobiologia 170: 35-44

Ahlgren, I., T. Frisk and L. Kamp-Nielsen (1988) Empirical and theoretical models of phosphorus loading, retention and concentration vs. lake trophic state. Hydrobiologia 170: 285-303

Allen T.F.H and T.B Starr (1982) Hierarchy, perspectives for ecological theory. The University of Chicago Press, 310p

Allen T.F.H and T.W. Hoekstra (1992) Toward a unified ecology. Columbia, New York, 384p

Andersson, G. (1981) Influence of fish on waterfowl and lakes. Anser 20: 21-24 (in Swedish with English summary)

Andersson, G., W. Graneli and J. Stenson (1988) The influence of animals on phosphorus cycling in lake ecosystems. Hydrobiologia 170: 267-284

Appleyard B. (1992) Understanding the present. Pan Macmillan, London, 283p

Azam, F., T. Fenchel, J.G. Field, J.S. Gray, L.A. Meyer-Reil and F. Thingstad (1983) The ecological role of water-column microbes in the sea. Marine Ecology Progress Series 10:257-

Bailey-Watts, A.E. and A. Kirika (1987) A reassessment of phosphorus inputs to Loch Leven (Kinross, Scotland): rationale and an overview of results on instantaneous loadings with special reference to runoff. Transactions of the Royal Society of Edinburgh: Earth Sciences 78: 351-367

Bannister, T.T. (1974a) Production equations in terms of chlorophyll concentration, quantum yield and the upper limit to production. Limnology and Oceanography 19: 1-12

Bannister, T.T. (1974b) A general theory of steady state phytoplankton growth in a nutrient saturated mixed layer. Limnology and Oceanography 19: 13-30

Bannister, T.T. (1979) Quantitative description of steady-state, nutrient saturated algal growth including adaptation. Limnology and Oceanography 24: 76-96

Banse, K. (1992) Grazing, temporal changes of phytoplankton concentrations, and the microbial loop in the open sea. pp. 409-440 in "Primary productivity and biogeochemical cycles in the sea", eds. P.G. Falkowski and A.D. Woodhead, Plenum, New York

Bartell, S.M., W.G. Cale, R.V. O'Neill and R.H. Gardner (1988) Aggregation error: research objectives and relevant model structure. Ecological Modelling 41: 157-168

Bates, S.S., A.S.W. de Freitas, J.E. Milley, et al. (1991) Controls on domoic acid production by the diatom *Nitzschia pungens* f. *multiseries* in culture: nutrients and irradiance. Canadian Journal of Fisheries and Aquatic Sciences 48: 1136-1144

Bays, J.S. and T.L. Crisman (1983) Zooplankton and trophic state relationships in Florida lakes. Canadian Journal of Fisheries and Aquatic Sciences 40: 1813-1819

Beaver, J.R. and T.L. Crisman (1982) The trophic response of ciliated protozoans in freshwater lakes. Limnology and Oceanography 27: 246-253

Benndorf, J. (1988) Limnologica 19, 116p

Benndorf, D. (1990) Conditions for effective biomanipulation: conclusions derived from whole lake experiments in Europe Hydrobiologia 200/201: 187-203

Berlinski, D. (1976) On systems analysis: an essay concerning the limitations of some mathematical methods in the social, political and biological sciences. MIT Press, Boston, 185p.

Bird, D.F. and J. Kalff (1984) Empirical relationships between bacterial abundance and chlorophyll concentration in fresh and marine waters. Canadian Journal of Fisheries and Aquatic Sciences. 41: 1015-1023

Blindow, I., G. Andersson, A. Hargeby and S. Johansson (1993) Long term pattern of alternative stable states in two shallow eutrophic lakes. Freshwater Biology 30: 159-167

Body, D.N. (1979) Australia's surface water resources in "Land and Water Resources of Australia", E.G Hailsworth and J.J. Woodcock (eds) Australian Academy of Technological Sciences, Melbourne

Boudreau, P.R. and L.M. Dickie (1992) Biomass spectra of aquatic ecosystems in relation to fisheries yield. Canadian Journal of Fisheries and Aquatic Science 49: 1528-1538

Box, E.O. (1981) Macroclimate and plant forms: an introduction to predictive modelling in phytogeography. Junk, The Hague, ???p

Bronmark, C. and S.E.B. Weisner (1992) Indirect effects of fish community structure on submerged vegetation in shallow, eutrophic lakes: an alternative mechanism. Hydrobiologia 243/244: 293-301

Brooks, J.L. and S.I. Dodson (1965) Predation, body size and the composition of the plankton. Science 150: 28-35

Brown, V.B. and S.A. Davies (1991) The environmental quality of north-western Port Phillip Bay. State Environmental Policy Review, Melbourne Water, Environmental Services Series No. 91/005, Melbourne, Victoria

Brylinsky, M. and K.H. Mann (1973) An analysis of factors governing productivity in lakes and reservoirs. Limnology and Oceanography 18: 1-14

Burmaster, D.E. (1979) The continuous culture of phytoplankton: mathematical equivalence among three unsteady state models. American Naturalist 113: 123-134

Canfield, D.E. and R.W. Bachmann (1981) Prediction of total phosphorus concentrations, chlorophyll a and secchi depths in natural and artificial lakes. Canadian Journal of Fisheries and Aquatic Science 38: 414-423

Caraco, N.F., J.J. Cole and G.E. Likens (1989) Evidence for sulphate controlled phosphorus release from sediments of aquatic systems. Nature 341: 316-318

Carney, H.J. (1990) A general hypothesis for the strength of food web interactions in relation to trophic state. Verhandlungen der Internationalen Vereinigung fur Theoretische und Angewandte Limnologie 24: 487-492

Carpenter, S.R. (1988) ed. Complex interactions in lake communities. Springer Verlag, Berlin

Carpenter, S.R. (1989) Temporal variance in lake communities: blue-green algae and the trophic cascade. Landscape Ecology 3: 175-184

Carpenter, S.R., J.J. Elser and K.M. Olson (1983) Effects of the roots of *Myriophyllum verticillatum* L. on sediment redox conditions. Aquatic Botany 17: 243-250

Carpenter, S.R., J.F. Kitchell and J.R. Hodgson (1985) Cascading trophic interactions and lake productivity. BioScience 35: 634-639

Carpenter, S.R. and nine others (1987) Regulation of lake primary productivity by food web structure. Ecology 68: 1863-1876

Carpenter, S.R., C.E. Kraft, R. Wright, X. He, P.A. Soranno and J.R. Hodgson (1992) Resilience and resistance of a lake phosphorus cycle before and after food web manipulation. American Naturalist 140: 781-798

Chapra, S.C. (1980) Simulation of recent and projected total phosphorus trends in lake Ontario. Journal of Great Lakes Research. 6: 101-112

Charlton, M.N. (1980) Hypolimnion oxygen consumption in lakes: discussion of productivity and morphometric effects. Canadian Journal of Fisheries and Aquatic Sciences. 37: 1531-1539

Clark, J.S. (1988) Effect of climate change on fire regimes in north-western Minnesota. Nature. 334: 233-235

Clementson, L.A., G.P. Harris, F.B. Griffiths and D.W. Rimmer (1989) Seasonal and interannual variability in chemical and biological parameters in Storm Bay, Tasmania: 1. Physics, chemistry and the biomass of components of the food chain. Australian Journal of Marine and Freshwater Research. 40: 25-38

Cohen, J.E. (1978) Food webs and niche space. Princeton University Press, 189p

Cohen J.E., S.L. Pimm, P. Yodzis and J. Saldana (1993) Body sizes of animal predators and animal prey in food webs. Journal of Animal Ecology 62: 67-78

Cole, J.J., S. Findlay and M.L. Pace (1988) Bacterial production in fresh and saltwater ecosystems: a cross-system overview. Marine Ecology - Progress Series 43: 1-10

Conley, D.J., C.L Schelske and E.F. Stoermer (1993) Modification of the biogeochemical cycle of Silica with eutrophication. Marine Ecology Progress Series 101: 170-192

Connell, J.H. (1978) Diversity in tropical rain forests and coral reefs. Science 199: 1302-1310

Cornett, R.J. and F.H. Rigler (1979) Hypolimnetic oxygen deficits: their prediction and interpretation. Science 205: 580-581

Cosser, P.R. (1989) Nutrient concentration - flow relationships and loads in the South Pine River, South-eastern Queensland. 1. Phosphorus loads. Australian Journal of Marine and Freshwater Research, 40: 613-30

Costanza, R. and F.H. Sklar (1985) Articulation, accuracy and effectiveness of mathematical models: a review of freshwater wetland models. Ecological Modelling 27: 45-68

Cullen, P. (1991) Scope of the eutrophication problem. Chemical Summit 1991, Impact of Eutrophication, Key Note Address

Cullen, P. and C. Forsberg (1988) Experiences with reducing point sources of phosphorus to lakes. Hydrobiologia 170: 321-336

Cullen, P and E.M. O'Loughlin (1982) Non point sources of pollution. p.437-453 in "Prediction in water quality" eds E.M. O'Loughlin and P.Cullen, Australian Academy of Science, Canberra

Cullen, P. and R. Rosich (1979) Effects of rural and urban sources of phosphorus on Lake Burley Griffin. Progress in Water Technology 11: 219-230

Cullen, P., R. Rosich and P. Bek (1978) A phosphorus budget for Lake Burley Griffin and management implications for urban lakes. Australian Water Resources Council, Technical paper 31, AGPS, Canberra

Cullen, P. and I. Smalls (1981) Eutrophication in semi-arid areas - the Australian experience. World Health Organisation, Water Quality Bulletin 6(3) Part 1: 79-83 and 90

Currie, D.J. (1990) Phosphorus deficiency and its variation among lakes. Canadian Journal of Fisheries and Aquatic Science. 47: 1077-1084

Currie, D.J., E. Bentzen and J. Kalff (1986) Does algal-bacterial phosphorus partitioning vary among lakes? A comparative study of orthophosphate uptake and alkaline phosphatase activity in freshwater. Canadian Journal of Fisheries and Aquatic Sciences. 43: 311-318

Cushing, D.H. (1989) A difference in structure between ecosystems in strongly stratified waters and those that are only weakly stratified. Journal of Plankton Research 11: 1-13

Cyr, H. and M.L. Pace (1993a) Magnitude and patterns of herbivory in aquatic and terrestrial systems. Nature 361: 148-150

Cyr, H. and M.L. Pace (1993b) Allometric theory: extrapolations from individuals to communities. Ecology. 74: 1234-1245

De Angelis, D.L. (1992) Dynamics of nutrient cycling and food webs. Chapman and Hall, London, 270p

DeAngelis, D.L. and J.C. Waterhouse (1987) Equilibrium and non equilibrium concepts in ecological models. Ecological Monographs 57: 1-21

De Angelis, D.L., P.J. Mulholland, A.V. Palumbo, A.D. Steinman, M.A. Huston and J.W. Elwood (1989) Nutrient dynamics and food web stability. Annual Reviews of Ecology and Systematics 20: 71-95

del Giorgio, P.A. and Peters, R.H. (1993) Balance between phytoplankton production and plankton respiration in lakes. Canadian Journal of Fisheries and Aquatic Science 50: 282-289

De Melo, R., R. France and D.J. McQueen (1992) Biomanipulation: hit or myth? Limnology and Oceanography 37: 192-207

Dennett, D.C. (1993) Consciousness explained. Penguin Books, London, 511p

Dickie, L.M., S.R. Kerr and P.R. Boudreau (1987) Size dependant processes underlying regularities in ecosystem structure. Ecological Monographs 57: 233-250

Diehl, S. (1988) Foraging efficiency of three freshwater fishes: effects of structural complexity and light. Oikos 53: 207-214

Dillon, P.J. and Kirchner W.B. (1975) Reply. Water Resources Research. 11: 1035-1036

Dillon, P.J. and F.H. Rigler (1974a) A test of a simple nutrient budget model predicting the phosphorus concentration of lake water. Journal of the Fisheries Research Board of Canada. 31: 1771-1778

Dillon, P.J. and F.H. Rigler (1974b) The phosphorus-chlorophyll relationship in lakes. Limnology and oceanography 19: 767-773

DiToro, D.M. (1980) Applicability of cellular equilibrium and Monod theory of phytoplankton growth kinetics. Ecological Modelling. 8: 201-218

Drake, J.A. and nine others (1993) The construction and assembly of an ecological landscape. Journal of Animal Ecology 62: 117-130

Droop, M.R. (1974) The nutrient status of algal cells in continuous culture. Journal of the Marine Biological Association of the United Kingdom. 54: 825-855

Edmondson, W.T. and J.T. Lehman (1981) The effects of changes in the nutrient income on the condition of Lake Washington. Limnology and Oceanography 26: 1-29

Einsele, W. (1936) Ueber die Beziehungen des Eisenkreislaufts zum Phosphatkreislauf im eutrophen See. Archiv fur Hydrobiologie. 29: 664-686

Eklov, P. and S.F. Hamrin (1989) Predatory efficiency and prey selection: interactions between Pike *Esox lucius*, Perch *Perca fluviatilis* and Rudd *Scardinus erythropthalamus*. Oikos 56: 149-156

Elser, J.J., M.M. Elser, N.A. MacKay and S.R. Carpenter (1988) Zooplankton mediated transitions between N and P limited algal growth. Limnology and Oceanography. 33: 1-14

Elser, J.J., E.R. Marzoff and C.R. Goldman (1990) Phosphorus and nitrogen limitation of phytoplankton growth in the freshwaters of North America: a review and critique of experimental enrichments. Canadian Journal of Fisheries and Aquatic Sciences 47: 1468-1477

Elton, C.S. (1958) The ecology of invasions by animals and plants. Chapman and Hall, London

Eppley, R.W. and B.J. Peterson (1979) Particulate organic matter flux and planktonic new production in the deep ocean. Nature 282: 677-680

Evans, M.S. (1992) Historic changes in Lake Michigan zooplankton community structure: the 1960s revisited with implications for top-down control. Canadian Journal of Fisheries and Aquatic Science 49: 1734-1749

Ferris, J.M. and Tyler, P.A. (1985) Chlorophyll - total phosphorus relationships in Lake Burragorang, New South Wales and some other southern hemisphere lakes. Australian Journal of Marine and Freshwater Research 36: 157-168

Ferris, J.M. and Tyler, P.A. (1992) The effects of inflow and outflow on the seasonal behaviour of a stratified reservoir in temperate Australia - a 20 year analysis. Archiv fur Hydrobiologie 126: 129-162

Fong, P., J.B. Zedler and R.M. Donohoe (1993) Nitrogen vs. phosphorus limitation of algal biomass in shallow coastal lagoons. Limnology and Oceanography. 38: 906-923

Fukuyama, F. (1992) The end of history and the last man. Hamish Hamilton, London, 418p

Gachter, R. (1987) Lake restoration: why oxygen and artificial mixing cannot substitute for a decrease in the external phosphorus loading. Schweizerische Zeitzschrift fur Hydrobiologie 49: 170-185

Gachter, R and J.S. Meyer (1993) The role of micro-organisms in mobilization and fixation of phosphorus in sediments. Hydrobiologia 253: 103-121

Ganf, G.G., R.L. Oliver and S.J.L. Stone (1982) Phytoplankton growth. p. 201-221 in "Prediction in water quality" eds E.M. O'Loughlin and P.Cullen, Australian Academy of Science, Canberra

Gascon, D. and W.C. Leggett (1977) Distribution, abundance, and resource utilization of littoral zone fishes in response to a nutrient/production gradient in Lake Memphremagog. Journal of the Fisheries research Board of Canada. 34: 1105-1117

Gasol. J.M. and D. Vaque (1993) Lack of coupling between heterotrophic nanoflagellates and bacteria: a general phenomenon across aquatic systems? Limnology and Oceanography 38: 657-665

Geddes, M.C. (1984) Limnology of Lake Alexandrina, River Murray, South Australia, and the effects of nutrients and light on the phytoplankton. Australian Journal of Marine and Freshwater Research 35: 399-415

Gehrke, P.C. and J.H. Harris (1994) The role of fish in cyanobacterial blooms in Australia. Australian Journal of Marine and Freshwater Research (in press).

Gleick, J. (1987) Chaos, making a new science. Viking Penguin, New York, 352p

Godbout, L. and R.H. Peters (1988) Potential determinants of stable catch in the Brook Trout (*Salvelinus fontinalis*) sport fishery in Quebec. Canadian Journal of Fisheries and Aquatic Sciences. 45: 1771-1778

Goldman, J.C. (1977) Steady state growth of phytoplankton in continuous culture: comparison of internal and external nutrient equations. Journal of Phycology. 13: 251-258

Gophen, M. (1990) Biomanipulation: retrospective and future development. Hydrobiologia 200/201: 1-11

Gulati, R.D. (1990) Structural and grazing responses of zooplankton community to biomanipulation of some Dutch water bodies. Hydrobiologia 200/201: 99-118

Gutelmakher, B.L. and E.S. Makartseva (1990) The significance of zooplankton in the cycling of phosphorus in lakes of different trophic categories. Internationale Review der gesamtem Hydrobiologie 75: 143-151

Hairston, N.G., F.E. Smith and L.B. Slobodkin (1960) Community structure, population control and competition. American Naturalist 94: 421-425

Hallegraeff, G.M. (1993) A review of harmful algal blooms and their apparent global increase. Phycologia 32: 79-99

Hanson, J.M. and W.C. Leggett (1982) Empirical prediction of fish biomass and yield. Canadian Journal of Fisheries and Aquatic Sciences 39: 257-263

Hanson, J.M. and R.H. Peters (1984) Empirical prediction of crustacean zooplankton biomass and profundal macrobenthos biomass in lakes. Canadian Journal of Fisheries and Aquatic Sciences. 41: 439-445

Hanson, M.A. and M.G. Butler (1990) Early responses of plankton and turbidity to biomanipulation in a shallow prairie lake. Hydrobiologia 200/201: 317-329

Harris, E. (1959) The nitrogen cycle in Long Island Sound. Bulletin of the Bingham Oceanographic College. 17: 31-65

Harris, G.P. (1978) Photosynthesis, productivity and growth: the physiological ecology of phytoplankton. Ergebnisse der Limnologie. (beiheft Archiv fur Hydrobiologie) 10: 1-171

Harris, G.P. (1980) Temporal and spatial scales in phytoplankton ecology. Mechanisms, methods, models and management. Canadian Journal of Fisheries and Aquatic Science 37: 877-900

Harris, G.P. (1983) Mixed layer physics and phytoplankton populations: studies in equilibrium and non-equilibrium ecology. Progress in Phycological Research 2: 2-52

Harris, G.P. (1985) The answer lies in the nesting behaviour. Freshwater Biology 15: 261-266

Harris, G.P. (1986) Phytoplankton ecology, Chapman and Hall, London, 384p

Harris, G.P. (1987) Time series analysis of water quality data from Lake Ontario: implications for the measurement of water quality in large and small lakes. Freshwater Biology 18: 389-403

Harris, G.P.(1988) Structural aspects of phytoplankton successions. Verh. Internat. Verein. Limnol. 23: 2221-2225

Harris, G.P. (1994) Pattern, process and prediction in aquatic ecology - a limnological view of some general ecological problems. Freshwater Biology. (in press)

Harris, G.P. and B.B. Piccinin (1980) Physical variability and phytoplankton populations IV. Temporal changes in the phytoplankton community of a physically variable lake. Archiv fur Hydrobiologie 89: 447-473

Harris, G.P. and A.M. Trimbee (1986) Phytoplankton population dynamics of a small reservoir: physical/biological coupling and the time scales of community change. Journal of Plankton Research 8: 1011-1025

Harris, G.P. and F.B. Griffiths (1987) On means and variances in aquatic food chains and recruitment to the fisheries. Freshwater Biology 17: 381-386

Harris, G.P., G.G. Ganf and D.P. Thomas (1987) Productivity, growth rates and cell size distributions of phytoplankton in the SW Tasman Sea: implications for carbon metabolism in the photic zone. Journal of Plankton Research 9: 1003-1030

Harris, G.P., G.D. Haffner and B.B. Piccinin, (1980) Physical variability and phytoplankton communities II. Primary productivity by phytoplankton in a physically variable environment. Archiv fur Hydrobiologie 88: 393-425

Harris, G.P., P. Davies, M. Nunez and G. Meyers (1988) Interannual variability in climate and fisheries in Tasmania. Nature 333: 754-757

Harris, G.P., F.B. Griffiths and L.A. Clementson (1992) Climate and the fisheries off Tasmania: interactions of physics, food chains and fish. in "Benguela Trophic Functioning" ed A.I. Payne, K.H. Brink, K.H. Mann and R. Hillborn: South African Journal of Marine Science 12: 585-597

Harris, G.P., G.C. Feldman and F.B. Griffiths (1993) Global oceanic production and climate change. p 237-270 in "Ocean colour: theory and applications in a decade of CZCS experience" eds V. Barale and P.M. Schlittenhardt, ECSC, EEC, EAEC, Brussels and Luxembourg

Hasler, A.D. and E. Jones (1949) Demonstration of the antagonistic action of large aquatic plants on algae and rotifers. Ecology 30: 359-364

Havens, K. (1993a) Effect of scale on food web structure. Science 260: 242-243

Havens, K.E. (1993b) Responses to experimental fish manipulations in a shallow, hypereutrophic lake: the relative importance of benthic nutrient cycling and trophic cascade. Hydrobiologia 254: 73-80

Havens, K.E. (1993c) Pelagic food web structure in Adirondack Mountain, USA, lakes of varying acidity. Canadian Journal of Fisheries and Aquatic Science 50: 149-155

Heaney, S.I. (1987) The influence of lake morphology and algal composition on nitrogen cycling and hypolimnetic deoxygenation (abstract). in M. Dokulil, "Report of the International Association of Phytoplankton Taxonomy and Ecology (IAP)", Mondsee, Austria, Sept 15-25 1986. Schweizerische Zeitschrift fur Hydrologie. 49: 384

Heaney, S.I., W.J.P Smyly and J.F. Talling (1987) Interactions of physical, chemical and biological processes in depth and time within a productive English lake during summer stratification. Internationale Revue der gesamten Hydrobiologie 71: 441-494

Heaney, S.I., J.W.G. Lund, H.M. Canter and K. Gray (1988) Population dyanmics of *Ceratium* spp. in three English Lakes, 1945-1985. Hydrobiologia 161: 133-148

Heaney, S.I., J.E. Corry and J.P. Lishman (1992) Changes of water quality and sediment phosphorus of a small productive lake following decreased phosphorus loading. p 119-131 in "Eutrophication: research and application to water supply", eds. D.W. Sutcliffe and J.G. Jones, Freshwater Biological Association, Ambleside, Cumbria

Hecky, R.E., P. Campbell and L.L. Hendzel (1993) The stoichiometry of carbon, nitrogen and phosphorus in particulate matter of lakes and oceans. Limnology and Oceanography 38: 709-724

Hecky, R.E. and P. Kilham (1988) Nutrient limitation of phytoplankton in freshwater and marine environments: a review of recent evidence on the effects of enrichment. Limnology and Oceanography 33: 796-822

Hentschel, E. and H. Wattenberg (1931) Plankton und phosphat in der Oberflachenschicht des Sudatlantischen Ozeans. Annales der Hydrographie, Berlin 58: 273-277

Hern, S.C., V.W. Lambou, L.R. Williams and W.D. Taylor (1981) Modifications of models predicting trophic state of lakes: Adjustment of models to account for the biological manifestations of nutrients. EPA-600/S3-81-001, US EPA Environmental Monitoring Systems Laboratory, Las Vegas

Hessen, D.O. (1992) Nutrient element limitation of zooplankton production. American Naturalist 140: 799-814

Holling, C.S. (1992) Cross-scale morphology, geometry and dynamics of ecosystems. Ecological Monographs 62: 447-502

Holtan, H., L. Kamp-Nielsen and A.O. Stuanes (1988) Phosphorus in soil, water and sediment: an overview. Hydrobiologia 170: 19-34

Horn, H. and W. Horn (1990) Growth of blue-green algae in the Saidenbach Reservoir and its relationship to the silicon budget. Internationale Revue der gesamten Hydrobiologie 75: 461-474

Howarth, R.W. (1988) Nutrient limitation of net primary production in marine ecosystems. Annual Reviews of Ecology and Systematics. 19: 89-110

Hutchinson, G.E. (1938) On the relation between the oxygen deficit and the productivity and typology of lakes. Internationale Revue des Gesamtes Hydrobiologie. 36: 336-355

Irvine, K., B. Moss and H. Balls (1989) The loss of submerged plants with eutrophication. II Relationships between fish and zooplankton in a set of experimental ponds and conclusions. Freshwater Biology 22: 89-107

Jack, J.D., S.A. Wickham, S. Toalson and J.J. Gilbert (1993) The effect of clays on a freshwater plankton community: an enclosure experiment. Archiv fur Hydrobiologie 127: 257-270

Jameson, F. (1991) Postmodernism, or the cultural logic of late capitalism. Verso, London, 438p

Jansson, M., H. Olsson and K. Pettersen (1988) Phosphatase; origin, characteristics and function in lakes. Hydrobiologia 170: 157-175

Janus. L.L. and R.A. Vollenweider (1981) The OECD cooperative program on eutrophication. Summary report, Canadian contribution. Scientific Series No. 131, National Water Research Institute, Canada Centre for Inland Waters, Burlington, Ontario.

Janus, L.L. and R.A.Vollenweider (1984) Phosphorus residence time in relation to trophic conditions in lakes. Verh. Internat. Verein. Limnol. 22: 179-184

Johansson, L. and L. Persson (1986) The fish community of temperate eutrophic lakes. p. 237-266 in "Carbon dynamics of eutrophic temperate lakes: the structure and function of the pelagic environment" eds B. Riemann and M. Sondergaard, Elsevier, Amsterdam.

Jones, G.J. (1993) LWRRDC Report

Jones, J.R. and M.V. Hoyer (1982) Sportfish harvest predicted by summer chlorophyll a concentration in Midwestern lakes and reservoirs. Transactions of the American Fisheries Society 111: 176-179

Jones, R.A. and G.F. Lee (1982) Recent advances in assessing impact of phosphorus loads on eutrophication related water quality. Water Research 16: 503-515

Judson, O.P. (1993) The rise of the individual based model in ecology. Trends in Ecology and Evolution 9: 9-14

Kamenir, Y.G. (1992) Further evidence of nonnutrient constraints on phytoplankton abundances. Limnology and Oceanography 37: 681-683

Kaufmann, S.A. (1993) The origins of order. Oxford University Press, 709p.

Kedem, B. and L.S. Chiu (1987) On the lognormality of rain rate. Proceedings of the National Academy of Sciences, USA 84: 901-905

Kelly, J.R. and S.A. Levin (1986) A comparison of aquatic and terrestrial nutrient cycling and production processes in natural ecosystems, with reference to ecological concepts of relevance to some waste disposal issues. p. 165-203 in "The role of the oceans as a waste disposal option", ed. G. Kullenberg, D.Reidel, Amsterdam.

Kerfoot, W.C. and D.L. DeAngelis (1989) Scale dependant dynamics: zooplankton and the stability of freshwater food webs. Trends in Ecology and Evolution. 4: 167-171

Kilham, P. and S.S. Kilham (1990) Endless summer: internal loading processes dominate nutrient cycling in tropical lakes. Freshwater Biology. 23: 379-389

Kingsland, S.E. (1985) Modelling nature. University of Chicago Press, 267p

Kira, T. (1991) State of the environments of world lakes - from the survey by ILEC/UNEP. p 48-54 in Proceedings of the Symposium on Water Resources Management with the Views of Global and regional Scales. International Lake Environment Committee/ UN Environment Program. Shiga, Japan

Kirchner, W.B. and P.J. Dillon (1975) An empirical method of estimating the retention of phosphorus in lakes. Water Resources Research. 11: 182-183

Kirk, J.T.O. (1983) Light and photosynthesis in aquatic ecosystems. Cambridge University Press, 401p

Lafontaine, Y. de and R.H. Peters (1986) Empirical relationship for marine primary production: the effect of environmental variables. Oceanologica Acta. 9: 65-72

Lammens, E.H.R.R., R.D. Gulati, M.-L. Meijer and E. van Donk (1990) The first biomanipulation conference: a synthesis. Hydrobiologia 200/201: 619-627

Larsen, D.P. and H.T. Mercier (1976) Phosphorus retention capacity of lakes. Journal of the Fisheries Research Board of Canada. 33: 1742-1750

Laronne, J.B. and I. Reid (1993) Very high rates of bedload sediment transport by emphemeral desert rivers. Nature 366: 148-150

Lazenby, D.G. (1975) Development of oxygen deficits in 14 Southern Ontario lakes. Limnology and Oceanography 20: 993-999

Lazerte, B.D. and S. Watson (1981) The prediction of lacustrine phytoplankton diversity. Canadian Journal of Fisheries and Aquatic Sciences 38: 524-534

Lewin R. (1993) Complexity. Dent, London, 208p.

Logofet, D.O. and Y.M. Svirezhev (1986) Averaging and aggregation in ecological models: an attempt at a non-linear approach. Ecological Modelling 34: 217-229

Lohammar, G. (1966) Some observations on horizontal variations in a eutrophic lake. Verhandlungen der Internationalen Vereinigung fur Theoretische und Angewandte Limnologie 16: 89-96

Luckyanov, N.K. (1983/84) Linear aggregation and separability of models in ecology. Ecological Modelling 21 (1983/1984): 1-12

Luckyanov, N.K., Y.M. Svirezhev and O.V. Voronkova (1983) Aggregation of variables in simulation models of water ecosystems. Ecological Modelling 18: 235-240

Lund, J.W.G. and C.S. Reynolds (1982) The development and operation of large limnetic enclosures in Blelham Tarn, English Lake District, and their contribution to phytoplankton ecology. Progress in Phycological Research 1: 1-65

Magnusson, J.J., B.J. Benson and T.K. Kratz (1990) Temporal changes in the limnology of a suite of lakes in Wisconsin, USA. Freshwater Biology 23: 145-159

Margalef, R. (1963) Succession in marine populations. p. 137-188 in "Advancing frontiers of plant sciences" 2, ed. R. Vira, Institute for Advanced Science Culture, New Delhi, India

Margalef, R. (1978) Life forms of phytoplankton as survival alternatives in an unstable environment. Oceanologica Acta 1: 493-509

Margalef, R. (1980) La Biosfera. Ediciones Omega, Barcelona

Marshall, T. and R.H. Peters (1989) General patterns for the seasonal development of chlorophyll a for temperate lakes. Limnology and Oceanography 34: 856-867

Marston, F., Young, W and Davis, R. (1993) Nutrient generation rates, data book - draft version. Catchment Management Support System, Ver. 3.0, CSIRO Division of Water Resources, Canberra ACT

Martinez, N.D. (1993) Effect of scale on food web structure. Science 260: 242-243

Martinova, M.V. (1993) Nitrogen and phosphor compounds in bottom sediments: mechanisms of accumulation, transformation and release. Hydrobiologia 252: 1-22

May, R.M. (1973) Stability and complexity in model ecosystems. Princeton University Press, Princeton, NJ.

May, R.M (1974a) Biological populations with non overlapping generations: stable points, stable cycles and chaos. Science 186: 645-647

May, R.M. (1974b) General introduction. p 1-14 in "Ecological Stability" eds M.B. Usher and M.H. Williamson, Chapman and Hall, London

May, R.M. (1976) Simple mathematical models with very complicated dynamics. Nature 261: 459-467

Mazumder, A. (1994a) Patterns of algal biomass in dominant odd- vs. even-link lake ecosystems. Ecology. 75(4): 1141-49

Mazumder, A. (1994b) Phosphorus-chlorophyll relationships under contrasting herbivory and thermal stratification: predictions and patterns. Canadian Journal of Fisheries and Aquatic Sciences. 51: 390-400

Mazumder, A. (1994c) Phosphorus-chlorophyll relationships under contrasting zooplankton community structure: potential mechanisms. Canadian Journal of Fisheries and Aquatic Sciences. 51: 401-7

McCauley, E. and J. Kalff (1981) Empirical relationships between phytoplankton and zooplankton biomass in lakes. Canadian Journal of Fisheries and Aquatic Sciences. 38: 458-463

McIntosh, R.P.(1985) The background of ecology, concept and theory. Cambridge University Press, 383p

McQueen, D.J. (1990) Manipulating lake community structure: where do we go from here? Freshwater Biology 23: 613-620

McQueen, D.J., J.R. Post and E.L. Mills (1986) Trophic relationships in freshwater pelagic ecosystems. Canadian Journal of Fisheries and Aquatic Science 43: 1571-1581

McQueen, D.J. and D.R.S. Lean (1987) Influence of water temperature and nitrogen to phosphorus ratios on the dominance of blue-green algae in Lake St George, Ontario. Canadian Journal of Fisheries and Aquatic Science 44: 598-604

McQueen, D.J., M.R.S. Johannes, J.R. Post, T.J. Stewart, and D.R.S. Lean (1989) Bottom-up and top-down impacts on freshwater pelagic community structure. Ecological Monographs 59: 289-309

McQueen, D.J., E.L. Mills, J.L. Forney, M.R.S. Johannes and J.R. Post (1992a) Trophic level relationships in pelagic food webs: comparisons derived from long term data sets for Oneida Lake , New York (USA) and Lake St. George, Ontario (Canada) Canadian Journal of Fisheries and Aquatic Science 49: 1588-1596

McQueen, D.J., R. France and C.Kraft (1992b) Confounded impacts of planktivorous fish on freshwater biomanipulations. Archiv fur Hydrobiologie 125: 1-24

Meijer, M.-L., M.W. de Haan, A.W. Breukelaar and H. Buiteveld (1990) Is reduction of the benthivorous fish an important cause of high transparency following biomanipulation in shallow lakes. Hydrobiologia 200/201: 303-315

Melack, J.M. (1976) Primary productivity and fish yields in tropical lakes. Transactions of the American Fisheries Society. 105: 575-580

Molot, L.A. and P.J. Dillon (1991) Nitrogen/phosphorus ratios and the prediction of chlorophyll in phosphorus limited lakes in central Ontario. Canadian Journal of Fisheries and Aquatic Sciences 48: 140-145

Monod, J. (1942) Recherches sur la croissance des cultures bacteriennes. 2nd ed. Herman et cie, Paris

Mortimer, C.H. (1941-42) The exchange of dissolved substances between mud and water in lakes. Journal of Ecology. 29: 280-329, 30: 147-201

Moss, B. (1990) Engineering and biological approaches to the restoration from eutrophication of shallow lakes in which aquatic plant communities are important components. Hydrobiologia 200/201: 367-377

Murdoch, W.W. (1966) Population stability and life history phenomena. American Naturalist 100: 5-11

Nicholls, N. (1985) Impact of Southern Oscillation on Australian crops. Journal of Climatology 5: 553-560

Nielsen, S.L. and K. Sand-Jensen (1990) Allometric scaling of maximal photosynthetic growth rate to surface/volume ratio. Limnology and Oceanography 35: 177-181

Nurnberg, G.K. (1984) The prediction of internal phosphorus load in lakes with anoxic hypolimnia. Limnology and Oceanography 29: 111-124

Nurnberg, G.K. (1988) Prediction of soluble phosphorus release rates from total and reductant-soluble phosphorus in anoxic lake sediments. Canadian Journal of Fisheries and Aquatic Science 45: 453-462

Nurnberg, G.K., M. Shaw, P.J. Dillon and D.J. McQueen (1986) Internal phosphorus load in an oligotrophic precambrian shield lake with an anoxic hypolimnion. Canadian Journal of Fisheries and Aquatic Science 43: 574-580

Oglesby, R.T. (1977a) Phytoplankton standing crop and annual productivity as functions of phosphorus loadings and various physical factors. Journal of the Fisheries Research Board of Canada. 34: 2255-2270

Oglesby, R.T. (1977b) Relationships of fish yield to lake phytoplankton standing crop, production and morphoedaphic factors. Journal of the Fisheries Research Board of Canada. 34: 2271-2279

Oksanen, , L., S.D. Fretwell, J. Arruda and P.Niemela (1981) Exploitation ecosystems in gradients of primary productivity. American Naturalist 118: 240-262

Olive, L.J. and P.H. Walker (1982) Processes in overland flow - erosion and production of suspended material. p. 87-119 in "Prediction in water quality" eds E.M. O'Loughlin and P.Cullen, Australian Academy of Science, Canberra

Oliver, R.L., B.T. Hart, G.B. Douglas and R. Beckett (1993) Phosphorus speciation in the Murray and Darling Rivers. Water, Official Journal of the Australian Water and Wastewater Association 20(4): 24-26 and 29

Ostrofsky, M.L. (1978) Modification of phosphorus retention models for use with lakes with low areal water loadings. Journal of the Fisheries Research Board of Canada. 35: 1532-1536

Pace, M.L. (1984) Zooplankton community structure, but not biomass, influences the phosphorus-chlorophyll a relationship. Canadian Journal of Fisheries and Aquatic Sciences. 41: 1089-1096

Pace, M.L. (1986) An empirical analysis of zooplankton community size structures across lake trophic gradients. Limnology and Oceanography 31: 45-55

Padisak, J., C.S. Reynolds and U. Sommer (1993) Eds. Intermediate disturbance hypothesis in phytoplankton ecology. Hydrobiologia 249 (1-3).

Paerl, H.W. (1988) Nuisance phytoplankton blooms in coastal, estuarine and inland waters. Limnology and Oceanography(4 part 2) 823-847

Pahl-Wostl, C. (1992) The hierarchical organisation of the aquatic ecosystem: an outline how reductionism and holism may be reconciled. Ecological Modelling 66: 81-100

Peters, R.H. (1983) The ecological implications of body size. Cambridge University Press. 329p

Peters, R.H. (1986) The role of prediction in limnology. Limnology and Oceanography 31: 1143-1159

Peters R.H. (1991) A critique for ecology. Cambridge University Press, 366p.

Peters, R.H. (1992) Lessons from the size efficiency hypothesis II: the mire of complexity. Hydrobiologia 235/236: 435-455

Peters, R.H. and J.A. Downing (1984) Empirical analysis of zooplankton filtering and feeding rates. Limnology and Oceanography 29: 763-784

Pick, F.R. and D.R.S. Lean (1987) The role of macronutrients (C,N,P) in controlling cyanobacterial dominance in lakes. New Zealand Journal of Marine and Freshwater Research 21: 425-434

Pimm, S.L. (1982) Food webs. Chapman and Hall, London 219p

Pimm, S.L. (1991) The balance of nature? University of Chicago Press, 434p

Pimm, S.L., J.H. Lawton and J.E. Cohen (1991) Food web patterns and their consequences. Nature 350: 669-674

PLUARG (1978) Environmental management strategy for the Great Lakes System. International Reference Group on Great Lakes Pollution from Land Use Activities. International Joint Commission, Windsor, Ontario.

Prentice, I.C., W. Cramer, S.P. Harrison, R.Leemans, R.A. Monserud and A.M. Solomon (1992) A global biome model based on plant physiology and dominance, soil properties and climate. Journal of Biogeography 19: 117-134

Prepas, E.E. (1983) Orthophosphate turnover time in shallow productive lakes. Canadian Journal of Fisheries and Aquatic Sciences. 40: 1412-1418

Prepas, E.E. and D.O. Trew (1983) Evaluation of the phosphorus-chlorophyll relationship for lakes off the Precambrian Shield in Western Canada. Canadian Journal of Fisheries and Aquatic Sciences. 40: 27-35

Prepas, E.E. and A.M. Trimbee (1988) Evaluation of indicators of nitrogen limitation in deep prairie lakes with indicatory bioassays and limnocorals. Hydrobiologia. 159: 269-276

Rast, W., R.A. Jones and G.F. Lee (1983) Predictive capability of the US OECD phosphorus loading-eutrophication response models. Journal of the Water Pollution Control Federation. 55: 990-1003

Rast, W. and G.F. Lee (1978) Summary analysis of the North American (US portion) OECD eutrophication project: nutrient loading-lake response relationships and trophic state indices. US EPA, EPA-600/3-78-008, Corvallis, Oregon

Redfield, A.C. (1958) The biological control of chemical factors in the environment.. American Scientist 46: 205-222

Reynolds, C.S. (1980) Phytoplankton assemblages and their periodicity in stratifying lake systems. Holarctic Ecology. 3: 141-159

Reynolds, C.S. (1982) Phytoplankton periodicity: its motivation, mechanisms and manipulation. Report of the Freshwater Biological Association 50: 60-75

Reynolds, C.S. (1984a) Phytoplankton periodicity: the interactions of form, function and environmental variability. Freshwater Biology 14: 111-142

Reynolds, C.S. (1984b) The ecology of freshwater phytoplankton Cambridge University Press.

Reynolds, C.S. (1986) Experimental manipulations of the phytoplankton periodicity in large limnetic enclosures in Blelham tarn, English Lake District. Hydrobiologia 138: 43-64

Reynolds, C.S. (1987) Community organisation in the freshwater plankton. p.297-325 in "Organisation of communities, past and present", eds. J.H.R. Gee and P.S. Giller, Blackwell Scientific Publications, Oxford

Reynolds, C.S. (1988) Potamoplankton: paradigms, paradoxes and prognoses. p285-311 in "Algae and the aquatic environment" ed F.E. Round, Biopress, Bristol

Reynolds, C.S. (1990) Temporal scales of variability in pelagic environments and the response of phytoplankton. Freshwater Biology 23: 25-53

Reynolds, C.S., P.A. Carling and K.J. Beven (1991) Flow in river channels: new insights into hydraulic retention. Archiv fur Hydrobiology 121: 171-179

Reynolds, C.S., R.L. Oliver and A.E. Walsby (1987) Cyanobacterial dominance: the role of buoyancy regulation in dynamic lake environments. New Zealand Journal of Maine and Freshwater Research. 21: 379-390

Reynolds, C.S., S.W. Wiseman, B.M. Godfrey and C. Butterwick (1983) Some effects of artificial mixing on the dynamics of phytoplankton populations in large limnetic enclosures. Journal of Plankton Research 5: 203-234

Rigler, F.H. (1964) The phosphorus fractions and the turnover time of inorganic phosphorus in different type of lakes. Limnology and Oceanography 9: 51-518

Rigler, F.H. (1966) Radiobiological analyses of inorganic phosphorus in lake water. Verhandlungen der Internationalen Vereinigung fur Theoretische und Angewandte Limnologie 16: 465-470

Rodriguez, J and M.M. Mullin (1986) Relation between biomass and body weight of plankton in a steady state oceanic ecosystem. Limnology and Oceanography 31: 361-370

Rosenzweig, M.L. (1971) Paradox of enrichment: destabilisation of exploitation ecosystems in ecological time. Science, 171: 385-7

Rosich, R.S. and Cullen, P. (1982) Nutrient runoff. In "Water Quality Management" ed. Hart, B.T., Australian Society of Limnology

Royle, R.N. and R.J. King (1992) The phytoplankton of Lake Liddell, New South Wales: chlorophyll a concentrations, species seasonal succession and covariation with nutrients. Hydrobiologia 245: 41-52

Rucker, R. von B. (1988) Mind tools. Penguin Books, London, 328p

Ryder, R.A., S.R. Kerr, K.H. Loftus and H.A. Regier (1974) The morphoedaphic index, a fish yield estimator - review and evaluation. Journal of the Fisheries Research Board of Canada. 31: 663-688

Sakamoto, M. (1966) Primary production by phytoplankton community in some Japanese lakes and its dependence on lake depth. Archiv fur Hydrobiologie 62: 1-28

Sawyer, C.N. (1947) Fertilisation of lakes by agricultural and urban drainage. Journal of the New England Water Works Association 61: 109-127

Scavia, D. (1980) An ecological model of Lake Ontario. Ecological Modelling 8: 49-78

Schaffer, W.M. and M. Kot (1985) Do strange attractors govern ecological systems? BioScience 35: 342-350

Schiemer, F. and Prosser, M. (1976) Distribution and biomass of submerged macrophytes in Neusiedlersee. Aquatic Botany, 2: 289-307

Schindler, D.W. (1978) Factors regulating phytoplankton production and standing crop in the world's freshwaters. Limnology and Oceanography 23: 478-486

Schindler, D.W., F.A.J. Armstrong, S.K. Holmgren and G.J. Brunskill (1971) Eutrophication of lake 227, Experimental Lakes Area, North-western Ontario by addition of nitrate and phosphate. Journal of the Fisheries Research Board of Canada 28: 1763-1782

Seip, K.L. and H. Ibrekk (1988) Regression equations for lake management - how far do they go? Verhandlungen der Internationalen Vereinigung fur Theoretische und Angewandte Limnologie 23: 778-785

Sephton, D.H. and G.P. Harris (1984) Physical variability and phytoplankton communities VI. Day to day changes in primary productivity and species abundances. Archiv fur Hydrobiologie 102: 155-175

Shan, Y., I.D. McKelvie and B.T. Hart (1994) An enzymatic flow injection method for the determination of alkaline phosphatase hydrolysable phosphorus in natural water and wastewater systems. Limnology and Oceanography (submitted)

Shapiro, J. (1990) Biomanipulation: the next phase - making it stable. Hydrobiologia 200/201: 13-27

Shinbrot, T., C. Grebogi, E. Ott and J.A. Yorke (1993) Using small perturbations to control chaos. Nature 363: 411-417

Simon, M., B.C. Cho and F. Azam (1992) Significance of bacterial biomass in lakes and the ocean: comparison to phytoplankton biomass and the biogeochemical implications. Marine Ecology Progress Series 86: 103-110

Simpson, H.J., M.A. Cane, A.L. Herczeg, S.E. Zebiak and J.H. Simpson (1993) Annual river discharge in South-eastern Australia related to El Nino-Southern Oscillation forecasts of sea surface temperatures. Water Resources Research 29: 3671-3680

Slobodkin, L.B. (1988) Intellectual problems of applied ecology. BioScience 38: 337-342

Slobodkin L.B. (1992) Simplicity and complexity in games of the intellect. Harvard University Press, Cambridge, Mass. 266p.

Smith, V.H. (1983) Low nitrogen to phosphorus ratios favour dominance by blue-green algae in lake phytoplankton. Science 221: 669-671

Smith, V.H. (1985) Predictive models for the biomass of blue-green algae in lakes. Water Research Bulletin 21: 433-439

Smith, V.H. (1986) Light and nutrient effects on the relative biomass of blue-green algae in lake phytoplankton. Canadian Journal of Fisheries and Aquatic Science 43: 148-153

Sommer, U. (1985) Comparison between steady state and non-steady state competition: experiments with natural phytoplankton. Limnology and Oceanography 30: 335-346

Sommer, U. (ed) (1989) Plankton Ecology. Springer-Verlag, Berlin, 369p

Sommer, U. (1990) Phytoplankton nutrient competition - from laboratory to lake. p 193-214 in "Perspectives on plant competition" eds J.B. Grace and D. Tilman, Academic Press, New York.

Sommer, U. (1991) A comparison of the Droop and Monod models of nutrient limited growth applied to natural populations of phytoplankton. Functional Ecology 5: 535-544

Sommer, U., M. Gliwicz, W. Lampert and A. Duncan (1986) The PEG model of seasonal succession of planktonic events in fresh waters. Archiv fur Hydrobiologie 106: 433-471

Sommer, U., J. Padisak, C.S. Reynolds and P. Juhasz-Nagy (1993) Hutchinson's heritage: the diversity-disturbance relationship in phytoplankton. Hydrobiologia 249: 1-8

Sondergaard, M., E. Jeppesen, E. Mortensen, E. Dall, P. Kristensen and O. Sortkjaer (1990) Phytoplankton biomass reduction after planktivorous fish reduction in a shallow, eutrophic lake: a combined effect of reduced internal P loading and increased zooplankton grazing. Hydrobiologia 200/201: 229-240

Sprules, W.G. and R. Knoechel (1984) Lake ecosystem dynamics based on functional representations of trophic components. p. 383-403 in "Trophic interactions within aquatic ecosystems. eds. D.G. Meyers and J.R. Strickler, AAAS Selected Symposium 85, American Association for the Advancement of Science, Washington.

Sprules, W.G. and M. Munawar (1986) Plankton size spectra in relation to ecosystem productivity, size and perturbation. Canadian Journal of Fisheries and Aquatic Science 43: 1789-1794

Sprules, W.G., J.M. Casselman and B.J. Shuter (1983) Size distribution of particles in lakes. Canadian Journal of Fisheries and Aquatic Science 40: 1761-1769

Stauffer, R.E. (1991) Environmental factors influencing chlorophyll v. nutrient relationships in lakes. Freshwater Biology 25: 279-295

Steinberg, C.E.W and H.M. Hartmann (1988) Planktonic bloom forming cyanobacteria and the eutrophication of lakes and rivers. Freshwater Biology 20: 2790287

Steinberg, C.E.W. and G. Zimmermann (1988) Intermittent destratification: a therapy measure against cyanobacteria in lakes. Environmental Technology Letters 9: 337-350

Sterner, R.W. (1990) The ratio of nitrogen to phosphorus resupplied by herbivores: zooplankton and the algal competitive arena. American Naturalist 136: 209-229

Sterner, R.W., J.J. Elser and D.O. Hessen (1992) Stoichiometric relationships among producers, consumers and nutrient cycling in pelagic ecosystems. Biogeochemistry 17: 49-67

Stevens, R.J. and R.V. Smith (1978) A comparison of discrete and intensive sampling for measuring the loads of nitrogen and phosphorus in the River Main, County Antrim. Water Research 12: 823-830

Suttle, C.A. and P.J. Harrison (1988) Ammonium and phosphate uptake rates, N:P supply ratios and evidence for N and P limitation in some oligotrophic lakes. Limnology and Oceanography 33: 186-202

Talling J.F. (1950) The element of chance in pond populations. The Naturalist (Oct-Dec) 157-70

Talling, J.F. (1976) The depletion of carbon dioxide from lake water by phytoplankton. Journal of Ecology 64: 79-121

Talling, J.F. (1985) Inorganic carbon reserves of natural waters and eco-physiological consequences of their photosynthetic depletion: microalgae. p 403-420 in "Inorganic carbon uptake by aquatic photosynthetic organisms" eds W.J. Lucas and J.A. Berry, The American Society of Plant Physiologists

Talling, J.F. (1986) The seasonality of phytoplankton in African lakes. Hydrobiologia 138: 139-160

Talling J.F. (1993) Comparative seasonal changes, and interannual variability and stability, in a 26 year record of total phytoplankton biomass in four English lake basins. Hydrobiologia 268: 65-98

ten Winkel E.H. and J.T. Meulemans (1984) Effects of fish upon submerged vegetation. Hydrobiological Bulletin 18: 157-158

Thomann, R.V. (1977) Comparison of lake phytoplankton models and loading plots. Limnology and Oceanography 22: 370-373

Thomann, R.V., D.M. DiToro, R.P. Winfield and D.J. O'Connor (1975) Mathematical modelling of phytoplankton in Lake Ontario. US EPA, EPA-660/3-75-005, Corvallis, Oregon, USA

Thomann, R.V., D.M. DiToro, D. Scavia and A. Robertson (1981) Ecosystem and water quality modelling. p 353-366 in "IFYGL - The International field year of the Great Lakes" eds E.J. Aubert and T.L. Richards, US NOAA Gt. Lakes Env. Res. lab. US Dept of Commerce, Ann Arbor, Michigan

Thomas, E.A. (1955) Stoffhaushalt und Sedimentation im oligotrophen Agerisee und im eutrophen Pfaffiker- und Greifensee. Memorie dell'Instituto Italiano di Idrobiologia. Suppl. 8: 357-465

Thomas, E.A. (1956) Sedimentation und Stoffhaushalt in Tulersee. Bull. Schweizerische Ver. Gas-und Wasserforschung 12: 1-11

Tilman, D.A. (1977) Resource competition between planktonic algae: an experimental and theoretical approach. Ecology. 58: 338-348

Tilman, D.A. (1982) Resource competition and community structure. Princeton University Press, Princeton, NJ

Tilman, D.A. and J.A. Downing (1994) Biodiversity and stability in grasslands. Nature 367: 363-365

Tilman, D.A., S.S. Kilham and P. Kilham (1981) Phytoplankton community ecology: the role of limiting nutrients. Annual Reviews of Ecology and Systematics. 13: 349-372

Tilman, D., R. Kiesling, R. Sterner, S.S. Kilham and F.A. Johnson (1986) Green, blue-green and diatom algae: taxonomic differences in competitive ability for phosphorus, silicon and nitrogen. Archiv fur Hydrobiologie 106: 473-485

Tilzer, M.M. (1988) Secchi disk - chlorophyll relationships in a lake with a highly variable phytoplankton biomass. Hydrobiologia 162: 163-171

Timms, R.M. and B. Moss (1984) Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing, in the presence of planktivorous fish, in a shallow wetland ecosystem. Limnology and Oceanography 29: 472-486

Titman, D.A. (1976) Ecological competition between algae: experimental confirmation of resource-based competition theory. Science. 192: 463-465

Trimbee, A.M. and G.P. Harris (1984a) Phytoplankton population dynamics of a small reservoir: effect of intermittent mixing on phytoplankton succession and the growth of blue-green algae. Journal of Plankton Research 6: 699-713

Trimbee, A.M. and G.P. Harris (1984b) Phytoplankton population dynamics of a small reservoir: use of sediment traps to quantify the loss of diatoms and the recruitment of summer bloom forming blue-green algae. Journal of Plankton Research 6: 897-918

Trimbee, A.M. and E.E. Prepas (1987) Evaluation of total phosphorus as a predictor of the relative biomass of blue-green algae with emphasis on Alberta lakes. Canadian Journal of Fisheries and Aquatic Sciences 44: 1337-1342

Urabe, J. (1993) N and P cycling coupled by grazers' activities: food quality and nutrient release by zooplankton. Ecology 74: 2337-2350

van Donk, E., M.P. Grimm, R.D. Gulati and J.P.G. Klein Breteler (1990a) Whole lake food web manipulations as a means to study community interactions in a small ecosystem Hydrobiologia 200/201: 275-289

van Donk, E., M.P. Grimm, R.D. Gulati, P.G.M. Heuts, W.A. de Kloet and L. van Liere (1990b) First attempts to apply whole-lake food-web manipulation in a large scale in the Netherlands. Hydrobiologia 200/201: 291-301

Vanni, M.J. (1987) Effects of nutrients and zooplankton size on the structure of a phytoplankton community. Ecology 68: 624-635

Varis, O. (1993) Cyanobacterial dynamics in a restored Finnish lake: a long term simulation study. Hydrobiologia 268: 129-145

Vollenweider, R.A. (1965) Calculation models of photosynthesis - depth curves and some implications regarding day rate estimates in primary production measurements. Memorie dell'Instituto Italiano di Idrobiologia. 18: 425-457

Vollenweider, R.A. (1968) Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to nitrogen and phosphorus as factors in eutrophication. OECD, Paris, Technical Report DAS/SCI/68.27: 182p

Vollenweider, R.A. (1969) Moglichkeiten und grenzen elementarer Modelle der Stoffbilanz von Seen. Archiv fur Hydrobiologie. 66: 1-36

Vollenweider, R.A. (1970) Models for calculating integral photosynthesis and some implications regarding structural properties of the community metabolism of aquatic systems. p. 455-472 in "Prediction and Measurement of Photosynthetic Productivity" Proceedings of the IBP/PP meeting, Trebon.

Vollenweider, R.A. (1975) Input - output models, with special reference to the phosphorus loading concept in limnology. Schweizerische Zeitzschrift fur Hydrologie. 37: 53-82

Vollenweider, R.A. (1976) Advances in defining critical loading levels for phosphorus in lake eutrophication. Memorie dell'Instituto Italiano di Idrobiologia 33: 53-83

Vollenweider, R.A. (1990) Eutrophication: conventional and non-conventional considerations and comments on selected topics. Memorie dell'Instituto Italiano di Idrobiologia 47: 77-134

Vollenweider, R.A. and L.L. Janus (1982) Statistical models for predicting hypolimnetic oxygen depletion rates. Memorie dell'Instituto Italiano di Idrobiologia 40: 1-24

Vollenweider, R.A. and P.J. Dillon (1974) The application of the phosphorus loading concept to eutrophication research. NRC No. 13690, NRC Associate Committee on Scientific Criteria for Environmental Quality, National Research Council, Canada. 42p.

Vollenweider, R.A. and J. Kerekes (1980) The loading concept as a basis for controlling eutrophication: philosophy and preliminary results of the OECD programme on eutrophication. Progress in Water Technology. 12: 5-38, IAWPR/ Pergamon Press

Vollenweider, R.A., W. Rast and J. Kerekes (1980) The phosphorus loading concept and Great Lakes eutrophication.. p. 207-234 Proceedings of the 11th Annual Cornell University Conference, "Phosphorus management strategies for the Great Lakes" eds R.C. Locke, C.S. Martin and W. Rast, Ann Arbor Science, Rochester, NY

Waldrop M.M. (1992) Complexity. Viking, New York 380p

Wallsten, M and P.-O. Forsgren (1989) The effects of increased water level on aquatic macrophytes. Journal of Aquatic Plant Management 27: 32-37

Watson, S. and J. Kalff (1981) Relationships between nanoplankton and lake trophic status. Canadian Journal of Fisheries and Aquatic Sciences. 38: 960-967

Watson, S., E. McCauley and J.A. Downing (1992) Sigmoid relationships between phosphorus, algal biomass and algal community structure. Canadian Journal of Fisheries and Aquatic Sciences 49: 2605-2610

White, E., G. Payne, S.Pickmere and F.R. Pick (1982) Factors influencing orthophosphate turnover times: a comparison of Canadian and New Zealand lakes. Canadian Journal of Fisheries and Aquatic Sciences. 39: 469-474

Williams, W.D. (1982) Australian conditions and their implications. p. 1-10 in "Prediction in water quality" eds E.M. O'Loughlin and P.Cullen, Australian Academy of Science, Canberra

Wilson, E.O. (1992) The diversity of life. Allen Lane (Penguin), London 424p.

Wofsy, S.C. (1983) A simple model to predict extinction coefficients and phytoplankton biomass in eutrophic waters. Limnology and Oceanography. 28: 114-155