

**PROCESSES CONTROLLING THE QUANTITIES OF BIOGENIC MATERIALS  
IN LAKES AND RESERVOIRS SUBJECT TO CULTURAL EUTROPHICATION**

by

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**ABSTRACT**

The processes which control the growth, composition, succession and loss from suspension of phytoplankton algae are briefly reviewed, with special reference to function in eutrophic reservoir systems. The ecology of larger algal biomasses supported by high nutrient loading rates are more likely to be subject to physical (wash-out, underwater light penetration, thermal stability and mixing) than to chemical constraints. Sudden changes in the interactions between physical factors temporarily impair the growth of dominant algal species, and advance the succession. Certain algae may be cropped heavily, but selectively, by zooplankton feeding, but they are rarely the species which cause problems in waterworks practice. Grazing, however, does influence succession. A deeper understanding of the operation of loss control mechanism is urgently required. Potentially, manipulation of the physical environment provides an important means of alleviating day-to-day algal problems in eutrophic reservoirs; in terms of cost effectiveness these may prove to be more attractive than reducing nutrient loads at source.

**INTRODUCTION**

The rapid eutrophication of lakes has been a major preoccupation of limnological research for more than a decade. A large literature is now available, perhaps numbering 2000 separate titles, which includes several excellent reviews (Lund 1972, 1978a; Rohlich 1969; Rossolimo 1971; Porter 1975). Undoubtedly, a much clearer appreciation of the fundamental causes and consequences of the problem now exists. In essence, an increase in specific nutrient loading rate upon a given hydrological system frequently stimulates primary production in the open water, enabling a larger average biomass of phytoplankton to be maintained. In turn, this can promote production by consumer and decomposer species, and alter the relative status of macrophyte communities. Many of these changes are considered undesirable: apart from recreational and amenity losses, they add significantly to treatment costs in the water supply industry. Not surprisingly, there are strong popular and economic incentives to reducing phytoplankton production in lakes and reservoirs.

Do we yet have the knowledge required to alleviate the effects of eutrophication? The answer is a qualified "yes". Research has shown that in a wide range of the world's temperate freshwaters, phytoplankton production is limited by phosphorus availability. The only natural source of phosphorus in a lake is its hydrological catchment. If the natural supply is augmented by domestic, industrial or agricultural effluents, all of which are relatively rich in biologically active phosphates, then phytoplankton production will inevitably be stimulated. Indeed, direct relationships between phytoplankton biomass (variously expressed as annual or seasonal mean or maximal chlorophyll concentration) and the availability of phosphorus (expressed as mean or maximal concentrations of total – or dissolved reactive – P) have been resolved quantitatively (eg Sakamoto 1966, Vollenweider 1968, Lund 1970, Dillon and Rigler 1974; for other references see Nicholls and Dillon 1978). Considerable variation in empirical evaluation among these models can be attributed to sampling differences, and variation in the chlorophyll content of the dominant algae (Nicholls and Dillon 1978). To a greater or

lesser extent, the potential algal response is modified by basin morphometry, latitude and local climate, and by their mutual interaction in controlling flushing rate, hydraulic recharge and water column stability. Quantitative allowance for these "morphoedaphic" factors is incorporated in some recent versions of the phosphorus—chlorophyll relationship (eg Oglesby 1977). These models are easily applied to predict the approximate levels of algal biomass (the confidence intervals cover almost one order of magnitude) that could be maintained in response to increased nutrient loadings, or in new impoundments of waters of ascertained chemical composition. Cases have been advanced for the reduction of phosphorus at point source as a means of achieving smaller average phytoplankton populations (eg Alexander 1978; Dillon et al. 1978). The spectacular recovery of Lake Washington (Edmondson 1972) after diversion of all main sewage outfalls is a testimony to the success of such schemes. Other experimental or pilot schemes in recent years (see Dillon et al. 1978; Forsberg et al. 1978 for references) have resulted in algal biomass reductions to a greater or lesser extent.

Of course, phosphorus is not the only factor known to control phytoplankton abundance. Numerous instances of limitation by nitrogen, especially in phosphorus-rich lakes (eg Lund 1970, 1978a; Toerien et al. 1975; Reynolds 1976a), iron (Lund, Jaworski and Bucka 1971), trace elements (Goldman, 1972) and organic chelators (Box 1977) have been reported in the literature. In these lakes, enrichment with respect to phosphorus will not necessarily result in higher standing crops. Moreover, many lakes, including some storage reservoirs, are so enriched that chemical limitation may not occur before the biomass has already reached intolerable levels, if at all. Nevertheless, nutrient stripping at point sources, or reduction in the original effluents may still be advocated: in accord with Liebig's "Law of the Minimum", the reduction would reimpose the chemical constraint (or impose a new one) upon algal production in the water body. In more fertile waters, nutrient removal would need to be almost complete to achieve the desired effect (Reynolds 1978a).

The qualification is two-fold. The first is whether such schemes can be justified. They are, in any event, extremely expensive, or they may exact a high price in social and industrial convenience or in agricultural efficiency. The limnologist can offer constructive advice to the relevant authorities, but implementation depends upon economic factors, compounded by popular attitudes. Ultimately, the issue may be resolved as a question: "what sort of lake are we prepared to accept?" And if we accept that some lakes and reservoirs should remain eutrophic, are we able to devise ways of minimising algal problems?

This brings us to the second qualification: that whereas limnology may have reached a point where the causes and effects of eutrophication can be conveniently summarised, the fundamental biology of planktonic algae is not so clearly understood that it can be invoked to predict and avert algal problems on a day-to-day basis. This inability is particularly frustrating to engineers in the water industry. Frequently their difficulties are caused by specific algal populations over relatively short periods of time. Moreover, the problems are as often related to the qualitative composition of the phytoplankton as to quantity alone.

In acknowledging these difficulties, this paper attempts to identify the factors which control phytoplankton growth in eutrophic waters. Areas for profitable research are also indicated, particularly where they are directly applicable to management needs. Special reference is made to past and present work carried out by the Freshwater Biological Association towards meeting those needs. The opinions expressed are personal, and are not necessarily shared by the FBA or its other employees.

## MECHANISMS CONTROLLING PHYTOPLANKTON GROWTH

The environmental factors which govern autotrophic production in lakes can be conveniently reduced to light, temperature and nutrient availability. The intensity, duration and underwater attenuation of solar radiation interact with temperature in controlling net photosynthetic productivity. The availability of nutrients determines the extent to which photosynthetic potential is translated into new cell material. Both processes are profoundly modified by the effects of water movements and column stability. In optically-deep lakes, net production is frequently limited by light when the water column is fully mixed. After stratification, nutrient availability may become the prominent controlling agent, even in many eutrophic lakes (Reynolds 1976a). If nutrients are more freely available, production may continue to the upper photic limit (Ganf 1974; Talling et al 1973).

Planktonic photosynthesis is well-documented (for major reviews, see Talling 1971; Harris 1978). Some classical studies have produced a series of useful conceptual and empirical models describing (*inter alia*) the areal and temporal integration of photosynthetic rate with respect to attenuation (Talling 1957, Vollenweider 1965, Patten 1968, Fee 1969), the depth of isothermal mixing (Talling 1971) and the upper light-limited maximum biomass (Steeman-Nielsen 1962, Steel 1973). These models have been constructed from observations on natural populations exposed in closed bottles to defined photic conditions. Experience has shown that they can provide reasonable predictions of photosynthetic production in other lakes of known optical properties.

Although good correlations between measured rates of photosynthesis and cell division have been obtained (Talling 1955), extrapolation of net growth from primary production estimates is not always reliable (Jassby and Goldman 1974). Models developed to predict the maximum light-limited standing crop (Talling 1955, Steel 1972, 1975) are more generally applicable to gauging the highest algal biomass likely to be encountered in eutrophic lakes. As an example, I (Reynolds 1978a) applied Steel's (1972) model to field measurements made in a small, naturally eutrophic lake (Croze Mere, England) to determine the size limit on vernal diatom maxima. The predicted values (100–130 mg chlorophyll  $a\ m^{-3}$ ) had been approached in several previous years. I used this result to support the view that further nutrient enrichment would be unlikely to increase vernal crops significantly. Re-examination of the data (in Reynolds 1978b) reveals another important deduction. Steel's model is particularly sensitive to the values ascribed to components quantifying the ratio  $I'_0/I_k$  (where  $I'_0$  and  $I_k$  are respectively, the irradiances obtaining immediately beneath the water surface and at the depth coinciding with the onset of light-saturated photosynthetic rates) and  $r$  ( $= R/P$ , the relative respiration coefficient, where  $P$  is the maximum photosynthetic rate and  $R$  is the dark respiration rate). If optimal values are interpolated, a rather higher standing crop (200–240 mg chlorophyll  $a\ m^{-3}$ ) can be predicted. A similar result is obtained by extrapolation from Talling's (1971, Figure 12) representation of the limiting mixed depth: euphotic depth ratio for given daily incident radiation values, and the increment in light extinction per unit of chlorophyll  $a$ . In 1968, Croze Mere did produce a vernal maximum of this magnitude (196 mg chlorophyll  $a\ m^{-3}$ ; Reynolds 1973a). The question arises why it should not have done so in other recent years. Losses through sinking, grazing and parasitism do not explain the shortfall. Major nutrients (silica, phosphorous and nitrogen) are not normally limiting either, and there was no significant difference in their availability during the growth phase in 1968. Moreover, both models permit much higher hypothetical standing crops to be maintained during the winter, well before net annual growth commences. If the models are substantially correct, then the observations demand that the values of the interpolated factors alter over the period prior to and during growth, and after the maximum has been achieved. The ratio  $I'_0/I_k$  varies during the time course of a day, due to changes in incident radiation. In addition,  $I_k$  and  $r$  are to some extent subject to physiological regulation by the algae in question. This raises the possibility that the physiological responses of the phytoplankton to the environmental conditions integrated over the mixed water column as a whole are more complex than is commonly supposed.

In a series of papers Harris and his co-workers describe manipulations of natural phytoplankton populations from differing environments which produced varied rates of photo-inhibition and recovery (Harris 1973, Harris and Piccinin 1977, Harris et al. 1979). Part of the variation is attributable to surface irradiance levels; but inhibition was most rapid in diatom populations taken from deep isothermally mixed layers, and least in *Ceratium* collected from near the surface in a stably stratified system. Harris (1978) argues that fluctuations in photosynthetic production are most likely to occur in water columns in which the vertical distribution of algal populations is constantly modified by turbulence. The adaptability of algae to changing environmental conditions, upon which their survival depends, includes both short-term metabolic controls of carbon utilisation and longer-term (in the order of cell generation time) responses (eg of cell pigment content: cf. Nicholls and Dillon 1978). Both kinds of response are important in two ways. In field determinations of photosynthesis, cells taken from mixed layers and enclosed in bottles at a fixed depth for 2 to 4 hours may yield appreciably different photosynthesis rates. Recent attempts to overcome this problem (eg Jewson and Wood 1975, Harris and Piccinin 1977, Marra, 1978) have resulted in higher estimates of net column photosynthesis. On the other hand, Jewson and Wood (1975) have demonstrated the depression in net rates arising when cells are artificially circulated beyond the limits of the euphotic zone. These arguments can be extended to predict the second point, at least in general terms: that an abrupt change in the depth of mixing is likely to reduce net photosynthetic production, at least until the algae have adapted adequately to the new conditions. There is obviously a case for further studies of photosynthetic production under conditions similar to those experienced by natural populations in mixed water columns, and for these to be related to net growth of the populations. In particular, the impact upon production of fluctuations in the vertical extent of mixing requires closer definition, since these may control the size and timing of maxima in waters not subject to nutrient limitation.

That growth of the population can continue to limits imposed by the underwater light climate, provided that nutrients are freely available, suggests that biomass is not ultimately constrained by the photosynthetic capacity of individual cells. In soft waters, however, the generation of high pH as a direct result of photosynthetic uptake of carbon dioxide imposes some rate limitation of photosynthesis, and hence limit population size below the theoretical light-limited maximum (Reynolds and Butterwick 1979). This may be because cells become starved of carbon, as shown experimentally by Talling (1976); although Lehman et al (1975) have shown that in the majority of natural lakes, invasion of atmospheric carbon dioxide into the surface mixed layer will normally offset this possibility. Alternatively, the high pH may not be acceptable to the dominant algae, which enhance their loss rates accordingly (eg through accelerated sinking velocities or the production of resting stages; but see later).

Except in the most eutrophic lakes, however, epilimnetic nutrient depletion sooner or later inhibits the increase in algal biomass (though not necessarily specific production rates: see above). Subject to limitations discussed earlier (Section 1), mean chlorophyll levels are correlated well with nutrient availability, especially of phosphorus. Specific effects of nutrient limitation vary among the algal groups: silica deficiency may well result in the mass death of actively-growing *Asterionella* populations, since dividing cells are unable to construct new frustules (Lund 1950); phosphorus deficiency impairs the buoyancy regulation mechanism in *Anabaena*, with the result that populations remain preferentially within the epilimnetic circulation (Reynolds 1972, 1976b). In many instances, ensuing loss of biomass detracts from the concept of "mean chlorophyll" which is compensated by the size of maxima. Indeed, it is the size of the maxima which is constrained by nutrient availability. I have argued elsewhere (Reynolds 1978a) that the efficiency of nutrient utilisation is reduced in progressively larger maxima; the poorer is the nutrient status of a lake, then the greater is its relative sensitivity to mild increases in nutrient availability. Conversely, the occurrence of algal maxima in only moderately eutrophic reservoirs may occasionally present water treatment problems equal to those which occur (albeit more frequently) in richer ones.

From the management point of view, it is useful to predict the scale of specific algal maxima before they occur. Within the period of a single season this is best achieved through frequent monitoring of phytoplankton population changes through the season, in relation to the nutrient capacity of the water for sustaining biomass increase. In the longer term, fundamental planning may depend upon forecasts of future loading trends in relation to the sources of raw water available, especially if transfers between one river catchment and another are contemplated; this is a field in which water engineers in the Soviet Union have considerable experience. Both sorts of prediction can be greatly enhanced by the technique of algal bioassay of reservoir water (for a fuller discussion, see Lund 1978a, Skulberg 1975). Such procedures serve principally to identify elements which control growth of test-organisms under laboratory conditions (eg Lund et al 1971, Lund, Jaworski and Butterwick 1975). Difficulties are sometimes encountered in the interpretation of results, which do not necessarily apply simultaneously to all species of algae represented in the plankton. Modifications to the growth medium, during both the preparation and execution of the assays, may also give misleading results (Reynolds and Butterwick 1979). When carried out in conjunction with a monitoring programme, however, bioassay constitutes a useful addition to the techniques employed in waterworks practice.

#### MECHANISMS CONTROLLING PHYTOPLANKTON QUALITY

Much of the literature on eutrophication has been directed towards the quantitative responses of the phytoplankton as a whole. There are certain instances in which the same algal species remained the prominent member of the phytoplankton throughout an extended period of known cultural eutrophication (eg *Oscillatoria agardhii* Gomont in Lake Washington: but see Edmondson 1972). However, clear differences in the species composition, diversity and dominance between lakes of different trophic status have long been apparent (Pearsall 1932, Rawson 1956, Gorham et al. 1974). There is considerable palaeolimnological evidence that major shifts in species dominance have occurred in response to changes in fertility (Pennington 1943). Important recent changes in species composition have been observed by Lund in Esthwaite Water (Lund 1973) and Blelham Tarn (Lund 1978b). As these lakes have become enriched by sewage and agricultural run-off some species of algae have become relatively more numerous (*Asterionella*, *Ceratium*) while others declined (*Oscillatoria*, *Dinobryon*, *Tabellaria*). Other species appeared for the first time during this period and are now prominent in the annual succession: *Stephanodiscus*, *Aphanizomenon*, *Anabaena* and *Microcystis*. The advent of bloom forming genera of prokaryotic blue-green algae (or Cyanobacteria) in lakes subject to cultural eutrophication has aroused concern throughout the developed world (Topachevskiy 1968, Fogg 1969, Reynolds and Walsby 1975).

Such "qualitative responses" to eutrophication (Reynolds 1978a) are often of greater practical consequence than abundance alone: certain planktonic diatom species are notorious amongst water engineers for their filter-clogging properties; blue-green algal blooms are generally more objectionable in fisheries and recreational waters, even when the biomass of offending organisms is actually small (Reynolds and Walsby 1975). It would be of considerable advantage to understand the biological characteristics of these organisms which enable them to flourish under certain conditions: the practical benefits arising from this knowledge would contribute to the alleviation of the worst consequences of eutrophication if the growth of undesirable species could be suppressed in favour of that of more tolerable algae. As yet, this understanding has not developed to the point where realistic artificial control measures can be proposed. This should perhaps be the objective of one line of future research.

At the present time, the most profitable approach appears to lie in the elucidation of factors controlling the seasonal fluctuations in abundance of the same algae in lakes where they are already dominant. Major reviews (eg Lund 1965, Hutchinson 1967, Round 1971, Porter 1977) have emphasised the controlling interactions of a multiplicity of environmental factors which operate during seasonal cycles. These interactions need not be discussed in detail here, except to point out that different algal groups do have different growth optima (Fogg 1975, Lehman et al 1975), which are influenced by cell size (Laws 1975), day length and average light intensity (Foy et al. 1976), temperature (Hammer 1964, Patrick 1969), and nutrient uptake kinetics (Tilman and Kilham 1976, Tilman 1977). Grazing by filter-feeding zooplankton (Nauwerck 1963, Haney 1973, Porter 1977), sinking (Lund 1966, Lund et al 1963, Reynolds 1973b, 1976c, Knoechel and Kalff 1975), pathogenic infections by protozoa, fungi and viruses (Canter 1973, Safferman and Morris 1967) and allelopathy (Keating 1977) have been instanced as factors governing differential loss rates.

All these contributions are instructive, but it is difficult to draw overall conclusions from the abundant literature: the sequence and combination of critical environment factors is bewildering by complex, and they will be virtually unique to a given lake. Against this observation must be placed the evident general similarities in seasonal succession that occur from year to year in individual lakes, and from one lake to another of similar trophic status. Indeed, successional patterns, at least at the taxonomic group level, are recognizable over a great many meso- and eutrophic waters. A seasonal progression of species-assemblages, from diatoms and cryptomonads, through green algae, blue-green algae to dinoflagellates seems typical for a wide diversity of more eutrophic lakes (Nauwerck 1963, Schelske and Stoermer 1972, Reynolds 1973a, Lewis 1978a). It can only be concluded that some fundamental principles override the detail differences which inevitably characterise the individual water bodies. The changes in species dominance are, moreover, usually abrupt, and occur in response to far-reaching changes in the ambient environment. Lewis (1978a) has shown that this is particularly true in some tropical lakes.

Round (1971), I believe, did not overstate the significance of environmental variations when he termed them "shock periods". One such "shock" follows the onset of thermal stagnation in lakes. The sharp increases in average day length and epilimnetic water temperature have, as discussed in the previous section, have a profound physiological effect upon the vernal algal assemblage (typically diatoms and cryptomonads) adapted to fully mixed conditions. Work in progress at the FBA has already demonstrated that this may be manifest in a significant reduction of growth rate and increase in intrinsic sinking rate. Given that the vertical extent of turbulent mixing, upon which diatoms, at least, depend for suspension, is simultaneously reduced, these algae will be rapidly eliminated from the trophogenic zone: the combination of these factors can account for the observed sinking out of *Asterionella* populations in Windermere, described by Lund et al (1963), and in other lakes whose epilimnia are still chemically capable of supporting diatom growth (Reynolds 1973b, Reynolds and Butterwick 1979). Relative delays in the onset of stagnation, induced by weather, have been observed to prolong the period of diatom dominance (Reynolds 1978b). In any case, diatoms can survive in stratified columns provided adequate nutrients (especially silica) are supplied, but losses of cells nevertheless represent a large proportion of those produced (Reynolds 1976c, and in prep.). Equally, their survival and net growth is considerably enhanced if the epilimnion is deepened (Reynolds 1973b, 1976a).

The newly stratified conditions clearly call for a different growth and survival strategy. Fast growth rate, tolerance for high light intensities and some means of maintenance within stable layers seem to be prime requirements. Some green algae (including members of the Chlorococcales and Volvocales) seem best adapted in this respect, and it is therefore unsurprising that these often become established. In many lakes, however, large populations take some time to develop; indeed, a phase of low biomass and high water clarity following stratification seems typical. One contributing factor is an increase in grazing pressure, as

populations of filter-feeding crustaceans become increasingly active in response to higher water temperatures, and reproduce more rapidly (Steel, et al 1972). There is some debate as to the effect of food selectivity upon algal succession: some species are either sufficiently large to escape filtration, or are rejected on other grounds; others may survive ingestion (Porter 1977). Except at the extremes of the trophic spectrum (see for instance, Pavoni 1963), it is usually the larger algal units which eventually dominate. In this way, zooplankton grazing may fail to control total algal biomass, but it may profoundly condition species succession.

Further shifts in dominance occur in response to the depletion of nutrients. In a stratified lake, depletion extends from the surface downwards. A gradient of growth conditions is thus established wherein different organisms may develop differentially. This in turn may lead to a greater diversity of species, each subject to subtly different limiting constraints (Peterson 1975). Dominance may be determined less by the nutrient requirements of the competing algae than by their specific means of obtaining them and storing them (Reynolds 1976a, 1976b). For example, the energy expenditure in vertical migrations undertaken by *Ceratium* may be offset by the competitive advantage gained by nutrient uptake at depth. Blue-green algae regulate their buoyancy during growth, and may gain some positive advantage if they are able to stratify in the metalimnion (Reynolds and Walsby 1975). However, both *Ceratium* and the blue greens are characterised by generally slower rates of growth. But it is perhaps of equal importance that both species minimise the rates of loss, either through sinking or grazing, as pointed out by Kalff and Knoechel (1978): it is clear that these algae have a different survival strategy from those previously considered, which seems well adapted to stably stratified systems. Not only are large populations likely, but they may persist for several months, even though their net growth rate is minimal. Other mechanisms exhibited by blue-green algae which are of potential selective advantage include a capacity (among filamentous forms) for nitrogen fixation (Fogg et al. 1973) and an efficient means of perennation on the sediments (Topachevskiy et al. Reynolds and Rogers 1976, Rother and Fay 1977, Reynolds in prep.)

More persistent nutrient availability seems to result in less diversity among the epilimnetic phytoplankton (Reynolds and Butterwick 1979, Reynolds in prep). There is some evidence (Harris and Piccinin 1977, Sze and Kingsbury 1972) that green algae (especially members of the Chlorococcales including *Oocystis*, *Chlorella* and *Scenedesmus*) continue to dominate such waters. The same effect might be produced in eutrophic waters of weaker thermal stability and having larger epilimnetic volumes. In some smaller lakes, where thermal micro-stratification alternates with sharp increases in wind-mixing, instability may promote renewed diatom growth, by effectively reverting the seasonal progression back to the pioneer stage (Reynolds 1976, Lewis 1978b). Increase in inflow rate of raw water to the epilimnion may increase the nutrient pool, and hence revert the succession to an earlier post-stratification stage.

Many of the variations in dominance that can be attributed directly to differences in nutrient availability and uptake kinetics, or to selective attack by pathogens are superimposed upon the broad seasonal trends outlined. They may affect the balance of organisms within one successional association, without materially advancing the succession as a whole. Examples of within-group variations of this kind have been given in Reynolds (1973b) Knoechel and Kalff (1978) and Stoermer et al. (1978) in each of these examples one species of diatom replaced another.

From this brief consideration, it is apparent that weather and water movements exert an overriding influence on the composition of the phytoplankton. If the biological mechanisms can be clarified, and their effects better predicted, it should be possible to anticipate algal problems in reservoirs, and to propose means of modifying succession by mechanical means.

## MECHANISMS CONTROLLING ALGAL DISTRIBUTION

It has long been known that the vertical distribution of planktonic algae is often heterogeneous, especially in stably stratified systems. Differences in horizontal distribution are also well-known but, until recently, have received relatively little attention. There is now increasing evidence of discontinuities in horizontal distribution ("patchiness") similar to those which occur in the sea, although the "large scale" distinctions between major current-borne water masses probably only occur where waters of adjacent basins of different trophic status interact (eg Harris and Smith 1977). "Mesoscale" variations (cf. Riley 1976) are found in lakes (eg Sandusky and Horne 1978), but the ways in which these develop are obscure. In the sea they are often related to grazing, and Riley's (1976) model allows diel migration to segregate specific populations, which may then be separated by turbulence currents and drift. Upwelling and seiches may contribute a similar effect in lakes, especially near shores. Small-scale "clustering" of the type described by McAlice (1970), where significant underdispersion occurs on scales of  $< 10$  m, are often evident in lakes. Some interaction between scales is evident (Sandusky and Horne 1978), and patterns are reduced for many species in winter (Sandusky and Horne 1978) and under stronger wind stress ( $> 3-5 \text{ m s}^{-1}$ ; Therriault et al. 1978).

Of more direct consequence in storage reservoirs is the tendency for plankton to collect disproportionately on one side of the lake. Buoyant blue-green algae accumulate above areas of downwelling near leeward shores (Yamagishi and Aoyama 1972, George and Edwards 1978); organisms whose gravity exceeds that of water are moved across the lake in return currents and then accumulate in areas of upwelling. Examples in the latter category include crustacea (Colebrook 1960) and *Ceratium* (Heaney 1976). These distributional patterns are influenced by basin size and morphometry, but clear horizontal differences only develop below a critical average wind velocity ( $\sim 3 \text{ m s}^{-1}$ ); as wind speed increases, however, some heterogeneity is likely to persist.

Heaney's work (George and Heaney 1976, Heaney 1976) is of special interest since it demonstrates the superimposition of wind-induced currents upon the alga's attempts to regulate vertical position. The alga may modify its behaviour in response to local growth conditions obtaining while the velocity and direction of limnetic currents is inherently variable. In this way an infinite range of distributional responses seems possible. Potentially, the outcome of this work might influence reservoir design and management, so that water masses relatively free of filter-blocking algae might be exploited. Flexibility in the use of existing abstraction points is a desirable design feature in eutrophic reservoirs.

## LOSS CONTROL MECHANISMS

Almost all the algal biomass generated by planktonic production is destined eventually to be removed from the open waters as a result of natural losses, including wash-out and dilution, sedimentation, grazing, death and decomposition. Compared to the effort expended in the study of anabolic growth mechanisms, these processes have received scant attention, either individually or in concert, in respect to specific algal populations, although Uhlmann's (1971) work on hyperfertilized systems does give consideration to the interactions of production and losses. The same general principles apply to lakes, although the nutrient levels and dilution rates are on smaller scales. They are currently under investigation at the FBA, in the belief that it may be possible to enhance the loss mechanisms as a means of regulating phytoplankton biomass in eutrophic lakes. The work, which is supported, under contract, by the Department of the Environment, has required the development of quantification techniques. At this stage, formal presentation of the results would be premature, but some provisional findings can be indicated.



The experimental work is centred on the Lund Tubes installed in Blelham Tarn, Cumbria (see Lack and Lund 1974). These are closed systems in which lake phytoplankton assemblages can be maintained indefinitely (Lund 1975) though its abundance and, to a limited extent, its specific composition can be regulated by controlled additions of inorganic nutrients (Lund 1978c). The enclosures eliminate the effects of wash-out and dilution but, conversely, the products of algal synthesis remain within the system and should be recoverable. By following the fate of specific populations, the magnitude of loss partitioning can be approximated and checked against retrospective measurements at the concentration points. In spite of the generous confidence intervals which have to be applied to the results, different species partition in significantly different ways. Moreover, these differences must be consistent with specific adaptations to planktonic life and growth strategies. Quantification of sinking losses is approached through three independent techniques. One is based upon the changes in the ratio of live:dead cells, using a calculation essentially similar to the one employed by Knoechel and Kalff (1978), though this holds only for colonial algae in which dead cells are retained in the colonies; its accuracy depends upon the randomness of sampling and the counting efficiency. The second relies on the recovery of algae from sediment traps placed strategically in the water column; here catches are influenced by water movements in the vicinity of the traps themselves, and this factor may bias the results (Reynolds 1979). The third method depends upon the measurement of the areal increment rate of cells arriving at the sediment surface, using a modified Jenkin sampler (Collins 1977). Substantial agreement between these methods has been observed. A further apparatus, comprising artificial substratum placed in open boxes arranged to present a collective 'solid' surface to the overlying water, is currently under test.

Observations on three separate diatom populations has shown that direct sinking to the sediments accounts for > 67% of their total biomass production; moreover, the majority of the cells are still alive when they reach the bottom (11 m). Sedimentation is most intense after the onset of stratification (see Section 3). In contrast the daily fractional loss rate during active growth in the freely mixed column is < 0.01.

The arrival of some other algae (*Microcystis*, *Staurastrum*) is consistent with removal by sinking. On the other hand, smaller proportions of dominant *Eudorina*, *Aukyra* and *Cryptomonas* populations could be accounted at the sediment surface, although some sedimentation was observed in the traps. Death and disintegration in the hypolimnion may explain part of this shortfall, but grazing by crustacea, and to a lesser extent, by rotifers was significant in these cases.

Grazing efficiency is influenced by food selectivity, either on the basis of size (Gliwicz 1970) or of genuine food preferences (Edmondson 1964), and by the physiological activity, age structure and size of specific populations. Rotifers can be numerically the most abundant members of the zooplankton, but their individual daily filtration rates (in the order  $10 - 100 \mu\text{l day}^{-1}$ : Pourriot 1977) are much smaller than those of planktonic *Daphnia* ( $0.5 - 30 \text{ ml day}^{-1}$  according to age and water temperature: Burns 1969). Filtration rates are also said to alter during the day (Nauwerck 1963, Haney and Hall 1975), and they probably decline when the ration requirement is met by large populations of suitable food organisms.

To assess the impact of community grazing upon the phytoplankton, it is necessary to sum the products of individual filtration rates of each size category in each species and their standing populations. At best, this gives an estimate of maximum potential grazing pressure, since it takes no account of rejection of some algae, nor of failure to ingest. It also assumes that grazers enjoy continuous access to their food, an assumption which is misplaced if the animals migrate away from the trophogenic zone during part of each day. Moreover, ingestion is no guarantee of assimilation (see Porter 1977). With these limitations in mind, the maximum filtration rates that we have been able to derive ( $0.5 - 0.75$  of the epilimnetic volume each day) will not prevent the net increase of an algal whose generation time is 1.25 days. As the

rate at which the animal population can mature and increase is rather longer than algal generation time, it is unlikely a. that grazing will prevent the growth of the alga before it encounters some other limiting constraint (eg nutrient stress) and b. that any relationship between food and feeder will not remain constant for long. Grazing pressure may, however, limit the potential algal population whilst its growth rate is reduced. Since the numbers of animals will decline when the food supply becomes suboptimal, it can be seen that grazing is only likely to be effective against existing algal populations: it is fallacious to assume that any stable relationship between phytoplankton and zooplankton is always struck in the temperate lake environment (cf Lewis 1977).

What is likely to be important is that intense grazing pressure will reduce the resource competition between the smaller (grazed) algae and the energetically-less efficient larger algae. Generally, it is the latter which become dominant and which create problems in waterworks practice. The practical husbanding of zooplankton as a means of controlling algal abundance therefore seems unpromising. Rather, the control of zooplankton by fish predation might have more potential, if reduced grazing were to favour the growth of "tolerable" algal species over "nuisance" species. Both possibilities remain largely untested and deserve further investigation.

## CONCLUSIONS

In this brief review, I have attempted to show the extent, or rather the deficiencies, of present knowledge concerning the biology of phytoplankton growth in eutrophic waters. If we assume that schemes to limit the average size of phytoplankton populations are unlikely to be adopted everywhere, then it is advisable that we try and understand more of the natural controlling processes, and seek ways to manipulate the balance between them. An important first step in this direction is the acceptance that phytoplankton comprises a variety of species, which do not necessarily all share the same strategy for growth and survival. Moreover the differences between them are not explicable in purely chemical terms. The more eutrophic the water body in which they occur, then the relatively more important are light, temperature and water movements in controlling the growth conditions. Of these, light and temperature interactions have been studied intensively; the physics of water movements also have a long history of study, but as I have indicated above, ecologists are still largely ignorant of their impact in phytoplankton ecology. Water-movements are of course extremely complex, not least because they are constantly in a state of flux. In previous publications (Reynolds 1979, Walsby and Reynolds 1979), the view has been advanced that once the behaviour of individual particles in relation to characteristic water motions (eg in convectional rotations, in open turbulence, and in boundary layers) can be established, then the effects of movement on distribution might be broadly predictable. The consequences in terms of phytoplankton growth will vary specifically, and in relation to other physical variables which alter seasonally. I believe that these responses should be predictable and ultimately controllable by artificial mixing.

The idea of regulating phytoplankton biomass through artificial destratification is not a new one, and the results of a number of experiments have been published (Symons et al. 1966, Robinson et al. 1969, Ridley 1970, Sirenko et al. 1972; See also Lackey 1973, for further references). Indeed, modern eutrophic reservoirs are now designed to optimise artificial mixing as far as possible (Steel 1972). These various installations have produced conspicuously different results, which are in part attributable to the duration and extent of mixing, and partly to differences between the morphometric properties of the basins concerned. Some experiments led to a net increase in algal biomass (see Wildman et al. 1975). Ridley (1970) showed that different species responded to differing extents. This is in accord with the predictive model proposed by Lorenzen and Mitchell (1975), since the model components are not equal for all algae.

Haynes (1975) took the experiments one stage further, through controlled fluctuations in the extent of mixing. Changes in species dominance were effected, increasing instability favouring the growth of green algae over blue-greens in Kezar Lake. I would suggest that this approach might be developed profitably: for if, as I have argued here, the growth of specific algal populations is directly correlated with physical characteristics of the medium then it ought to be possible to first establish one set of growth conditions (for instance by consistent artificial mixing) until a moderate but manageable phytoplankton developed, and then to alter them (ie allow the column to stratify) so that another set of conditions obtain. The mixing phase of the cycle would be reintroduced at the desired stage to suppress the growth of the phytoplankton community responding to the stable column. It must be stressed, however, that until specific survival strategies and growth responses are better understood, the possibilities remain speculative and the proposition hypothetical.

Other aspects of this account have touched on biological control mechanisms. At present, those involving zooplankton seem less attractive for potential manipulation than physical controls, but that does not mean that they should not be explored further. Clarification of more specific phytoplankton-zooplankton interactions is still required before they can be usefully exploited in practice.

One final point requiring emphasis is that many of the current problems caused by algae in waterworks are intermittent and, because they depend upon a combination of physical, chemical and biotic factors which is virtually unique to a given water body, are unlikely to arise simultaneously in all the storage reservoirs available for supply. Lund (1975) has proposed a scheme for the rotational use of compartments of a reservoir isolated by (eg) impermeable butyle-rubber barriers, on the same principle as Lund Tubes. Lund envisaged that water would be abstracted from the compartment whose phytoplankton had entered a nutrient-limited decline phase. In highly eutrophic reservoirs, however, the exhaustion of nutrients and the elimination of the phytoplankton standing crop might be relatively delayed. But the system has the additional advantage of flexibility: selection could be substituted for rotation so that the water abstracted would be the best available. The possible future introduction of reservoir management schemes of the type I have envisaged here would not replace Lund's system, but rather enhance its use.

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