



# How green is my river? A new paradigm of eutrophication in rivers

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## Abstract

Although the process of eutrophication is reasonably well understood in lakes, there is currently no conceptual understanding of how eutrophication develops in rivers. This issue is addressed here. A review of the main processes controlling the development of eutrophication in lakes has been carried out as a precursor to considering the effect in rivers. The importance of hydraulic flushing in controlling algal growth suggests that short-retention-time rivers will show different effects compared to long retention-time, impounded rivers. The latter are likely to operate like lakes, moving from macrophyte domination to phytoplankton domination whereas the former move to benthic and filamentous algal domination. Subsequently, a conceptual model of the development of eutrophic conditions in short-retention-time rivers is developed. Although there is general agreement in the literature that an increase in nutrients, particularly phosphorus, is a pre-requisite for the eutrophic conditions to develop, there is little evidence in short-retention-time rivers that the plant (macro and micro) biomass is limited by nutrients and a good case can be made that the interaction of hydraulic drag with light limitation is the main controlling factor. The light limitation is brought about by the development of epiphytic algal films on the macrophyte leaves. The implications of this conceptual model are discussed and a series of observable effects are predicted, which should result if the model is correct.

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## 1. Introduction

The Water Framework Directive of the European Community (WFD; Council of European Communities, 2000) provides one of the most significant environmental targets for improving surface water quality across Europe. While considering a host of pollutants, a key focus is placed on the role of nutrients in eutrophication. For example, in England and Wales alone, it has been estimated that the current costs of eutrophication in terms of increased costs of water treatment for public supply, loss of biodiversity and amenity value will be

around £100 million per year and that the costs of remediation to address this damage amounts to about £55 million (Pretty et al., 2003). There is considerable debate over the relative importance of point (sewage) and diffuse (agriculture and, for nitrogen, atmospheric deposition) pollution with regards to river eutrophication, and climate variability complicates the situation further (Jarvie et al., in press; Neal and Jarvie, 2005). There are also questions as to the rate and extent to which freshwater systems might recover following nutrient reductions; reducing nutrient fluxes might not necessarily result in an ecological change back to pre-impacted conditions (Jarvie et al., 2004). A proper analysis and understanding of biological processing and ecosystem functioning within surface water systems is vital if environmental management strategies are to be

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based on sound science (Neal and Heathwaite, 2005; Wade, 2006-this volume). In this paper we will review our current understanding of the main processes governing eutrophication in lakes and use this as a basis for developing a conceptual model of eutrophication in rivers.

## 2. Background

In most of the developed world, pollution of waters brought about by the microbial breakdown of easily degraded organic matter, resulting in low oxygen concentrations, has been controlled by the introduction of effective sewage treatment facilities. However, there is a common acceptance that major increases in the primary production of water bodies, i.e. the excessive growth of plants, mainly in the form of algae and large rooted plants (macrophytes) due to high inputs of nutrients (mainly phosphorus and nitrogen), is now the most important polluting effect in lakes and rivers in the developed world (e.g. Mainstone and Parr, 2002). This process, which is termed eutrophication, has a limited effect on human health (with the exception of occasional blue-green algal blooms, which can produce toxic substances in the water) but has major economic consequences. Increased algal blooms in lakes and rivers are considered to be aesthetically unattractive and can have significant negative effects on tourism and the prices of waterfront properties. Excessive growth of algae in water supply reservoirs can increase the cost of water treatment significantly; increased growth of rooted plants can increase flooding whereas the loss of rooted plants and associated communities due to eutrophication is considered to lower biodiversity (e.g. Mainstone and Parr, 2002).

The concept of the progressive eutrophication of a water body, i.e. a change from low to high productivity due to an increase in the input of inorganic nutrients, was established relatively early in the development of limnology (Naumann, 1919). As a result, it is often forgotten that eutrophication is, in fact, defined subjectively. An observer classifies a water body in the range ultra-oligotrophic through to hyper-trophic on the basis of experience and a few qualitative criteria. A major step forward in developing a number of commonly accepted, quantifiable descriptors of trophic status in lakes was made by Vollenweider (Vollenweider, 1968; OECD, 1982) and, over the last forty years, a significant research effort has been devoted to determining the mechanisms by which anthropogenically induced eutrophication occurs. As a result, our level of understanding of the

processes by which increases in a limiting nutrient (OECD, 1982) can increase the biomass of phytoplankton in lakes are sufficiently well understood that a number of reliable models have been developed, capable of predicting phytoplankton biomass and community structure over time (e.g. PROTECH, Reynolds et al., 2001). These types of model are now sufficiently well developed that good predictions of concurrent changes in nutrient concentrations, planktonic algal biomass, zooplankton biomass and algal community (group) structure can be made, enabling their use for quite sophisticated comparisons of a suite of management options for a given lake (Hilton et al., 1992, 2001; May et al., 2001; Lewis et al., 2002, 2003). However, although Ohle (1955) applied the term eutrophication to rivers as early as the mid fifties, our understanding of eutrophication in rivers remains extremely limited. A compilation of statements from Water Quality Managers and other water managers in the late 1990s (Hilton and Irons, 1998) reported the following problematic conditions in rivers which they considered to have resulted from the effects of anthropogenically enhanced eutrophication:

- Excessive growth of planktonic (suspended) algae
- Excessive growth of benthic and filamentous algae
- Excessive growth of aquatic macrophytes (a description particularly prevalent amongst flood defence engineers)
- Reductions in the numbers of species of macrophytes present
- A move from macrophyte to benthic, filamentous or planktonic algal dominance
- Frequent occurrence of low dissolved oxygen events (particularly overnight)
- Large pH changes
- Regular blue-green algal blooms
- Green or brown coloration of the water.

This is a fairly wide range of effects which cannot be explained by current hypotheses of the mechanisms by which the effects of eutrophication might be generated in rivers. A number of workers have looked at specific, observed effects of increasing nutrients, e.g. macrophyte biodiversity and species succession (Dawson et al., 1999; Wilby et al., 2001) and interactions between epiphytic algae and macrophytes (Flynn et al., 2002; Wade et al., 2002). However, there appears to be no over-arching hypothesis of the development of eutrophication in rivers, which can predict the course of events and account for all the observable effects listed above. As a result, the research community is unable to

supply the science required to underpin management decisions to reduce the supposed effects of eutrophication, which is now of major importance for achieving good ecological status for the WFD (Council of European Communities, 2000).

### 3. A short review of the process of eutrophication in lakes

Lakes tend to become naturally more eutrophic with (geologic) time; as they become shallower due to silt inputs, the incoming nutrients are distributed amongst a smaller volume of water increasing their concentration and, hence, the resulting biomass of algae (Moss, 1980). However, the increased interest in eutrophication studies over the past few decades has been generated by the accelerated rates of eutrophication brought about by human activities and the need to re-establish a more ecologically acceptable state. In lakes, the change usually appears (superficially) to be simple with turbid, often coloured (brown, green or blue-green) water replacing macrophyte-dominated, clear waters. The turbidity is the result of an increase in the biomass of planktonic (suspended) algae in the open water. Aesthetically, this is considered to be unsightly and can significantly increase treatment costs when the water is used for potable water supply.

A series of major improvements in our understanding of eutrophication was reported by Vollenweider (Vollenweider, 1968; OECD, 1982), who led an international research programme into the subject. Substantial data sets were collated for over 100 northern temperate lakes, which had been subjectively classified into one of 5 classes: ultra-oligotrophic, oligotrophic, mesotrophic, eutrophic and hypertrophic, using the normally accepted range of qualitative measures. A simple classification was then carried out to identify both fixed and probabilistic boundaries between the five classes on the basis of a number of quantifiable environmental measures, including nutrient concentrations, turbidity and chlorophyll concentrations. It should be recognised that this was, essentially, an expert system and simply achieved a consensus opinion of how the qualitative trophic classification translated into quantifiable parameters (NB the classification, itself is still arbitrary). However, for the first time, it allowed measurable targets to be set for management which, in itself, was a major step forward.

A second significant development (OECD, 1982) was the introduction of the concept of the “limiting nutrient.” The basis of this approach, which built on the work of Hutchinson (1973), was that planktonic algal cells contain approximately the same relative propor-

tions of carbon, nitrogen and phosphorus (Redfield, 1934) and, for diatoms, silicon. Population growth takes place by each cell splitting into two identical cells. To achieve this, all the nutrients must be available in sufficient quantities to allow a doubling of the cell numbers. Eventually, the amount of one or more nutrients will drop below a concentration at which further increases in biomass can no longer occur at the rate determined by the temperature and light input. At this stage growth is deemed to be “nutrient limited” and the total biomass achievable will be determined by the “limiting nutrient.” In freshwater lakes, over the annual cycle, the limiting nutrient is usually phosphorus (P) although there are a few situations where nitrogen (N) or a combination of nitrogen and phosphorus (jointly) is limiting, such as some low nutrient/acidic lakes, (Maberly et al., 2002, 2003) and some hypertrophic lakes with large phosphorus inputs (e.g. James et al., 2003). Generally, P (or N) is the nutrient which is limiting for most of the growing season, but within this longer-term limitation, other nutrients can limit growth for a few weeks, such as silicon during the spring diatom bloom (Gervais, 1991; Interlandi et al., 1999). The identification of a limiting nutrient in a given lake, in conjunction with the class boundaries, allows a target nutrient concentration to be set and the development of a management plan to achieve that target.

Vollenweider (OECD, 1982) supplied a third key to our understanding of the mechanisms of eutrophication in lakes. He applied some simple chemical engineering equations to the data and showed that the “flushing rate” (flow rate/volume) or the inverse, the “water retention time” in a lake determines how efficiently the algae can use the nutrients. In short, if the lake flushing rate were faster than the algal growth rate then the algae would be unable to grow to their maximum biomass and use up all the nutrients. This is because a large proportion of the algae and nutrients would be washed out via the outflow before any increases in algal biomass could occur. Hence, lakes with relatively short retention times would not develop large planktonic algal biomass, irrespective of the nutrient load. Conversely, lakes with long retention times would allow algae to fully utilise any nutrients added to the lake and allow the development of large algal biomass, which would eventually become nutrient limited.

It took two decades of research to fully explore and understand the consequences of these insights. However, by the early 1990s, a number of models, e.g. PROTECH (Reynolds et al., 2001), had been developed which could predict changes in algal biomass and species composition quite successfully, by linking these

three keystone developments with a number of other simplifying assumptions (Reynolds, 1989, 1992). On the basis of these predictions, management scenarios can be tested and the most appropriate can be implemented. An increasing number of examples of the use of the PROTECH model as a management tool can be cited, e.g. Hilton et al., 1992; May et al., 2001. Analysis of data from a number of lakes to which management controls have been applied over the last twenty years has shown that, as a general rule, deep lakes, i.e. those which stratify permanently throughout the summer season, typically respond rapidly to reductions in nutrient loads, whereas shallow lakes can take decades to recover (Osborne, 1980; Sas, 1989; Phillips, 1984; Edmonson and Lehman, 1981). The internal cycling of nutrients from the sediment (Sas, 1989), which are much more effectively recycled in shallow lakes than in deep lakes, is a key factor limiting poor recovery. There is currently no quantitative understanding of the process, which would allow it to be included in models, although there is some evidence that it may result from stochastic, wind driven resuspension of anaerobic sediments with high interstitial P concentrations (Hilton et al., 2001). However, once macrophytes become re-established then other positive feedback processes push the system towards macrophyte dominance (Scheffer et al., 1993). For example, plants stabilise the water column increasing the sedimentation of suspended particles, which increases the amount of light getting to plants. Further, many plants release oxygen into the sediment making it less anoxic and thereby reducing the dissolved P in the interstitial water which could be recycled. Roots stabilise the sediment making them less susceptible to resuspension by wind driven turbulence.

Almost all models that attempt to predict the course of eutrophication and any remedial measures in lakes simulate phytoplankton behaviour alone at the eutrophic/hyper-eutrophic end of the spectrum. There are very few, if any, practical models which attempt to simulate the macrophyte dynamics in lakes as eutrophication worsens or improves. Scheffer et al. (1993) reviewed hypotheses proposing that in this situation, in shallow systems, where nutrient concentrations are medium to low ( $30\text{--}300 \mu\text{g P l}^{-1}$ ), two equally likely states are possible: in one, phytoplankton dominates and in the other, at the same nutrient concentration, macrophytes dominate. On the basis of this hypothesis, biomanipulation was proposed as a remediation technique to flip the system from plankton dominated to macrophyte-dominated (at the same nutrient concentration). In this approach, fish were removed and excluded from lakes thought to be in the bimodal

equilibrium situation; the objective being to reduce fish predation of zooplankton, allowing the latter to graze on the algae. This reduced the turbidity and allowed the macrophytes to utilise more light and nutrients and attain dominance, e.g. Moss et al. (1996). Reynolds (1994) showed that there were many situations where this restoration technique had worked, even though ecological theories of nutrient utilisation and recycling were incompatible with the zooplankton mechanism. (Theoretically, grazing on algae would recycle nutrients which, given sufficient time, should be taken up by large algae that could not be eaten by zooplankton but would give an equivalent biomass to the initial biomass of the smaller algal community.) It is only recently that Jones and Sayer (2003) have identified a more likely mechanism. They showed that, at low nutrient concentrations, where bimodal equilibria were possible, the biomass of algae was not related to either zooplankton numbers or nutrient concentrations but to the numbers of macroinvertebrates grazing on epiphytic algae on the macrophytes. Phillips et al. (1978) had previously suggested that growth of epiphytes on macrophytes, blocking out light to the higher plants, was probably the mechanism by which systems were driven from the macrophyte dominated state to the phytoplankton dominated state. However, the fact that the same process was operating when eutrophication was reversed using biomanipulation, and that it was mediated through macroinvertebrate grazing had not been proposed before. Jones and Sayer (2003) also showed an inverse correlation between fish numbers and invertebrate numbers at these low to medium nutrient concentrations. Hence, removal of the fish reduced predation on the macroinvertebrate grazers, allowing them to reduce the amount of epiphytes covering the macrophytes which, in turn, received more light allowing them to grow more rapidly. At these intermediate nutrient concentrations, the increased macrophyte biomass stored sufficient nutrient that concentrations of free nutrients in the water column reduced, causing the phytoplankton biomass to reduce and the system to move towards macrophyte dominance. The discovery of this mechanism suggests that the removal of fish as a remediation method is only suitable for shallow lakes and not deep lakes, where macrophytes can fill, and hence influence, only a small proportion of the total lake volume.

Even with a limited knowledge of the effects of nutrient recycling from the sediments and of the processes involved in moving from phytoplankton dominance to macrophyte dominance (and vice-versa), the current level of understanding of the processes is sufficient to design and implement effective management strategies to control eutrophication in lakes, even though in most shallow

systems the time scales for achieving targets may be longer (decades) than public expectation (immediate). The understanding of eutrophication in rivers is much more limited.

#### 4. Eutrophication in rivers

Given the large amount of work which has been carried out on eutrophication in lakes, a good starting point in developing a mechanism of eutrophication in rivers is to consider the effect of the major factors shown to be important in lakes.

##### 4.1. Retention time

Vollenweider (OECD, 1982) demonstrated the importance of lake retention time as a major control on the ability of planktonic algae to utilise nutrients. If the retention time of a lake, which is assumed to be completely mixed, is shorter than the doubling time of planktonic algae in the system, then the development of a biomass of planktonic algae large enough to cause nuisance conditions will not occur irrespective of the nutrient conditions, because the algae are flushed out at a rate faster than they can grow. A similar, but not completely comparable situation will occur in rivers where, rather than complete mixing, plug flow occurs, i.e. mixing across the river takes place quickly but mixing along the river is very limited so that a tracer that is introduced over a short length of time will pass through the system as a plug, rather than mixing throughout the length of the river. As a result, the relevant, equivalent parameter for rivers is the time of travel, which theoretically is the same as the retention time but, in practice tends to be longer because of dispersion processes in the river. Planktonic (suspended) algal biomass will increase along the length of a river but, in the upper reaches of the river at least, the biomass in the water column will never reach nuisance concentrations. This is because the initial inoculum (the biomass of algae at the start of the growing period) of planktonic algae at the source of the river will always be small, due to the high rate of flushing that occurs, and a large number of cell doublings will be required to increase the concentration of cells to visually unacceptable levels. Hence, planktonic algae are unlikely to develop significant populations in the upper reaches of all rivers (the length depending on the retention time) and over the whole length of short rivers with a retention time less than a few algal cell doubling times. Conversely large rivers and deep, impounded rivers (including canals) have long retention times, of similar order to the range of lake retention times, which are much longer than algal doubling times so that a large biomass of phytoplankton can develop in the middle

and lower reaches of the river. This suggests that eutrophication in rivers is likely to express itself in two different forms, depending on the type of river. Deep, impounded rivers with long hydraulic residence times and the lower reaches of large rivers are likely to be dominated by planktonic algae when nutrient concentrations are high and lake models are likely to be applicable. This is consistent with work by Reynolds et al. (1998) who successfully modelled algal biomass and composition change in the lower River Thames (UK) using a minor modification of the PROTECH lake model and the work of Thebault and Qotbi (1999) who modelled phytoplankton changes in the River Lot (France). Conversely, in the lower reaches of the River Frome (Dorset, UK; catchment area of 400 km<sup>2</sup>; maximum length of 58.5 km; calculated median travel time from source to mouth approximately 60 h) Marker and Gunn (1977) showed that all the suspended algae in the river were resuspended benthic species and none were planktonic species. These observations are consistent with the existence of at least two different mechanisms of eutrophication in rivers, depending on the retention time. Rivers downstream of eutrophic lakes constitute a special case since they are likely to show a prevalence of planktonic algae due to the high inoculum of algae from the lake, but they will only continue to show measurable growth in long retention-time rivers. In short-retention-time rivers the planktonic algae from the lake will add to the total turbidity but not increase significantly by growth during transit. The cut-off point between phytoplankton dominance and other forms of plant domination is likely to be very variable, depending on the specific circumstances at a site, but the change could, potentially, occur at around two to three doubling times for planktonic algae. Reynolds (1984) suggested that the maximum doubling rate of planktonic algae is of the order two days, and hence the lower end of the range of retention times covering the transition range is likely to be between 4–6 days transit time. However, since the inoculum of planktonic algae is small in river headwaters, an observable change is only likely to occur after a much longer time. At sites on a river with transit times from source longer than this cut-off, planktonic algae are likely to dominate. At shorter transit times macrophytes and attached algae almost certainly will dominate.

##### 4.2. Limiting nutrients

It is generally recognised that an increase in nutrient loading is a prerequisite of increased eutrophication in rivers (Schneider and Melzer, 2003). However, it has still not been unequivocally established which of the main nutrients, if any, is generally limiting in rivers. There is

some evidence suggesting that phosphorus has a significant effect on macrophyte community structure (Dawson et al., 1999) and Carr and Chambers (1998) showed that macrophyte biomass was related to sediment P concentrations. Carr and Goulder (1990) showed that periphyton (defined throughout our paper as a generic term for all attached algae, including epiphytic, epilithic, benthic, etc.) in the River Hull (UK) were P limited, in agreement with work by Stockner and Shortreed (1978) and Peterson et al. (1983) on other rivers. Conversely Marcus (1980) found nitrogen to limit periphyton growth in his system. Matlock et al. (1998) found a number of sites where either P or N was limiting periphyton but a much greater number where both N and P appear to be jointly limiting. The likelihood is that the nutrient limiting growth probably changes depending on both the plant type (macrophyte, epiphyte, benthic algae, attached filamentous algae, etc.) and the trophic state of the river. Although raised concentrations of nutrients in the water column (and pore water) are required to induce hyper-eutrophic conditions, Schneider and Melzer (2003) and Carr and Chambers (1998) noted that all requirements for plant growth, such as light levels, trace nutrient concentrations, etc., must be in excess for plants to achieve their full growth potential, i.e. the maximum amount of growth which could be achieved at a given temperature if a specific nutrient were limiting and all other factors were in excess. Hence, if the river flows through a shaded area, such as a forest, then that growth potential will not be achieved due to light limitation and the river may not show any apparent signs of hyper-eutrophication. At low to medium productivity, nutrients probably limit macrophyte biomass but at high concentrations they are probably not limiting. Westlake (1981) suggested that nutrients will not be limiting in rivers waters with phosphate concentrations  $>30 \mu\text{g P l}^{-1}$  and nitrate  $>1 \text{ mg N l}^{-1}$ ; conversely it is likely that periphytic algal biomass will be limited by nutrient availability across a wide spectrum of nutrient concentrations. In the following we assume that a nutrient is the driver but is not necessarily limiting at the hypereutrophic end of the spectrum, where management interest is most intense.

#### 4.3. Load or concentration?

Vollenweider (OECD, 1982) showed a clear relationship between the total annual phosphorus load ( $\text{kg a}^{-1}$ ) to a lake and both the mean and maximum annual chlorophyll-a concentration ( $\text{mg m}^{-3}$ ). This relationship infers both that the phosphorus must be trapped efficiently in lakes, which is consistent with the work of Canfield et al. (1982), and that phosphorus entering the lake in mainly

solid-bound forms (Bowes and House, 2001), which are not immediately available to phytoplankton, is transformed into bioavailable forms (Bostrom et al., 1988; Ekholm, 1994) by microbially driven processes occurring within the time period that the P remains in the lake. However, in rivers, which are much more dynamic, these conditions are not maintained and both the timing of discharges relative to the plant growth period and the availability to different aquatic plants of nutrients from different sources is likely to be much more important in rivers than in lakes. This is because, in lakes, peaks of nutrient input are smoothed and there is sufficient time for inter-conversion between nutrient forms to occur.

The main growing season, and hence requirement for nutrients, for aquatic plants in northern temperate regions is from March to the end of September. However, the main period for the transport of diffuse, agricultural sources of P is during the winter and particularly the autumn rains (Mainstone and Parr, 2002; Cooper et al., 2002), which are key drivers of the transport processes involved. Conversely, the output of phosphorus for most STWs, in terms of flux, is approximately constant over the year (Mainstone and Parr, 2002; Cooper et al., 2002). This is the reason why, in rivers downstream of STW, the classical, straight line dilution relationship between the logarithm of in-river P concentration and the logarithm of flow is so pronounced (House and Warwick, 1998; Jarvie et al., 1998). As a result, the P concentration from these sources will be at its highest during the low summer flows (Bowes et al., 2005a,b; Cooper et al., 2002). Interpolation of data from the River Thame (Cooper et al., 2002; Cooper, personal communication) suggest that ca. 75% (66% to 84%) of the total annual diffuse P load was transported during the period October to February inclusive, leaving only 25% transported during the growing season. Conversely the same data set indicates that approximately 57% of the total P derived from STW was transported during the growing season. Hence, as suggested by Mainstone et al. (1996), the annual total phosphorus load may well be a less useful parameter for predicting the level of eutrophication in short-retention-time rivers than in lakes (although it will remain a useful parameter for identifying the relative importance of different sources in a river catchment and for the prediction of trophic status in lakes and estuaries, fed by rivers).

In addition to the difference in timing between diffuse and STW inputs of phosphorus, it is instructive to consider the chemical form of the phosphorus from each source when compared to the forms of P that can be utilised by different types of plant. Clearly, planktonic algae, suspended in the water column can only obtain their nutrients directly from the water column in dissolved, bioavailable forms. However, since the

timescales for phytoplankton production to develop problem biomass concentrations from a small algal inoculum are quite long, there is likely to be time for transformations between chemical forms of P in long retention-time rivers where phytoplankton can be a problem. Conversely, macrophytes can obtain their nutrients from either the sediments or the water column. Carignan (1982) developed an empirical equation to estimate the percentage of P taken up by the roots, compared to the whole plant uptake. If this equation is generally applicable it would suggest that at equal concentrations of P in the sediment pore water and open water column only 27% of the P would be derived from the sediment, whereas the percentage of P taken up by the roots would be 72% and almost 100% if the sediment pore water P concentration were 10 times and 100 times the water column P concentration respectively. Typically sediment pore water P concentrations are much higher than those in the overlying water (e.g. Woodruff et al., 1999) so that percentage uptake by roots is likely to be closer to the latter two values than the former. Periphyton (attached algae) are intermediate and their main nutrient source may well depend on the type of periphyton. Epiliths (plants attaching to stones) and large filamentous algae (e.g. cladophora) can only access nutrients from the water column. Conversely, benthic algae will also be able to access nutrients from both the sediment and the water. Finally, although epiphytic algae (living on plants) can obtain some nutrients by parasitic uptake from the plant they grow on, their main source of nutrients is from the water column. Although particulate and other unavailable forms of phosphorus can be transformed into bioavailable forms in the sediment (House, 2003), it is highly likely that, in short-retention-time rivers, there will be insufficient sufficient time for breakdown processes to transform unavailable forms of P, suspended in the water column into bioavailable forms, except to a minimal extent. Given that the most obvious nuisance plant species (filamentous algae and epiphytic algae) obtain the majority of their phosphorus directly from the water column and require it to be in bioavailable form, the median growing-season concentration of SRP (assuming macrophytes and algae cannot utilise short term pulses efficiently) may well be a better indicator of the likely level of nuisance eutrophication than the annual total P load. This is consistent with the observations of Wilby et al. (1998) that low flows and elevated SRP concentrations during summer favour the growth of filamentous algae to the detriment of the macrophyte, *Ranunculus*. It is also consistent with results from House et al. (2001) who showed that macrophytes in the River

Thame (UK) took up only a few percent of the annual total P load. However, this proportion is likely to increase significantly as the total P load reduces to the extent that annual total P load may have some potential for predicting macrophyte production in low to medium trophic status, short-retention-time rivers, where biodiversity and rare plant habitat protection are the legal drivers for remediation. Total P load will remain a useful predictor of phytoplankton biomass concentrations in large and/ or long retention-time rivers.

#### 4.4. Multiple stable states

From the review of the current evidence from lakes, it is clear that a major cause of the shift from macrophyte dominance to phytoplankton dominance in lakes is the development of epiphytic algal growths on macrophytes which reduce the amount of light the macrophytes receive. However, a key feature in lakes when the level of eutrophication is either increasing or, following remediation, decreasing is the influence of positive feedback effects. When eutrophic status gets worse and macrophyte dominance begins to be replaced by phytoplankton dominance, the reduced macrophyte growth, caused by the epiphytes intercepting light from the macrophytes, allows the phytoplankton to utilise more of the P in the system and make it unavailable for macrophyte use by incorporating it into algal biomass. The higher turbidity brought about by the increased phytoplankton biomass further reduces the light to the macrophytes, further reducing the ability of the macrophytes to grow. Conversely, when large grazing macro-invertebrate populations increase the light incidence to the higher plants by reducing the epiphytic film, then the macrophytes take up P from the water column and incorporate it into macrophyte biomass, thus reducing its availability to the phytoplankton. This, in turn, reduces the algal biomass and the turbidity, which increases the light to the macrophytes and the system moves further towards macrophyte dominance.

Ham et al. (1981) reported that, in some years, epiphytic algae covering *Ranunculus* in the River Lambourn caused delays of several months in the development of the high percentage coverage of *Ranunculus* usually seen in the river. On the basis of this they proposed a conceptual model, where the build up of epiphytes was the cause of macrophyte decline in low-flow years [but no link was made with nutrients in the river.] Hence, there is evidence that a similar mechanism to lakes may be working as rivers become more eutrophic. However, in a short-retention-time river there is too little phytoplankton biomass present to form the second stable state observed in lakes. It is difficult

to see how macrophytes and benthic algae (indicative of extreme riverine eutrophication) can interact in a positive feedback loop, since they both have access to a large pool of nutrients in the sediment and are not dependent on a limited P resource in the water column. As a result, it is unlikely that multiple stable states exist in a riverine system. The main cause of macrophyte decline is likely to be light limitation by epiphytes, rather than, as implied by Holmes and Newbold (1984), an aversion to high phosphorus concentrations, per se. At low dissolved inorganic carbon concentrations, the light limitation will be exacerbated by competition for inorganic carbon, between the epiphytic film and the macrophytes (Jones et al., 2002). This will result in the effects of eutrophication occurring at much lower nutrient concentrations in low alkalinity waters than in high alkalinity waters. However, in general, for lakes and rivers with equal (high or low) alkalinity, extinction of macrophytes (but not necessarily community composition change) is likely to occur at much higher nutrient concentrations in short-retention-time rivers than in lakes (unless high river flows or high inorganic turbidity increase the stress on the macrophytes). Since phytoplankton concentrations never achieve high levels in short reten-

tion-time rivers, no positive feedback loop can develop to increase stress on macrophytes. This is consistent with the existence of vigorously growing macrophyte communities in rivers with relatively high P concentrations, compared to lakes. For example, in the River Frome (UK), strongly growing *Ranunculus* beds occur in areas where the SRP concentration is typically  $200 \mu\text{g P l}^{-1}$ . It is also consistent with observations made by Spink et al. (1993) who reported no visible algal growth in an experimental flowing system at  $40 \mu\text{g P l}^{-1}$ , a concentration of P that would result in significant planktonic algal growth in a lake. At  $200 \mu\text{g P l}^{-1}$ , Spink et al. (1993) reported significant reduction in the biomass of *Ranunculus* and *Potamogeton* in the same experimental facility to the benefit of filamentous algae, which showed a significant increase in biomass.

#### 4.5. Light limitation

Macrophytes have evolved a number of strategies which should increase the efficiency of their light interception and utilisation. A key strategy is the positioning of leaves higher into the water column (Fig. 1A), either through morphological plasticity within

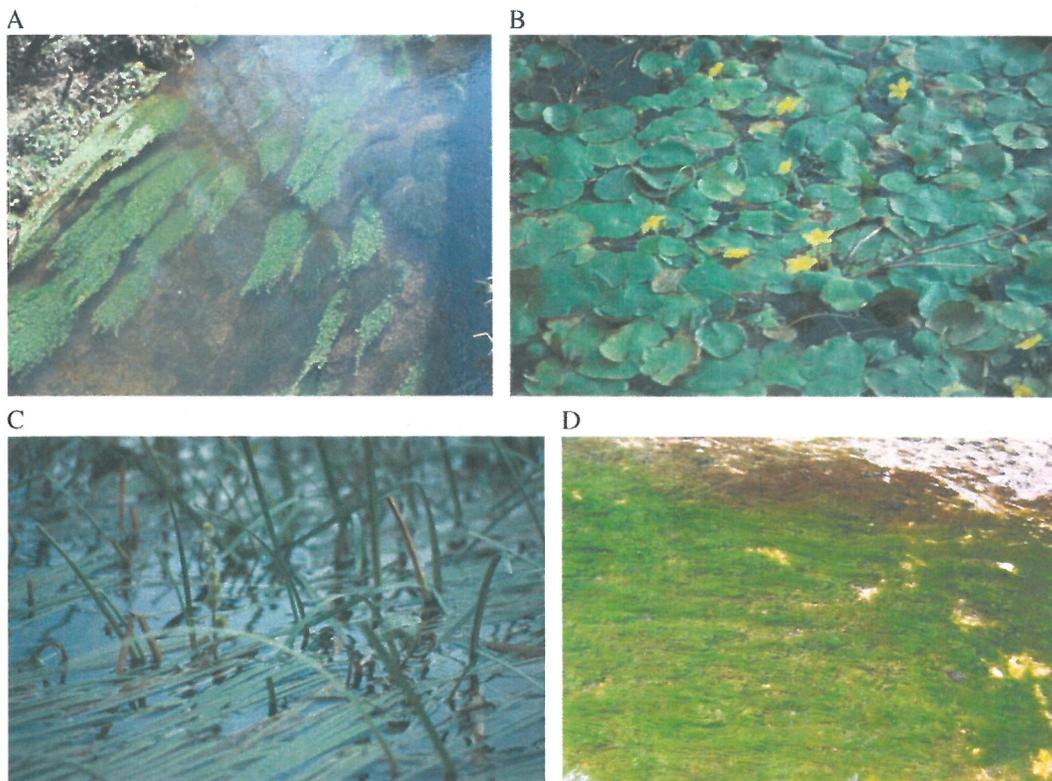


Fig. 1. Examples of the types of plants identified in the different stages of eutrophication in short-retention-time rivers. A). Tall submerged plants: *Callitriche stagnalis* and *Fontinalis antipyretica* B). Floating plants: *Nymphaeoides peltata* C). Emergent plants (mixed with tall submerged plants): *Sparganium emersum* D). Filamentous algae.

a species or by changes in species dominance (Wade et al., 1990). All submerged species are shade tolerant with known light saturation points ranging from 10% to 50% of full sun, whilst floating and emergent species are capable of using full sun irradiance (Spencer and Bowes, 1990). Plastic changes include increasing shoot elongation and changes in plant shape to increase their rate of intercepting light (Spencer and Bowes, 1990). Ultimately these intra-species morphological or community changes move towards dominance by floating-leaved plants (Fig. 1B) and eventually dominance by emergent plants with increasing eutrophication (Fig. 1C). However, this is only achieved at a significant cost in increased hydraulic drag resulting in increased vulnerability to damage by high water velocities.

A second strategy is efficient utilisation of light; a low light compensation point is beneficial in low light conditions. This stress-tolerant strategy may result in changes in species dominance with light regime (Brown et al., 1974). Finally, in the situation proposed here where epiphytic algae colonise the leaf surface, those macrophytes which grow faster than the rate of colonisation on the macrophyte leaves will have a better competitive edge than macrophytes which are slow growing. *Cladophora* (and other large, attached, filamentous algae (Fig. 1D)) is likely to benefit from this mechanism, since it has a relatively high growth rate. If the driver for change to more eutrophic conditions in short-retention-time rivers is light limitation, then plant communities in eutrophic waters would be likely to be dominated by plants which capture or utilise light efficiently, rather than a move to nutrient (P) tolerant plants per se. Since the evidence suggests that light limitation is brought about by epiphytic algal cover on the macrophyte leaves, light reception by the macrophyte will be influenced by the epiphyte film thickness. At least three processes could influence the thickness of epiphytic algal films on macrophytes: (1) self-shading, (2) sloughing (i.e. loss of the algal film due to turbulence at the leaf surface at high water velocities) and (3) grazing by invertebrates.

Self-shading of the epiphytes occurs when the film grows so thick that no light can get through to the bottom layer of epiphytes. They senesce and lose their adhesive properties, causing the epiphyte film to slough off and new algal films begin growing on the leaf. At this stage the macrophytes are severely light limited and are likely to struggle to take advantage of these short time windows (a few days each, since the epiphyte inoculum on the leaves is likely to be high at the start of epiphyte re-growth) of light availability.

At high water velocities, the epiphytic algae will experience significant hydrodynamic drag. Hence the

epiphytic film will tend to be pulled off the plant by the flow as the algal film thickens and the adhesion strength of the lower layers weakens. If this were an important process then, for the same nutrient concentrations in the water column, macrophytes in faster flowing waters would be likely to be subjected to less light limitation than slower flowing waters with a subsequent lower selection pressure on macrophyte communities for light efficient or fast growing species. However, Williams (1981) inferred that the flow reductions in and around plant stands were such that the sloughing effect would be considerably reduced compared to the same leaf in the open water. In addition, plant modifications to counter low light conditions tend to increase the hydraulic drag of the plant and reduce the water velocity where macrophytes are uprooted. As a result, sloughing of the biofilm (if any occurs) appears unlikely to benefit the macrophytes to any great extent.

The third factor limiting epiphyte film thickness is grazing by invertebrates. Work by Ledger and Hildrew (1998, 2000) showed that invertebrate grazing has a significant effect on the periphyton biomass. As a result, step reductions in the grazing invertebrate population, are likely to cause rapid increases in epiphytes and subsequent damage to macrophytes. This is consistent with observations that a spill of sheep dip into the River Derwent and its tributary the River Cocker, near Cockermonth (UK) in late April 1997, resulted in a major loss of the macrophyte community and its replacement with an extremely productive benthic algal mat (R. Prigg, personal communication). The sheep dip was not toxic to the macrophytes but was very toxic to grazing invertebrates. Other potential causes of macrophyte loss induced by loss of the macroinvertebrate grazers could be a synchronous emergence of adult insects from aquatic grazing larvae or a rapid increase in fish predation brought about by intensive fish stocking.

#### 4.6. Velocity

A factor which is not considered in lake eutrophication models is water velocity. In rivers, it is generally accepted as a major driver defining plant (including algae) distributions through the turbulence it develops, which imposes strong forces on plants and ultimately uproots or dislodges them. These disturbances are another way in which plant distributions can be altered, apart from the effects of eutrophication, and any model of eutrophication development must, ultimately, include the effects of flow as well as the those of increasing nutrients.

Based on Grime's theory of community succession (Grime, 1977), Briggs (1996) developed a conceptual model of macrophyte and periphyton succession in rivers. The resources were assumed to be light, nutrients (N, P, C) and temperature. The disturbances, which remove biomass, were described by three factors: temporal scale hydraulics (velocity instabilities caused by floods); spatial scale hydraulics (including local turbulence and bed sediment particle size) and (in specific areas) grazing. Petts (1996) later refined the flow related disturbances by setting them into the context of the hydrograph, suggesting that four flow descriptors relevant to habitat suitability were important: flood magnitude, flood duration, flood timing (through the growing season) and flood return period (frequency). On the basis of Grime's model, Briggs (1996) predicted that no plants would grow in rivers with a high frequency of flood flows, unstable bed sediments and high, interspace water velocities, but as the severity of the hydraulic conditions decreased, periphyton would dominate, followed by bryophytes, then, at the most stable conditions, macrophytes. This is consistent with observations at the national and international scales which identify two key factors influencing aquatic macrophyte species and community distributions: alkalinity (Westlake, 1969) and a measure of disturbance, often approximated by a combination of stream power (Dawson, 1988) and flood magnitude and frequency (Riis and Biggs, 2003). Hence, macrophytes can be removed and periphyton dominance established simply by the development of inhospitable flow (velocity) conditions, without the need to increase nutrient input (although the biomass is likely to be much smaller when the change is induced by flow).

#### 4.7. The interaction of nutrients, light limitation and water velocity

As outlined above, the major mechanisms by which macrophytes increase the efficiency of their light capture (e.g. increase leaf size, change shape, move leaves nearer the water surface, grow faster) usually result in a physical structure which has a much higher hydraulic drag. For example, rooted macrophytes with floating leaves are most common in slow flowing or margin conditions. Hence, the more a macrophyte tries to combat shortages of light, brought about by epiphyte film growth, the more vulnerable it becomes to severe damage by high water velocities. As a result it becomes important to understand the effects of light limitation and velocity, since the response of the river may be different at different combinations of light limitation and flow.

A number of general theories of species succession strategies have been developed. In the context of eutrophication in rivers, Grime's (1977) theory of species development appears to form a sensible framework within which to discuss the interaction of light limitation and hydrodynamic drag on macrophytes.

Grime proposed that plant communities move across a two dimensional continuum, with three end-members (Fig. 2). The 2D continuum is defined by two main stressors: (1) limitation of resources limiting growth (nutrients, light) and (2) removal of biomass by physical disturbance. He proposed that plant distributions would result from the adaptation of one of three strategies to combat different conditions resulting from combinations of the two stressors. He called these strategies: competitive, stress-tolerant and ruderal. Elliott et al. (1999) confirmed the validity of this theory for predicting the species succession of phytoplankton in a lake.

In the case of the development of eutrophic conditions in short-retention-time rivers, resulting in changes in community and ultimately loss of macrophytes, the biomass removal mechanism would be high drag stress/uprooting on the plants induced at high water velocity and the growth limiting resource for macrophytes would be light limitation (by epiphytic algae), i.e. high stress occurs at low light levels. The measure of physical disturbance would probably be represented by one of Petts' (1996) flow descriptors or a combination of all of them. In our case, the growth limitation stressor, light, could also be represented by an inverted nutrient scale, where high stress occurs at high nutrient concentrations; this is the inverse of the normal situation in terrestrial and river systems where the shortage of nutrients causes the stress.

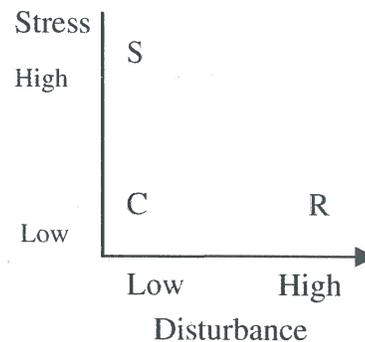


Fig. 2. The stress disturbance space hypothesised by Grime (1977). C = competitive, i.e. low resource stress, low disturbance; S = stress tolerant, i.e. high resource stress, low disturbance; R = ruderal plants, i.e. low resource stress, high disturbance environments. No plants survive in high resource stress-high disturbance environments.

Simple application of Grime's hypothesis would then suggest that under low flow and high light conditions, plant growth would be limited only by inter- and intra-species competition for resources with little biomass loss by physical damage. Conversely, at high flows, physical damage would be high and ultimately, no macrophytes could survive and periphytic algae would dominate. On the vertical axis, as light limitation increases, macrophytes adapt and become more susceptible to damage by high flows. The implication is that at the same level of light limitation, the condition of the river will always be worse at higher levels of physical damage (higher flows, however defined) than at lower physical damage levels: the higher the level of physical disturbance, the more foreshortened the pattern of change from macrophytes to benthic algae becomes. Macrophyte species richness frequency is known to decrease with the frequency of flood disturbance (Riis and Biggs, 2003). Wilby et al. (1998) reported a negative correlation between the frequency of large, day-to-day increases in flow and the percentage cover of macrophytes (*Callitriche* spp., *B. erecta* and *Ranunculus* spp.) although they suggested that this was the result of scour losses alone during the rising limb of the hydrograph, rather than a joint effect with eutrophication. However, Ham et al. (1981) pointed out that things are slightly more complicated than this. In the River Lambourn, macrophyte biomass increased with increasing mean discharge in March whereas, in the River Wye, Brooker et al. (1978) had shown a decrease in macrophyte growth with increasing flow. This apparent dichotomy can be resolved if we consider the type of river, and hence the flood frequency. The Wye has a hard rock catchment with a relatively low base-flow index so that the flow is relatively flashy. Hence a high summer flow indicates a large number of storm events creating high turbulence with a short return period, i.e. a short time period between high flows, and a resulting negative effect on macrophyte growth. Conversely, the Lambourn is a groundwater fed river with a high base-flow index. Flow changes are relatively slow and a high mean March flow will be indicative of a high summer flow, but with few high turbulence peaks. In addition, the measurement site on the Lambourn has a sewage treatment discharging into it upstream, which is the major source of P at the site (Ham et al., 1981). The high summer flow will dilute the P concentration so that less epiphytic algae grow, reducing light competition and allowing the macrophytes to grow more quickly. The result is a positive relationship with flow.

## 5. The conceptual model for the development of eutrophic conditions in short-retention-time rivers

On the basis of a comparison with lake systems and the behaviour of some of the other factors considered above, it is possible to propose a conceptual model of the development of eutrophic conditions in rivers, particularly short-retention-time rivers, which can explain most of the observed features. The key features are:

- 1) Long retention-time rivers respond differently to short retention-time rivers when exposed to excess nutrients. The former move to dominance by phytoplankton, whereas the latter tend to dominance by benthic and periphytic algae.
- 2) In short retention-time rivers macrophyte growth becomes limited by light as a result of epiphytic algal growth rather than by nutrients.
- 3) Because macrophyte growth is limited by light, a succession of macrophyte species from plants with submerged leaves, through plants with leaves in the upper water column, plants with floating leaves to emergent plants would be expected as the river becomes more eutrophic. However, this sequence might be modified by the flow conditions in the river.
- 4) In eutrophic/hypereutrophic short retention-time rivers, macrophytes will have a heavy coating of epiphytic algae. As the macrophytes die out they will be replaced by strong growths of filamentous algae which will eventually be replaced by benthic algae.
- 5) The median SRP concentration is likely to be a better predictor of trophic status in short retention-time rivers than the total P load.
- 6) The SRP concentrations at which the eutrophic/hypereutrophic boundary lies is much higher in short retention-time rivers than in lakes.
- 7) For a given relatively high average flow in a short retention-time river with high SRP load, repeated pulse high flows are likely to reduce macrophyte growth whilst a continuous flow with the same average flow rate is likely to increase macrophyte growth, compared to low flows.
- 8) Because of the effect of epiphytic algae on the light climate to macrophytes, rapid changes in grazing invertebrates are likely to result in a major change to the health of the macrophytes.

The interactions involved in this model, excluding the effects of biomass destruction by high flows, are represented in Fig. 3. The resulting predicted succession

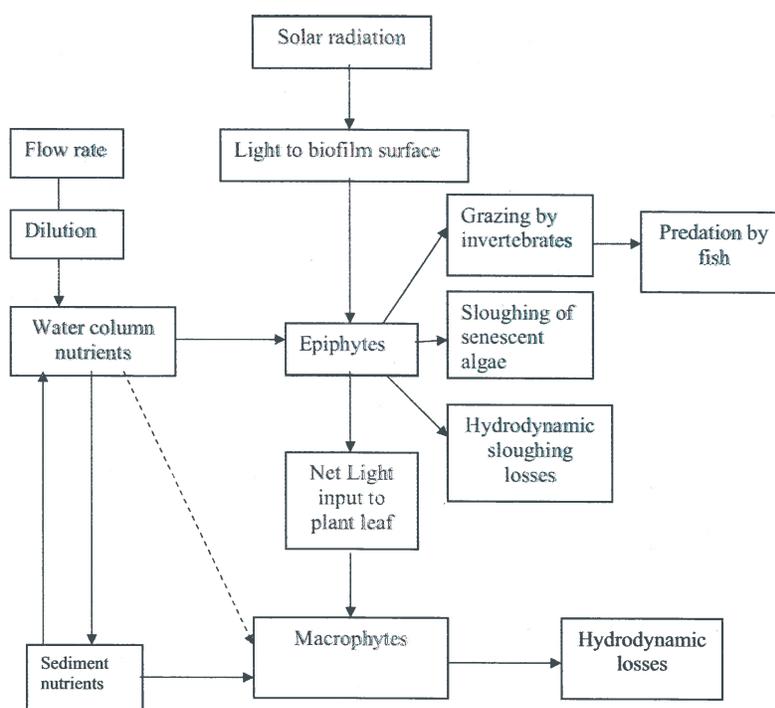


Fig. 3. A schematic diagram of the mechanism of eutrophication development in rivers.

of effects can be represented diagrammatically by Fig. 4 where the  $x$ -axis, represented in arbitrary units of increasing phosphorus concentration, is equivalent to the situation close to the  $Y$  axis on Grime's plot (Fig. 2) with low disturbance stress. On the basis of this model the following stages of development of eutrophication in short retention-time rivers could be envisaged.

### 5.1. Low nutrient concentrations

In short-retention-time rivers with low nutrient concentrations, macrophytes tend to dominate in the slower flowing reaches and haptophytes tend to dominate in the faster flowing, mainly upland reaches (Briggs, 1996). For plants rooted in muddy sediments, much of the nutrient utilised by the plant is likely to be taken up via the sediment, where nutrients are often concentrated, compared to the water column (Carignan, 1982). In plants that are simply anchored on stones, most of the uptake is likely to occur through the leaves. At these low nutrient concentrations, slow growing, nutrient efficient plants are likely to dominate. Plants that can rapidly switch on the ability to take up nutrients through the leaves, even though their main source of nutrients may be from the sediment, are likely to gain an ecological advantage and dominate macrophyte communities.

### 5.2. Low-medium nutrient concentrations

Macrophytes increase sedimentation locally in rivers resulting in carbon, nitrogen and phosphorus rich sediments around the plant base (Chambers et al., 1992; Sand-Jensen, 1998) and significant amounts of any dissolved nutrient in the water column, particularly phosphorus, are likely to be rapidly adsorbed by the sediment (House and Denison, 2002). Nutrient mass balance studies on the downstream sections of the River Frome and River Swale (UK) have shown bed-sediment uptake rates of SRP from the water column of 83 and 53  $\mu\text{mol P m}^{-2} \text{h}^{-1}$  respectively, during summer low-flow conditions (Bowes and House, 2001; Bowes et al., 2005a,b). Up to 80% of the total phosphorus entering the lower River Frome during summer low-flows was retained within the river channel, due to deposition of particulate-bound phosphorus, the adsorption of dissolved P to the bed sediments and, to a lesser extent, bioaccumulation into plants and algae. The resulting phosphorus-rich sediment deposits will encourage colonisation by rooted plants that obtain most of their nutrient via the roots. They will become dominant and develop increasing amounts of biomass as the nutrient in the sediment increases. Recent work suggests that much of the nitrogen taken up will be recycled many times, via processes in the sediment

(Trimmer, personal communication). At these low to medium nutrient loads, concentrations of available nutrient in the water column are likely to remain low because of the efficient uptake by sediments, so that epiphytic algae, which obtain most of their nutrients (but not all) from the water column, are likely to be limited. Alternatively, benthic algae are likely to begin to develop a significant biomass by utilising the sedimentary pool of nutrients.

### 5.3. Medium to high nutrient concentrations

As the flux of phosphorus to a site increases, there will become a point (a gradual change, rather than a step change) where the sediments become “saturated” with nutrients, particularly phosphorus, since the Equilibrium Phosphorus Concentration ( $EPC_0$ ) of the sediments, i.e. the concentration of phosphorus in water in contact with sediment (or particles) above which sorption onto solids takes place and below which desorption of particulate P occurs (House and Denison, 2000, 2002; Taylor and Kunishi, 1971), will become greater than the water column P concentration. At this point, sorption to the sediments will stop, allowing any dissolved P to remain in solution, resulting in an observed rise in phosphorus concentrations in the water. At this point, it is also likely that the macrophytes will no longer be nutrient limited and so will be unable to take advantage of any additional available nutrient in the water column. Possibly self-shading or competition will become the limiting factor, which has not been considered in the model presented here. Conversely, epiphytic algae will benefit from the available nutrient in the water column, which is their main source of nutrient. The epiphytic algae will begin to colonise leaf surfaces and develop significant biomass, probably to levels that are visible to observers. By covering the macrophyte leaves the algae will, in effect, “steal” light from the macrophytes and shade them out at increasing rates as the epiphyte film thickens. At this concentration of phosphorus, P is probably no longer limiting and an increase in available P results in no apparent increase in epiphyte biomass which is consistent with experiments reported by Scrimgeour and Chambers (1997) and Bowes (unpublished). In response, macrophytes (species and/or individuals) will use a number of strategies to maximise light capture and/or utilisation to continue growing. Macrophytes that can grow in low light conditions will have an advantage, as will macrophytes that can maintain their access to light by rapid growth, growing faster than the epiphytes can colonise and cover the leaves. *Cladophora* is likely to have a major advantage under these circumstances and would be expected to gain

dominance at high dissolved phosphorus concentrations. *Cladophora* obtains its nutrients direct from the water column and so could not grow well in lower nutrient conditions, but grows quickly under high P concentrations, competing effectively with the epiphyte growth. Hence, under these conditions light, rather than phosphorus (or other nutrients), is likely to be the factor limiting macrophyte growth and the higher plant communities will become dominated by macrophytes which can either grow at low light levels in the water or at sufficiently high rates that they can outgrow the epiphytes. This would, presumably, result in a move towards dominance by emergent species in areas where the flow is sufficiently low. As the epiphyte cover increases, macrophytes find it increasingly difficult to capture the light they need to grow. Eventually, a stage will be reached where the macrophyte community cannot counteract the light loss brought about by the epiphytes and macrophyte biomass will crash. At slightly higher nutrient concentrations, rapidly-growing, attached, filamentous algae such as *Cladophora*, will no longer be able to compete and the system will become dominated by thick growths of benthic algae alone. From the discussions above, it would appear that as the disturbance stress increases, the sequence of events shown in Fig. 4 would be compressed towards lower nutrient concentrations, in particular the nutrient concentrations at which complete macrophyte loss occurs and benthic algae become dominant.

Recalling from the Introduction that the boundaries between different trophic levels are subjective, Fig. 4 allows us to describe the observable features of four levels of eutrophication which have meaning for short-retention-time rivers.

1. Healthy stands of macrophytes, dominated by submerged species (oligotrophic)
2. Healthy macrophyte stands with an increasing relative abundance of light efficient and/or near-surface or floating-leaved and emergent plants with slight occurrence of epiphytic algal cover on the leaves and some benthic algae visible (mesotrophic)
3. Macrophytes appear to be under severe stress with increasingly heavy epiphyte cover. Dominance by near surface or floating-leaved and emergent plants. Significant benthic algal cover (eutrophic)
4. Very sparse or no macrophyte stands leaving heavy *Cladophora* and/or benthic algal cover (hyper-eutrophic)

These visual markers will occur at different nutrient concentrations in rivers with different flow characteristics. A repeat, in rivers, of the type of study carried out by

Vollenweider for lakes would allow these boundaries to be transcribed into specific nutrient concentrations suitable for use as the class boundaries for WFD classifications.

Figs. 3 and 4 highlight the wide range of factors and interactions involved in the development of eutrophic conditions in short-retention-time rivers. This complexity may well be the reason why the literature, as reviewed by Carr and Chambers (1998), is so ambivalent about the importance of nutrients, particularly phosphorus, as the factor limiting macrophyte growth in rivers. Since epiphytic algae appear to be such important players in the degradation of eutrophic rivers, measurement of their density per unit surface area of macrophyte may well be a useful parameter to monitor in order to assess the rate of change in eutrophic status in short-retention-time rivers.

### 6. Consequences for remediation

If this mechanism for the development of eutrophication in rivers is correct, then a number of consequences ensue. Any remedial management of eutrophic and hyper-eutrophic rivers will aim to return the river to macrophyte dominance. On the basis of the hypothesis outlined in this

paper it is likely that, in many lowland British rivers, light rather than P is the main factor limiting growth, since the phosphorus concentrations are relatively high. The appropriate management approach would still be to limit phosphorus inputs since the excessive growths of epiphytes result from excessive inputs of nutrients, particularly P. However, it is highly likely that the initial stages of P removal will not show any observable effects, because the P concentrations are so high that P is not limiting. Continued reductions in P concentrations will eventually bring them into the range where they begin to be limiting. At this stage, further reductions in phosphorus load would reduce the epiphytic biofilm on the plants, which may not be easily observed by non-specialists and even more P must be removed before a positive effect on the macrophytes will be observable. As a result, it is likely that in severely eutrophic rivers, the removal of phosphorus from a large number of sources may be required before the macrophytes are seen to begin to recover.

Macrophytes in enriched systems tend to develop shallow roots. As a result, they are more easily pulled out of the sediment by high flows (Mainstone et al., 1996), removing the rootstock from which any macrophytes

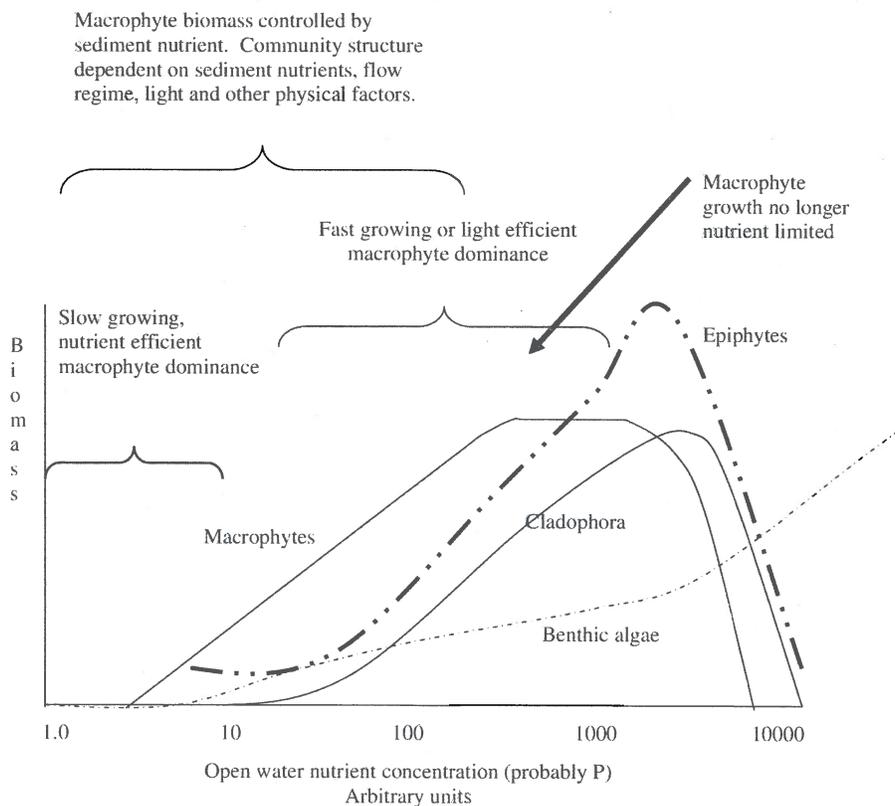


Fig. 4. The relationship between the concentration of a limiting nutrient in a river and the effect on the biomass of different plant types.

might regenerate when sympathetic growing conditions are returned. Because of this interaction between eutrophication and flow, replanting schemes may be required for some plants to recover their stocks.

Our earlier discussion on the efficacy of load as a predictor of trophic status in short retention-time rivers can be extended to consider the effect of the hypotheses presented here on remediation strategies. It is now well accepted (Haygarth and Jarvis, 1997; Sharpley and Smith, 1989; Gerdes and Kunst, 1998; Reynolds and Davies, 2001) that a significant part of the phosphorus from diffuse agricultural sources is in particulate forms that are not immediately available to plants without changes in chemical form. Data for the River Swale (Bowes et al., 2003) suggest that 20% of the total P load is present as SRP at a site unaffected by sewage treatment discharges, whereas data for the River Thames (Cooper et al., 2002) suggest a value nearer 50%. It is clear that this proportion is highly variable between rivers and through the year. Since Haygarth et al. (2005) showed that the proportion of SRP in agricultural land run-off varied through the year with a higher proportion of SRP in spring, we will use the higher, 50% SRP value for the rest of this discussion. Conversely, a significant proportion of point-source sewage treatment works (STW) effluent P is in the form of soluble reactive P (Mainstone and Parr, 2002; Jarvie et al., 2002; Gerdes and Kunst, 1998). Cooper et al. (2002) presented data which indicated that 96% (standard deviation=1.4%) of the phosphorus in sewage treatment works effluent discharging to the River Thames was in the form of soluble reactive P (SRP). However, some of this SRP rapidly reacts with particulate material in the river (Bowes and House, 2001) and data for the River Frome (Bowes, unpublished) suggest that the proportion of SRP in the river settles down to about 80% of the total P load within a short distance downstream from the effluent discharge. If we take an example catchment where the contribution to the total P load is 50% from point source sewage treatment works and 50% from agricultural diffuse pollution and apply the ratios of percentage growing season load and percentage bioavailable P then, during the growing season, (25% × 50% =) 12.5% of the diffuse pollution is likely to be effective whereas (57% × 80% =) 45.6% of the sewage treatment effluent is effective. As a result, a much greater emphasis on the removal of phosphorus from point sources, rather than the current efforts to target STW and farms equally, is likely to be a much more cost effective route for controlling eutrophication in short retention-time rivers (Mainstone and Parr, 2002; Jarvie et al., in press). However, when initial remediation work has brought eutrophication levels back

to low to mid levels and biodiversity of macrophyte communities becomes the driver then reduction of diffuse sources of pollution may well become important.

Finally it is not clear what effect nutrients stored in the sediment will have on recovery. Obviously, if the enriched sediments are washed out in the autumn and winter storm flows, then the memory will be very limited, but if significant amounts of sediment remain, they may increase the water column P concentrations particularly during the growing season (House and Warwick, 1998; Mainstone and Parr, 2002; Jarvie et al., 2005b). However, it is not clear at this stage whether the resulting water column P concentrations will be sufficiently high that damaging amounts of epiphytic algal films will be developed.

## 7. Conclusions and recommendations

A hypothesis of the development of eutrophic conditions in rivers has been developed, based on mechanisms known to be important in lakes but modified by additional processes known to be important in rivers. The proposed model is consistent with a number of observations in eutrophic rivers. In addition, the model predicts a number of effects which should be tested by experiment and field observation to add further weight to the arguments in favour (or otherwise) of this proposed model. The predictions include:

1. The lower reaches of long rivers, slow flowing impounded rivers and rivers downstream of lakes should move towards phytoplankton domination in nutrient-enriched conditions whereas short-retention-time rivers will tend towards dominance by benthic algae.
2. The median concentrations of bio-available dissolved nutrients are likely to be a more useful predictor of the trophic status of rivers than nutrient load, particularly at those trophic levels where management intervention to reduce the trophic status is being considered (i.e. benthic algal dominance).
3. A large number of interacting processes involving several biotic and physical factors are involved in the development of eutrophication in short-retention-time rivers. As a result the system is complex.
4. The key factor in the degradation and eventual loss of macrophyte communities is the development of epiphytic algal communities which reduce the amount of light reaching the macrophyte.
5. In eutrophic and hyper-eutrophic systems, nutrients, particularly phosphorus, are drivers of the system, forcing light limitation, but seldom become limiting in their own right.

6. In low to medium productivity systems, nutrients may well limit macrophyte growth.
7. Macrophytes which survive best in eutrophic conditions in short-retention-time rivers are likely to be those which either grow very rapidly or can grow best at low light levels.
8. Rivers that are subjected to frequent, high pulse flows of long duration during the growing season are likely to show the undesirable effects of eutrophication at lower nutrient concentrations than rivers which are not subject to additional high velocity stresses.
9. Qualitative descriptors of different trophic levels in rivers can be based on the succession of plants described by the model. Oligotrophic — strong macrophyte stands with a good representation by submerged plants; Mesotrophic — evidence of slight epiphyte cover and the appearance of benthic algae; Eutrophic — increasingly heavy epiphyte cover with dominance by floating-leaved and emergent plants; Hyper-eutrophic — collapse of macrophyte stands leaving heavy attached filamentous and/or benthic algal cover.
10. The biomass of epiphytic algae per unit area of macrophyte may be a useful parameter for monitoring the trophic status in short-retention-time rivers.
11. An immediate response to P reductions may not be observable in many British lowland rivers because P concentrations are so high. Many sources may need to be reduced before any beneficial effect on the macrophytes is seen.

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