PHYTOPLANKTON PERIODICITY: ITS MOTIVATION, MECHANISMS AND MANIPULATION

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Introduction

Regular cyclical fluctuations in abundance and species composition constitute one of the most striking characteristics of the freshwater phytoplankton, yet the factors that regulate the periodic wax and wane of specific populations are many and complex and they are incompletely understood. This review summarizes some recent work at the FBA to find a generalized explanation of phytoplankton periodicity in lakes. Much of the observational and experimental evidence is drawn from ongoing projects centred on the large enclosures ("Lund Tubes") installed in Blelham Tarn and described by Lack & Lund (1974) and Lund & Reynolds (in press). These structures are sufficiently large (capacity: 18 500 m³) to maintain open-water communities, perhaps indefinitely, yet are small enough to permit convenient manipulation of physical, chemical and biotic variables. However, they cost so much to make and run that we are unable to operate enough of them to provide statistical replication of experimental treatments. We have therefore to study them as if they were separate water bodies, except that we can influence them in particular ways (for instance, by controlling the nutrient loading).

In this article, I try to relate our observations on the phytoplankton in the tubes to the periodic changes that occur in natural lakes. I hope to show that such changes have common patterns, that they are due to common causes ('motivation'), that they are effected by similar processes and that they are therefore predictable and, potentially, manipulable.

I wish to thank the many members of FBA staff, students and visitors who have contributed to the work, even though they may not agree with everything I say in this article. The work has been financially supported by the Department of the Environment (Contract DGR/480/310).

Phytoplankton periodicity

Phytoplankton has been studied for many years in many countries. The earliest work was essentially descriptive, establishing *what* lived in the open water of lakes. This quickly prompted secondary questions – *why* and *how* do they live there? Many aspects of the morphological and physiological adaptations of planktonic organisms have been probed during the last 80 years or so, though not all to the same extent. Much of the effort has implicitly sought explanations for the characteristic seasonal progressions in species dominance, which have come to be known as the 'seasonal succession' (or, for reasons which are outlined below, what I prefer to call the 'seasonal periodicity').

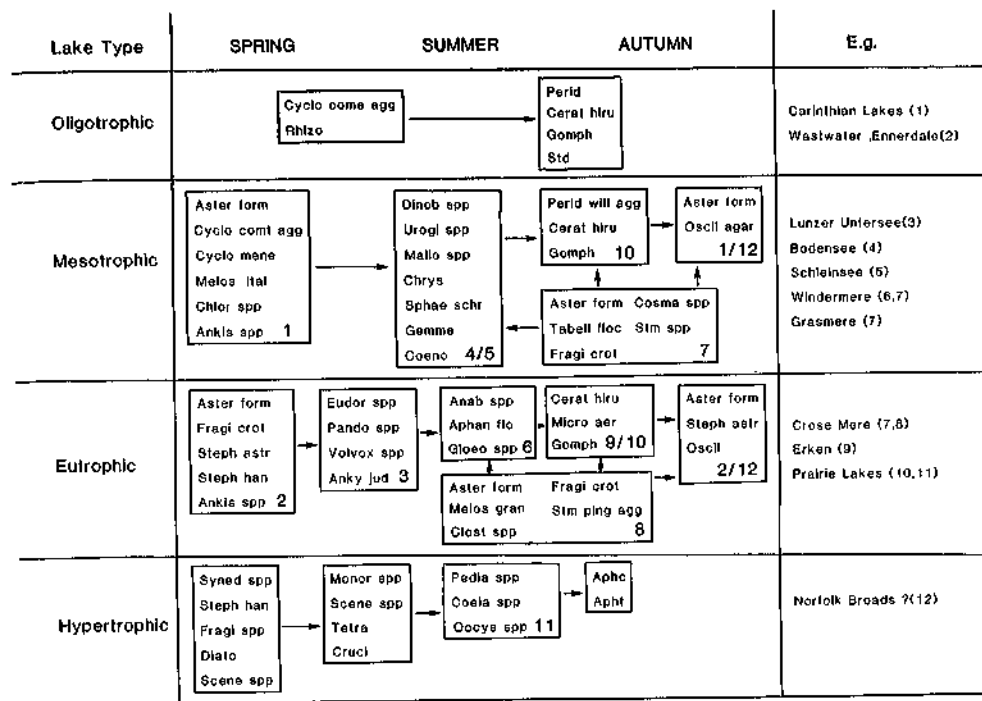| Lake Type	SPRING	SUMMER	AUTUMN	E.g.
Oligotrophic	Cyclo come agg / Rhizo	→	Perid / Cerat hiru / Gomph / Std	Carinthian Lakes (1) / Wastwater, Ennerdale (2)
Mesotrophic	Aster form / Cyclo comt agg / Cyclo mene / Melos Ital / Chlor spp / Ankis spp **1**	Dinob spp / Urogl spp / Mallo spp / Chrys / Sphae schr / Gemme / Coeno **4/5**	Perid will agg / Cerat hiru / Gomph **10** → Aster form / Oscil agar **1/12** ; Aster form Cosma spp / Tabell floc Stm spp / Fragi crot **7**	Lunzer Untersee (3) / Bodensee (4) / Schleinsee (5) / Windermere (6,7) / Grasmere (7)
Eutrophic	Aster form / Fragi crot / Steph astr / Steph han / Ankis spp **2**	Eudor spp / Pando spp / Volvox spp / Anky jud **3**	Anab spp / Aphan flo / Gloeo spp **6** ; Cerat hiru / Micro aer / Gomph **9/10** → Aster form / Steph astr / Oscil **2/12** ; Aster form / Melos gran / Clost spp ; Fragi crot / Stm ping agg **8**	Crose Mere (7,8) / Erken (9) / Prairie Lakes (10,11)
Hypertrophic	Syned spp / Steph han / Fragi spp / Diato / Scene spp	Monor spp / Scene spp / Tetra / Cruci	Pedia spp / Coela spp / Oocys spp **11** → Aphc / Apht	Norfolk Broads ?(12)

FIG. 1. Generalized successional pathways in lakes of different trophic status: the boxes represent assemblages of species (whose names are listed below) one or more of which may be abundant; bold numbers refer to assemblage-labels of Reynolds (1980a). Examples of each sequence are referenced 1-12. 1: Findenegg (1943); 2: Pearsall (1932); 3: Ruttner (1930); 4: Grim (1939); 5: Vetter (1937); 6: Lund, in Macan (1970); 7: Reynolds (1980a); 8: Reynolds (1978c); 9: Nauwerck (1963); 10: Lin (1972); 11: Kling (1975); 12: Leah et al. (1980). Abbreviations to species: Ankist = *Ankistrodesmus* spp; Anky =*Ankyra judayi*; Anab = *Anabaena* spp.; Aphan flo = *Aphanizomenon flos-aquae*; Aphc = *Aphanocapsa*; Apht = *Aphanotheca*; Aster form = *Asterionella formosa*; Cerat hir = *Ceratium hirundinella*; Chlor = *Chlorella* spp.; Chrys = *Chrysochromulina*; Clost spp includes *Closterium aciculare*, *C. acutum*, *C. tortum*; Coela = *Coelastrum* spp; Coeno = *Coenococcus*; Cosma = *Cosmarium* spp, (*C. abbreviatum, C. contractum, C. depressum*); Cruci = *Crucigenea* spp.; Cyclo come agg = *Cyclotella comensis* aggregate; Cyclo comt agg = *C. comta* aggregate; Cyclo mene = *Cyclotella meneghiniana*; Diato = *Diatoma*; Dinob = *Dinobryon* (chiefly *divergens*); Eudor spp. = *Eudorina* spp.; Fragi spp. = *Fragilaria* spp.; *Fragilaria crotonensis* (Fragi crot) is distinguished; Gemme = *Gemellicystis* cf. *neglecta*; Gloeo = *Gloeotrichia*; Gomph = *Gomphosphaeria* spp. including forms ascribable to *Coelosphaerium*; Mallo = *Mallomonas* (e.g. *M. caudata*) Melos gran = *Melosira granulata*; Melos ital = *M. italica*; Micro aer = *Microcystis aeruginosa*; Monor spp. = *Monoraphidium* spp.; Oocys. spp. = *Oocystis* spp. (e.g. *O. borgei*); Oscil = *Oscillatoria* spp., usually ascribable to *O. agardhii* (Oscil agar); Pando spp. = *Pandorina* spp. (e.g. *P. morum*); Pedia spp. = *Pediastrum* spp. (*P. boryanum, P. duplex, P. tetras*); Perid =*Peridinium* spp.; the *P. willei* aggregate (Perid will agg) is distinguished; Rhizo = *Rhizosolenia*; Scene = *Scenedesmus* spp.; Sphae schr = *Sphaerocystis schroeteri*; Std = *Staurodesmus*; Steph astr = *Stephanodiscus astraea* (= *S. rotula*); Steph han = *Stephanodiscus hantzschii*; Stm spp = *Staurastrum* spp.; the *S. pingue* aggregate (Stm ping agg) is distinguished; Syned spp. = *Synedra* spp. Tabell floc = *Tabellaria flocculosa*; Tetra = *Tetrastrum*; Urogl spp = *Uroglena* spp.; Volvox spp = *Volvox* spp.

Hutchinson's (1967) detailed review of known periodicities among temperate lakes established that broadly similar annual cycles of specific abundances occur in geographically remote lakes sharing similar trophic and morphometric properties. Typical progressions are summarized in Fig 1; additional data from Reynolds (1980a) and a tentative scheme for hyper-eutrophic lakes are included. The species-representations grouped in boxes should be regarded as alternative dominants of those assemblages; it is the assemblage which invariably characterizes a given stage in a given sequence, though the quantitative and temporal extent of its representation can vary. The model is not designed to accommodate precisely all observable sequences so much as to describe the basic kinds of sequential change that naturally occur. That evidently similar sequences have been so frequently described in the literature and that they have been imitated in the Lund Tubes (Lund & Reynolds in press) suggests that the direction and controlling mechanisms of change are common to all of them.

Motivation of change: environmental variability

Which, then, of the many types of environmental variability are critical to the regulation of phytoplankton periodicity? Since Pearsall's (1932) important observations on the phytoplankton periodicity of the English Lakes were published, many subsequent workers have tried to explain periodic change primarily in terms of specific nutrient requirements and changes in time of nutrient availability (for reviews see Lund (1965); Fogg (1975)). This approach has identified a number of important relationships, for instance, that between *Asterionella* and silica in Windermere (Lund 1950). However, the absolute requirements of most algae for nitrogen and phosphorus, the two elements whose availability perhaps varies most significantly during the year, are, weight for weight, generally similar (Reynolds 1978a, 1980b). Nevertheless, specific growth rates (k') of algae vary with the concentrations of these nutrients, conforming to Monod-type kinetics (Fig. 2), and the curves are often different for different species. When two species having different half-saturation coefficients (K_s) are grown together the one with the faster rate of growth for a given availability of a limiting nutrient is likely to dominate (e.g. Tilman & Kilham 1976). The ability of certain cyanobacteria (or 'blue-green algae') to fix dissolved nitrogen gas must give them an advantage over other species of phytoplankton at times when supplies of combined nitrogen are limiting. In general, however, it is difficult to see how relatively subtle and overlapping interspecific differences in nutrient-dependent growth kinetics could be solely or consistently responsible for the known, broadly repeatable changes in community composition observed in so many different lakes. Moreover, similar changes in biomass and species dominance have been imitated in the Lund Tubes, even when the concentrations of major nutrients (N, P, Si, Fe) are deliberately
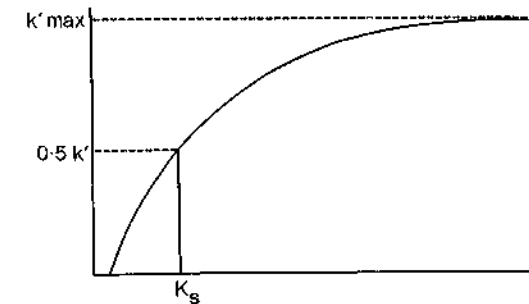
FIG. 2. The relationship defined by the Monod growth model relating growth (k', vertical axis) to nutrient availability (horizontal axis). K_s, the half-saturation constant, is the nutrient level required to sustain half the theoretical growth rate (to which the model curve is asymptotic).

maintained at supra-optimal levels (Reynolds 1980a, Reynolds & Wiseman in press). The supply of nutrients *is* important, especially in regulating the total biomass of phytoplankton that can be maintained (as evidenced by the now familiar phosphorus-chlorophyll models of eutrophication: e.g. Sakamoto 1966; Dillon & Rigler 1974; Lee et al. 1978); its influence on quality (i.e. species composition) probably depends on more complex interactions with other environmental factors.

Similarly, interspecific differences in light and temperature preferences seem insufficiently dissimilar to account, by themselves, for gross periodic changes in species composition. Photosynthetic activity may exert a selective influence through its effect on the carbon supply: species that can use bicarbonate as a source or carrier of carbon will be favoured at high pH-levels (Talling 1976). If algae are to survive, then their photosynthetic physiologies must be compatible with the average light conditions in the water column in which they are distributed (the "underwater light climate" of Talling (1971)). As the understanding of light adaptation has advanced (reviewed by Harris 1978, 1980), it has become clear that the suites of adaptive responses, both biochemical (involving alternative internal metabolic pathways) and behavioural (regulation of station in the light gradient), vary among planktonic species. Those of diatoms seem better suited to the high-frequency, high-amplitude oscillations of light perceived by cells circulating in well-mixed columns, whereas those of many motile species (e.g. *Ceratium*) may be tailored to the lower frequency variations in light at the depths where, potentially, they maintain station.

The vertical extent of mixing often changes with season. Warming of the surface waters in spring and summer tends to set up gradients of temperature (and, hence, of density); the warmer and lighter the water becomes, the greater is its resistance to mixing with the colder, denser

water below. Where the energy of the (largely wind-driven) surface flow is insufficient to overcome the density gradient, turbulence subsides, flow becomes laminar or viscous and a thermocline (metalimnion) is formed. Density gradients may persist for a matter of hours or, at most, days in shallow or exposed lakes, or for months on end in deep or well-sheltered ones. Even in the latter, metalimnia can extend towards the surface during warm, still, anticyclonic weather and then be depressed during cooler, windier conditions.

Few phytoplankton organisms can resist turbulent diffusion and tend to become randomized in diffusive flow (vertical diffusivity coefficients >0.01 cm^2s^{-1}); where density gradients are sufficiently stable (>0.02 kg $m^{-3}m^{-1}$; vertical diffusivity <0.001 cm^2s^{-1}), however, organisms are segregated according to their intrinsic settling behaviours, that is, whether they either sink or float, or if motile, they move towards a preferred depth (Reynolds 1976a). In this way, a well-mixed lake provides a quite different environment from a stably-stratified one: each favours different morphological, physiological and behavioural characteristics for algal growth and survival. We may anticipate that those species that do well under one set of conditions may fare less well under another.

Mixing (or the lack of it) influences other features of the environment. If the depth of turbulent mixing (Z_m) exceeds the depth to which sufficient light penetrates to support photosynthesis (Z_{eu}), then the organisms suspended in the flow must, on average, pass part of the daylight period in darkness (cf. Talling 1971). If $Z_{eu}>Z_m$, the growth of organisms can be enhanced, so long as they remain in the light and do not sink irretrievably therefrom. At the same time, algal uptake may deplete the dissolved nutrients in the surface waters at a faster rate than weak mixing recycles them from depth. Net depletion is accentuated by sedimentary losses of intact cells and the faecal pellets of animals feeding on them. The stratified water column tends to be differentiated (or to segregate) into the upper, nutrient-limited epilimnion and a lower, potentially dark, hypolimnion.

Such segregation is most clearly demonstrated in small eutrophic lakes (e.g. Crose Mere (Reynolds 1976b)). Soon after the onset of the summer stratification sedimentation eliminates the spring assemblage dominated by non-motile diatoms, even though the water may remain chemically capable of supporting continued growth (Reynolds 1973, Reynolds & Butterwick 1979). This assemblage is replaced first by ones dominated by motile (e.g. *Eudorina*) or buoyancy-regulating organisms (e.g. *Anabaena*) and eventually by species (e.g. of *Ceratium, Microcystis*) capable of performing substantial vertical migrations between the epilimnion and the nutrient-rich hypolimnion (Heaney & Talling 1980a; Reynolds 1978b). Populations of diatoms (Fig. 1) can become re-established during summer after episodes of increased wind-mixing and metalimnetic depression.

The transitions between these successive periodic stages are therefore correlated with either the intensification or the weakening of the vertical segregation of the environment (Reynolds 1976b, 1980a).

Corresponding transitions are less well-defined in Windermere, where the spring *Asterionella* maxima are rarely achieved before the column has stratified (Lund et al. 1963) but they are eventually replaced by motile chrysophytes and dinoflagellates and by non-motile colonial green algae characterized by relatively slow sinking rates; diatoms reappear after episodes of wind-mixing (Reynolds 1980a). In the oligotrophic Carinthian lakes, studied by Findenegg (1943), diatoms dominated single annual maxima in mid-summer, some months after stratification. These differences may be related to the greater absolute depth (>10 m) and relative transparency of their epilimnia ($Z_{eu} \geqslant Z_m$).

Such considerations have led me to regard the periodic formation and collapse of near-surface density gradients as the major cause of phytoplankton periodicity in lakes, both directly (through its various interactions with morphological and behavioural characteristics of individual species) and indirectly (through its overriding influence on the distribution of other physical and chemical factors) (Reynolds 1980a, 1980b). Although I have not investigated the periodicities of shallow, unstratified lakes in any detail, they need not be excluded from this concept, if the waters they inhabit are analogized to the epilimnia of stratified lakes.

Directionality of change: analogies with terrestrial ecosystems

Much of the modern theory of succession has been developed by terrestrial-plant ecologists (e.g. Pielou (1966), Odum (1971)) but few phycologists have sought to apply it to planktonic communities[1]. In essence, areas of the earth's surface are successively invaded and modified by recognizable communities in distinct sequences, passing from 'pioneer' to 'climax' associations (e.g. from bare ground to high forest) separated by relatively abrupt transitions. Successional series are characterized by increasing biomass, complexity and (usually) diversity and by declining productivity. Nevertheless, successions may be suspended at an intermediate steady state, or plagioclimax, by exploitation (in this example, say, the maintenance of permanent grassland) or may be reverted to a more primitive stage (clear-felling of forest, ploughing-up).

Analogous processes in the plankton can be related to the stability of the three-dimensional fluid environment (Reynolds 1980a). A newly-formed epilimnion is open to colonization by those species of phytoplankton which arrive there and to initial dominance by those maintaining higher relative

[1] The work of R. Margalef (e.g. 1962, 1968) is a conspicuous exception to this statement. His papers and our conversations have contributed many of the initial ideas that we have investigated. I willingly and gratefully acknowledge my debt to him.

rates of net growth. Their activity modifies the environment to the extent that it becomes increasingly segregated. 'Pioneers' become nutrient-limited and the competitive advantage moves to species better-suited to the modified conditions (Reynolds 1976b), even though their absolute rates of growth are lower (see Fig. 3). Thus, nitrogen-limited populations of *Eudorina* may be replaced by nitrogen-fixing strains of *Anabaena* (recalling the increase of clover in a field of rye-grass as the effects of fertilization wears off) and, ultimately, by relatively slow-growing species (e.g. *Ceratium*) which may derive nutrients from greater depths (Reynolds 1978c).

These responses are *autogenic* (determined by the species themselves) and may be equated with strict succession (Reynolds 1980a). However, the balance between successional advance and its exploitation is delicate (cf. Margalef 1968). Changes in turbulent circulation and structural stability occur at irregular and unpredictable intervals. The more severe the perturbation, the relatively greater are the increases in epilimnetic volume and its vertical integration. These new conditions stimulate the renewed increase of diatoms, perhaps of desmids and other species characteristic of well-mixed water columns. If the increased mixing is sustained, as occurs in autumn, these algae may come to dominate a new community which is out of the successional sequence. This response (which I call 'shift') is *allogenic* (that is, it is imposed upon the species). Equally, if the perturbation is short-lived, and the epilimnion restratifies, at least a partial recapitulation of the earlier summer succession, or 'reversion', is favoured (for examples, see Reynolds 1980a). Provided the distinction is drawn between autogenic successional progression and allogenic changes, it is possible to accommodate the various directions of periodic change within a single explanatory theory.

Mechanisms of change:
Growth and attrition

Recent work at Windermere (Le Cren 1981) and elsewhere (e.g. Kalff & Knoechel 1978) has recognized that the dynamics of net population change are equally dependent upon growth and mortality. Thus, the attainment of a substantial population (N_t) depends on the maintenance of a high net growth-rate (k_n) or, if lower, for a longer period of time (t) or from a larger initial starting population (or inoculum, N_o). These quantities are related in equation (1):

$$N_t = N_o e^{tk_n}$$

(where e is the base of natural logarithms)

Whence $k_n = [\log_e(N_t/N_o)]t^{-1}$ (2)

The net rate of increase is usually lower than the true rate of cell increase (k': see Fig. 3) because cell stocks may be continually lost ('exploited'
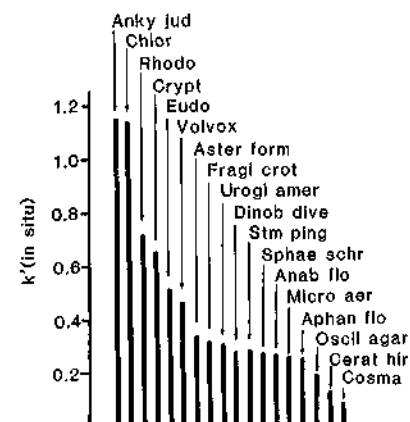
FIG. 3.   Comparison of the maximum *in situ* rates of growth (k') of species in Lund Tubes since 1976, reconstructed from (e.g.) equation (3). Values derived as in Reynolds et al. (in press).

(Margalef 1968)) through outwash (w), *in situ* death and decomposition (d), sedimentation (s) and grazing by animals (g). The rates of all these processes can be expressed as exponents. Thus:

$$k_n = k' - (k_w + k_d + k_s + k_g)$$

(3)

We have attempted to quantify these components through the waxing and waning of a number of specific populations husbanded in the Lund Tubes and to reconstruct the total production and losses attributable to the various processes in terms of cells (Reynolds et al. in press). Washout from the closed systems has been assumed to be zero. Decomposition was found to be mainly confined to the base of the hypolimnion (Jones & Simon 1980), cells frequently sinking from the epilimnion intact (Reynolds & Wiseman in press). Parasitism was negligible. *In situ* death rates were rarely separately quantifiable, and in most instances were included with the sinking losses. However, cell losses attributable to sedimentation (plus death) or grazing were generally large. Moreover, the partitioning of total loss between the different causes of loss differed greatly among the species studied. These are briefly described below.

Algal sedimentation

Reynolds & Wiseman (in press) measured the sedimentary flux of algal cells into two designs of sediment trap and to the sediment surface. The methods had been previously calibrated against known fluxes of *Lycopodium* spores introduced at the surface of a Lund Tube (Reynolds 1979). Rates of sinking loss (k_s) from the water column were successfully

modelled: in non-turbulent layers, the intrinsic (still-water) settling velocity (V') applies; under turbulent conditions, sinking loss is a hyperbolic, first-order reaction, analogous to dilution, which can be shown to be independent of turbulent intensity (Walsby & Reynolds 1980) but to be continuously related to the depth of the turbulent layer (Z_m):

$$k_s = \log_e[1/(1 - V'/Z_m)] \tag{4}$$

Results confirmed the sensitivity of diatoms ($V' = 0.2-0.9$ m d^{-1}) to the depth of mixing: k_s was low during the isothermal period (keeping V'/Z_m low) but increased after stratification (when an increase in V' coincided with the sharp decrease in Z_m (Reynolds & Wiseman in press)). More than 80% of the vernally-produced *Asterionella* cells in either tube were recovered intact on the sediment. In contrast, the summer dominants characteristically yielded much lower k_s values during growth (although their propagules – zygotes, akinetes, cysts or, in the case of *Microcystis*, vegetative colonies – were rapidly recruited to the sediment at the end of the growth phase (Reynolds et al. in press)). The same is apparently true in some natural lakes (Reynolds 1976b; Livingstone & Reynolds 1981).

Grazing

Filter-feeding crustacea (especially *Daphnia*) and, occasionally, rotifers have typically dominated the zooplankton biomass of the Lund Tubes (Ferguson et al. in press). By measuring the filtration rates of individual animals in various species- and size-categories and then multiplying the rates by their respective abundances, we calculated the total volume of water processed by the zooplankton population each day (a, expressed as a proportion of the total volume of the Lund Tube). This has been shown to vary from 0.002 d^{-1} in winter to up to 2 d^{-1} in summer (Thompson et al. in press).

However, algal particles are not removed uniformly from the inhalant current but are 'selected', probably exclusively by size (Ferguson et al. in press): algae whose unit size is greater than 60 µm in two or more planes (larger colonies of *Eudorina*, *Microcystis* and *Fragilaria*) are virtually immune from ingestion. Specific rates of loss to filter-feeding (k_g) were calculated according to equation (5):

$$k_g = \phi a \tag{5}$$

(where ϕ is a coefficient of selectivity, scaled between 1, for indiscriminate, complete removal of algae as food, and 0, for complete rejection). Precise evaluation of ϕ was not possible. Reynolds et al. (in press) deduced upper and lower limits of ϕ from field data each of which were separately interpolated into equation (5) to give the likely range of k_g.

High grazing pressures exert a heavy toll on smaller (<60 µm) algae (nanoplankton): for example, more than 89% of *Ankyra* cells produced in Tube A during July 1978 were removed by filter-feeders. The alga

nevertheless must have maintained a sufficiently high positive rate of net growth ($k' > 0.9$ d$^{-1} > k_g$; $k_g = 0.2$ initially, increasing to ~1.0 d^{-1}) to enable it to produce a dominant, almost monospecific, light-limited population. Once its growth slowed, however, it was very rapidly eliminated ($k_n \simeq k_g$). Other small algae (*Chromulina*, *Rhodomonas*) have also been shown to increase despite moderate filtration pressures ($a = 0.4$ to 0.6 d^{-1}) while their growth rate is not resource-limited. Their limitation or eventual removal by grazing favours the dominance of larger, 'inedible' species (which, in turn, leads to starvation and death for many of the animals (Ferguson et al. in press; Thompson et al. in press)).

The absence of a steady-state relationship between food and feeders thus contributes to the seasonal compositional changes observed in the Lund Tubes. It also explains why the typical sequences should be frequently dominated by larger algae: their relative immunity from grazing often means that their characteristically lower potential growth-rates (k'; see Fig. 4) nevertheless exceed the net growth rates (k_n) of the smaller, grazed species, giving them the prospect of relatively larger maximal populations (N_t). At the same time, they will lock-up nutrients which are then unavailable to nanoplankton: exploitation is reduced and the succession advances. Zooplankton grazing will not limit phytoplankton abundance *per se* but its intensity will influence its ultimate species composition. This is true whether or not the zooplankton is itself heavily predated by fish (Reynolds 1980b).

Growth and survival strategies

Since the species of phytoplankton are drawn from diverse and unrelated phylogenetic groups of aquatic organisms, it should not be surprising that their morphological and behavioural adaptations to planktonic life are correspondingly dissimilar. As a generalization, non-motile species with high sinking rates (chiefly diatoms) are dependent upon deep mixed layers, given adequate nutrients and light conditions. Species that sink less rapidly, if at all, are further sorted according to their growth rates, the capacity of the environment to satisfy their individual growth requirements and by their resistance to grazing. A species will have better prospects for survival if (1) it tolerates lower environmental limits than its competitors – whether of nutrient availability (e.g. of nitrogen by *Anabaena*), or of light availability (*Oscillatoria* spp.) – or (2) alternative sources of nutrients can be reached (e.g. *Ceratium*). Survival in the longer term (such as through periods unfavourable for growth) depends on the maintenance of a stock of potential cell material. The production of morphological or physiological propagules, which can pass many months or even years on the lake sediments until suitable conditions for 'germination' obtain, characterizes many of the species that are abundant on a seasonally recurring cycle. Indeed, perennation is an important factor contributing
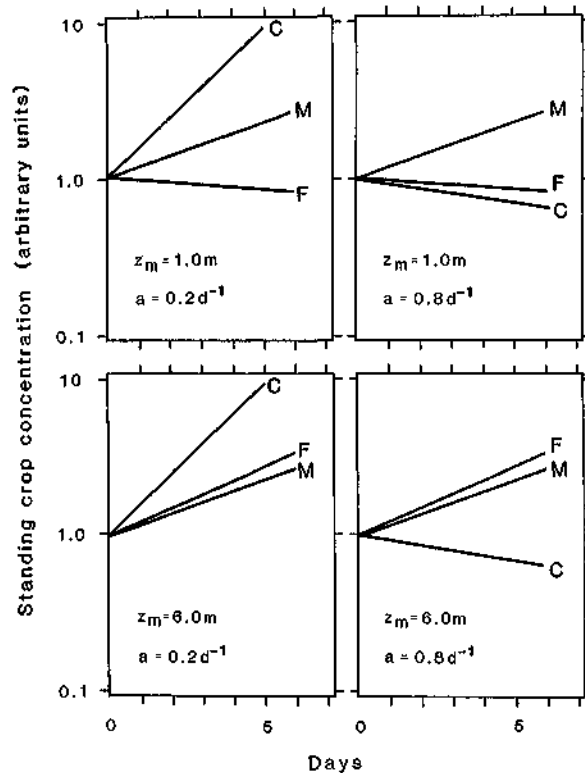
FIG. 4. The net growth rates (k_n) of three competing species of summer phytoplankton *Cryptomonas* spp. (C), *Fragilaria crotonensis* (F) and *Microcystis aeruginosa* (M) under different combinations of low or high column mixing (z_m), which differentiates between heavy, motile diatoms (F) and motile (C) or buoyant (M) species, and low or high community filtration pressure (a, expressed as a fraction of the total lake volume processed daily) which differentiates between small, edible (C) and large, inedible algae (F, M). Redrawn from Fig. 9 of Reynolds et al. (1982).

to year-to-year similarities in the successional sequences. Temporal phasing of propagule formation and germination also provides valuable clues to the specific environmental preferences and their limits.

Many species of pennate diatoms (e.g. *Asterionella, Fragilaria*) have no known resting stage: their growth and survival appears to rely upon the maintenance of stocks (albeit, at times, very sparse) of vegetative cells in suspension and upon 'bursts' of net increase whenever conditions permit. Cryptomonads are also evidently capable of growing under a wide variety of environmental conditions (Reynolds et al. in press). The coupling of the ability to survive in very small numbers and the potential

for rapid growth reaches its extreme among the 'opportunist' (cf. Reynolds 1980a) species that have occasionally produced substantial populations in the Lund Tubes (e.g. *Ankyra, Chromulina, Pedinomonas* spp. (Lund & Reynolds in press)). Thus, there seems to be a negative correlation between the provision of special over-wintering stages among phytoplankton and their potential rates of growth.

Motivation and mechanisms of periodicity: an interpretation

While our work has not yet achieved its objective of an explanation of phytoplankton periodicity, it has enhanced our appreciation of probable causative factors and the processes which bring about change. There is little doubt that the seasonal appearance, growth and replacement of dominant organisms in the phytoplankton of lakes (and, for that matter, in ponds and rivers) depend on many interactions between the typical ranges of fluctuation in environmental resources and the specific responses of the species thereto. Nevertheless, there do seem to be consistent underlying patterns to the interaction of these factors. I submit that overall temporal sequence represents a series of subsequences, each characterized by maturation of the planktonic community along a descending gradient in its characteristic limiting resource (whether it is phosphorus, nitrogen or other nutrient, or optical depth). The rate at which it proceeds depends on how rapidly the environment is autogenically altered by the algae themselves and by the extent to which each stage is 'exploited' by loss processes: grazing, sedimentation, death or hydrological washout. Allogenic changes in the relative stability may lead to a shift to an alternative subsequence. Figure 5 attempts to show, in stylized form, how the growth rates (k') of different species might respond to seasonal changes in light and temperature and to the declining availability of a limiting nutrient. It also shows how seasonal changes in mixed depth and in grazing intensity can differentially detract from k' among the various species. The model, which is based on the data we have obtained in the Lund Tubes, traces the periodic sequence in terms of the *properties* of organisms (i.e. whether they have high nutrient half-saturation coefficients or not, adapt to well-mixed and optically deep or to stable water columns, are large or small, are motile or non-motile) and, thus, of those 'available', in terms of probable species dominance. Sequences often seem to pass from species with fast rates of growth, net of losses, to those with slower ones. In this way, it is possible to interpret both the general similarities in the phytoplankton of lakes of similar trophic status, and the consistent differences (Fig. 1) among the sequences of oligotrophic lakes (characteristically limited by phosphorus), eutrophic lakes (frequently nitrogen- and, occasionally, carbon-limited) and hyper-eutrophic lakes (nutrients not limiting, but light climate critical). Sequences remain
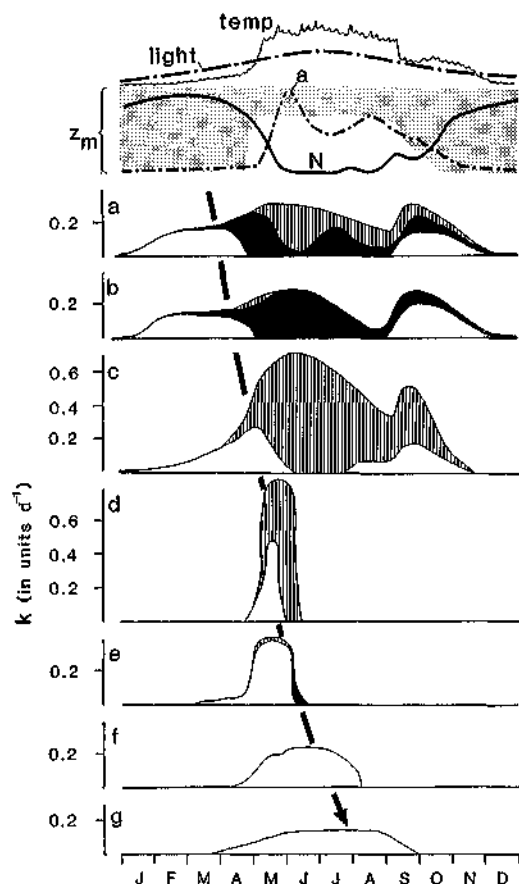
FIG. 5. Schematic representations of the growth rates of phytoplankton in relation to major environmental factors (top): income of light radiation, surface water temperature, mixed depth (Z_m, stippled), relative volume filtered daily by zooplankton (a) and limiting nutrient concentration (N). The seasonal changes in growth rate (k') of six species of phytoplankton, a-f are shown, partitioned according to the relative rates of loss experienced, if any: (solid – sinking loss rate; vertical hatching – grazing loss rate). The white areas correspond to net growth rate, k_n. The vertical arrow traces the probable succession of dominant species: (a) is a diatom (e.g. *Asterionella*) that is grazed by zooplankton; (b) is another diatom which is often immune to grazing (e.g. *Fragilaria*); (c) is a cryptomonad that grows for most of the year but is often heavily grazed; (d) is an opportunist (e.g. *Ankyra*); (e), (f) and (g) are larger motile algae which have low sinking and grazing losses: they are exemplified (respectively) by *Eudorina*, *Anabaena*, *Microcystis* or *Ceratium* in eutrophic lakes and by *Dinobryon* or *Uroglena*, *Sphaerocystis*, *Ceratium* or *Peridinium* in (P-limited) mesotrophic lakes.

liable to suspension ('plagioclimax'), under steady-state conditions, or to be taken back to a more primitive stage, by allogenic perturbations.

This interpretation of phytoplankton periodicity also offers a basis for interpolation of appropriate quantitative values to predict the composition in response to climatic variations or persistent nutrient enrichment (eutrophication), where these potentially alter the level of the limiting resources.

Manipulation of periodicity

Our current work is directed towards testing the accuracy of simple predictions, based on the above interpretation, of the responses of the phytoplankton community of the Lund Tubes to an artificially altered (manipulated) balance between growth and potential losses. The scope of the manipulations, conveniently carried out in the Lund Tubes, offer three dimensions for variation – nutrient loading, mixed depth and zooplankton filter feeding. So far, we have attempted to stimulate substantial net increase of diatoms in response to artificial increases in the epilimnetic circulation and to produce a dominant nanoplankton by limiting filter-feeding. The initial results have been encouraging; their detailed reporting here is inappropriate but will be published elsewhere in due course.

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