FRESHWATER BIOLOGY SPECIAL REVIEW

# Phytoplankton periodicity: the interactions of form, function and environmental variability

C. S. REYNOLDS Freshwater Biological Association Windermere Laboratory, Ambleside

SUMMARY. 1. This review considers the periodic cycles of species dominance in a wide selection of temperate lakes. By ascribing individual species to assemblages, a high incidence of similarity among periodic cycles is demonstrated. Reference to lakes at high and low latitudes, as well as to rivers, shows conformity to parts of the same broad patterns.

2. The role of population dynamics in shaping community structure is emphasized. Two types of change are recognized: autogenic, undirectional subsequences (successions), regulated by specific responses to critically changing resource-ratio gradients; and allogenic changes, regulated by variability in the physical environment.

3. Analysis of the responses of representative species to allogenic change permits further grouping of the assemblages. These groupings coincide with clear morphological distinctions among the same phytoplankton species according to their unit sizes and surface area/volume ratios.

4. It is argued that these properties condition the physiological responses of algae to seasonal variations in temperature, mixing and exposure to the underwater light field. The responses are compounded by relative resistances to loss processes (sinking, grazing), by short-term photosynthetic adaptation and vertical migratory behaviour.

5. Graphical summaries are presented that relate the morphologically-, physiologically- and behaviourally-mediated responses to a hierarchy of physical, chemical and biotic environmental variables. Phytoplankton periodicity is the outcome of these interactions.

## Introduction

Since Pearsall (1930, 1932) established that the abundance and species composition of freshwater phytoplankton undergo regular seasonal fluctuations, a considerable research effort has been expended into the environmental factors

Correspondence: Dr C. S. Reynolds, Freshwater Biological Association Windermere Laboratory, Ambleside, Cumbria LA22 0LP.

that might regulate its distribution. In spite of this activity and of an enormous expansion in documented knowledge, it is acknowledged that the conceptual understanding and predictability of seasonal change have scarcely advanced during the subsequent 50 years (Kalff & Knoechel, 1978). The approaches adopted have nevertheless identified several important contributory mechanisms, including specific differences in the optimal light and temperature

8

preferences of phytoplankton, in their photo-synthetic behaviour and physiology and, not-ably, in their nutrient-uptake and -saturation requirements (for recent reviews, see Paerl, 1982; Rhee, 1982; Tilman, Kilham & Kilham, 1982). That these differences respond to season-al variations in environmental conditions is not to be doubted but the basis and outcome of the supposed competition is, generally, still poorly understood.

It is not the purpose of this review to duplicate these recent literature surveys and syntheses. Rather, I wish to adopt an alternative approach to the problem of periodic change in species composition (or, as it has become misleadingly styled, 'the seasonal succession'). I shall first attempt to classify the periodic sequences that occur in natural lakes and to show the common patterns to which they conform. This is followed by an examination of the transitions in commun-ity dominance, of the manner and direction in which changes occur and the scales of environ-mental variation that generate them. Individual species are then categorized into groups accord-ing to their responses to the major sources of environmental variability. In the later sections of the review I shall show how closely these same categories coincide with those that distinguish among the sizes, shapes and physiological characteristics of the same organisms. I shall also suggest that this correspondence is not coin-cidental, rather that it is indicative of the existence of several sets of adaptive specializa-tions among the phytoplankton; each has evolved to suit particular characteristics of water-bodies but none is ideal under all cir-cumstances. As environmental characteristics vary with season so the selective advantage moves in train, from one category to another.

## Temporal variations in phytoplankton composition

I estimate that, since Hutchinson (1967) re-viewed the annual phytoplankton periodicities in selected lakes, at least 200 descriptions of the cycles in other lakes and water-bodies have been added to the literature. Some 80% of these titles concern lakes in Europe or in North America; the others refer mainly to African and Austra-lian waters, while several concentrate upon lakes at high latitudes (Kalff et al., 1975; Moore,

1979; Jónasson & Adalsteinsson, 1979; Light, Ellis-Evans & Priddle, 1981). Relatively little information is yet available for lakes in South America or in Asia (other than Israel and Japan). The scope for between-year variations in the phasing, sequencing, duration and rate of increase, and the eventual biomass achieved by each species in a given water-body borders on the infinite, even before between-lake variations are even considered. Yet, at a higher level of categorization, where individual species are assigned to 'assemblages' of species that share closely similar phasing of increase, relative abundance and decrease, the sequence-patterns of seasonal change can be readily established. Moreover, the patterns discerned among geog-raphically remote but morphometrically- and trophically-similar lakes are often remarkably similar.

I was able to propose fourteen such species-assemblages in order to characterize the phyto-plankton periodicities of five limnologically distinct British lake systems (Reynolds, 1980). The addition of a further five categories (see Reynolds, 1982) was adequate to accommodate the periodicities reviewed in Hutchinson (1967), together with those of selected shallow hyper-trophic systems, exemplified by Brundall Broad, England (Leah, Moss & Forrest, 1980) and Neusiedlersee, Austria (Dokulil, 1979). With little modification these assemblages are res-tyled (A−S, X, Y) and arranged in Fig. 1 to show their approximate sequential relationships and the contrasted patterns among lakes of differing trophic status and morphometry.

Such a deliberately oversimplified summary cannot be expected to accommodate precisely every known seasonal sequence, but the major-ity of these will be seen to follow one or other the horizontal progressions shown or to be in-termediate between an adjacent pair. Thus, the periodic sequences in very oligotrophic, sub-alpine lakes, such as Millstättersee and Klopeinersee in Austria (as described by Fin-denegg, 1943) and Ennerdale Water and Wast-water in the English Lake District (Pearsall, 1932; FBA, unpublished data), in which a single summer or early autumn biomass peak (total cell volume $<2$ $\mu$l $1^{-1}$) is dominated initially by centric diatoms (e.g. *Cyclotella comensis*,* *Rhi-zosolenia eriensis*) and then by dinoflangellates

* A full list of algal taxa, together with authorities, is appended (Appendix I).
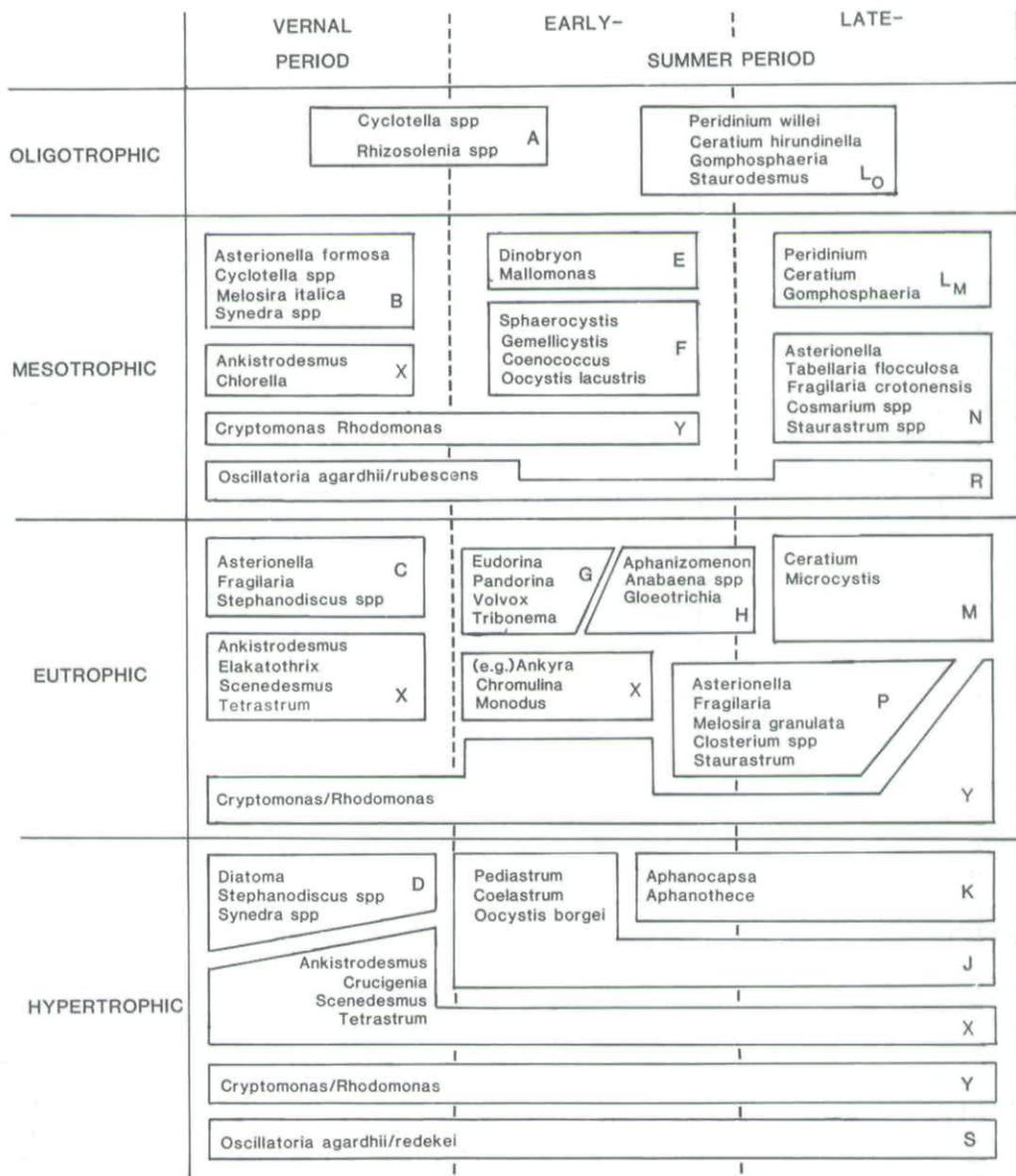
| | VERNAL PERIOD | EARLY– SUMMER PERIOD | | LATE– |
|---|---|---|---|---|



FIG. 1. Assemblages of temperate freshwater phytoplankton (*A–S, X, Y*) and some representative species, one or more of which may grow well, relatively well or become abundant in the types of lake and during the approximate seasons of the year indicated (separated by the vertical broken lines). Modified after Fig. 1 of Reynolds (1982).

(e.g. *Peridinium willei, Ceratium hirundinella*), are represented in Fig. 1 by the progression $A \rightarrow L_0$. In somewhat less oligotrophic large lakes, like Lunzer Untersee, Austria (Ruttner, 1930), Bodensee, Germany/Switzerland (Grim, 1939; see also Sommer, 1981) and Windermere (Lund, in Macan, 1970; Reynolds, 1980), the peak biomass tends to be larger (total cell volume $<5 \ \mu l \ l^{-1}$), to be attained earlier in the year (generally late spring) and to be followed by several small maxima, each separated by distinct minima. The vernal growth is dominated by diatoms (represented from among: *Asterionella formosa*, various *Cyclotella* spp. including *C. comta*, *C. glomerata* and *C. melosiroides*, *Melosira italica*, *M. islandica* and *Synedra* spp.)

with subdominant populations of small chlorophytes, chrysomonads and, frequently, cryptomonads. Late-spring and early summer peaks, dominated either by chrysophyceaen flagellates (*Mallomonas, Dinobryon, Uroglena* spp. or by gelatinous colonial chlorophyceae (e.g. *Sphaerocystis schroeteri, Gemellicystis neglecta, Coenococcus, Radiococcus* spp.), ultimately give place to a phase of *Ceratium*- or *Peridinium*-dominance, in which the cyanobacterium *Gomphosphaeria* is usually well-represented. Such mestotrophic sequences may be represented as $B{\rightarrow}E/F{\rightarrow}L_M$.

An abrupt late-summer or early autumn re-establishment of diatom-dominated assemblages frequently occurs in both Windermere (Reynolds, 1980) and Bodensee (Sommer, 1981). The species representation in spring and summer is not identical: *Cyclotella* spp. tend to be rare, while conspicuous additions include *Tabellaria flocculosa* var. *asterionelloides* (in Windermere), *Melosira granulata* (in Bodensee) and *Fragilaria crotonensis* (in both) and, frequently, desmids (e.g. *Staurastrum, Cosmarium* spp.). The assemblage is therefore distinguished ('*N*').

Several features distinguish the phytoplankton of lakes that are either naturally eutrophic in character (they are typically smaller and/or shallower than the first two lake types; nutrient loadings tend to be more concentrated with depth, while a relatively small hypolimnetic volume is subject to severe oxygen deficit) or as a consequence of anthropogenic enrichment. Its average biomass is greater and is particularly abundant in two marked and well-separated maxima $(5-20 \ \mu l \ l^{-1})$, one 'vernal' (March to June: dominated by diatoms, especially *Asterionella formosa, Fragilaria crotonensis* and *Stephanodiscus* spp., with cryptomonads a major subdominant), and one in late summer (generally dominated by *Ceratium* and/or *Microcystis aeruginosa*). Between these characteristic peaks, there may be several more or less pronounced smaller pulses: the more so in richer lakes (e.g. Crose Mere, England; Reynolds, 1973a), where they are frequently dominated by species of Volvocales (e.g. *Volvox aureus, Eudorina* spp., *Pandoria* spp.) with a subdominant nanoplankton and, later on, by filamentous cyanobacteria (*Anabaena, Aphanizomenon* spp.); the less so in mildly eutrophic lakes (e.g. Sjön Erken, Sweden, at the time of Nauwerck's

(1963) extensive investigation) where various chrysophytes, including *Erkenia, Chromulina, Dinobryon, Mallomonas* and *Uroglena*, and then filamentous cyanobacteria, notably *Gloeotrichia*, were the dominants. These lakes also tend to briefly support late summer or autumnal populations of diatoms (especially *Asterionella, Fragilaria* or *Melosira granulata*) and desmids (especially *Closterium* spp.), analogous to those of Windermere. The generalized sequences of many eutrophic lakes may thus be represented $C{\rightarrow}E$ or $G{\rightarrow}H{\rightarrow}L$ or $M$ with, to varying extents, returns through *P, X* or *Y*.

The fourth progression in Fig. 1 attempts to reconcile the relatively scant information for ponds and shallow lakes subject to high nutrient loading. The vernal assemblages may become abundant soon after the winter solstice. Biomass is dominated by various diatoms (especially *Diatoma*, small *Synedra, Nitzschia* and *Stephanodiscus* spp., assemblage *D*), by euglenoids or by such chlorococcalean genera as *Ankistrodesmus, Chlorella* and *Scenedesmus* (assemblage *X*) which, in some instances, may persist through much of the year (see Reynolds, 1973b). Elsewhere, diatoms may give way to larger colonial chlorococcales (assemblage *J*), represented by *Pediastrum, Coelastrum, Oocystis* (e.g. Gt Budworth Mere, England; Reynolds, 1978a), and then, as in Neusiedlersee and Brundall Broad, to small colonial cyanobacteria (assemblage *K*), represented by *Aphanothece* and *Aphanocapsa* (Dokulil, 1979; Leah *et al.*, 1980). There are examples of sequences (see Reynolds, 1973b) which share some affinities with those of eutrophic lakes, progressing from $C-D$ assemblages (*Diatoma, Synedra nana, Stephanodiscus hantzschii, Cyclotella pseudostelligera*) to filamentous or colonial cyanobacteria (*H, K*) with perhaps intermediate phases of dominance by colonial chlorophyceae (*G, J*) or even chrysophyceae (*Synura, Dinobryon* spp.). Cryptomonads can feature as prominent subdominants in these sequences or may even dominate for much of the time (Reynolds, 1978a). This type of progression ($C/D{\rightarrow}J/X{\rightarrow}H/K$) also applies to the phytoplankton periodicities of the much larger highly-enriched Onondaga Lake, U.S.A. (cf. Sze, 1980), Hamilton Harbour (a near-isolated embayment of Lake Ontario: Haffner, Harris & Jarai, 1980) and Pfäffikersee, Switzerland (Pavoni, 1963).

The frequent occurrence and persistence of

populations of *Oscillatoria* sp. in many temperate lakes requires separate treatment in Fig. 1. The peculiarities in seasonal growth and buoyant behaviour of *Oscillatoria* spp. which contribute to their ecology in lakes are reviewed in Reynolds (1983a). Examples of lakes dominated by *Oscillatoria* populations are of two distinct types. Lough Neagh, Northern Ireland (Gibson *et al.*, 1971), Drontermeer and Wolderwijd, Netherlands (Berger, 1975), are nutrient-rich, relatively shallow or exposed stretches of water that are more or less continuously wind-mixed and in which vernal diatom assemblages (*C*, *D*) are succeeded, *inter alia*, by large populations of *O. agardhii* and/or *O. redekei* Van Goor (assemblage *S*). The second category includes mildly eutrophied, deep sub-alpine lakes like Zürichsee (Pavoni, 1963) and Vierwaldstättersee, Switzerland (Zimmerman, 1969), Lago Maggiore, Italy (Ravera & Vollenweider, 1968) and Lake Washington, U.S.A. (before sewage diversion; Edmondson, 1970), and some shallower mid-continental lakes that stratify intensely during summer (Eberley, 1959; Brook, Baker & Klemer, 1971; Klemer, 1976). Here, the most abundant species (either *O. rubescens* or *O. agardhii* var. *isothrix* Skuja; assemblage *R*) tend to achieve their best growth when the water column is well-mixed, passing the summer stratified in the metalimnion.

Even such an incomplete summary of temporal variability in phytoplankton dominance in temperate lakes should make reference to periodicities elsewhere. Although much less information is available on which to base the assertion, analogous sequences can be discerned among tropical lakes. Some of the large and nutrient-deficient lakes support small populations of diatoms, desmids and cyanobacteria through longer growing seasons (Melack, 1979; Hecky & Kling, 1981) in sequences approximating to *P*→*H*. Shallower and more productive lakes may be more persistently dominated by cyanobacteria, such as *Spirulina* sp. (the tropical analogue of assemblage *K* or *S*?) or *Microcystis* (Talling *et al.*, 1973; Ganf & Viner, 1973). Lewis' (e.g. 1978a) work on Lake Lanao, Philippines, suggests that others may produce analogous sequences to temperate lakes (resembling *P*/*Y*→*H*→*K*/*M*) over truncated time spans that may be recapitulated two or three times annually. As a generalization, there is a tendency among tropical phytoplankton sequences for a relative preponderance of centric diatoms (especially *Melosira*) over pennate species, of *Peridinium* over *Ceratium*, of many-armed *Staurastrum* spp. over *Cosmarium* and *Closterium* and of cyanobacteria generally.

Among those temperate rivers that are either sufficiently long or sluggish to permit a significant growth of phytoplankton, species representation commonly shows greatest affinities with that of small, unstratified lakes, with abundant small centric diatoms and chlorococcalean algae. The species correspondingly abundant in natural and artificial impoundments will also be periodically well-represented in the rivers that drain them (see Reynolds, 1983a, for references).

In concentrating upon patterns common to numbers of water-bodies, this survey deliberately omits consideration of many plankton associations responding to overriding specialized environmental factors—extreme acidity, salinity, heavy metal content and so on—as being beyond its scope. The section is concluded by reference to the work on the three large limnetic enclosures in Blelham Tarn, England (for reviews, see Lund, 1975, 1981; Lund & Reynolds, 1982; Reynolds, 1982). These enclosures have been used to isolate the natural waters of the Tarn for periods of months or years and to subject them to various experimental manipulations involving altered nutrient loading, zooplankton grazing and hydraulic column stability. Throughout these manipulations, the enclosures have continued to support limnetic phytoplankton associations, which, moveover, developed sequentially according to outlines given in Fig. 1. 'Mesotrophic' (*B*→*E*/*F*→*L*ₘ), eutrophic (*C*→*G*→*X*/*Y*→*M*) and various intermediate progressions (involving *H*, *N*, *P* and *R*) have been successfully imitated, mainly by adjustments in the scale and frequency of nutrient loads (Lund & Reynolds, 1982). The imposition of artificial destratification has repeatedly altered the temporal phasing of compositional changes but not the fundamental sequences (Reynolds *et al.*, 1983, 1984).

## Environmental control of phytoplankton periodicity

The factors that regulate the periodic wax and wane are acknowledged to be many and complex

(Lund, 1965). It is something of a truism that the environmental factors that have been considered important in the past—nutrients, temperature and light—have been those which are relatively convenient to measure. Until recently, little account has been taken of those factors which have long been recognized to influence phytoplankton ecology but which are more difficult either to measure (e.g. the effects of organic chelating agents, chemical antagonisms) or to interpret (the interaction between algal requirements for micronutrients and their chemistries in natural waters). Moreover, there has been an evident tendency to relate specific algal abundances (yields), rather than the processes (growth) by which they are attained, to particular environmental variables. This approach assumes the widespread existence of stable environmental equilibria, whereas this is unlikely to be the case (Harris, 1980, 1983). Ecologists, whilst acknowledging the special adaptations of algae to pelagic life-modes, often overlook the striking morphological differences (of size, shape and colonial organization). Surely such variety cannot have been achieved amongst organisms adapting to identical environmental constraints?

If the preceding overview of phytoplankton sequences is accepted and, implicitly, that their mutual similarities are the product of common selective interactions among critical environmental variables and the biological responses of the organisms themselves, then it should be possible to deduce the major driving variables of change and the appropriate adaptive features that they invoke. This section is devoted to discerning which of the many dimensions and scales of environmental variability are critical to the regulation of specific population and community changes.

Perhaps the most profitable approach is to first consider how such changes manifest themselves. It must be presumed at the outset that algae will grow wherever and whenever they are able. For a species to grow requires the simultaneous satisfaction of two conditions: (i) that the complete spectrum of its minimum environmental requirements is fulfilled; and (ii) that it is present to be able to exploit those opportunities when they arise. The second condition introduces several conceptual problems: how are algae transmitted among waterbodies to the extent that planktonic flora are so cosmopolitan? How important is successful perennation? And, how do those algae that produce no known perennating propagule survive between growing seasons? I do not intend to explore these problems here; they have been variously addressed by Atkinson (1980), Heaney, Chapman & Morison (1983) and Reynolds (1983a). On the other hand, the species most likely to figure in the periodicity of a given water-body will be those that have regularly produced populations at the corresponding stages in the past, presumably because they are just the species that are most likely to be able to furnish the relatively large 'inocula' of vegetative cells required to initiate tangible increase when conditions favour their growth. This expression of 'biological inertia' (cf. Gorham, 1957) is a powerful bias favouring the recapitulation of specific seasonal abundance from year to year.

Seasonal dominance is nevertheless strongly influenced by the comparative dynamics of net population increase and by the time periods over which they apply. These quantities are interrelated in the mathematical expression of exponential population increase:

$$N_t = N_0 e^{k_n t} \tag{1}$$

(where $N_0$ represents the specific population biomass existing at zero time, $N_t$ is the corresponding quantity after time $t$ and $k_n$ is the exponential coefficient of net increase, expressed as a natural logarithm, to the base e). Species that dominate will be those that either maintain the fastest rates of net increase (i.e. $k_n$ is large) or maintain slower rates of growth for longer periods of time ($t$ is large) or if the initial inoculum ($N_0$) is sufficiently large to confer an advantage over faster-growing organisms. $N_0$ relates to the second condition (ii, above); $k_n$ and $t$ relate to the first and are subject to regulation by the organisms' perception of their environment.

It is also important to stress that $k_n$ is a net coefficient, expressing the instantaneous outcome of several simultaneous conflicting processes, broadly summarized by equation (2):

$$k_n = k' - \Sigma k_L \tag{2}$$

Here $k'$ is the true rate of growth of a population and $\Sigma k_L$ is the sum of the negative coefficients of the rates of population attrition. The latter
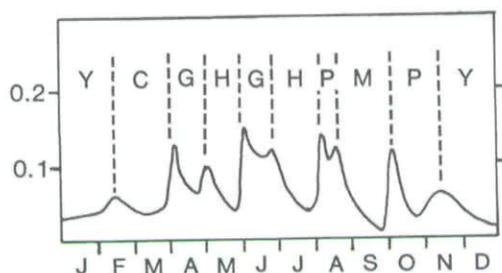
FIG. 2. The rate of periodic change ($\sigma$, day$^{-1}$) in Crose Mere, 1973. Higher values ($\sigma > 0.1$ day$^{-1}$) are associated with abrupt transitions in community dominance between species ascribed to their respective assemblages identified in Fig. 1. Stylized after part of Fig. 4 of Reynolds (1980).

include the rate of 'dilution' by outwash ($k_w$), *in situ* death and decomposition ($k_d$), by 'permanent' settling to the sediments ($k_s$) and through the feeding activities of zooplankton ($k_g$). Thus,

$$\Sigma k_L = k_w + k_d + k_s + k_g \qquad (3)$$

Reynolds *et al.* (1982) showed that each process represents an 'environmental variable' in its own right but specific differences in, for instance, net sinking rates or sensitivity to grazing determine that the species present are simultaneously affected to differing extents. Loss processes thus contribute to selective alterations in phytoplankton composition.

Changes in community structure respond to the changing relative rates of growth and attrition of (at least) the more abundant species. The mathematical expression of community change introduced by Jassby & Goldman (1974) has been applied (albeit in slightly modified forms) to natural plankton sequences by Lewis (1978b) and Reynolds (1980).

$$\sigma = \frac{\Sigma i \left[ \{ b_i (t_1)/\beta(t_1) \} - \{ b_i(t_2)/\beta(t_2) \} \right]}{t_1 - t_2} \qquad (4)$$

[where $b_i(t)$ is the biomass or weighted abundance of the *i*th species at time $t$ and $\beta(t)$ is the total biomass or abundance of the entire phytoplankton community; $\sigma$, the sum of the fractional differences between $t_1$ and $t_2$, expressed per unit time (generally 1 day), is the index of community change]. A single example, stylized from data for Crose Mere, 1973, and presented in Reynolds (1980), of the application of the index is given in Fig. 2: the value of $\sigma$ is low ($<0.05$ day$^{-1}$) when community composition

fluctuates little (all major species present increasing or decreasing simultaneously) but increases as one dominant population is replaced by another. High values ($>0.1$ day$^{-1}$) generally represent abrupt changes, where several species decline simultaneously and other species increase rapidly to fill the 'vacuum'. Thus, the rate of change serves to identify the transitions in community organization that, by implication, respond to critical shifts in the perceived environment.

Reference to Reynolds' (1976) more detailed investigation of the phytoplankton periodicity in Crose Mere, 1973, indicates that the transitions were associated with two distinct sets of environmental variables: either they occurred (e.g. G→H) whilst the water column remained stably stratified but epilimnetic nutrient concentrations (in this case, of dissolved inorganic combined nitrogen) were declining or they were correlated with abrupt changes in the stability of the stratification (C→G; H or M→P; P→M). The former are identifiable in Fig. 2 as approximately symmetrical fluctuations in the rate of change, $\sigma$; the latter are distinctly skewed leftwards. These two patterns of responses were also discernible for the other sets of assemblages in the lakes considered by Reynolds (1980). They may be distinguished among the broad subdivisions shown in Fig. 1: horizontal differentiation of the assemblages corresponds to the changes in given lakes that may be associated with major seasonal alterations in hydraulic stability (zero-, early- and late stratification stages); vertical differentiation distinguishes phytoplankton assemblages in lakes of different trophic status at the *corresponding* periodic stages. Indeed, relative environmental stability and nutrient availability can be discerned to be among the principal factors governing the spatial and temporal distribution of phytoplankton.

*Periodic change in relation to the chemical environment*

The almost universal acceptance of the importance of the role of limiting nutrients in the ecology of phytoplankton is acknowledged in the vertical arrangement of periodic progressions in Fig. 1. In part, the various categories of trophic status relate to differing morphometric and physiographic features of individual lake basins—their areas, mean and maximum

depths, wind exposure, internal water circulations and so on. Greater significance is rightly attached to (usually parallel) differences in the availability of essential nutrients in the lakes concerned. 'Availability' is a catch-all covering the supply of nutrients to the lake ('loading'), their dissipation in time and with depth, their retention in forms assimilable by phytoplankton and the efficiency with which they can be cycled through the limnetic ecosystem. Though the absolute minimum elemental requirements of most algae are apparently very similar, the environmental demands made by growing populations are not identical. Moreover, the nutrients available to each species present simultaneously may differ, since each specific quantity includes the nutrients already present ('cell-quotas') within existing cells (Droop, 1974; Rhee, 1978). Limiting nutrients are either supplied in low concentrations relative to their constitution within healthy algal tissue or they are depleted to low levels as a consequence of uptake and assimilation by the existing algal biomass which may render them unavailable to support growth of other, later species. The nutrients that have been shown (or have been presumed) most frequently to limit the rates of growth $(k')$ of algae and their apparent yields are inorganic carbon, inorganic combined nitrogen and assimilable phosphorus (Owens & Esaias, 1976). The growth of diatoms is also subject to limitation by available silicon. Indeed, the numerous recorded observations wherein severe silicon depletion has selected against the further growth of diatoms (Lund, 1950; Paasche, 1980) and in favour of non-siliceous algae are familiar examples of the regulation of phytoplankton composition by nutrients. Algae are not all equally efficient in obtaining carbon dioxide at high pH (Moss, 1973a; Talling, 1976; see also Lehman, 1978); provided that there is an abundant light energy supply. A shortage of combined nitrogen (ammonia, nitrate) presents a distinct advantage to those filamentous cyanobacteria (assemblage $H$) that are able to fix atmospheric nitrogen (Bothe, 1982). Phytoplankton composition in lakes of low bicarbonate alkalinity or which receive chronically low inputs of nitrates is biassed accordingly, especially during periods of high demand.

Among temperate lakes, however, phosphorus availability commonly occupies the critical role in limiting algal production and biomass (Schindler, 1977). The strong positive correlation between the mean summer concentration of biomass in the trophogenic layers of such lakes (ranging from $<0.1$ to $>100$ g m$^{-3}$ or, expressed as chlorophyll $a$ content, from 0.3 to $\sim$1500 mg chl $a$ m$^{-3}$) and the phosphorus available for conversion to algal biomass (Dillon & Rigler, 1974; Lee, Rast & Jones, 1978; Vollenweider & Kerekes, 1980) is well known. Similarly, demonstrable relationships exist between annual gross photosynthetic carbon fixation $(4-700$ g C m$^{-2}$ ann$^{-1})$ and phosphorus availability (reviewed in Kalff & Knoechel, 1978). However, the larger sustainable biomasses among P-rich lakes are offset by relative reductions in light penetration so that, at times, productivity of the plankton biomass (*sensu* carbon fixed per unit biomass) in eutrophic lakes may fall from 2 g C (g C) day$^{-1}$ to below the levels characterizing oligotrophic lakes ($\leq 0.6$ g C (g C) day$^{-1}$; Elster, 1965; Talling, 1966). Zero net productivity occurs when photosynthetic gains are balanced by respirational losses of the whole population, which, assuming nutrients not to be limiting, occurs in nature at biomass levels equivalent to $300-500$ mg chl $a$ m$^{-2}$ (Steeman-Nielsen, 1962; Talling *et al.*, 1973). This is really another way of stating that nutrients limit biomass rather than photosynthetic productivity (Kalff & Knoechel, 1978). Nevertheless, the translation of photosynthetically-fixed carbon into new biomass depends upon an adequate rate of supply of other nutrients to the intracellular sites of anabolism. Thus, while such supplies are available, productive (i.e. fast-growing species) will be selectively favoured over slow-growing species. As their growth becomes increasingly subject to limitation by nutrients (in more oligotrophic waters) or light (in eutrophic waters) or by exploitation (grazing, sinking) so the advantage is lost and the possibility of a transition to dominance by slower-growing species becomes stronger (Moss, 1973b).

Extensive laboratory experimentation (e.g. of Kilham, 1975; Tilman & Kilham, 1976) established that the relationship between the growth rate of individual organisms and the availability of a given limiting nutrient generally conforms to a Monod-type model (see Fig. 3a). In fact, growth rate responds directly to the total concentration of the limiting nutrient within the cells, according to Droop's (1974) cell-quota model but, at steady state, the formulations are
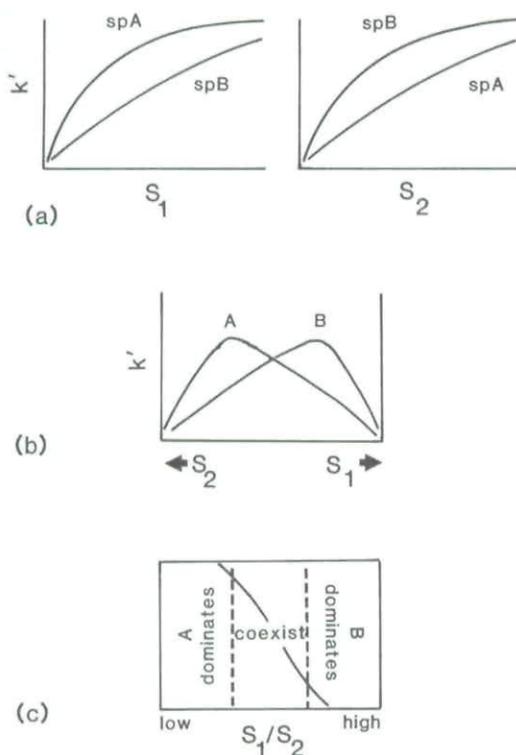
FIG. 3. Diagrammatic representation of the elements of the resource-based competition theory. The top figures (a) show the nutrient-limited growth rates of two algae, sp *A* and sp *B* in relation to the concentration of two nutrients $S_1$, $S_2$; (b) when grown together in $S_1$- or $S_2$-limited cultures, *A* should dominate when $S_1$ is absolutely low; *B* when $S_2$ is low. When both elements are simultaneously limiting (*C*) the ratio $S_1/S_2$ becomes critical: species *A* dominates at a low ratio; sp *B* dominates at a high one; the species coexist when *A* is limited more by $S_2$ and *B* is limited more by $S_1$. Redrawn from Fig. 61 of Reynolds (1983a) which was based on Figures in Tilman (1977), Tilman & Kilham (1976) and Kilham & Kilham (1980).

equivalent (Goldman, 1977; Burmaster, 1979; but see Droop, 1983). Such models have been combined to develop graphical-mechanistic models predicting the outcome of interspecific competition for two potentially-limiting resources (Tilman, 1977, 1981; Tilman *et al.*, 1982). The now-classic demonstration of resource competition between *Asterionella formosa* and *Cyclotella meneghiniana* showed that, although their nutrient-saturated growth rates were similar, growth of *Asterionella* was half-saturated at a lower P-concentration than was

that of *Cyclotella* but that the half-saturation concentration for silicon-limited growth was lower in *Cyclotella* than in *Asterionella* (Tilman & Kilham, 1976). When grown together, they co-existed well if their respective growth rates were each simultaneously limited by different nutrients. When both were P-limited, however, *Asterionella* would maintain a faster rate of growth than *Cyclotella*; *Cyclotella* would dominate when both were Si-limited (Fig. 3b). The successful direct application of the predictions to explain compositional variations in the near-shore region of Lake Michigan (Kilham, 1978; Tilman, 1981; Tilman *et al.*, 1982) provides a convincing illustration of the power of the resource competition concept.

The theory has been extended to cover interactions among other groups of species and along ratio gradients of other nutrients (Rhee, 1978; Rhee & Gotham, 1980; Holm & Armstrong, 1981) and interacting physical factors, such as light and temperature (Rhee & Gotham, 1981; Tilman *et al.*, 1982). Thus, a declining Si/P ratio gradient should differentially select among diatom species and, eventually, favour the replacement of diatoms by green algae or cyanobacteria; equally, a declining N/P ratio gradient ultimately favours the replacement of green algae by nitrogen-fixing cyanobacteria. Of added ecological importance is that, just as there are several potential and simultaneously limiting resources, so there is a corresponding diversification in the number of physiological 'niches' (Tilman *et al.*, 1982) and, hence, of a greater number of simultaneously co-existing species (cf. Petersen, 1975) and of successional changes in dominance along the ratio gradients.

While it is desirable that these approaches be further refined and extended, it is possible to discern how the characteristic assemblages may be broadly partitioned among lakes of different trophic status and characteristic resource ratios (i.e. vertically in Fig. 1) according to their individual specific growth-rate responses.

It is a logical corollary that seasonal variations in phytoplankton species composition (i.e. horizontal progressions in Fig. 1) might also be influenced directly by seasonally-changing resource-ratio gradients (Kilham & Kilham, 1980; Tilman *et al.*, 1982). Neither is this a new idea, since it follows the precedent established by Pearsall (1932), whose principal conclusions— that the sequence of species dominating the

phytoplankton of the English lakes after the demise of silicon-limited diatoms (corresponding to $E \to F \to L$) are related to changes in the N/P ratio and in the concentrations of dissolved organic matter—continue to enjoy popular acceptance, 50 years after they were propounded. Certainly, it is possible to relate seasonal changes in comparative performances of individual species in individual lakes to seasonally-changing nutrient-ratio gradients. To Pearsall's (1932) examples may be added Kilham's (1971) deductions concerning the sequential changes in diatom dominance along declining Si/P gradients (*Melosira* → *Asterionella* → *Tabellaria* → *Stephanodiscus*) among a wide variety of lakes, which approximate well to the predictions of the Tilman model (see Tilman *et al.*, 1982), and the replacement of *Eudorina* and *Volvox* by *Anabaena* in Crose Mere, as nitrogen falls to very low levels (declining N/P: Reynolds, 1978a), much in the manner predicted by Rhee & Gotham (1980). Three sequences of dominant species in Lund Enclosures may also be cited. In one, the sequence *Eudorina* (G)/*Rhodomonas* (Y) → *Sphaerocystis* (F) → *Anabaena* (H) → *Uroglena* (E) accompanied the weakening effect of heavy vernal P-fertilization through the summer period (increasing N/P gradient: see Reynolds, 1983a). On another occasion, when summer fertilization with P (but not N; N/P declined) was maintained, *Anabaena* (H) replaced *Dinobryon* (E) and *Sphaerocystis* (F) (Reynolds *et al.*, 1983). In a third, more continuous fertilizations with N, P and Si, designed to preserve more or less constant resource ratios, *Eudorina* (G), *Ankyra* (X) and *Cryptomonas* (Y) were prominent (Reynolds *et al.*, 1982).

Two striking features of these examples require comment. First, that these temporal sequences, to a greater or lesser extent, represent limited horizontal displacements among assemblages diagnostic of the same periodic stages. It is arguable that experimentally-changed nutrient-resource ratios selected either within the defined assemblages or among distinct (vernal, early summer) assemblages (B or C or D; E or F or G or H). The second is that changes in the resource-ratio gradients (albeit, artifically enhanced in the Lund Enclosures) are generated directly through the demands made by growing populations themselves. Such impacts include the depletion of carbon and

micronutrients and the reduction in light penetration. In each instance, as the environmental resources are depleted to the extent that the resource ratios are critically altered, so relative nutrient-limited growth rates and specific susceptibilities to loss processes assume selective importance. Ultimately, these factors influence subsequent changes in dominance. The species in contention, however, are always drawn from assemblage-groups representative of the relevant periodic stage.

Conceptually, such progressions are wholly analogous with autogenic seral successions among terrestrial plant communities (Reynolds, 1980, 1982; see also Margalef, 1968, 1978). Planktonic successions of the type $X/Y \to G \to H \to M$ or $E \to F \to L$ are thus directly comparable with the progressive change from bare ground to grassland and, ultimately, to high forest, albeit on a much shorter time scale. In each case, dominance passes ffom productive (fast-growing), opportunist species, that invest in reproduction of new individuals, to slower-growing conservative species, that are less vulnerable to exploitative loss processes and that are adapted to operate relatively close to the resource-determined carrying capacity of the environment. The same selective switch among differing specific life-cycle and survival strategies, encapsulated in the terms r- and K-selection (MacArthur & Wilson, 1967; see also Hairston, Tinkle & Wilbur, 1970; Pianka, 1970), can be applied equally to species of phytoplankton (Kilham & Kilham, 1980; Sommer, 1981; Reynolds *et al.*, 1983). In both cases the compositional changes are mediated by the specific responses of organisms to environmental modification consequential upon the maturation of community organization generated by the component species themselves. In the context of the freshwater phytoplankton, I have suggested that the term 'succession' be reserved to describe only such autogenic sequences of community dominance (Reynolds, 1980, 1982). 'Succession' should not be used as a synonym of 'periodicity', which, as will now be argued, is also driven by other, allogenic, variables.

*Periodic change in relation to the physical environment*

In much the same way that terrestrial successions may be sharply terminated by

catastrophic intervention (fire, drought, flood or anthropogenic activities) and returned abruptly to a more primitive stage, so the seasonal development of phytoplankton is subject to external influences. These allogenic factors include the conspicuous seasonal cycles in the intensity of irradiance, in photoperiod, water temperature (and, hence, density) and climatically-induced instances of flood and wind-mixing. Moreover, these factors interact to influence profoundly the relative stability of the perceived physical environment, which, in turn, also fluctuates seasonally. Although the general patterns of limnetic water movements, in both vertical and horizontal planes, and the spatial and temporal scales on which they operate are quantifiable (for reviews see Joseph & Sendner, 1957; Mortimer, 1974; Smith, 1975; Csanady, 1978; Ottesen Hansen, 1978), few attempts have been made to assess their integral effects on the freshwater phytoplankton (Walsby & Reynolds, 1980). However, there is now good evidence (Harris, 1983; Reynolds, 1983a; Reynolds *et al.*, 1984) that the vertical density profile of a natural water column can be usefully invoked both as a convenient summary of the stability and the extent of turbulent mixing during the preceding 1–3 days, as well as of its liability to further fluctuation in the immediate future. In winter, when the water is uniformly cold (but free of ice-cover), the velocity of the (largely wind-driven) surface flow is freely dissipated to greater depths by convection and turbulence. Solar heating at the surface, through spring and summer, lowers the miscibility of superficial water with colder water at depth and, equally, raises the level of kinetic energy required to integrate the whole column. Where the energy of wind-mixing is insufficient to overcome the density differences, turbulence rapidly subsides, flow becoming laminar or viscous. The water column stratifies, into two or more discrete layers, each separated by a metalimnion (pycnocline, thermocline) characterized by a steepened density gradient. Such gradients may persist for only hours or 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.

While planktonic organisms tend to be randomized in strong turbulent flow (vertical diffusivity coefficients $>0.01$ cm$^2$ s$^{-1}$), their intrinsic buoyant behaviours become increasingly manifest in the locality of suitably stable ($>0.02$ kg m$^{-3}$ m$^{-1}$, vertical diffusivity $<0.001$ cm$^2$ s$^{-1}$) density gradients: depending upon their densities, they then sink or float or, if they are motile, may make compensatory movements to a 'preferred' depth. In lakes, these behaviours can lead to secondary, horizontal variations in distribution (George & Edwards, 1976; Heaney, 1976).

The vertical extent of mixing has other important bearings upon the physicochemical environment. If the mixed depth ($z_m$: that upper part of the water column wherein the vertical density gradient is $<0.02$ kg m$^{-3}$ m$^{-1}$) exceeds the depth to which sufficient light penetrates to support net photosynthetic production ($z_{eu}$, or euphotic depth) then not only are entrained organisms forced to spend part of the daylight period in effective darkness (Talling, 1971) but, as they are transported through the full light gradient, they also experience rapid fluctuations in the intensity of irradiance (Harris, 1978; Farmer & Takahashi, 1982). If, on the other hand, $z_{eu}>z_m$, then net photosynthetic production can be potentially maintained both by algae entrained in the mixed layer, and by those beneath it, so long as they remain within the euphotic zone. These conditions are more likely to be met in the upper reaches of stably-stratified columns, where higher water temperatures contribute to enhanced rates of production. At the same time, increased production in a restricted volume may cause nutrients to be depleted at a faster rate than that of replenishment and weak recycling from depth, while the downward settling of non-buoyant phytoplankton and of the faecal pellets of zooplankton grazing near the surface remove potential nutrients from the epilimnion. Stably stratified columns thus tend to become progressively segregated into upper, nutrient-depleted epilimnia and lower, light-deficient hypolimnia.

In this way, well-mixed, often optically-deep ($z_m>z_{eu}$) water columns provide quite different environmental constraints from stably-stratified ones. In the first, adaptations for maximizing turbulent entrainment, for facultative maintenance of growth in a rapidly-fluctuating light field, often at low water temperatures, will be positively selected. In the second, the selective

advantage quickly passes to organisms adapted to resist permanent sinking losses and increasingly towards species ($K$-strategists) that use the available resources more efficiently.

Moreover, allogenic seasonal alterations between extensive vertical isothermal mixing (typical of autumn, early-spring and, in ice-free lakes, winter) and the formation of stable, near-surface density gradients (late spring and summer) implicitly constitute one of the principal selective variables driving phytoplankton periodicity in temperate lakes (horizontal progression in Fig. 1), through their regulating effect upon the dynamic performances of individual species (Round, 1971; Reynolds, 1980). For instance, the rates of decline in vernal diatom populations, which, in well-mixed lakes and epilimnia, are usually attributable to severe depletion of available silicon, are often equalled or exceeded in small eutrophic lakes even though silicon and other nutrients remain well above limiting levels (Paasche, 1980). In the latter instances, the critical factor appears to be the onset of summer stratification and the abrupt diminution of the mixed depth (Reynolds, 1973c, 1976). Equally, they may reappear and grow rapidly when wind-mixing increases $z_m$, either in early autumn or, in some cases, during mid-summer. Similar observations have been made in the Lund Enclosures, diatoms disappearing soon after stratification set in, even though the artificially fertilized water remained chemically capable of supporting their continued growth (Reynolds & Butterwick, 1979; Reynolds et al., 1983). Of particular interest are the 1978 experiments in which the enclosures were frequently fertilized to maintain approximately constant concentrations of dissolved nutrients (atomic ratio, 26 Si:33N:2P). In spite of supposedly steady resource ratios, major shifts in dominance from diatoms (assemblage $B$) to green algae ($G$, $X$) and then to Microcystis (M) nevertheless occurred (Reynolds & Wiseman, 1982). In a subsequent analysis (Reynolds et al., 1982), it was shown that net increase in diatoms occurred only when $z_m > 1-2$ m. A descriptive equation fitted to the data for Fragilaria showed that the sinking loss rate ($k_s$) alone exceeded the growth rate ($k'$) when $z_m < {\sim}1.2$ m. (This model has since been refined to account for the effect of optical depth upon $k'$: see Reynolds et al., 1983.)

In much the same way, certain green algae

(Eudorina, Ankyra, Sphaerocystis) and cyanobacteria (Anabaena, Microcystis) share an apparent preference for stably stratified columns (Reynolds, 1980; Reynolds et al., 1982, 1983), although the optical depth seems to be more critical than the absolute depth of mixing, $z_m$ (Reynolds et al., 1984). These evidently different responses of individual phytoplankton species to various environmental gradients can be related to each other to predict their distributions in nature. A preliminary graphical representation of these relationships has been attempted in which the various assemblages were incorporated into a simple two-dimensional matrix describing the variables 'nutrient availability' and 'depth of mixing' (Fig. 7 of Reynolds, 1980). A more refined version of this conceptual matrix is presented here (Fig. 4a). The 'nutrient availability' axis of the original is itself shown in two dimensions to accommodate variations in the N/P ratio, as absolute concentrations of either nutrient fluctuate. The vertical axis now represents physical stability of the environment: 'high stability' may be equated with low absolute mixed depths typical of warm, microstratified epilimnia, 'low stability' signifies either a much increased absolute mixed depth or increased optical depth of the mixed layer; because cold water can be more freely mixed than can warm, there is also an implicit temperature component. The matrix is divided into spaces, each labelled according to the algal assemblage most likely to be selected at those coordinates. As the extent to which the boundary planes are either rigid or immutable is still unknown, evaluation of the axes would be speculative and is thus omitted deliberately. The arrangement of the assemblages nevertheless attempts to relate their spatial and temporal distributions and the periodic sequences of their development as far as is practicable. From given starting coordinates, defined by the relevant physical conditions and nutrient concentrations obtaining, subsequent environmental changes can be tracked through the matrix to predict the likely changes in community dominance. The directions that may be followed and the types of change that they represent are shown in Fig. 4(b). Autogenic successional changes are described in the plane nutrient availability versus nutrient ratio, progressing in the general direction of the broad arrow but allowing for lateral drift as nutrient resource ratios alter. Abrupt
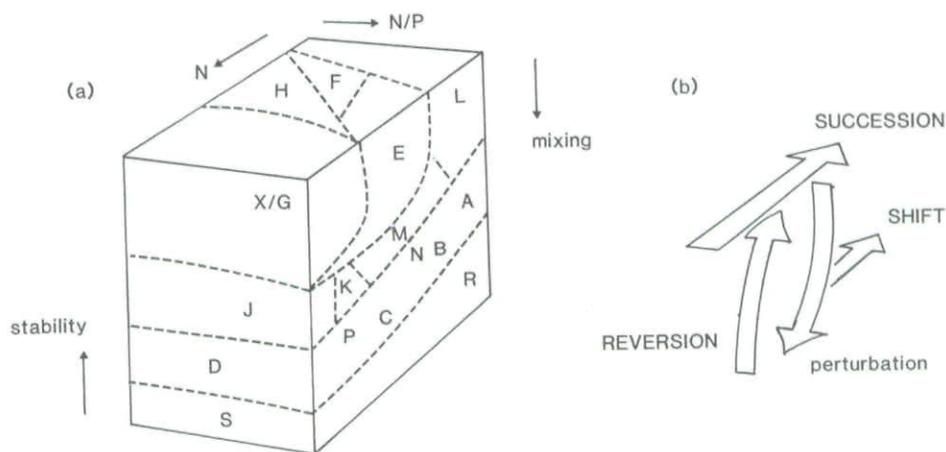
FIG. 4. (a) A hypothetical three-dimensional matrix, bounded by axes defining (i) mixing/stability, (ii) the concentrations of nitrogen (N) and phosphorus (P) and (iii) the N/P ratio and accommodating most of the algal assemblages. (b) The three directions of periodic progression from one dominant assemblage to another: from given starting coordinates, autogenic successional changes are traced in the nutrient concentration/ratio plane; increased mixing ('perturbation'), at any time, causes movement in all three planes to new coordinates whence a 'shifted' succession may be initiated or, as the system becomes less mixed, a 'reversion' to a previous dominant may occur. Developed from Fig. 7 of Reynolds (1980).

allogenic decreases in column stability (perturbation) cut downwards across the successional progression and, as relatively nutrient-rich water may become simultaneously entrained, backwards along the 'nutrient-availability' axis. If persistent, a new, '*shifted*' succession is initiated lower on the stability axis. Alternatively, re-establishment of stratification allows an upward drift through the matrix, before the successional direction is resumed ('*reversion*').

The rate of successional change is governed by the responses of individual species to the rate at which they deplete the available resources. The extent of the community responses to allogenic perturbation depends upon its severity and duration. Species capable of rapid growth (*r*-strategists) are always more likely to dominate the early stages of succession and shift. Equally, such species are most easily replaced during the course of succession or perturbation. Loss-resistant K-strategists are not only likely to dominate the later stages of autogenic succession but have an enhanced capacity to survive adverse perturbations and so, potentially, to field larger inocula ($N_0$ in equation 1) when favourable conditions are restored.

The proposed existence of an overriding influence of physical mixing upon phytoplankton periodicity is strongly supported by the results of experimental manipulations of the mixed depth in one of the Lund Enclosures (in Reynolds *et al.*, 1983, 1984). On each of several occasions during 1981, mixing of the water column to >8 m was accompanied by the renewed net growth of diatoms (*Stephanodiscus hantzschii, Asterionella formosa, Fragilaria crotonensis, Tabellaria flocculosa*: assemblages C, B, N) and, especially when optical depth was greater in late season, of *Oscillatoria agardhii* var. *isothrix* (assemblage *R*). Re-stratification ($z_m$<2 m) led simultaneously to the elimination of diatoms (mostly by sinking) and, variously, to the enhanced growth of *Ankyra* (*X*), cryptomonads (*Y*), *Sphaerocystis* (*F*), *Dinobryon* and *Uroglena* (*E*), *Anabaena* (*H*) and *Ceratium* (*L*). Though net growth of the *Anabaena* was suppressed during mixing, the stock persisted well to resume growth during subsequent restratification episodes and, eventually, to dominate during late-summer. During 1982 the enclosure was fertilized more heavily and the alterations in stability were applied more frequently (1–2 week bursts of mixing; 2–3 week periods of restratification). *Ankyra*, cryptomonads, *Eudorina* (*G*), *Sphaerocystis* and *Anabaena* produced the strongest net growth during the earlier restratification episodes but *Volvox* (*G*) and *Microcystis* (*M*) dominated the late-

season episodes. Mixing stimulated the renewed increase of diatoms (particularly of *Fragilaria*), *Staurastrum* and *Oscillatoria*. Despite the bias in favour of more 'eutrophic' indicator-species during 1982, the average biomass (15.5 μg chl *a* l$^{-1}$) was kept at an artificially low level, more reminiscent of a P-deficient mesotrophic lake and well below the mean (~50 μg chl *a* l$^{-1}$) predicted from the P-loads, according to the equations of Dillon & Rigler (1974) and Lund & Reynolds (1982).

The 'goodness of fit' of these various community responses to artificially-enhanced physical variability, imposed on a markedly non-seasonal time scale, suggests that it is to the natural, seasonal fluctuations in these factors which typical periodic cycles respond. There is little doubt that the seasonal appearance, growth and replacement of particular species are determined by many complex interactions among the fluctuating environmental resources (many of which are not considered here) and their individual dynamic responses thereto. The same statement applies to the assemblages, though less emphatically. The broadly consistent underlying periodic patterns among lakes (Fig. 1) can be interpreted as an assembly of brief successional progressions (or subsequences) along declining gradients of a characteristically critical resource (be it phosphorus, nitrogen or other nutrient, or optical depth). Each subsequence is terminated by an abrupt allogenic change in structural stability that establishes an alternative subsequence. Thus, while it is possible to relate subsequences, such as E→F→L or G→H→M to the nutrient status of the lakes in which they occur, changes (say) from vernal diatom assemblages (B, C, D) in favour of early summer opportunists (X, Y) or to mid-summer dominants (E, F, G, H, L, M) and late-summer or autumn dominants (N, P, R) that characterize all the progressions shown in Fig. 1, are directly related to annually-recurrent fluctuations in physical stability and relative mixing. The relationship between these fundamental shifts and quantifiable aspects of the basic biological adaptations of the participating species of phytoplankton is discussed in the following sections.

## Morphological criteria

Quite as striking as the differential dynamic responses of phytoplankton to environmental variability is the extreme interspecific variation in their sizes, shapes and organization into colonial structures. Another conspicuous morphological variable is the presence of swimming organelles: cells of most planktonic species of Chrysophyceae (e.g. of assemblage *E*), Volvocales (*G*), dinoflagellates (*L, M*) and Cryptophyceae (*Y*) possess one or, more usually, two flagella, whereas diatoms, desmids and chlorococcales (*A–D, F, J, N, P*) are inherently non-motile. Cyanobacteria also lack swimming organelles but many planktonic species (of assemblages *H, M, R* and *S*) possess intracellular gas vacuoles that, through a delicate balance between their production and their 'dilution' by growth and pressure-collapse, enable the cells to adjust their buoyancy to be either more or less dense than the surrounding water (for a full explanation, see Walsby, 1978).

Variety among the phytoplankton is further enriched by differences in pigmentation—the relative contents of chlorophyll and accessory photosynthetic pigments—though these variations tend to be segregated more according to major taxonomic affinities.

These traits are not unique to freshwater phytoplankton. Similar diversity of size, shape, colony formation, motility and pigmentation is evident among the marine phytoplankton (Malone, 1980; Taylor, 1980). The adaptive significance of the morphological categories, proposed by Schütt (1892) and Gran (1912), has been invoked by several workers (Margalef, 1958, 1967; Smayda, 1970; Malone, 1980; Sournia, 1981) but, as Sournia's (1982) stimulating review points out, many specific properties and the supposed advantages they confer have not been adequately investigated. This is scarcely less true of the freshwater phytoplankton but, as I shall now attempt to establish, morphological adaptations are central to the different responses of individual species to environmental variability.

### Size and shape

The essential evolutionary adaptation common to all phytoplankton—the need to prolong suspension—is manifest in their universally microscopic sizes (Reynolds, 1983a). Within this constraint, typical specific cell volumes of freshwater species (e.g. Table 3 of Reynolds, 1983a and Fig. 5) range over four orders of magnitude, from about 5–18 μm$^3$ (in *Synecho-*
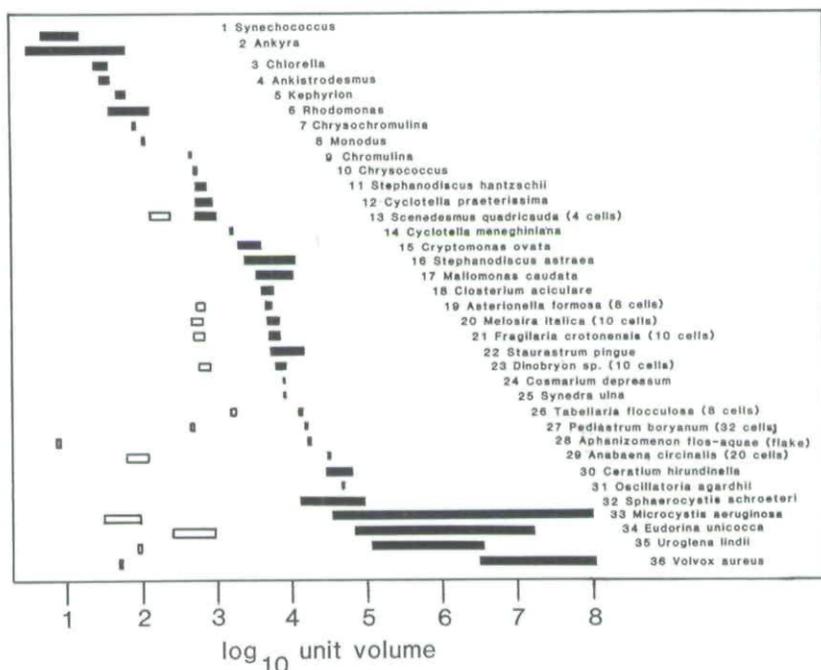
FIG. 5. Mean volumes (in μm³) of discrete algal 'units' (free unicells, colonies and including mucilage, where appropriate; mean cell volumes of colonial species shown as open figures) of some species of freshwater phytoplankton. Original, based on data and sources given in Table 3 of Reynolds (1983a).

*coccus*) to about $30-70\times10^3\mu m^3$ (in *Ceratium hirundinella*). Whereas the cells of the smaller species generally tend to be spherical or ellipsoidal in shape, those of 'larger' species (generally $>500$ $\mu m^3$) exhibit an increasing tendency either to become elongated in one ('attenuated' shapes, e.g. of *Closterium* and *Synedra* spp.) or two planes ('flattened' shapes e.g. of *Trachelomonas*) or to possess protuberances in two or three planes that give much more complex shapes (e.g. in *Ceratium* and many *Staurastrum* spp.). These relative departures from the spherical form counteract the geometrical loss of relative surface area consequential upon increasing spherical volume *per se*, to the extent that the ratios of surface area to volume (hereinafter, *SA/V*) among individual cells vary over little more than one order of magnitude, from about 0.2 $\mu m^{-1}$, in *Ceratium,* to about 3.6 $\mu m^{-1}$ in *Ankistrodesmus* (cf. Lewis, 1976).

The diversity of phytoplankton morphologies is enhanced by species habitually forming many-celled coenobial or colonial structures. The arrangements of the individual cells often

generate new shapes. Filamentous (e.g. in *Melosira, Oscillatoria*), stellate (e.g. in *Asterionella*), ribbon (e.g. in *Fragilaria*), and plate-like (e.g. in *Pediastrum*) structures minimize the area of contact between the individual cells, so that *SA/V* is largely preserved. On the other hand, binding of cells in common mucilaginous sheaths (e.g. in *Sphaerocystis, Eudorina, Microcystis*) often produces much larger, quasi-spherical colonies ($2.5\times10^3$ to $100\times10^6$ $\mu m^3$). So far as the *SA* of such colonies can be estimated, *SA/V* would appear to be inherently low ($0.01-0.2$ $\mu m^{-1}$). Coiling (in many *Anabaena* spp.), and radial (in *Gloeotrichia*) or linear aggregation of filaments, to form 'flakes' or 'rafts' (in *Aphanizomenon*), often accompanied by mucilage sheathing, also contributes to secondary structures having low *SA/V* ratios (Reynolds & Walsby, 1975; Reynolds, 1983a).

An elegant graphical representation of the relationships between morphological diversification and *SA/V* was devised by Lewis (1976). The same method of construction was adopted to derive Fig. 6, in which average measurements
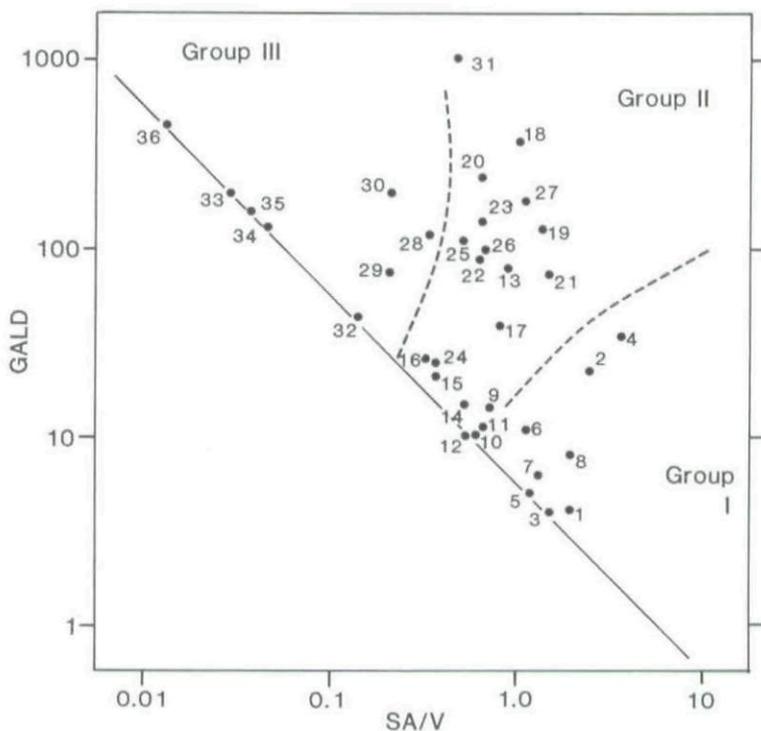
FIG. 6. Freshwater phytoplankton morphology—the greatest axial linear dimension (GALD, in $\mu$m) plotted on a log scale against $SA/V$ ($\mu$m$^{-1}$) ratio distinguishes among near-spherical shapes (close to the diagonal line representing the diameter of spheres of given $SA/V$) and larger algae which are morphologically distorted and in which $SA/V$ is increased (points well above the diagonal line). The grouping of the points is on the basis of periodic position (see text)—the figure therefore shows the remarkable concordance between algal size, shape and colonial organization and seasonal behaviour. Original plot of data given in Table 3 of Reynolds (1983a) and constructed according to Lewis' (1976) Fig. 1. Numbered points refer to species listed in Fig. 5.

(taken from Table 3 of Reynolds, 1983a) of the greatest axial linear dimension ($GALD$) are plotted against corresponding measurements of $SA/V$ for each of a selection of phytoplankton units (cells or colonies, according to typical habits). Like Lewis' (1976) original, Fig. 6 emphasizes the decrease in $SA/V$ that accompanies increase in unit size and the effect of structural attenuation upon $SA/V$ among larger individual units.

These representations of cell- or colony-size (Fig. 5) and shape (Fig. 6) reveal clear segregations among species ascribable to one or other of the three periodic categories. Thus, the early-summer opportunist group (I: assemblages $X$, $Y$) comprises mainly unicellular species of small size and simple shape ($V < 500$ $\mu$m$^3$; $SA/V > 0.7$). The species characterizing the assemblages of well-mixed vernal- or late-summer water columns (Group II: $A$, $B$, $C$, $D$, $N$, $P$) tend to have larger individual cells or colonies ($V$: 600–20,000 $\mu$m$^3$) but whose complex shapes generally preserve a high $SA/V$ ratio ($> 0.3$). The 'summer dominants' (Group III: $F$, $G$, $H$, $K$, $L$, $M$) characteristically form large individual units ($> 10^4$ $\mu$m$^3$) of low $SA/V$ ($< 0.3$ $\mu$m$^{-1}$). It is of interest that, of the species of Chrysophyceae (assemblage $E$) for which data are available, only *Uroglena* falls among Group III summer forms; the others are apparently allied more closely to group II. The high $SA/V$ ($\sim 0.5$) of the fine, solitary threads of *Oscillatoria agardhii* ($R$, $S$) places it in Group II, while certain small centric diatoms (*Cyclotella* spp., *Stephanodiscus hantzschii*) and large cryptomonads fall close to the arbitrary boundary between Groups I and II.

It is doubtful that this concordance between the morphological features of these species and the periodic position of the assemblages they represent is entirely coincidental. Indeed, the existence of a close interdependence between

the environmentally-determined dynamic responses of species and the morphological organization of their cells is strongly implied. Recognition of this functional relationship opens additional perspectives on the mechanisms that regulate phytoplankton periodicity.

## Phytoplankton morphology and function

It is probable that several morphologically-related mechanisms contribute to periodicity. In this section I discuss two sets of such mechanisms—those related to prolonging residence in the trophogenic zone and those influencing cell physiology and growth. The arrangement of this discussion does not imply any relative importance of either set of mechanisms or of any other: it is chosen to facilitate the logical development of the argument.

### Morphology and prolonged suspension

Most freshwater phytoplankton are more dense than water and therefore sink in relation to the water immediately adjacent to it. This condition applies even in fully developed turbulence, wherein planktonic organisms are constantly randomized but are nevertheless liable to be lost from suspension in a given mixed depth ($z_m$) into the non-turbulent water below (the metalimnion or basal boundary layer). Loss from suspension follows a first-order exponential decay curve (cf. dilution) determined by the intrinsic settling velocity ($u'$) of the particles relative to the depth of the mixed layer (Smith, 1982). If growth is zero and sinking is the only source of change,

$$N_t \times N_0 \, e^{-u't/z_m} \qquad (5)$$

It follows, from equations (1) to (3), that the exponential rate of sinking loss ($k_s$) is given by:

$$k_s = u'/z_m \qquad (6)$$

The intrinsic settling velocities of smaller planktonic algae are assumed to conform to the modified Stokes Equation (Hutchinson, 1967; Walsby & Reynolds, 1980):

$$u' = 2gr^2(\varrho' - \varrho)/(9\eta \cdot \phi_r) \qquad (7)$$

where $g$ is gravitational acceleration, $\eta$ is the coefficient of viscosity of the medium, $\varrho$ its density, $\varrho'$ the density of the alga and $r$ is the radius of a sphere of identical volume to the alga. The term ($\varrho' - \varrho$) is known as the 'excess

9

density'; $\phi_r$, the coefficient of 'form resistance', expresses the effect on sinking rate of the relative departure of the algal shape from the spherical form: i.e.

$$\phi_r = u'/u_s \qquad (8)$$

where $u_s$ is the sinking velocity of the sphere of the same volume and excess density. Values of $\phi_r$ have rarely been independently calculated for non-spherical algae, except when all of the other factors in equations (7) and (8) have been determined (e.g. Walsby & Xypolyta, 1977; Reynolds, 1979; Wiseman, Jaworski & Reynolds, 1983). Stokes' Law nevertheless serves to illustrate the effects of morphological diversity upon sinking velocity (and, by implication, on suspension). For a given excess density, increasing size ($r$) confers an obvious disadvantage. If particle size is increased simply by enveloping the cell in mucilage, increase in $r$ may be more than compensated by a decrease in excess density (see Walsby & Reynolds, 1980). Frequently, secondary aggregation of cells in colonies has the effect of increasing $r$ but, depending upon their mutual arrangement, the new shape may exaggerate $\phi_r$. This particular adaptation offers an advantage to diatoms whose opaline cell walls considerably raise their excess densities ($\varrho'$: 1100–1300 kg m$^{-3}$; Reynolds, 1983a; Wiseman et al., 1983). Of possibly greater significance than any lowering of sinking rate is the demonstrable increase in capacity for passive entrainment in turbulent eddies that high $\phi_r$ confers (for examples, see Reynolds, 1983a). Even so, the dependence of larger, non-motile algae (especially Group II diatoms: sinking rates generally 0.2–1.2 m day$^{-1}$) upon relatively deep mixing, that preserves low values of the ratio $u'/z_m$, is clear.

Motility (including buoyancy regulation) offers a counter to permanent sinking from the mixed layer and, when turbulence subsides, a means of regaining station at a (supposedly) desired depth. In both instances the rapidity of compensatory vertical movements will be enhanced by a lowered form resistance. Swimming speeds of dinoflagellates and colonial Volvocales and the buoyant flotation rates of colonial cyanobacteria probably exceed passive sinking rates by one or more orders of magnitude (Reynolds & Walsby, 1975; Sournia, 1982). This 'alternative strategy' of morphological adaptation, shown by Group III genera (*Eudorina*,

*Uroglena, Microcystis*), in which large size and lowered form resistance ('streamlining') are coupled with efficient motility, will be of maximum benefit in waters mixed infrequently or only superficially ($z_m < z_{eu}$).

The smaller algae of Group I appear to adopt an intermediate position between these two extremes. Small size contributes to low sinking velocities even in non-mixed layers, wherein motile forms are capable of directing movements towards or away from particular depths (Baker, 1970; Fee, 1976; Reynolds, 1983a).

A second size-related constraint upon maintenance in suspension is the influence of grazing of algae by zooplankton. The dynamic interdependence between producer and consumer is complex and frequently misunderstood (Frost, 1980; Gliwicz, 1980). Knowledge of the feeding habits and food selection of individual animal species is also still incomplete. What is relevant to the present discussion, however, is (i) that larger filter-feeding crustacea (e.g. *Daphnia* spp.) potentially make the biggest impact upon phytoplankton, (ii) that their abundance depends upon earlier growth, fecundity and recruitment of juveniles, and (iii) that these processes, in turn, are subject, *inter alia*, to adequate concentrations (for *Daphnia*, $>0.4 \mu g$ C ml$^{-1}$: Lampert, 1977) of suitable foods being available. Food selection in *Daphnia* spp. appears to be exclusively on the basis of size, determined by the spacing of the filtering setules on the phyllopods ($1-2 \mu m$ apart) and the width of the carapace gape (Gliwicz, 1980). The maximum dimensions of ingested food particles is related to body-size (Burns, 1968): particles up to $50-60 \mu m$ in two or three planes can be ingested by *Daphnia hyalina* (Ferguson, Thompson & Reynolds, 1982) and possibly filaments, longer ($<110 \mu m$) in one plane only (Nadin-Hurley & Duncan, 1976).

Filter-feeding thus primarily affects the dynamics of small algae (mostly of Group I, some Group II). The extent of the effect depends upon the relative magnitudes of the rates of growth ($k'$) and grazing loss ($k_g$) (see equations 2 and 3). In turn, $k_g$ is dependent upon the community filtration rate (CFR), which amounts to the product of the concentration of filter-feeding animals and the volume of water filtered by each individual at the water temperature obtaining. $k_g$ will not necessarily be identical for all species present simultaneously,

owing to feeding selectivity ($\psi$; scaled from 0, for total rejection, to 1 for indiscriminate ingestion). Thus,

$$k_g = \psi(CFR) \tag{9}$$

Reynolds *et al.* (1982) recorded several instances in which CFR exceeded the equivalent of 0.9 epilimnetic volumes day$^{-1}$. For small algae ($\ll 60 \mu m$), $k_g$ may have also approached 0.9 day$^{-1}$. In effect, such algae must maintain a growth rate of similar order if their populations are to be maintained. Larger algae (including colonies of *Fragilaria, Microcystis*), for which $\psi \rightarrow 0$, may be unaffected directly by grazing and continue to increase even when $k' \ll CFR$. The implication is that intense grazing generally selects in favour of large algae and against small species, at least when ($k' - k_g$) of grazed species is less than $k_n$ of the ungrazed species. Reynolds *et al.* (1982) presented dynamic simulations of the simultaneous net growth rates of *Cryptomonas, Fragilaria* and *Microcystis* under various combinations of community filtration rate (regulating $k_g$ values) and of mixed depth (regulating $k_s$). Assuming neither light nor nutrients to be limiting, *Microcystis* (Group III) would dominate when $z_m$ was low and CFR was simultaneously high.

Such theoretical outcomes, distinguishing between relative performances of organisms ascribable to Groups I, II and III, correspond with broad seasonal variations in the interaction of these loss processes, associated with the onset of stratification and with the development of zooplankton populations. That their respective roles are contributory rather than causal is emphasized by the fact that changes in phytoplankton species dominance frequently occur at subcritical levels of either $k_g$ or $k_s$. Moreover, these components ($\Sigma k_L$) constitute only one half of the dynamic equation (2): some further consideration of the factors influencing $k'$ is also required.

*Morphology and physiological processes*

The second category of morphologically-determined mechanisms concerns the physiological functioning of phytoplankton cells. Increase in specific biomass depends upon a net organic assimilation of materials gained from the environment. All such exchanges of energy, gases, nutrients and waste between the cell and the external medium must take place across the
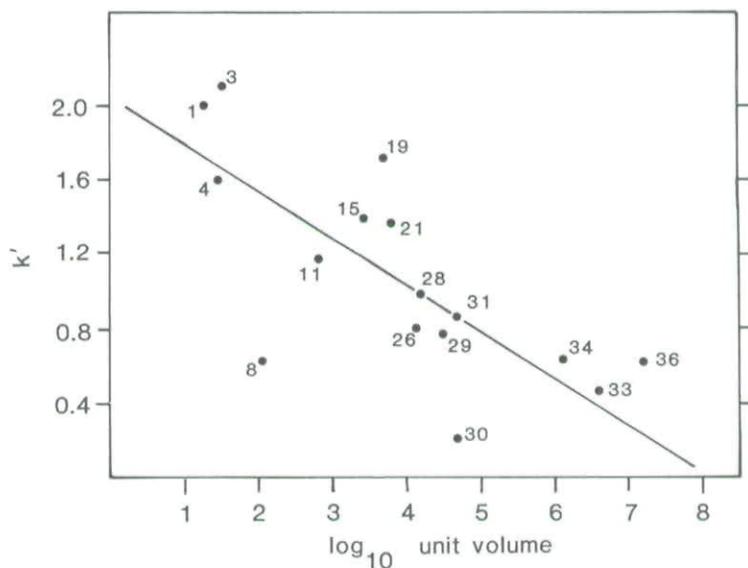
FIG. 7. Algal growth rates ($k'$) in culture, generally continuously light- and nutrient-saturated at about 20°C, plotted against mean unit volumes. Data from Tables 3 and 16 of Reynolds (1983a), with unpublished data for *Volvox aureus*. Numbers refer to species listed in Fig. 5. The equation of the regression fitted to the points is $k' = 1.929 - 0.216 \log V$ ($r - 0.731$, $P < 0.05$).

cell wall. To a greater or lesser extent they also involve intracellular transfer of metabolites (by diffusion or through enzymic reactions) between the cell wall and the sites of assimilation. The surface area of the cell thus assumes an obvious relevance to the present argument, as it relates the exchange potential to the biomass of the cell material (cf. Sournia, 1981). It may be contended that increasing the size of a spherical cell *per se* depresses the average rate of intracellular assimilation per unit mass but that structural distortions, increasing $SA/V$, have an opposite effect (Sournia, 1981, 1982). Thus, if the external supplies of light and nutrients are saturating, then the maximum sustainable (i.e. assimilation-limited) growth rates of algae may be expected to be inversely correlated to cell size and positively correlated to cell $SA/V$. The available evidence for freshwater phytoplankton, taken from Tables 3 and 16 of Reynolds (1983a) and replotted in Figs 7 and 8(a), suggests that both statements apply to morphological units grown under idealized culture conditions, at least as well as they have been shown to do so in marine phytoplankton (see Margalef, 1957; Eppley & Sloan, 1966; Banse, 1976). Moreover, it remains possible to distinguish the various periodic groupings.

The morphological impact on cell metabolism applies equally to rates of catabolic respirational losses from cells which, as a function of cell biomass, will be relatively greater among small, high $SA/V$ forms (Laws, 1975). The significance of respirational losses in regulating growth rate has been questioned by Banse (1976): while they continue to represent constant fractions (between 0.02 and 0.2) of the maximum photosynthetic rate over a wide range of temperatures, no size dependence of relative respirational rate will be necessarily evident. When cells are prevented from photosynthesizing at the maximum rate (e.g. when deprived of light), however, the small, high-$SA/V$ forms seem likely to respire larger relative fractions of cell biomass per unit times in accord with Laws' (1975) view.

It is not immediately clear either which metabolic process or processes are so constrained by the morphological and cytological structure of cells to limit their overall growth rates or why units of conspicuously differing morphologies should respond differently to environmental variability in their natural habitats. However, the limited available data describing specific growth responses to controlled variations in temperature and light suggest the
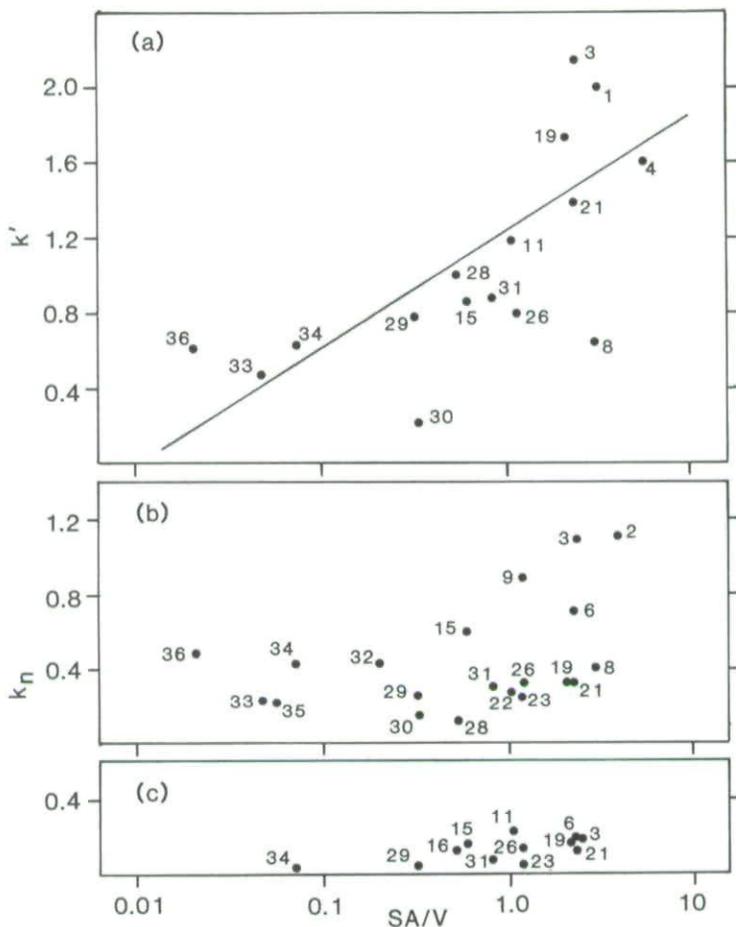
FIG. 8. (a) Algal growth rates ($k'$) in culture, generally continuously light and nutrient-saturated at about 20°C plotted against mean unit $SA/V$. Maximum net growth rates ($k_n$, corrected for grazing, but not sinking, losses) of natural phytoplankton in (b) the summer epilimnia ($z_m<5$ m; $\theta$: 16−20°) and (c) the pre-equinoxial mixed layers ($z_m$: 9−11 m; $\theta$: 4−7°) of the Lund Enclosures in Blelham Tarn. Data from Tables 3, 16 and 17 of Reynolds (1983a) and some, later unpublished entries. Numbers refer to species listed in Fig. 5. The equation of the regression fitted to the points in Fig. 8(a) is $k'=1.290+0.547$ log $SA/V$ ($r=+0.698$, $P<0.05$).

existence of potentially selective interactions. The temperature dependence of light-saturated growth rates of six species in culture may be greater among species whose individual cells have low $SA/V$ ratios (see Fig. 9). This relative dependence is expressed by the $Q_{10}$ value (here representing the factor by which $k'$ is increased for a given 10°C-rise in temperature). The values shown may be compared with the generally-accepted $Q_{10}$ values for photosynthetic carbon-fixation and respiration rates (2.0−2.3: see Harris, 1978). Although there is a clear need for additional experimental evidence, it is possible to deduce that whereas the growth rates of higher $SA/V$ forms may be limited by net photosynthetic rates, those of low-$SA/V$ cells may be limited more by the rates of surface exchange and internal transport, both of photosynthetic gases and of the other components (nutrients) required to assemble new biomass. Both the exchange and the transport processes are themselves temperature-dependent but are independent of light. It follows that, while the water remains warm (>15°C), these processes should be correspondingly less responsive than photosynthesis to reductions in total insolation, perceived irradiance levels and photoperiod (but see later). Dark respiration should remain
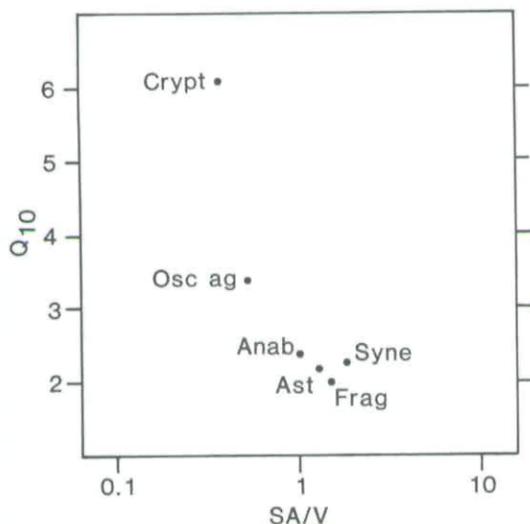
FIG. 9. $Q_{10}$- values of light- and nutrient-saturated growth rates of six species of phytoplankton (*Anabaena flos-aquae, Asterionella formosa, Cryptomonas ovata, Fragilaria crotonensis, Oscillatoria agardhii* and *Synechococcus* sp.) at various temperatures plotted against mean cell *SA/V* ratios. Sources of data, Table 3 and Fig. 68 of Reynolds (1983a).

vernal period that Group III is poorly represented in Fig. 8(c). Although it is the higher-*SA/V* species that show the greatest capacity to grow under these conditions, it is apparent that the performance of (Group I) smaller algae is apparently no better and, indeed, may be poorer than those of the algae with larger cells in Group II. This is perhaps the consequence of the relatively larger respirational losses sustained by small cells during the long dark periods obtaining under conditions of short winter days and full column-mixing. There is some evidence (discussed in Reynolds, 1983a) that under conditions of winter ice cover those same species can maintain faster rates of growth than diatoms, despite the low ambient water temperatures, so long as they remain within the euphotic zone. In this context it would be valuable to investigate the phytoplankton composition of high-altitude, tropical lakes, offering the combination of high solar irradiances and low water-temperatures. More experimental data on the responses of laboratory cultures to extremes of temperature at different irradiances and photoperiods are also desirable.

## Photosynthetic regulation and behaviour

The preceding discussion presupposes that photosynthetic carbon fixation is always maintained at the highest sustainable levels under the given hydrological conditions. This section draws attention to the existence of interspecific differences in the regulation of photosynthesis that contribute to differences in specific growth rates and, potentially, in phytoplankton composition. The discussion impinges upon the structural arrangement and functioning of the photosynthetic apparatus and the biochemical pathways followed in carbon fixation and metabolism. Detailed description of these topics is not included here; where amplification is required, Harris' (1978) excellent review should be consulted.

At a given temperature, maximum photosynthetic rate ($P$) is kinetically related to perceived light intensity (Fig. 10). The relationship may be specified in terms of four characteristics: the light-saturated photosynthetic rate ($P_{max}$), the points of its onset ($I_k$) and its inhibition ($L_i$) and the photosynthetic efficiency at subsaturating (limiting) irradiance intensities ($P/I$). In essence, the $P_{max}$ characteristic is

unchanged but will detract from growth rate to an increasing extent as the dark period is extended. Such a relationship is implied by the plot (Fig. 8b) of maximum specific rates of increase observed (after correction for grazing losses) in the nutrient-enriched summer epilimnia of the Blelham enclosures ($\theta > 15°C$). *In situ* growth rates are markedly depressed compared to the maximal rates in culture (Fig. 8a) but the relative depression is least among low-*SA/V* colonies of Group III and greatest among high *SA/V* unicells of Group I, although the latter remain capable of maintaining the fastest absolute rates of growth.

Under conditions of full isothermal mixing, during winter and spring, both the light period and water temperature are severely reduced. Here, temperature-limitation might be expected to act more upon the light-independent processes of low-*SA/V* species than of high-*SA/V* species, while the growth rates of the latter continue to be limited more by net photosynthesis (Tamiya *et al.*, 1953; Foy, Gibson & Smith, 1976). So few of the low-*SA/V* unicells and colonial algae, if present, grow at measurable rates in the Blelham Enclosures during the
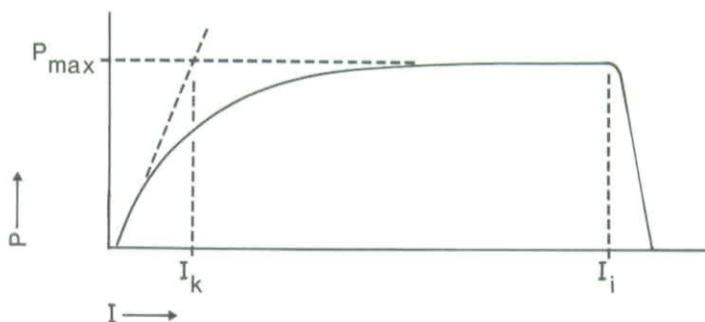
FIG. 10. A simplified plot of the relationship of photosynthetic rate ($P$) and irradiance intensity ($I$) in phytoplankton, showing the onset of light saturation ($I_k$) and inhibition ($I_i$) of $P_{max}$.

determined by the well-defined light-interception properties and electron-transport activity of chlorophyll, the principal photosynthetic pigment. Thus, the inflection in the $P$ vs $I$ curve at $I_k$ (see Fig. 10) represents a switch from a rising light-limited portion to a light-saturated, temperature-sensitive plateau (Harris, 1978).

Photosynthesis in intact cells passively transported through the full light gradient follows similar characteristics of light-limitation, -saturation and inhibition (albeit subject to variable time lags). Constant turbulent transport through or beyond the euphotic depth inevitably exposes the entrained algae to frequent and rapid fluctuations ranging from near full-sunlight ($I > 800 - 1600 \, \mu E \, m^{-2} s^{-1}$ of photosynthetically-active radiation, or PhAR) to total darkness. Where the mixed depth ($z_m$) is less than the contemporary euphotic depth ($z_{eu}$), the diel fluctuations in light experienced by entrained algae will be no less extreme, but the fluctuations will be both less frequent and more gradual (Farmer & Takahashi, 1982). Where $z_{eu} \gg z_m$, there is considerable scope for motile organisms to optimize their vertical position during the daylight period; the frequency of fluctuation is diel.

In order that algae may survive and grow, it is axiomatic that their photosynthetic physiologies should be well-adapted to the characteristic light conditions of the water column in which they are distributed ('the underwater light climate' of Talling, 1971). Several such physiological adaptations are evident among phytoplankton. For instance, the content of chlorophyll and accessory pigments of individual cells (especially of Group II diatoms and *Oscillatoria*) circulating

through optically deep mixed layers can be facultatively increased, by a factor of 2−5 (Reynolds, 1983a). This enables the cells to raise the rate of carbon fixation per unit of biomass during the short periods of exposure to light and to increase photosynthetic efficiency in the light-limited layers. As Cosper (1982) has demonstrated with laboratory cultures of a marine diatom, *Skeletonema*, exposure to rapid fluctuations in light intensity cannot, by itself, raise the efficiency of cell productivity and growth, relative to that under constant, saturating irradiances. On the other hand, the extreme efficiency of light-harvesting and of conversion into growth in *Oscillatoria agardhii* has been shown to be of considerable selective advantage in well-mixed, turbid water columns (Mur, Gons & van Liere, 1978). Thus by making as much 'hay' as possible in the brief interludes of 'sunshine', light-adapted, Group II organisms may optimize their growth potential under the high-frequency light fluctuations perceived in optically-deep columns.

Passive transport in mixed layers inevitably brings cells close to the water surface. Depending upon the intensity of the incident irradiance and its vertical attenuation with depth, the risk of photosynthetic inhibition may be restricted to within the upper metre or so. While this layer is convectively wind-mixed (current velocities $> 0.03 \, m \, s^{-1}$) entrained cells are unlikely to remain within the layer for long enough for marked photoinhibition effects to develop (5−10 min: Harris & Piccinin, 1977) before they are removed again to depth (see also Harris & Lott, 1973). The risks are proportionately greater in the restricted mixed depths of summer

epilimnia, particularly when water transparency and incident irradiances are high. Indeed, Group II diatoms (see Reynolds & Wiseman, 1982; Reynolds, 1983b) and *Oscillatoria* spp. (Reynolds *et al.*, 1983) 'stranded' near the surface when mixed depth is abruptly reduced (e.g. at the onset of thermal stratification) quickly develop symptoms of photoinhibition, contraction of plastids, damage to the photosynthetic apparatus and, ultimately, cell lysis. The sinking rates of diatoms also increase sharply; this coupled with the decreased capacity for entrainment, contributes to their rapid elimination from the epilimnion (see Fig. 24 of Reynolds, 1983a).

Evidence from short-term exposures to a range of high irradiances ($>\sim200$ $\mu$E m$^{-2}$ s$^{-1}$; see Harris, 1973; Harris & Piccinin, 1977) indicates that photoinhibition of gross photosynthetic rate is probably common to all algae exposed to high light intensities but that marked differences in susceptibility and subsequent recovery exist among them (see also Harris, 1978). Also, algae have the option of controlling their net carbon-fixation by excreting excess photosynthates or photosynthetic intermediates (e.g. glycollate) and, at least among green algae, of photorespiration (see Raven & Beardall, 1981). These differences are reflected in the rates at which photoinhibition occurs. Inhibition apparently occurs less rapidly (taking between 30 min and 3 h) among 'sun-adapted' green algae and dinoflagellates taken from surface waters of stratified lakes in summer (Harris, 1978). Thus, there seems to be a close link between the low photosynthetic efficiencies and slow photoinhibition of summer assemblages (Group III) that contrasts with the 'shade' adaptations of deep-mixed diatom populations (Group II).

Motility (including buoyancy control) offers an additional mechanism for the self regulation of photosynthesis. If convection alone fails to transport the algae away from the irradiance levels obtaining near the surface, directed movements away from the surface may achieve a similar result. Equally, the same algae can avoid settling out of the open water and regain position in the euphotic zone after mixing episodes ($z_m > z_{eu}^*$). The net effect of these processes will be to concentrate the algae within restricted depth ranges. Migrations of flagellates (Baker, 1970; Heaney, 1976; Fee, 1976) and cyanobacteria (Reynolds & Walsby, 1975;

Klemer, 1976) resulting in pronounced mid-water maxima are well known. The focus of such movements is frequently at depths where photosynthetic rate is markedly submaximal (Baker, Brook & Klemer, 1969; Reynolds, 1975, 1978b). This behaviour has sometimes interpreted as a way of gaining access to metalimnetic and hypolimnetic nutrient reserves when supplies are depleted in the epilimnion (Fogg & Walsby, 1971; Reynolds & Walsby, 1975). This explanation may have been overstated. A more plausible deduction might be that while assimilation and growth rates are limited by an epilimnetic nutrient deficiency or, perhaps, by a morphological constraint (see above), excess photosynthate must be excreted or otherwise metabolized. Stratification deep in the light gradient offers a means of reducing photosynthetic rate to a level compatible with the maximum growth rate sustainable by the limiting resource. This alternative view is supported by the experimental observation that nitrogen supplied to N-limited *Oscillatoria* populations enables them to move higher in the light gradient (Walsby & Klemer, 1974; Klemer, Feuillade & Feuillade, 1982).

It will be seen that, in much the same way that the striking morphological differences among planktonic arguably represent separate adaptations to the various scales of physical variability in natural water bodies (see above), differing physiological mechanisms apparently enable the respective organisms to optimize their photosynthetic productivity under the appropriate conditions. Although some photosynthetic adaptation can occur over as few as one or two generations and is to some extent the consequence, rather than the cause, of the dynamic responses to environmental variability, it is nevertheless an integral component of each specific growth and survival strategy and so contributes to the regulation of periodic community change.

### Phytoplankton periodicity: a perspective

Earlier in this review, I suggested that planktonic algae will grow when and where they are able to do so. 'When' is the key to periodic change; 'where' differentiates periodic sequences in different types of water-body. Both determine the ability to grow through a complex series of interactions among environ-

mental variables. There appears to be no single factor ultimately determining seasonality in activity and dominance of the phytoplankton. Rather there is a group of factors—involving nutrient preferences, nutrient-limited kinetics, resistance to losses, motility and photosynthetic physiologies, each of which may be directly or indirectly influenced by morphological criteria—that selects among potentially competing species. Nevertheless these factors may be provisionally arranged in a hierarchial sequence based on the extent of the community responses that they invoke. In descending order, the sequence moves from interactions involving primarily physical (temperature, mixing, relative light penetration), chemical (ionic environments, nutrient availabilities and relative gradients) and then biotic (grazing, parasitism) factors. Each hierarchial level then selects among the relative growth potentials of phytoplankton on progressively finer adaptive criteria, much in the manner of a dichotomous key to the identification of plants or animals. I wish to conclude by restating the differential adaptations of phytoplankton that determine their responses to environmental variability and by offering the rudiments of a diagnostic key to their spatial and temporal distributions.

Correlations exist among the morphologies, physiologies and periodic positions of freshwater phytoplankton, similar to those that have been detected in marine phytoplankton (Margalef, 1957, 1978; Smayda, 1970; Malone, 1980; Sournia, 1981, 1982). The present review goes further, perhaps, in seeking to identify fundamental causal interactions between the dynamic responses of phytoplankton to environmental variability, on the one hand, and basic aspects of form and function, on the other. The general morphological and ecological characteristics of the three main periodic groupings are summarized in Table 1. High (>0.3) $SA/V$ favours high rates of metabolic exchange, net photosynthetic yield, nutrient uptake, assimilation and, ultimately, growth over a wide range of temperatures. These can be subdivided among those algae (periodic Group I) whose relatively high $SA/V$ is a geometrical consequence of a small unit size and those larger individuals and colonial units (of Group II) that achieve comparable $SA/V$ values through structural distortions (morphological attentuation). Larger units are less sensitive than small cells to

respirational losses in darkness but are more reliant upon turbulent entrainment for maintenance in suspension (this applies especially to the heavier, non-motile diatoms). Group II algae are thus better suited to the mixed water columns obtaining in small lakes during spring and autumn and, in larger lakes, for long periods in summer as well ($z_m > 3$ m). Photosynthetic adaptation may enhance their ability to growth under conditions of high-frequency light fluctuations. Group I algae can survive longer in stratified columns and also tolerate mixing unless $z_m \gg z_{eu}$. Population increase and maintenance in many species of Groups I and II are sensitive to deficiencies in nutrient availability and, variously, to in situ loss processes.

The combination of increasing unit size (either of cells or of colonial structures) and reducing $SA/V$ that distinguishes Group III organisms brings a general lowering of physiological activity and growth rate as well as an increase in sensitivity to low temperatures. The coupling of motility with large unit size counters the risk of permanent sinking from mixed columns and permits rapid, self-regulated adjustment of vertical station in stratified layers. These algae are always likely to perform relatively better at the temperatures obtaining in summer epilimnia (wherein their minimal photosynthetic light requirements are also frequently saturated) than in cold, isothermally-mixed columns. Photosynthetic adaptation here tends towards lowered photosynthetic efficiency and resistance to photoinhibition and is thus more closely tuned to low frequency oscillations in perceived light levels. The nutrient requirement to saturate growth rate is unlikely to be much lower than in low $SA/V$ forms but biomass conservation and low sensitivity to in situ losses contribute to improved survival prospects under extreme nutrient limitation. Many Group III organisms also produce overwintering propagules that may contribute inocula of vegetative cells in future growing seasons.

These morphologically-determined, selective responses to major, seasonally-changing features of the physical environment underpin the conspicuous periodic cycles in lakes. Low average insolation selects against Group I, low mixed-depth against Group II and low temperature against Group III. Vernal isothermal mixing (cold; poor light), will normally favour Group II; stable summer stratification will be

TABLE 1. Summary of morphometric and physiological features of periodic groups and phytoplankton asemblages

| Group | Unit volume ($V$, in $\mu m^3$) | SA/V | Motility | Photosynthetic efficiency | Photoinhibition | $k'_{max}$ at ~20°, $day^{-1}$ | $Q_{10}$ of growth rate | Light dependence of growth rate | $\psi$ | Adaptive strategies | Representative assemblages |
|---|---|---|---|---|---|---|---|---|---|---|---|
| I | <500 | 0.7–3.0 | + | ? | Potentially avoid | High, probably > 1.5 | < 2.5 | High | →1 | r | X, Y |
| | | | – | Facultatively high | Slow? | 0.6–2.2 | < 2.5 | High | →1 | r | X |
| | 500–5000 | 0.3–2.0 | + | Facultatively high | Avoid | 1.0–1.4 | > 3.0 | Moderate | →1 | r | Y |
| II | 500–10,000 | 0.3–2.0 | – | Usually high | Rapid | 0.8–1.8 | 2.0–3.0 | High | 0→0.6 | r | A, B, C, D, N, P |
| | | | – | Probably high | Slow? | ? | ? | Moderate | Low? | r–K | J |
| | | | + | ? | Avoid? | ? | ? | Moderate? | ? | r–K | Some E |
| | 3000–100,000 | 0.3–0.5 | + | Usually high | Avoid | c. 0.8 | > 3.0 | Low | Generally →0 | K | R, S |
| III | 10,000–$10^8$ | < 0.3 | – | Low? | Slow | < 0.7 | > 2.5 | Low | Generally low | r | F |
| | | | + | Mostly low | Avoid | < 0.7 | > 2.5 | Low | 0→low | r–K | G, Some E |
| | | | + | Mostly low? | Slow or avoid | < 0.7 | > 2.5 | Low | 0 | K | H, L, M |

expected to favour Group I initially and Group III sooner or later (other chemical and biotic, features of the environment also contribute to selection between them). Where gross physical fluctuations occur on cycles markedly shorter than one calendar-year (as in some tropical lakes) or are artificially shortened (see Reynolds et al., 1984), then entirely analogous responses occur on correspondingly truncated cycles. Where annual physical variations are suppressed (e.g. in rivers and some lakes) so phytoplankton periodicity, at least at group level, tends to be suspended in favour of within-group successional sub-sequences. So long as the general physical conditions persist, autogenic selection moves from the faster-growing, more $r$-selected species within the group and towards slower growing $K$-strategists. Successive dominance may be influenced by changing nutrient- and light-resource gradients and by differing sensitivities to loss processes (especially grazing and parasite epidemics). Collectively, such periodic progressions are exemplified by the replacement of assemblages $B$ or $C$ by $E$ or $R$ and by the $X \rightarrow G \rightarrow H \rightarrow M$ succession (note: Group I→III) of eutrophic epilimnia.

Many other within-group sequences along physical, chemical and biotic gradients are possible. Table 2 is advanced as a means of both tracing and unifying the seasonal periodicities of a wide spectrum of water-bodies, as well as of their tentative prediction, at assemblage level. The assemblages are arranged across the top of the table in approximate descending order of their resource-saturated growth rates and increasing $K$-selection. The tolerances of each assemblage to various physical, chemical and biotic variables to which they may be exposed are arbitrarily scaled by asterisks (from none—representing low or zero tolerance—to three—representing high tolerance or even obligate preference). Successional sequences are assumed to move horizontally to the right, principally involving in turn only species of those assemblages which are *simultaneously* tolerant of the limiting environmental constraints. The rate of progression cannot be determined but, as new or additional constraints become effective, so rightward movement to the next suitably-tolerant assemblage is generated.

In this way, it is possible to account for the seasonal periodicities exemplified in Fig. 1. Large, deep-mixed, P-deficient, oligotrophic lakes are shown to most favour $A/B$ species; increasing turbidity (say) would selectively favour *Oscillatoria* spp. (assemblage $R$); decreasing silicon would favour $E$. More enriched lakes increasingly select for $B/C$ in spring or perhaps $E$ or $R$. In summer, developing epilimnetic nutrient deficiencies and grazing activities lead to sequential replacement of $X$ and $Y$ (sensitive to both) and perhaps $G$ (sensitive to nutrient levels), $F$ (sensitive to nitrogen concentration) or $H$ (sensitive to phosphorus) before $M$ or $L$ eventually become dominant. Increased mixing during, or at the end of, summer favours assemblages $N$, $P$ or $R$.

Table 2 thus lends graphical expression to the concept that phytoplankton periodicity is the outcome of morphologically-, physiologically- and behaviourally-mediated responses of phytoplankton to the various dimensions of environmental variability. It is this concept that this review seeks to project. It is, of course,

TABLE 2. Environmental growth tolerances of phytoplankton assemblages

| Factor | X | Y | C/D | A/B | P | N | J | R/S | E | H | G | F | M | L |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Physical** | | | | | | | | | | | | | | |
| Temperature < 5° | ** | ** | *** | *** | * | * | * | * | * | | | | | |
| Mixed depth < 3 m | ** | ** | | | | | * | ** | *** | *** | *** | ** | *** | *** |
| $z_m/z_{eu} > 1.5$ | * | ** | *** | ** | ** | * | ** | *** | * | * | | * | ** | |
| **Chemical** | | | | | | | | | | | | | | |
| pH > 9 | * | * | ** | * | ** | * | ? | * | | *** | ** | * | *** | *** |
| [Si] < 200 $\mu$g l⁻¹ | *** | *** | | * | | * | *** | *** | ** | *** | *** | *** | *** | *** |
| [N] < 100 $\mu$g l⁻¹ | * | * | | * | | * | | * | * | *** | | * | * | * |
| [P] < 0.3 $\mu$g l⁻¹ | | * | | * | ** | * | * | * | * | ** | | * | | * |
| **Biotic** | | | | | | | | | | | | | | |
| CFR > 0.6 day⁻¹ | | | ** | ** | ** | ** | ** | ** | ** | *** | ** | ** | ** | *** |

incomplete in numerous details and it will not be immediately acceptable to all. However, it does embrace many recent advances in the fields of photosynthetic physiology, nutrient-uptake and growth kinetics and population dynamics as well as the results of large-scale experimental manipulations of environmental factors. My intention is to provoke the further thought and critical discussion that is still necessary if we are genuinely to advance upon Pearsall's (1932) understanding of phytoplankton periodicity.

## Acknowledgments

## References

Atkinson K.M. (1980) Experiments in dispersal of phytoplankton by ducks. *British Phycological Journal*, **15**, 49–58.

Baker A.L. (1970) An inexpensive microsampler. *Limnology and Oceanography*, **15**, 158–160.

Baker A.L., Brook A.J. & Klemer A.R. (1969) Some photosynthetic characteristics of a naturally occurring population of *Oscillatoria agardhii* (Gomont). *Limnology and Oceanography*, **14**, 327–333.

Banse K. (1976) Rates of growth, respiration and photosynthesis of unicellular algae as related to cell size—a review. *Journal of Phycology*, **12**, 135–140.

Berger C. (1975) Occurrence of *Oscillatoria agardhii* Gomont in some shallow eutrophic lakes. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **19**, 2689–2697.

Bothe H. (1982) Nitrogen fixation. *The Biology of Cyanobacteria* (Eds N. G. Carr and B. A. Whitton), pp. 87–104. Blackwell Scientific Publications, Oxford.

Brook A.J., Baker A.L. & Klemer A.R. (1971) The use of turbidimetry in studies of the population dynamics of phytoplankton populations with special reference to *Oscillatoria agardhii* var. *isothrix*. *Mitteilungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **19**, 244–252.

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

Burns C.W. (1968) The relationship between body size of filter-feeding cladocera and the maximum size of particle ingested. *Limnology and Oceanography*, **13**, 675–678.

Cosper E. (1978) Effects of diurnal fluctuations in light intensity on the efficiency of growth of *Skeletonema costatum* (Grev.) Cleve (Bacillariophyceae) in a cyclostat. *Journal of Experimental Marine Biology and Ecology*, **65**, 229–239.

Csanady G.T. (1978) Water circulation and dispersal mechanisms. *Lakes: Chemistry, Geology, Physics* (Ed. A. Lerman), pp. 21–64. Springer, New York.

Dillon P.J. & Rigler F.H. (1974) The phosphorus-chlorophyll relationship in lakes. *Limnology and Oceanography*, **19**, 767–773.

Dokulil M. (1979) Seasonal pattern of phytoplankton. *Neusiedlersee—the Limnology of a Shallow Lake in Central Europe* (Ed. H. Löffler), pp. 203–231. Den Haag, W. Junk.

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

Droop M.R. (1983) 25 years of algal growth kinetics. A personal view. *Botanica Marina*, **26**, 99–112.

Eberley W.R. (1959) The metalimnetic oxygen maximum in Myers Lake. *Investigations of Indiana Lakes and Streams*, **5**, 1–46.

Edmondson W.T. (1970) Phosphorus, nitrogen and algae in Lake Washington after diversion of sewage. *Science*, **169**, 690–691.

Elster H.-J. (1965) Absolute and relative assimilation rates in relation to phytoplankton populations. *Memorie dell'Istituto Italiano d'Idrobiologia*, **18** (Suppl.), 77–103.

Eppley R.W. & Sloan P.R. (1966) Growth rates of marine phytoplankton: correlations with light absorption by cell chlorophyll *a*. *Physiologia Plantarum*, **19**, 47–59.

Farmer D.M. & Takahashi M. (1982) Effects of vertical mixing on photosynthetic responses. *Japanese Journal of Limnology*, **43**, 173–181.

Fee E.J. (1976) The vertical and seasonal distribution of chlorophyll in lakes of the Experimental Lakes Area, northwestern Ontario: implications for primary production estimates. *Limnology and Oceanography*, **21**, 767–783.

Ferguson A.J.D., Thompson J.M. & Reynolds C.S. (1982) Structure and dynamics of zooplankton communities maintained in closed systems with special reference to the algal food supply. *Journal of Plankton Research*, **4**, 523–543.

Findenegg I. (1943) Untersuchungen über die Ökologie und die Produktionsverhältnisse des Planktons im Kärnter Seengebeite. *Internationale Revue der Gesamten Hydrobiologie und Hydrographie*, **43**, 368–429.

Fogg G.E. & Walsby A.E. (1971) Buoyancy regulation and the growth of planktonic blue-green algae. *Mitteilungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **19**, 182–188.

Foy R.H., Gibson C.E. & Smith R.V. (1976) The influence of day length, light intensity and

temperature on the growth rates of planktonic blue-green algae. *British Phycological Journal*, **11**, 151–163.

Frost B.W. (1980) Grazing. *The Physiological Ecology of Phytoplankton* (Ed. I. Morris), pp. 465–491. Blackwell Scientific Publications, Oxford.

Ganf G.G. & Viner A.B. (1973) Ecological stability in a shallow equatorial lake (Lake George, Uganda). *Proceedings of the Royal Society B*, **184**, 321–346.

George D.G. & Edwards R.W. (1976) The effect of wind on the distribution of chlorophyll *a* and crustacean plankton in a shallow eutrophic reservoir. *Journal of Applied Ecology*, **13**, 667–690.

Gibson C.E., Wood R.B., Dickson E.L. & Jewson D.M. (1971) The succession of phytoplankton in L. Neagh, 1968–1970. *Mitteilungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **19**, 146–160.

Gliwicz Z.M. (1980) Filtering rates, food size selection and feeding rates in cladocerans—another aspect of interspecific competition in filter-feeding zooplankton. *Evolution and Ecology of Zooplankton Communities* (Ed. W. C. Kerfoot), pp. 282–291. University Press of New England, Hanover, N.H.

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

Gorham E. (1957) The development of peatlands. *Quarterly Review of Biology*, **32**, 145–166.

Gran H.H. (1912) Pelagic plant life. *The Depths of the Ocean* (Eds J. Murray and H. Hjort), pp. 307–386. Macmillan, London.

Grim J. (1939) Beobachtungen am Phytoplankton des Bodensees (Obersee) sowie deren rechnerische Auswertung. *Internationale Revue der Gesamten Hydrobiologie und Hydrographie*, **39**, 193–315.

Haffner G.D., Harris G.P. & Jarai M.K. (1980) Physical variability and phytoplankton communities. III. Vertical structure in phytoplankton populations. *Archiv für Hydrobiologie*, **89**, 363–381.

Hairston N.G., Tinkle D.W. & Wilbur H.M. (1970) Natural selection and the parameters of population growth. *Journal of Wildlife Management*, **34**, 681–690.

Harris G.P. (1973) Diel and annual cycles of net plankton photosynthesis in Lake Ontario. *Journal of the Fisheries Research Board of Canada*, **30**, 1779–1787.

Harris G.P. (1978) Photosynthesis, productivity and growth: the physiological ecology of phytoplankton. *Ergebnisse der Limnologie*, **10**, 1–171.

Harris G.P. (1980) Temporal and spatial cycles in phytoplankton ecology. Mechanisms, methods, models and management. *Canadian Journal of Fisheries and aquatic Sciences*, **37**, 877–900.

Harris G.P. (1983) Mixed layer physics and phytoplankton populations: studies in equilibrium and non-equilibrium ecology. *Progress in Phycological Research*, **2**, 1–52.

Harris G.P. & Lott J.N.A. (1973) Light intensity and photosynthetic rates in phytoplankton, *Journal of the Fisheries Research Board of Canada*, **30**, 1771–1778.

Harris G.P. & Piccinin B.B. (1977) Photosynthesis by natural phytoplankton populations. *Archiv für Hydrobiologie*, **80**, 405–457.

Heaney S.I. (1976) Temporal and spatial distribution of the dinoflagellate *Ceratium hirundinella* O. F. Muller within a small productive lake. *Freshwater Biology*, **6**, 531–542.

Heaney S.I., Chapman D.V. & Morison H.R. (1983) The role of the cyst stage in the seasonal growth of the dinoflagellate *Ceratium hirundinella* within a small productive lake. *British Phycological Journal*, **18**, 47–59.

Hecky R.E. & Kling H.J. (1981) The phytoplankton and protozooplankton of the euphotic zone of Lake Tanganyika; species composition, biomass, chlorophyll content and spatio-temporal distribution. *Limnology and Oceanography*, **26**, 548–564.

Holm N.P. & Armstrong D.E. (1981) Role of nutrient limitation and competition in controlling the populations of *Asterionella formosa* and *Microcystis aeruginosa* in semicontinuous culture. *Limnology and Oceanography*, **26**, 622–634.

Hutchinson G.E. (1967) *A Treatise on Limnology*, Vol. II. Wiley, New York.

Jassby A.D. & Goldman C.R. (1974) A quantitative measure of succession rate and its application to the phytoplankton of lakes. *American Naturalist*, **108**, 688–693.

Jónasson P. & Adalsteinsson H. (1979) Phytoplankton production in a shallow eutrophic Lake Mývatn, Iceland. *Oikos*, **32**, 113–138.

Joseph J. & Sendner H. (1957) Über die horizontale Diffusion im Meere. *Deutsches Hydrographische Zeitschrift*, **11**, 51–77.

Kalff J., Kling H.J., Holmgren S.H. & Welch H.E. (1975) Phytoplankton, phytoplankton growth and biomass cycles in an unpolluted and in a polluted polar lake. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **19**, 487–495.

Kalff J. & Knoechel R. (1978) Phytoplankton and their dynamics in oligotrophic and eutrophic lakes. *Annual Reviews in Ecology and Systematics*, **9**, 475–495.

Kilham P. (1971) A hypothesis concerning silica and the freshwater planktonic diatoms. *Limnology and Oceanography*, **16**, 10–18.

Kilham P. & Kilham S.S. (1980) The evolutionary ecology of phytoplankton. *The Physiological Ecology of Phytoplankton* (Ed. I. Morris), pp. 571–597. Blackwell Scientific Publications, Oxford.

Kilham S.S. (1975) Kinetics of silicon-limited growth in the freshwater diatom *Asterionella formosa*. *Journal of Phycology*, **11**, 396–399.

Kilham S.S. (1978) Nutrient kinetics of freshwater planktonic algae using batch and semicontinuous methods. *Mitteilung der internationale Vereinigung für Theoretische und Angewandte Limnologie*, **21**, 147–157.

Klemer A.R. (1976) The vertical distribution of *Oscillatoria agardhii* var. *isothrix*. *Archiv für Hydrobiologie*, **78**, 343–362.

Klemer A.R., Feuillade J. & Feuillade M. (1982) Cyanobacterial blooms: carbon and nitrogen

limitation have opposite effects on the buoyancy of *Oscillatoria*. *Science*, **215**, 1629–1631.

Lampert W. (1977) Studies on the carbon balance of *Daphnia pulex* De Geer as related to environmental conditions. IV. Determination of the 'threshold' concentration as a factor controlling the abundance of zooplankton species. *Archiv für Hydrobiologie (Supplementband)*, **48**, 361–368.

Laws E.A. (1975) The importance of respiration losses in controlling the size distribution of marine phytoplankton. *Ecology*, **56**, 419–426.

Lee G.F., Rast W. & Jones R.A. (1978) Eutrophication of water bodies: insights for an age-old problem. *Environmental Science and Technology*, **12**, 900–908.

Leah R.T., Moss, B. & Forrest D.E. (1980) The role of predation in causing major changes in the limnology of a hyper-eutrophic lake. *Internationale Revue der Gesamten Hydrobiologie und Hydrographie*, **65**, 223–247.

Lehman J.T. (1978) Enhanced transport of inorganic carbon into algal cells and its implications for the biological fixation of carbon. *Journal of Phycology*, **14**, 33–42.

Lewis W.R. (1976) Surface/volume ratio: implications for phytoplankton morphology. *Science*, **192**, 885–887.

Lewis W.R. (1978a) Dynamics and succession of the phytoplankton in a tropical lake: Lake Lanao, Philippines. *Journal of Ecology*, **66**, 849–880.

Lewis W.R. (1978b) Analysis of succession in a tropical phytoplankton community and a new measure of succession rate. *American Naturalist*, **112**, 401–414.

Light J.J., Ellis-Evans J.C. & Priddle J. (1981) Phytoplankton ecology in an Antarctic lake. *Freshwater Biology*, **11**, 11–26.

Lund J.W.G. (1950) Studies of *Asterionella formosa* Hass. II. Nutrient depletion and the spring maxima. *Journal of Ecology*, **38**, 1–35.

Lund J.W.G. (1965) The ecology of the freshwater phytoplankton. *Biological Reviews of the Cambridge Philosophical Society*, **40**, 231–293.

Lund J.W.G. (1975) The use of large experimental tubes in lakes. *The Effects of Storage on Water Quality* (Ed. R. E. Youngman), pp. 291–311. Water Research Centre, Medmenham.

Lund J.W.G. (1981) Investigations on phytoplankton, with special reference to water usage. *Occasional Publication of the Freshwater Biological Association*, No. 13, 64 pp.

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

Macan T.T. (1970) *Biological Studies of the English Lakes*. London, Longman.

MacArthur R.H. & Wilson E.O. (1967) *The Theory of Island Biogeography*. Princeton University Press.

Malone T.C. (1980) Algal size. *The Physiological Ecology of Phytoplankton* (Ed. I. Morris), pp. 433–463. Blackwell Scientific Publications, Oxford.

Margalef R. (1957) Nuevos aspectos del problema de la suspension en los organismos planctonicos. *Investigación Pesquera*, **7**, 105–116.

Margalef R. (1958) Temporal succession and spatial heterogeneity in phytoplankton. *Perspectives in Marine Biology* (Ed. A. A. Buzzati-Traverso), pp. 323–349. University of California Press, Berkeley.

Margalef R. (1967) Some concepts relative to the organization of plankton. *Oceanography and Marine Biology Annual Review*, **5**, 257–289.

Margalef R. (1968) *Perspectives in Ecological Theory*. University of Chicago Press.

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

Melack J.M. (1979) Temporal variability of phytoplankton in tropical lakes. *Oecologia*, **44**, 1–7.

Moore J.W. (1979) Factors influencing the diversity, species composition and abundance of phytoplankton in twenty one Arctic and subarctic lakes. *Internationale Revue der Gesamten Hydrobiologie und Hydrographie*, **64**, 485–489.

Mortimer C.H. (1974) Lake Hydrodynamics. *Mitteilungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **20**, 124–197.

Moss B. (1973a) The influence of environmental factors on the distribution of freshwater algae: an experimental study. II. The role of pH and carbon dioxide-bicarbonate system. *Journal of Ecology*, **61**, 157–177.

Moss B. (1973b) The influence of environmental factors on the distribution of freshwater algae: an experimental study. IV. Growth of test species in natural lake waters, and conclusion. *Journal of Ecology*, **61**, 193–211.

Mur L.R., Gons H.J. & van Liere L. (1978) Competetion of the green alga *Scenedesmus* and the blue-green alga *Oscillatoria*. *Mitteilungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **21**, 473–479.

Nadin-Hurley C.M. & Duncan A. (1976) A comparison of Daphnid gut particles with the sestonic particles present in two Thames Valley reservoirs throughout 1970 and 1971. *Freshwater Biology*, **6**, 109–124.

Nauwerck A. (1963) Die Beziehungen zwischen Zooplankton und Phytoplankton im See Erken. *Symbolae Botanicae Upsaliensis*, **17(5)**, 1–163.

Ottesen Hansen N.-E. (1978) Mixing processes in lakes. *Nordic Hydrology* **9**, 57–74.

Owens O.v.H. & Esaias W.E. (1976) Physiological responses of phytoplankton to major environmental factors. *Annual Review of Plant Physiology*, **27**, 461–483.

Paasche E. (1980) Silicon. *The Physiological Ecology of Phytoplankton* (Ed. I. Morris), pp. 259–284. Blackwell Scientific Publications, Oxford.

Paerl H.W. (1982) Factors limiting productivity of freshwater ecosystems. *Advances in Microbial Ecology*, Vol. 6 (Ed. K. C. Marshall), pp. 75–110. Plenum Press, London.

Pavoni M. (1963) Die Bedeutung des Nannoplanktons im Vergleich zum Netzplankton. *Schweizerische Zeitschrift für Hydrologie*, **25**, 219–341.

Pearsall W.H. (1930) Phytoplankton in the English lakes. 1. The proportions in the water of some dissolved substances of biological importance. *Journal of Ecology*, **18**, 306–320.

Pearsall W.H. (1932) Phytoplankton in the English lakes. 2. The composition of the phytoplankton in relation to dissolved substances. *Journal of Ecology*, **20**, 241–262.

Petersen R. (1975) The paradox of the plankton: an equilibrium hypothesis. *American Naturalist*, **109**, 35–49.

Pianka E.R. (1970) On r- and K-selection. *American Naturalist*, **104**, 592–597.

Raven J.A. & Beardall J. (1981) Respiration and photorespiration. *Canadian Bulletin of Fisheries and Aquatic Sciences*, No. 210, 55–82.

Ravera O. & Vollenweider R.A. (1968) *Oscillatoria rubescens* D.C. as an indicator of pollution. *Schweizerische Zeitschrift für Hydrologie*, **30**, 374–380.

Reynolds C.S. (1973a) The phytoplankton of Crose Mere, Shropshire. *British Phycological Journal*, **8**, 153–162.

Reynolds C.S. (1973b) Phytoplankton periodicity of some north Shrophire meres. *British Phycological Journal*, **8**, 301–320.

Reynolds C.S. (1973c) The seasonal periodicity of planktonic diatoms in a shallow eutrophic lake. *Freshwater Biology*, **3**, 89–110.

Reynolds C.S. (1975) Interrelations of photosynthetic behaviour and buoyancy regulation in a natural population of a blue-green alga. *Freshwater Biology*, **5**, 323–338.

Reynolds C.S. (1976) Succession and vertical distribution of phytoplankton in response to thermal stratification in a lowland mere, with special reference to nutrient availability. *Journal of Ecology*, **64**, 529–550.

Reynolds C.S. (1978a) The plankton of the north-west Midland meres. *Occasional Publications of the Caradoc and Severn Valley Field Club*, No. 2, 36+xxii pp.

Reynolds C.S. (1978b) Stratification in natural populations of bloom-forming blue-green algae. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **20**, 2285–2292.

Reynolds C.S. (1979) Seston sedimentation: experiments with *Lycopodium* spores in a closed system. *Freshwater Biology*, **9**, 55–76.

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

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

Reynolds C.S. (1983a) *The Ecology of Freshwater Phytoplankton*. Cambridge University Press.

Reynolds C.S. (1983b) A physiological interpretation of the dynamic responses of population of a planktonic diatom to physical variability of the environment. *New Phytologist*, **95**, 41–53.

Reynolds C.S. & Butterwick C. (1979) Algal bioassay of unfertilized and artificially fertilized lake water

maintained in Lund Tubes. *Archiv für Hydrobiologie (Supplementband)*, **56**, 166–183.

Reynolds C.S., Thompson J.M., Ferguson A.J.D. & Wiseman S.W. (1982) Loss processes in the population dynamics of phytoplankton maintained in closed systems. *Journal of Plankton Research*, **4**, 561–600.

Reynolds C.S. & Walsby A.E. (1975) Water-blooms. *Biological Reviews of the Cambridge Philosophical Society*, **50**, 437–481.

Reynolds C.S. & Wiseman S.W. (1982) Sinking losses of phytoplankton maintained in closed limnetic systems. *Journal of Plankton Research*, **4**, 489–522.

Reynolds C.S., Wiseman S.W. & Clarke M.J.O. (1984) Growth- and loss-rate responses of phytoplankton to intermittent artificial mixing and their potential application to the control of planktonic algal biomass. *Journal of Applied Ecology*, **21** (in press).

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

Rhee G.-Y. (1978) Effects of N : P atomic ratios and nitrate limitation on algal growth, cell composition and nitrate uptake. *Limnology and Oceanography*, **23**, 10–25.

Rhee G.-Y. (1982). Effect of environmental factors and their interactions of phytoplankton growth. *Advances in Microbial Ecology*, Vol. 6 (Ed. K. C. Marshall), pp. 33–74. Plenum Press, London.

Rhee G.-Y. & Gotham I.J. (1980) Optimum N : P ratios and coexistence of planktonic algae. *Journal of Phycology*, **16**, 486–489.

Rhee G.-Y. & Gotham I.J. (1981) The effect of environmental factors on phytoplankton growth: temperature and the interactions of temperature with nutrient limitation. *Limnology and Oceanography*, **26**, 635-648.

Round F.E. (1971) The growth and succession of algal populations in freshwaters. *Mitteilungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **19**, 70–99.

Ruttner F. (1930) Das Plankton des Lunzer Untersees: seine Verteilung in Raum und Zeit warend der Jahre 1908–1913. *Internationale Revue der Gesamten Hydrobiologie und Hydrographie*, **23**, 1–138 and 161–287,

Schindler D.W. (1977) Evolution of phosphorus limitation in lakes. *Science*, **195**, 260–262.

Schütt F. (1892) Das Pflanzenleben der Hochsee. *Erbgenisse der Plankton-Expedition der Humboldt-Stiftung*, **1**, 243-314.

Smayda T.J. (1970) The suspension and sinking of phytoplankton in the sea. *Oceanography and Marine Biology Annual Review*, **8**, 353–414.

Smith I.R. (1975) Turbulence in lakes and rivers. *Occasional Publications of the Freshwater Biological Association*, No. 29, 75 pp.

Smith I.R. (1982) A simple theory of algal deposition. *Freshwater Biology*, **12**, 445–449.

Sommer U. (1981) The role of r- and K-selection in the

succession of phytoplankton in Lake Constance. *Acta Oecologia*, **2**, 327–342.

Sournia A. (1981) The morphological bases of competition and succession. *Canadian Bulletin of Fisheries and Aquatic Sciences*, No. 210, 339–346.

Sournia A. (1982) Form and function in marine phytoplankton. *Biological Reviews of the Cambridge Philosophical Society*, **57**, 347–394.

Steeman-Nielsen E. (1962) On the maximum quantity of plankton chlorophyll per surface unit of a lake or the sea. *Internationale Revue der Gesamten Hydrobiologie und Hydrographie*, **47**, 333–338.

Sze P. (1980) Seasonal succession of phytoplankton in Onondaga Lake, New York (U.S.A.). *Phycologia*, **19**, 54–59.

Talling J.F. (1966) Photosynthetic behaviour in stratified lake populations of a planktonic diatom. *Journal of Ecology*, **54**, 99–127.

Talling J.F. (1971) The underwater light climate as a controlling factor in the production ecology of freshwater phytoplankton. *Mitteilungen der Internationale Vereinigung für Theoretische and Angewandte Limnologie*, **19**, 214–243.

Talling J.F. (1976) The depletion of carbon dioxide from lake waters by phytoplankton, *Journal of Ecology*, **64**, 79–121.

Talling J.F., Wood R.B., Prosser M.V. & Baxter R.M. (1973) The upper limit of photosynthetic productivity by phytoplankton: evidence from Ethiopian soda lakes. *Freshwater Biology*, **3**, 53–76.

Tamiya H., Iwamura T., Shibata K., Hase E. & Nihei T. (1953) Correlation between photosynthesis and light independent metabolism in the growth of *Chlorella*. *Biochimica et Biophysica Acta*, **12**, 23–40.

Taylor F.J.R. (1980) Basic biological features of phytoplankton cells *The Physiological Ecology of Phytoplankton* (Ed. I. Morris), pp. 3–55. Blackwell Scientific Publications, Oxford.

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

Tilman D. (1981) Tests of resource competition using four species of Lake Michigan algae. *Ecology*, **62**, 802–815.

Tilman D. & Kilham S.S. (1976) Phosphate and silicate growth and uptake kinetics of the diatoms *Asterionella formosa* and *Cyclotella meneghiniana* in batch and semicontinuous culture. *Journal of Phycology*, **12**, 375–383.

Tilman D., Kilham S.S. & Kilham P. (1982) Phytoplankton community ecology: the role of limiting nutrients. *Annual Review of Ecology and Systematics*, **13**, 349–372.

Vollenweider R.A. & Kerekes J. (1980) The loading concept as basis for controlling eutrophication philosophy and preliminary results of the OELD programme on eutrophication. *Progress in Water Technology*, **12**, 5–38.

Walsby A.E. (1978) The gas vesicles of aquatic prokaryotes. *Relation between Structure and Function in the Prokaryotic Cell* (Eds H. J. Rogers and R. Y. Stanier), pp. 327–357. Cambridge University Press.

Walsby A.E. & Klemer A.R. (1974) The role of gas vacuoles in the microstratification of a population of *Oscillatoria agardhii* var. *isothrix* in Deming Lake, Minnesota. *Archiv für Hydrobiologie*, **74**, 375–392.

Walsby A.E. & Reynolds C.S. (1980) Sinking and floating. *The Physiological Ecology of Phytoplankton* (Ed. I. Morris), pp. 371–412. Blackwell Scientific Publications, Oxford.

Walsby A.E. & Xypolyta A. (1977) The form resistance of chitan fibres attached to the cells of *Thalassiosira fluviatilis* Hustedt. *British Phycological Journal*, **12**, 215–223.

Wiseman S.W., Jaworski G.H.M. & Reynolds C.S. (1983) Variability in sinking rate of *Asterionella* colonies: the influence of their excess density. *British Phycological Journal*, **18**, in press.

Zimmermann U. (1969) Okologische und physiologische Untersuchungen an der planktonischen Blaualge *Oscillatoria rubescens* D.C. unter besonderen Berucksichtung von Licht und Temperatur. *Schweizerische Zeitschrift für Hydrologie*, **31**, 1–58.

## Appendix I

Alphabetical list of specific names of algae named in this paper, with authorities

*Anabaena circinalis* Rabenh. *ex* Born. *et* Flah.
*Anabaena flos-aquae* Bréb. *ex* Born. *et* Flah.
*Ankyra judayi* (G.M.Sm.) Fott
*Aphanizomenon flos-aquae* Ralfs *ex* Born. Flah.
*Asterionella formosa* Hass.
*Ceratium hirundinella* O. F. Müll.
*Closterium aciculare* T. West
*Cosmarium depressum* (Näg.) Lund
*Cryptomonas ovata* Ehrenb.
*Cyclotella comensis* Grun.
*Cyclotella comta* (Ehrenb.) Kütz.
*Cyclotella glomerata* Bachmann
*Cyclotella melosiroides* Kirchner
*Cyclotella meneghiniana* Kütz.
*Cyclotella praeterissima* Lund
*Cyclotella pseudostelligera* Hust.
*Eudorina unicocca* G.M.Sm.
*Fragilaria crotonensis* Kitton
*Gemellicystis neglecta* Teiling
*Mallomonas caudata* Iwanoff
*Melosira granulata* (Ehrenb.) Ralfs
*Melosira islandica* O. F. Müll.
*Melosira italica* (Ehrenb.) Kütz.
*Microcystis aeruginosa* Kütz. emend. Elenkin
*Oocystis borgei* Snow

*Oocystis lacustris* Chodat
*Oscillatoria agardhii* Gom.
*Oscillatoria agardhii* Gom. var. *isothrix* Skuja
*Oscillatoria redekei* Van Goor
*Oscillatoria rubescens* D.C. *ex* Gom.
*Pediastrum boryanum* (Turp.) Meneghin
*Peridinium willei* Huitfield-Kaas
*Rhizosolenia eriensis* H. L. Smith
*Scenedesmus quadricauda* (Turp.) Bréb.

*Sphaerocystis schroeteri* Chodat
*Staurastrum pingue* Teiling
*Stephanodiscus astraea* (Ehrenb.) Grun.
*Synedra nana* Meister
*Synedra ulna* (Nitzsch) Ehrenb.
*Tabellaria flocculosa* (Roth.) Kütz. var. *aster-ionelloides* (Roth.) Knuds.
*Uroglena lindii* Bourrelly
*Volvox aureus* Ehrenb.