

Phytoplankton and Primary Production

Phytoplankton

The phytoplankton **are the primary producers of the pelagic zone of lakes and oceans.** Accordingly, the phytoplankton is the base of the food chain. [Macrophytes and allochthonous organic material are also important, especially in small lakes.] In addition, because phytoplankton are numerous, their presence can have a profound effect on water transparency and color. They can produce taste and odor problems for drinking water supplies.

Habitat designations

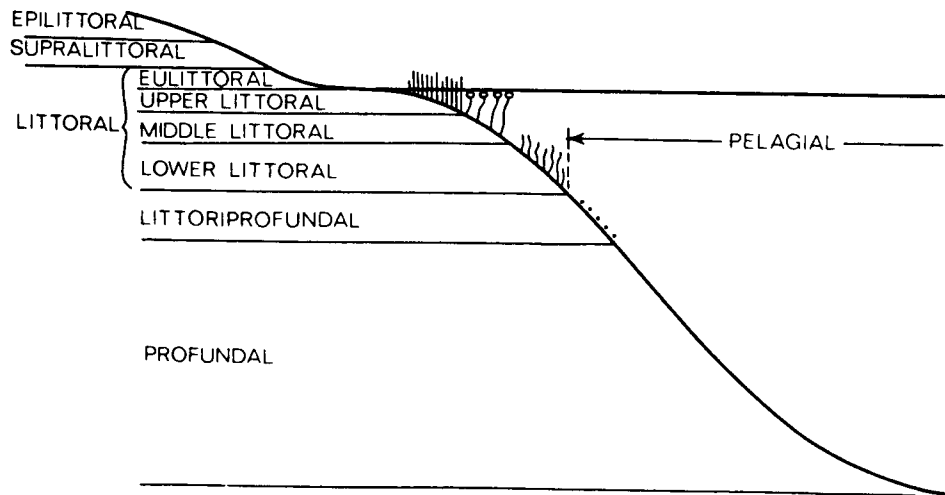


FIGURE 8-2 Lacustrine zonation (see text for discussion). (After Hutchinson, 1967.)

Benthic algae can be important primary producers in some lakes. A good local example is Waldo Lake. The low nutrient concentrations in the water column support little phytoplankton, but rather dense mats of benthic algae are present. In this circumstance all the primary producer action is on the bottom.

TABLE 7.3 Terms Used to Classify Aquatic Organisms by Habitat

<i>Habitat</i>	<i>Description</i>
Benthic	On the bottom
Emergent	Emerging from the water
Endosymbiotic	Living within another organism
Epilithic	On rocks
Epigeal	Above ground
Epipelagic	On mud
Epiphytic	On plants
Episammic	On sand
Hyporheic	In groundwater influenced by surface water
Lentic	In still water
Littoral	On lake shores, in shallow benthic zone of lakes
Lotic	In flowing water
Neustonic	On the surface of water
Pelagic	In open water
Periphytic (Aufwuchs, biofilm, microphytobenthos)	Benthic, in a complex mixture including algae
Profundal	Deep in a lake
Symbiotic	Living very near or within another organism
Stygophilic	Actively use groundwater habitats for part of life cycle
Stygobitic	Specialized for life in groundwater

Pelagic phytoplankton

The phytoplankton are all so small that they live in a **viscous** world. Their size and swimming or sinking velocities are such that their motion relative to the water is characterized by low Reynolds number. Contrary to what their name might suggest (plankton = “wandering”), most phytoplankton are heavier than water. They persist in the water column because of growth and mixing. Their presence could better be described as “suspended” rather than floating.

Phytoplankton are not “simple” organisms. They are taxonomically and ecologically diverse. They are capable of physiological adjustments to their sinking rate, their ability to assimilate scarce nutrients, and their ability to harvest light.

Phytoplankton are a central feature of the trophic classification system. Several of the features of the trophic classification system are directly related to the phytoplankton. Examples:

factor	oligotrophic	eutrophic
primary production	low (50-300 mg C/m ² day)	high (>1000 mg C/m ² day)
algal biomass	small (0.02-0.1 mg C/l) (0.3-3 µg Chl/l)	large (>0.3 mg C/l) (10-500 µg Chl/l)
development of cyanobacteria	absent, or little	massive

The central feature of the trophic classification system is the causal relationship between nutrient loading and algal growth. The other features of the system reflect the consequence of the degree of algal growth.

Phytoplankton associations.

Limnologists have long recognized distinct patterns in the species composition of the phytoplankton. Species that commonly appear together are sometimes labeled as “assemblages” or “associations”. For example, Hutchinson (1967, p396-397) describes 13 associations of phytoplankton species that can be related to environmental conditions.

For some authors, such a designation implies an ecological interdependence among the participating species, however, it may be that no such biotic interdependence is required, and may not exist. Individual species may simply be responding to common environmental conditions. Accordingly, absent direct evidence, it should not be assumed that the co-occurrence of species implies direct ecological interdependence.

Phytoplankton associations correlate with ecological conditions rather than with geographic location. For example, Kalff and Watson (1986, “Phytoplankton and its dynamics in two tropical lakes: a tropical and temperate zone comparison”, in *Hydrobiologia* 138:161-176, QK 935 .S5) report that **very few species are distinctively tropical**. For example, *Botryococcus braunii* is an important component in the phytoplankton in the two Kenyan lakes in their study, but is also the most important species under the ice in Char Lake during several months of polar night.

In several lakes that have been studied in sufficient detail, there is a characteristic annual **succession of phytoplankton species**. A well-documented case is the plankton of Lake Windemere, England. (See Maberly et al., 1994, *Freshwater Biology* 31:19-34. The rise and fall of *Asterionella formosa* in the South Basin of Windemere: analysis of a 45-year series of data” QH 96 A1 F73.

The average pattern of cell concentration in the South Basin of Windemere increases to an annual maximum in early spring followed by a rapid decline to a mid-summer minimum and a rise to a plateau in autumn and early winter.

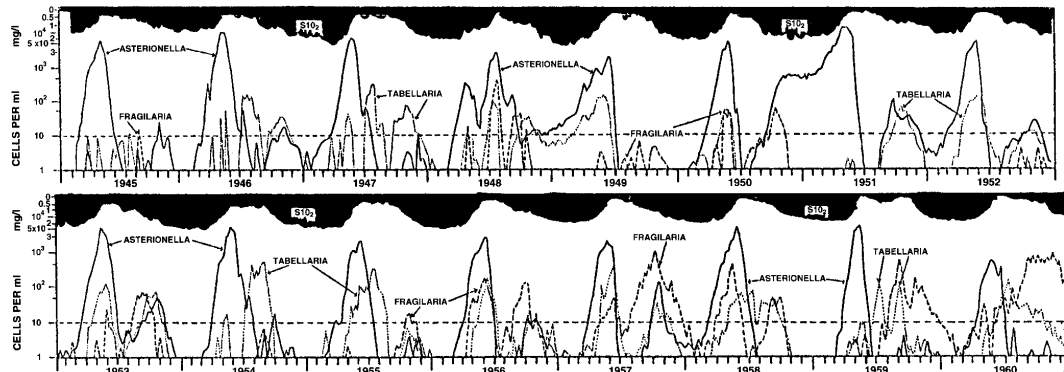


FIGURE 14-22 The periodicity of the diatom algae *Asterionella formosa*, *Fragilaria crotonensis*, and *Tabellaria flocculosa* in relation to fluctuations in the concentration of dissolved silica, 0–5 m in Lake Windemere, England, 1945–1960. (From Lund, J. W. G.: *Verhandlungen Int. Ver. Limnol.* 15:37, 1964.)

Typically in the Pacific Northwest, at least in mesotrophic lakes, we see a succession of dominant species through the seasons as in the example below from Lake Sammamish, East of Seattle.

- Spring diatoms

- Summer greens
- Late summer cyanobacteria (blue greens)
- Winter greens and diatoms

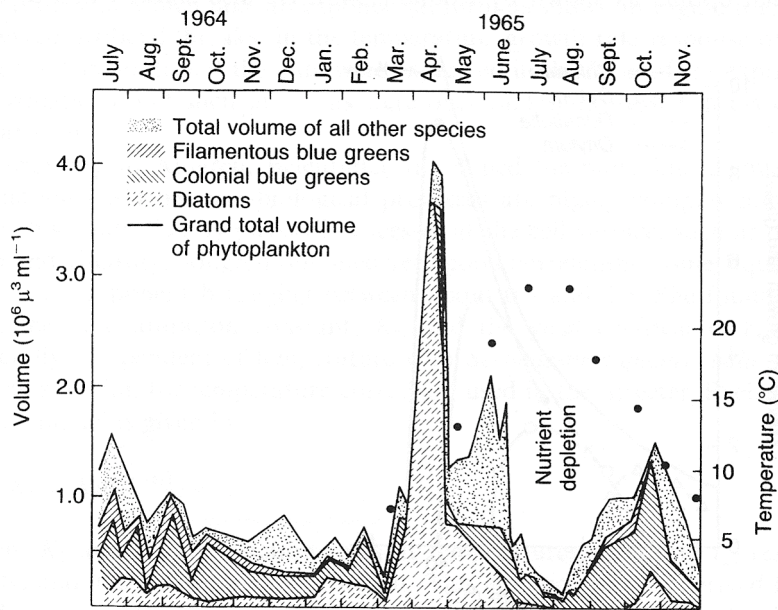


Figure 6.27 Surface phytoplankton composition at a centrally located station in Lake Sammamish. Temperature indicated by solid circles (after Isaac *et al.*, 1966).

The point: there is a distinct pattern of phytoplankton species rise and fall that is repeated each year. Other lakes apparently follow a distinct pattern as well (although few good long-term data sets have been collected.) Thus, there appears to be a general pattern for an orderly succession of species over the year that repeats year after year. Although considerable variation exists between one year and the next, the overall pattern is similar. Over the long term, the pattern may shift, especially if disturbed by anthropogenic disturbance.

We may infer from this that there must be “deterministic” mechanisms that regulate the species composition and succession of the phytoplankton. What are they?

Some of the important dimensions of phytoplankton ecology are:

- suspension mechanisms
- nutrient uptake
- light utilization
- influence of physical mixing
- loss factors (sinking, grazing, parasitism).

Some of the big questions are: What determines *species diversity* (and the “paradox of the plankton”). Why do particular *associations* develop? What explains the *patterns of species succession*? Can phytoplankton be “managed” (i.e. predictably manipulated)?

Paradox of the Plankton

A primary characteristic of phytoplankton communities is the number of species

populations that coexist simultaneously. The **Competitive Exclusion Principle** suggests that in a relatively uniform environment in which species are competing for the same resources, the species that is the best competitor for a critical limiting resource (or resources) should come to dominate the community. There are often, however, two or more co-dominant species in phytoplankton communities. Rare species always exist among the dominant and subdominant species. Thus, the diversity of most phytoplankton assemblages is higher than expected based on theory and mathematical derivations.

Why?

- For competitive exclusion to occur, conditions must be uniform for a sufficient period of time. If conditions change rapidly, the advantage gained by being a superior competitor may not last long enough to exclude other species. Also, differences in resource use may not be great enough for competitive exclusion to occur before conditions change, i.e., niche overlap is large. In lakes, both regular (e.g., temperature) and irregular (e.g. light) environmental changes occur on different time scales.
- Species differ in nutrient requirements and/or nutrient uptake kinetics, e.g., different Monod Model parameters, particularly K_s , but are able to coexist according to Resource Ratio gradient model. (see below for more on this)
- Predation on one algal species more than another would encourage co-existence, even if the preyed upon species is competitively superior, other factors being equal. Selective grazing by zooplankton occurs, mostly on the basis of size.
- Some species are planktonic all the time (**holoplankton**) and some enter resting stages in which they drop out of the community, often into the sediments (**meroplankton**) and rejoin opportunistically when conditions improve.
- Epilimnion is a patchy habitat so zooplankton distribution is patchy also, which results in “**contemporaneous disequilibrium**”, i.e., at any one time, many patches of water exist in which one species is at a competitive advantage relative to the others. These water masses are stable enough to permit a considerable degree of patchiness to occur in phytoplankton, but are obliterated frequently enough to prevent the exclusive occupation of each niche by a single species.

Taxonomy

Size and generation time considerations.

They are all “small”: from about $<0.2 \mu\text{m}$ to about 1 mm. All of them are thus small enough to live in a viscous (low Reynolds number) world.

However, in reality, they cover an **enormous size range**: In terms of volume, about 7 orders of magnitude, or about the same size range as moss to redwood trees.

Table 21-1 A division of phytoplankton, bacterioplankton, and protozooplankton on the basis of unit size.¹

Grouping	Maximum Diameter (D) or Length (L) (μm)	Phytoplankton Attributes
Femtoplankton	< 0.2 (D)	Consists of very small bacteria and viruses.
Picoplankton	0.2-2 (D)	Contains the smallest phytoplankton (~0.5-2 μm). All but the smallest are subject to significant predation by small rotifers, protozoa, and by some of the filter-feeding daphnid crustaceans; experience negligible sinking rates. Very high potential growth rates of the larger forms.
Nanoplankton	2-30 (D or L)	Many, often flagellated phytoplankton; principal food of the macrozooplankton and microzooplankton; very low sinking rates. High potential and realized growth rates.
Microplankton	30-200 (D or L)	Small microplankton (< ~70 μm). Subject to some macrozooplankton grazing and prone to moderate sinking when nonmotile or lacking buoyancy control. Moderate potential growth rates. Large microplankton (> ~70 μm). Retained by traditional ~70 μm mesh size plankton nets (<i>netplankton</i>). Highly prone to sinking in the absence of buoyancy control; principal food of pelagic and benthic zone omnivorous fish as well as sediment microbes. Moderate to low potential growth rates.
Mesoplankton	200-20,000 (L)	Large cells and colonies. For attributes, see large microplankton.
Macroplankton	> 20,000 (L)	Large free-floating plants such as duckweed (<i>Lemna spp.</i>) in ponds; and the notorious water hyacinth (<i>Eichornia</i>) and waterfern (<i>Salvinia</i>) in tropical and subtropical lakes and slowly flowing rivers (see Fig. 15-1 and Chapter 24). Lowest potential growth rates.

“Net plankton” (> 30 μm)

¹The present division differs from the one proposed by Sieburth et al. (1978) by expanding by 10 μm the maximum nanoplankton size range to include those organisms most subject to substantial predation by freshwater crustacean zooplankton.

Generation time and annual succession patterns.

Some species can divide as frequently as once per day and growth rates of 0.5/day are common. Such a population could theoretically increase at a very great rate:

growth rate	population growth in 30 days
0.1	20x
0.5	400x

Thus, very rapid population growth is possible – a years’ time is equivalent to 10,000 years of time for terrestrial forests in terms of the number of generations. The annual pattern of succession could be said to be equivalent to post-Pleistocene time for terrestrial plant communities.

Prokaryota: Cyanobacteria (=Cyanophyta, Myxophyta, Schizophyta, “Blue-green algae”)

Chroococcales: Solitary or colonial coccoid “blue-greens”: *Microcystis*, *Synechococcus*.

Nostocales: Filamentous blue greens, mostly capable of heterocyst formation (i.e., N-fixation) *Oscillatoria*, *Anabaena*, *Aphanizomenon*, *Spirulina*, *Trichodesmium*

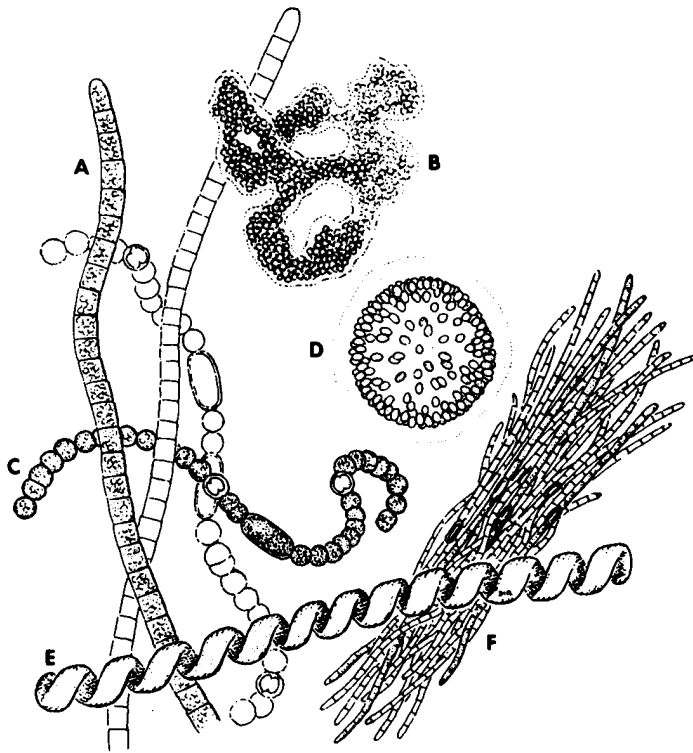


Figure 3-1
Some bluegreens (Cyanobacteria) from inland waters. **A**, *Oscillatoria*; **B**, *Microcystis aeruginosa*; **C**, *Anabaena*; **D**, *Coelosphaerium*; **E**, *Spirulina*; **F**, *Aphanizomenon flos-aquae*.

Eukaryota: eukaryotic algae, with chloroplasts, etc.

Cryptophyta: Naked, biflagellated algae with one or two large plastids.
Cryptomonas, *Rhodomonas*

Pyrrhophyta: dinoflagellates. Two flagella of different length and orientation.
Ceratium, *Glenodinium*, *Gymnodinium*

Chrysophyta: unicellular, colonial, filamentous, with a preponderance of carotenoid pigments, various biochemical characteristics.

Ochromonadales: *Dinobryon*, *Mallomonas*, *Synura*

Bacillariophyceae: Diatoms: centric and pennate

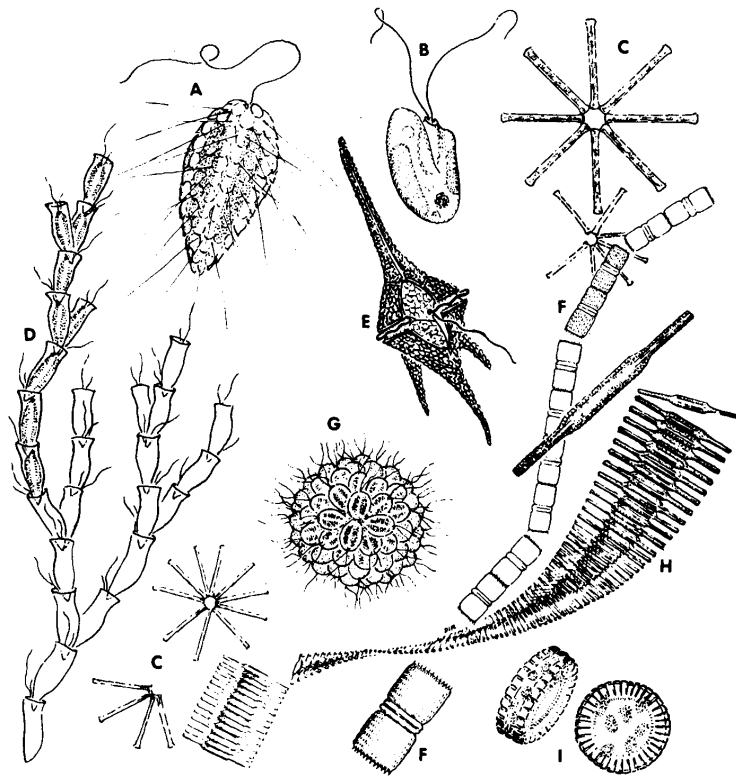


Figure 3-3
 Representatives of the golden brown phyla in inland waters. **A**, *Mallomonas*, Chrysophyceae; **B**, *Cryptomonas*, Cryptophyta; **C**, *Asterionella*, Bacillariophyceae; **D**, *Dinobryon*, Chrysophyceae; **E**, *Ceratium hirundinella*, Pyrrophyta; **F**, *Melosira*, Bacillariophyceae; **G**, *Synura*, Chrysophyceae; **H**, *Fragilaria*, Bacillariophyceae; **I**, *Cyclotella*, Bacillariophyceae.

Euglenophyta: *Euglena*

Chlorophyta: Green algae. Several orders.

TABLE 8.3 Characteristics of Major Groups of Freshwater Algae^a

Group (common name)	Dominant pigments	Cell wall	Habitats	Approximate No. of species (% freshwater)	Ecological importance
Cyanobacteria	Chl <i>a</i> , phycobilins	Peptidoglycan	Oligotrophic to eutrophic, benign to harsh environments	1,200–5,000 (50%)	Some fix nitrogen, some toxic, floating blooms characteristic of nutrient-rich lakes
Rhodophyceae (red algae)	Chl <i>a</i> , phycobilins	Cellulose	Freshwater species in streams	1,500–5,000 (5%)	Rare in freshwaters except <i>Batrachospermum</i> in streams
Chrysophyceae	Chl <i>a</i> , chl <i>c</i> , carotenoids	Chrysolaminarin	Freshwater, temperate, plankton	300–1,000 (80%)	<i>Dinobryon</i> a common dominant in phytoplankton
Bacillariophyceae (diatoms)	Chl <i>a</i> , chl <i>c</i> , carotenoids	Silica frustule	Plankton and benthos	5,000–12,000 (20%)	An essential primary producer, both in freshwaters and globally
Dynophyceae	Chl <i>a</i> , chl <i>c</i> , carotenoids	Cellulose	Primarily planktonic	230–1,200 (7%)	Some toxic, some phagotrophic, involved in many symbiotic interactions
Euglenophyceae	Chl <i>a</i> , chl <i>b</i>	Protein	Commonly in eutrophic waters, associated with sediments	400–1,000	Can be phagotrophic, indicative of eutrophic conditions
Chlorophyceae (green algae)	Chl <i>a</i> , chl <i>b</i>	Naked, cellulose or calcified	Oligotrophic to eutrophic, planktonic to benthic	6,500–20,000 (87%)	Very variable morphology, very important primary producers; filamentous types in streams, unicellular in plankton
Charophyceae	Chl <i>a</i> , chl <i>b</i>	Cellulose, many calcified	Benthic, still to slowly flowing water	315 (95%)	Often calcareous deposits

^aSee Figs. 8.4–8.6, 8.8, and 8.9 for representative genera and some morphological characteristics [after South and Whitrick (1987) and Vymazal (1995)].

TABLE 15-4 Characteristics of Common Major Associations of the Phytoplankton in Relation to Increasing Lake Fertility^a

General lake trophity	Water characteristics	Dominant algae	Other commonly occurring algae
Oligotrophic	Slightly acidic; very low salinity	Desmids <i>Staurodesmus</i> , <i>Staurastrum</i>	<i>Sphaerocystis</i> , <i>Gloeocystis</i> , <i>Rhizosolenia</i> , <i>Tabellaria</i>
Oligotrophic	Neutral to slightly alkaline; nutrient-poor lakes	Diatoms, especially <i>Cyclotella</i> and <i>Tabellaria</i>	Some <i>Asterionella</i> spp., some <i>Melosira</i> spp., <i>Dinobryon</i>
Oligotrophic	Neutral to slightly alkaline; nutrient-poor lakes or more productive lakes at seasons of nutrient reduction	Chrysophycean algae, especially <i>Dinobryon</i> , some <i>Mallomonas</i>	Other chrysophyceans, (e.g., <i>Synura</i> and <i>Uroglena</i>); diatom <i>Tabellaria</i>
Oligotrophic	Neutral to slightly alkaline; nutrient-poor lakes	Chlorococcal <i>Oocystis</i> or chrysophycean <i>Botryococcus</i>	Oligotrophic diatoms
Oligotrophic	Neutral to slightly alkaline; generally nutrient poor; common in shallow Arctic lakes	Dinoflagellates, especially some <i>Peridinium</i> and <i>Ceratium</i> spp.	Small chrysophytes, cryptophytes, and diatoms
Mesotrophic or eutrophic	Neutral to slightly alkaline; annual dominants or in eutrophic lakes at certain seasons	Dinoflagellates, some <i>Peridinium</i> and <i>Ceratium</i> spp.	<i>Glenodinium</i> and many other algae
Eutrophic	Usually alkaline lakes with nutrient enrichment	Diatoms much of year, especially <i>Asterionella</i> spp., <i>Fragilaria crotonensis</i> , <i>Synedra</i> , <i>Stephanodiscus</i> , and <i>Melosira granulata</i>	Many other algae, especially greens and cyanobacteria during warmer periods of year; desmids if dissolved organic matter is fairly high
Eutrophic	Usually alkaline; nutrient enriched; common in warmer periods of temperate lakes or perennially in enriched tropical lakes	Cyanobacteria, especially <i>Anacystis</i> (= <i>Microcystis</i>), <i>Aphanizomenon</i> , <i>Anabaena</i>	Other cyanobacteria; euglenophytes if organically enriched or polluted

^a After Hutchinson (1967).

Some dimensions of phytoplankton ecology.

Sinking and suspension.

For small particles sinking in a viscous medium, the rate of sinking is described by Stoke's law:

$$V_s = \frac{(2 g r^2 (q' - q))}{9 \mu \phi}$$

where: v_s = terminal sinking velocity
(attained almost instantly)

r = radius of the particle

g = acceleration of gravity (9.8 m/sec²)

q' = density of the particle

q = density of the medium (1.0 for water)

μ = dynamic viscosity of the medium

ϕ = coefficient of form resistance

(1 for a sphere)

Some sample values of *observed* sinking velocity

Alga	Observed sinking velocity ($\mu\text{m}/\text{sec}$)	24hr
<i>Stephanodiscus astrea</i> (6-7 μm diameter)	11.52 (+/- 0.81)	1 m
<i>Stephanodiscus astrea</i> (12-14 μm)	27.62 (+/- 2.64)	2.4 m
<i>Asterionella formosa</i> (8 cells)	7.33 (+/- 0.57)	0.6 m
<i>Melosira italica</i> (7-8 cells)	11.40 (+/- 4.11)	1 m



Asterionella and Melosira are shown in the figure above labeled 3.3. Stephanodiscus spp.

Phytoplankton may make adjustments in several of these terms as a means of regulating their rate of sinking and their vertical position in the water column.

r (**particle size**): Particle size is the most sensitive parameter, since the effect of the radius is squared in the formula.

$\rho' - \rho$ (**excess density**): A variety of possibilities exist for algae to regulate their excess density. Most phytoplankton cells are heavier than water, and therefore sink. Although there are only small differences in density among the various species, it is the excess density that determines sinking velocity. A diatom with a density of 1.2 g/ml is only 15% heavier than a green algal cell (1.04 g/ml), but if they were both the same size and had the same form resistance, the diatom would sink 5 times as fast.

Algae are heavier than water because of their biochemical composition. Nevertheless, the possibility exists that they could regulate their excess density by adjusting the proportions of various cell constituents. Some approximate densities for various cell constituents are:

<u>Constituent</u>	<u>Specific gravity</u>
Carbohydrate	1.5 g/ml
Protein	1.3
Nucleic acid	1.7
Minerals	2.5
Lipids	0.86
Gas vacuoles	0.12

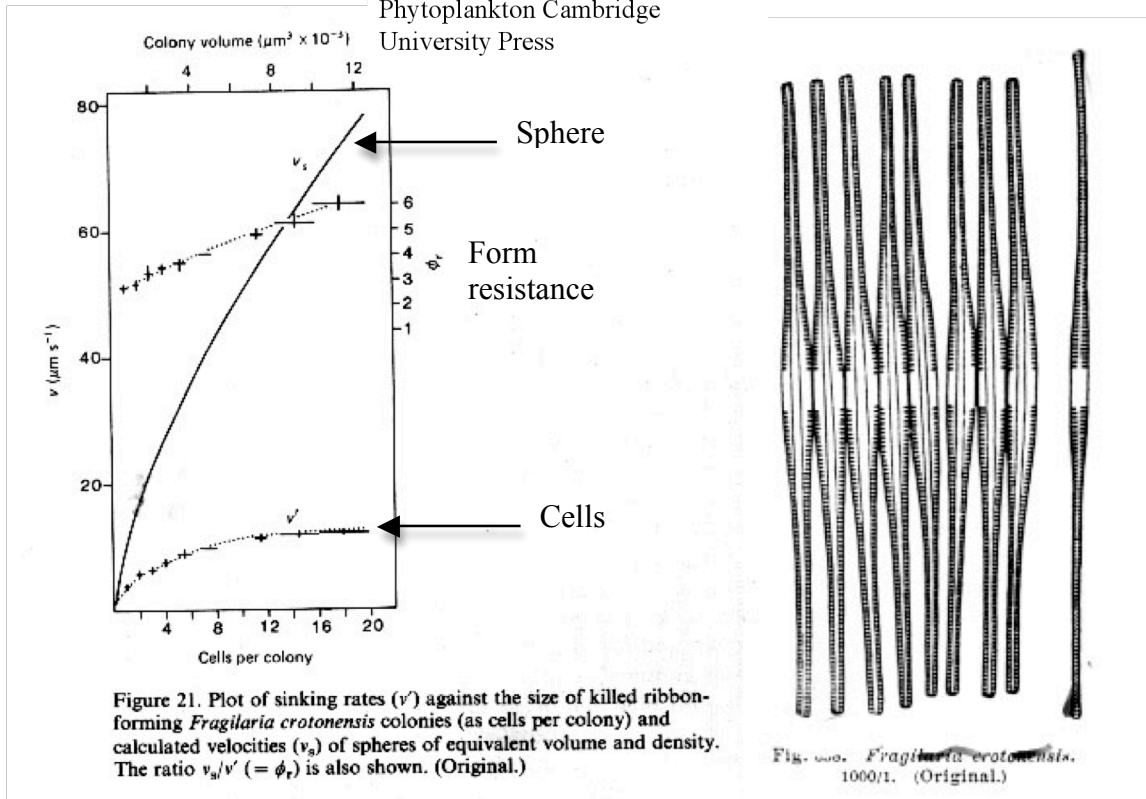
Other possibilities for density regulation include ion regulation and the secretion of mucilage. However, Reynolds presents arguments that seem to dismiss one by one the possibility of any adaptive value for the regulation of excess density by mechanisms other than gas vacuoles. Lampert and Sommer suggest that mucilage may instead be an “anti-predator” adaptation.

ϕ (**form resistance**): The shape of phytoplankton cells and colonies suggests that adjustments to form resistance are important as a means to regulate sinking. The sinking rate of a particle is altered from the sinking rate of a sphere by its shape even if density and volume remain unchanged. At low Reynolds number, “streamlining” will not produce a more rapid sinking rate. **Changes in shape can only reduce sinking rate. The amount by which the sinking rate is reduced compared to an equivalent sphere**

is described by the dimensionless coefficient ϕ (Phi). Its value can be predicted only for regular ellipsoids for which theoretical derivations have been verified experimentally (Reynolds, p65). Experimental results indicate that small projections or irregularities on cell surfaces do not greatly affect sinking velocity. However, ...”distortions of the spherical form, whether as cylinders, plates or other more elaborate forms, result in 2-5 fold reduction in the sinking rate with respect to the equivalent sphere.”

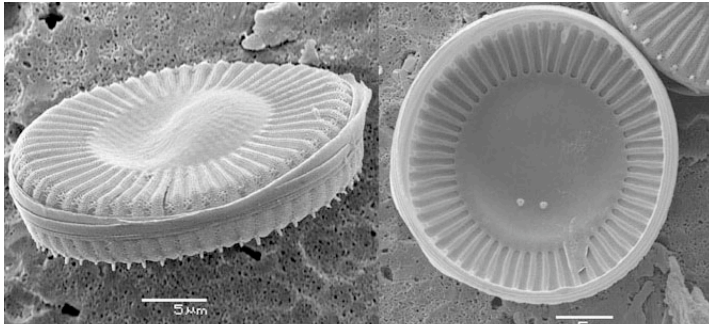
Estimation of form factor and effect of shape on sinking rate is illustrated below for *Fragilaria crotonensis*

From Reynolds C S 1984 The Ecology of Freshwater Phytoplankton Cambridge University Press



Some examples of observed values of form resistance (Table 10, Reynolds, p69)

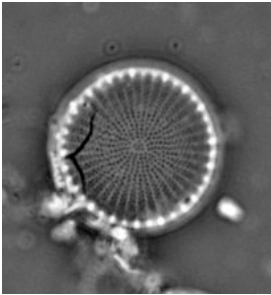
Alga	Shape	ϕ
<i>Cyclotella meneghiniana</i>	squat cylinder	1.03
<i>Stephanodiscus astrea</i>	squat cylinder	0.94-1.06
<i>Synedra acus</i>	attenuate cylinder	4.08
<i>Melosira italica</i> (7-8 cells)	cylinder	4.39
(1-2 cells)	cylinder	2.31
<i>Asterionella formosa</i> (4 cells)	stellate	3.15
(16 cells)	stellate	4.28
<i>Fragilaria crotonensis</i> (11-12 cells)	plate	4.83



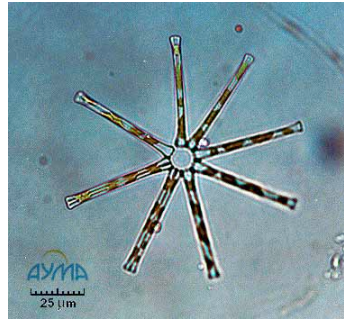
Cyclotella meneghiniana



Synedra acus

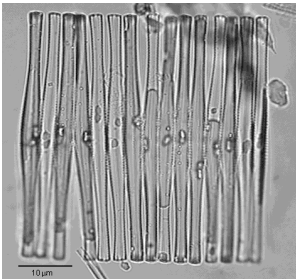


Stephanodiscus sp.



Asterionella

Formosa



Fragellaria crotensis

In short, it is clear that changes in shape can have a large effect on sinking rate. However, as Lampert and Sommer point out (p67), such shapes may well be more significant as defense mechanisms against grazers.

swimming:

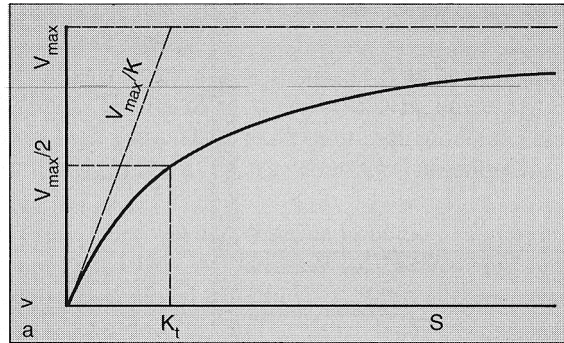
Reynolds, p97: “The swimming movements of motile organisms can appear very impressive...when observed under the microscope. In reality, the rates of progress are, at best, in the order of 0.1-1.0 mm/s. These movements are too feeble to overcome wind-driven current speeds having velocities an order or two greater. Nevertheless, the vertical direction of the movements will be important, for if the intrinsic movements were (say) all in the downward direction, the predicted effect would be analogous to the sinking of a non-motile particles. Vertical movements would always be more effective in non-turbulent layers and the latter are essential if vertical station is to be even approximately maintained.” Note that a swimming velocity of 1 mm/sec is equal to 86 m/day, more than 10x the sinking velocity of non-swimming particles!

Competition theory and the phytoplankton

Tilman model.

Tilman built on the simple Michaelis-Menten kinetics of nutrient uptake and developed a model to explain phytoplankton dynamics based upon resource availability.

He grew two species of diatoms (*Asterionella formosa* and *Cyclotella meneghiniana*) in semicontinuous culture under first phosphorus limitation and then under silica limitation. The growth rate of each species of diatom could be modeled as a function of each nutrient according to the Michaelis-Menten equation:



$$\mu = \mu_{\max} ([S]/K_{1/2} [S]),$$

where: μ = growth rate, under nutrient limitation, μ_{\max} = maximum growth rate, $[S]$ = concentration of the limiting nutrient, $K_{1/2}$ = the “half saturation” constant for the uptake of the particular limiting nutrient (K_t on the figure).

His results can be summarized by a table of the half-saturation constants for the uptake of each nutrient by each diatom:

$K_{1/2}$, or “half-saturation” constants for Silica and Phosphorus for two species of diatoms (See Tilman).

	Silica $K_{1/2}$	Phosphorus $K_{1/2}$
<i>Asterionella formosa</i>	3.94 $\mu\text{g Si/l}$	0.04 $\mu\text{g P/l}$
<i>Cyclotella meneghiniana</i>	1.44 $\mu\text{g Si/l}$	0.25 $\mu\text{g P/l}$

As is implied by the results, *Asterionella* has greater affinity for phosphorus, and will “win” a direct competition with *Cyclotella* if competition is based solely on the ability to assimilate phosphorus when the concentration is low. Conversely, *Cyclotella* has a greater affinity for Silicon, and will “win” a competition based on scarce supplies of Silicon. As can be seen in the figure below, the predictions of the model are born out, including the coexistence of the two species when each is limited by a different nutrient, P for *Cyclotella* and Si for *Asterionella*.

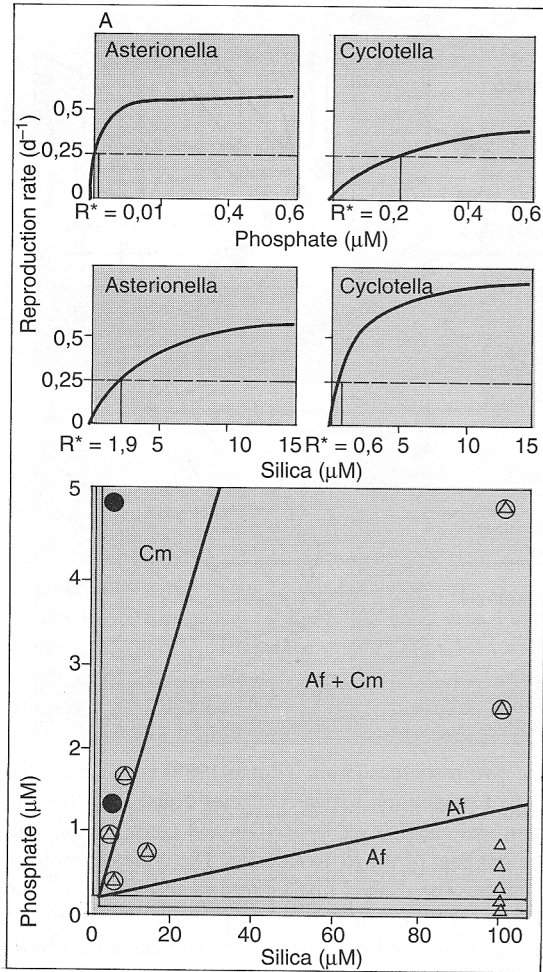


Figure 6.7 Summary of the competition experiments of Tilman (1977) with *Asterionella formosa* and *Cyclotella meneghiniana* at a dilution rate of 0.25 d^{-1} . (Above) Monod kinetics of P- and Si-limited growth, determination of the R^* values. (Below) A competition diagram with ZNGIs and consumption vectors. The symbols characterize the supply points (composition of the medium in the inflow) of each experiment and the taxonomic outcome of the competition. Circles: *Cyclotella* dominant; triangles: *Asterionella* dominant; combined symbols: coexistence.

Notice that when the ratio of P to Si is less than $0.04/3.94$, $P/Si < 0.01$, *Asterionella* wins the competition. In effect, P is in very short supply, and *Asterionella* is the more efficient at assimilating P, so ***Asterionella* wins the competition.**

On the other hand, if the ratio of P to Si is more than $0.25/1.44$, $P/Si > 0.17$, *Cyclotella* wins the competition. In this case, Si is in very short supply, and since *Cyclotella* is more efficient at assimilating Si, ***Cyclotella* wins the competition.**

Between these two inequalities, *Asterionella* is limited by the availability of Si while *Cyclotella* is limited by the availability of P, and **both species persist.**

The results then provide a more satisfactory cause/effect model of the outcome of competition, since the mechanistic basis of the competitive interaction is understood. Tilman's results provide a partial answer for the paradox of the plankton: species can coexist if limited by different nutrients.

Tilman later went on to apply this approach to terrestrial plants and became famous (at least among limnologists and plant ecologists). **His theory predicts that competition is most intense when resources (nutrients) are limiting.**

Ratios

Phytoplankton that are not limited by N or P are likely to have nutrient ratios of approximately 106C:16N:1P on a molar basis (The Redfield Ratio). If the composition of the phytoplankton departs from this ratio, it is an indication of nutrient limitation for the element underrepresented in the phytoplankton.

Models of plankton succession.

A number of authors have proposed models to explain the patterns of phytoplankton associations and phytoplankton succession commonly seen in lakes. Three different approaches (among many) are represented by:

- (1) Hutchinson's model, based on a reductionist approach,
- (2) Sommer's model (PEG) which is mainly descriptive, and
- (3) Reynolds' model, which integrates several ingredients, including the functional morphology of the phytoplankton.

Hutchinson's model of independent factors.

Hutchinson interpreted the patterns of seasonal succession of the phytoplankton in terms of the interplay of a variety of environmental factors. He identified the following list of factors as important in determining the succession of phytoplankton in a lake:

Partially independent physical factors

- Temperature

- Light

- Turbulence

Interdependent biochemical factors

- Inorganic nutrients

- Accessory organic materials, vitamins, etc.

- Antibiotics

Biological factors

- Parasitism in the broad sense

- Predation

- Competition.

He used this approach to describe the annual pattern of succession observed in Lake Windemere. Hutchinson admitted that this approach is "impeccable logically" and recognized that the outcome of competition may vary with environmental conditions.

PEG (Plankton Ecology Group) model

This model ascribes seasonal succession to a combination of autogenic (the accumulation of biomass, changes in relative metabolic rate, changes in nutrient availability and competition among algae for scarce nutrients, and herbivory by zooplankton) and

allogenic (such as temperature, light, stratification, mixing) processes. According to the PEG model, succession begins with ice breakup, and proceeds through 24 distinct sequential events and accounts for “typical” events that happen in a temperate zone lake.

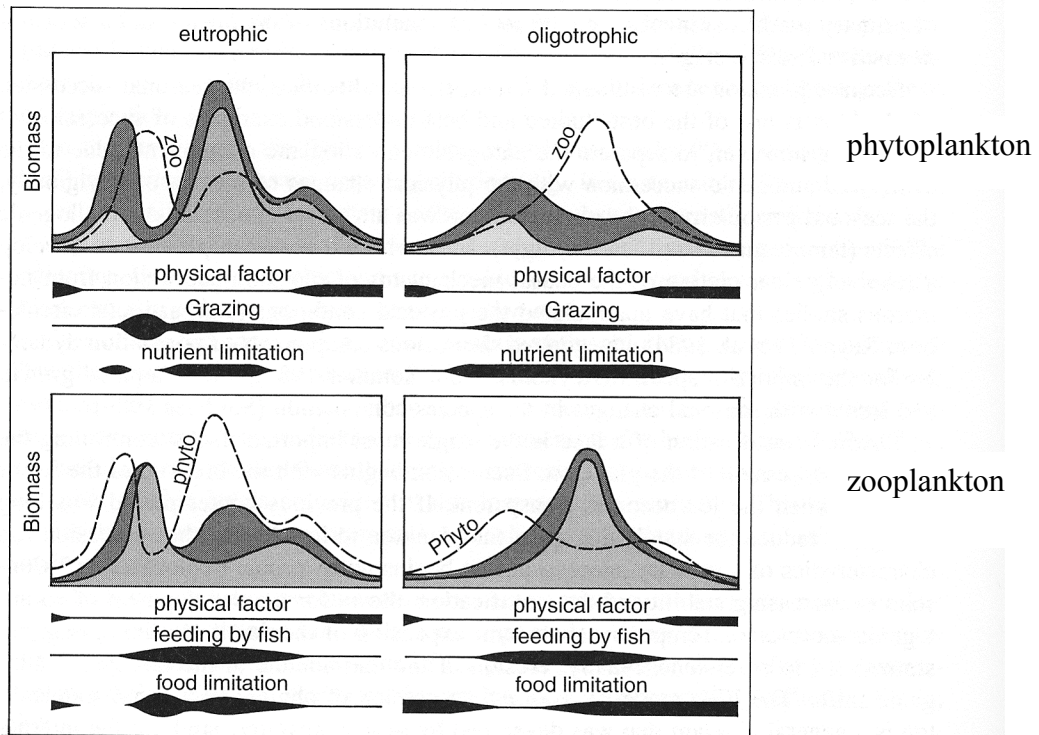


Figure 8.17 Graphic presentation of the PEG model of seasonal succession. Seasonal development of phytoplankton (above) and zooplankton (below) in eutrophic (left) and oligotrophic (right) lakes. Phytoplankton: dark shading, small species; medium shading, large nonsiliceous species; light shading, large diatoms. Zooplankton: dark shading, small species; medium shading, large species. The black horizontal symbols indicate the relative importance of the selection factors (from Sommer et al. 1986).

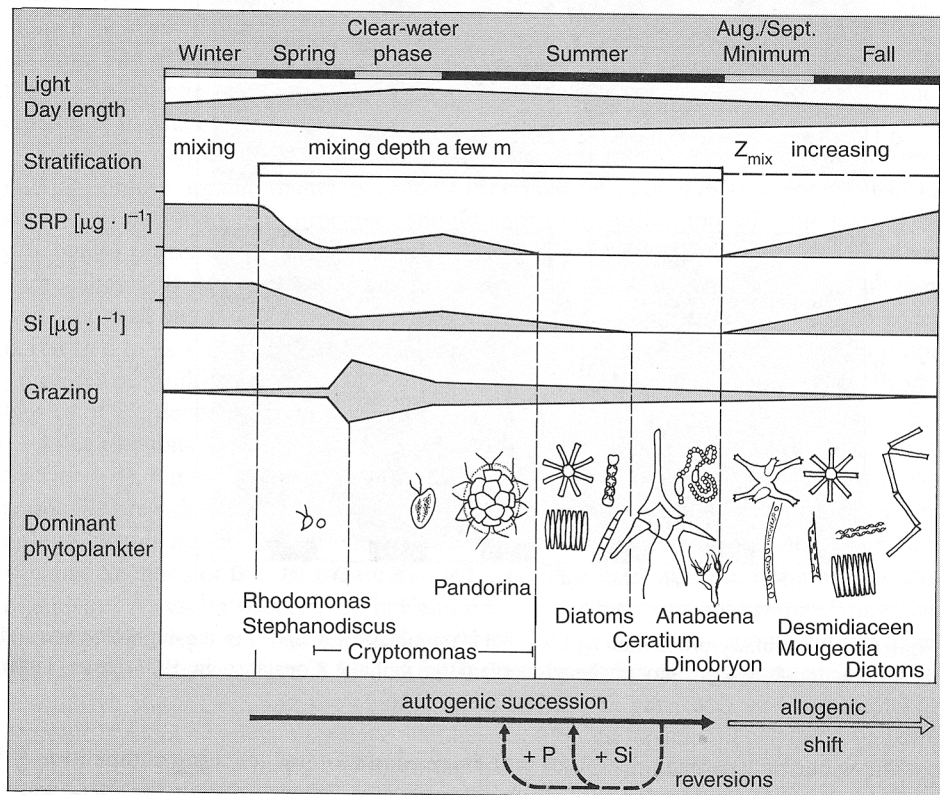


Figure 8.18 Diagram of the seasonal succession of phytoplankton and the relevant environmental conditions in Lake Constance (from Sommer 1987).

Reynolds model: C,S, and R associations.

See Reynolds, 1996 "The plant life of the pelagic", in SIL Proceedings 26:97-113.

Where Tilman first developed his ideas with phytoplankton and then applied them to terrestrial plants, Reynolds applied work in terrestrial plant ecology by Grimes to phytoplankton. In his model he links various characteristics of lakes and algae into a model of succession. These characteristics include:

- the chemical and physical characteristics of the epilimnion,
- the "strategies" of the species of algae to be expected to thrive under various combinations of these chemical and physical conditions,
- the individual groups of species of algae which can be associated with these strategies ("associations"), and
- a consideration of the "functional morphology" of the algae which confers the ability to prosper under the particular chemical and physical conditions where they are found.

Chemical and physical conditions. Reynolds points out that the epilimnion of a lake can be thought of as presenting various combinations of physical and chemical conditions that offer contrasting opportunities to individual species of algae. He organizes these

chemical and physical conditions into a 2 x 2 matrix according to the availability of light (high or low) and the availability of nutrients (high or low). These patterns are presented in his figure 1b (below). In the upper left quarter of the diagram, nutrients (resources) and light (energy) are generously available. The upper right quarter of the diagram represents conditions of light limitation (“energy limited”), either because light is not very available (winter or high turbidity) or because it is dilute (deep mixing). The lower left panel represents conditions of nutrient limitation, as might be expected in summer in an oligotrophic lake after algal growth has depleted available nutrients. The lower right panel, where both energy and nutrients are limited is uninteresting because the conditions are untenable for any algae.

Types of species to be expected with these combinations of conditions. The species which can be expected to thrive under these various conditions may be assigned to a general “*strategy*” according to their means of coping with the combination of light and nutrient availability. (He adopts Grimes notation {C, S, R} for identifying the “strategy” of each of the contrasting groups of algae.)

		Light	
		High	Low
Nutrients	High	Competitive	Ruderal
	Low	Stress Tolerant	No viable strategy

Note that this theory predicts that competition is most intense when resources are abundant. Remember Tilman’s prediction mentioned above? This sets up some nice opportunities for research to test ecological theory, which many graduate students have taken advantage of to find a dissertation topic.

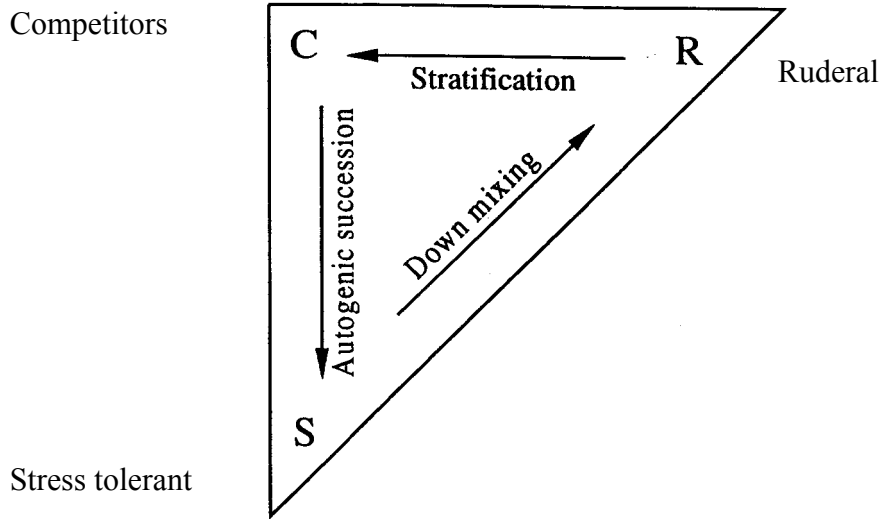


Fig. 8. Strategic triangle deduced from Figs. 1, 3 and 4b, with selective shifts brought about by stratification, succession and intermediate disturbance by mixing. Original.

C species: Species which can be expected to do best when both light and nutrients are readily available are those species capable of rapid growth. C species are small-celled and therefore have a high ratio of surface area to volume. Hence, they are able to assimilate nutrients and grow rapidly when light is adequate.

S species: Species which can be expected to do best when nutrients are scarce but light is adequate are those that are efficient at nutrient uptake. A general characteristic is the ability to conserve biomass by avoiding sinking or grazing. In general, cell sizes are large. When light is available, such large cells are able to assimilate scarce nutrients and, because of their size, retain and conserve them. Many are also motile and thus avoid sinking losses. Their large size makes them more resistant to grazers.

R species: Species which can be expected to do best when nutrients are plentiful but light is limiting are those that are efficient at light utilization. They are medium-sized but often have a shape much distorted from the spherical. Such shapes (flat disks or long needle-like shapes) allow a more efficient dispersal of light harvesting centers. It is therefore not surprising that there is an association between such medium size and distorted shape and the ability to use scarce or dilute light. These species are capable of light adaptation (more chlorophyll per cell) or chromatic adaptation (more accessory pigments to absorb remaining light frequencies). Such species are more tolerant of vertical mixing (“disturbance”) because of their ability for “light tuning”.

Reynolds has identified a number of phytoplankton associations which can be identified with one or another of the conditions of light and nutrients in his matrix (see table below).

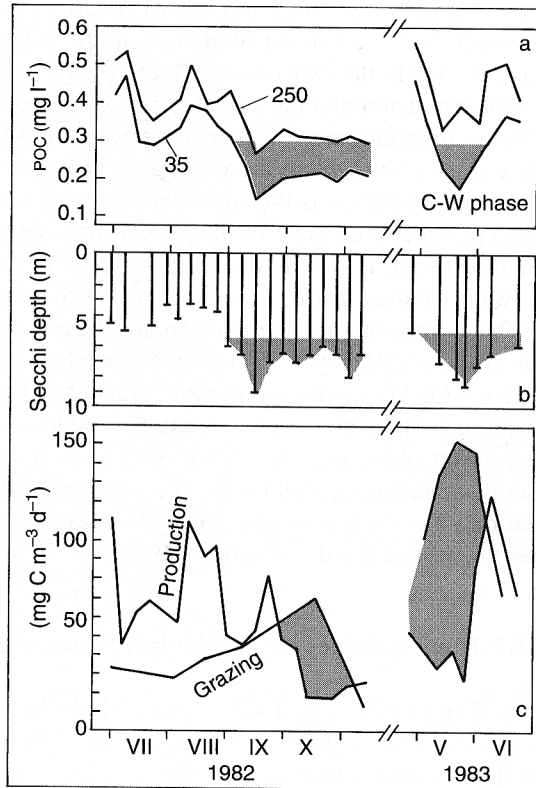
CONDITION	ENERGY LIMITED	ENERGY AND RESOURCES REPLETE	RESOURCES LIMITED
TYPICAL SEASONALITY	VERNAL PERIOD	EARLY - LATE - SUMMER PERIOD	
OLIGOTROPHIC		<i>Cyclotella</i> spp <i>Urosolenia</i> spp A	<i>Peridinium willei</i> <i>Ceratium hirundinella</i> <i>Gomphosphaeria</i> <i>Staurodesmus</i> L O
MESOTROPHIC	<i>Asterionella formosa</i> <i>Cyclotella</i> spp <i>Melosira italica</i> <i>Synedra</i> spp B	<i>Dinobryon</i> <i>Mallomonas</i> E	<i>Peridinium</i> <i>Ceratium</i> <i>Gomphosphaeria</i> L M
	<i>Ankistrodesmus</i> <i>Chlorella</i> X	<i>Sphaerocystis</i> <i>Gemmelicystis</i> <i>Coenococcus</i> <i>Oocystis lacustris</i> F	<i>Asterionella</i> <i>Tabellaria flocculosa</i> <i>Fragilaria crotonensis</i> <i>Cosmarium</i> spp <i>Staurastrum</i> spp N
	<i>Cryptomonas / Rhodomonas</i> Y		
	<i>Planktothrix rubescens / mougeotii</i>		R
EUTROPHIC	<i>Asterionella</i> <i>Fragilaria</i> <i>Stephanodiscus</i> spp C	<i>Eudorina</i> <i>Pandorina</i> G <i>Volvox</i> T <i>Tribonema</i>	<i>Aphanizomenon</i> <i>Anabaena</i> spp <i>Gloeotrichia</i> H
	<i>Ankistrodesmus</i> <i>Elakatothrix</i> <i>Scenedesmus</i> <i>Tetrastrum</i> X	e.g. <i>Ankyra</i> <i>Chromulina</i> <i>Monodus</i> X	<i>Ceratium</i> <i>Microcystis</i> M
	<i>Cryptomonas / Rhodomonas</i>		<i>Asterionella</i> <i>Fragilaria</i> <i>Melosira granulata</i> <i>Closterium</i> spp <i>Staurastrum</i> Y
HYPERTROPHIC	<i>Diatoma</i> D <i>Stephanodiscus</i> spp <i>Synedra</i> spp	<i>Pediastrum</i> <i>Coelastrum</i> <i>Oocystis borgeti</i>	<i>Aphanocapsa</i> <i>Aphanothece</i> K
	<i>Ankistrodesmus</i> <i>Crucigenia</i> <i>Scenedesmus</i> <i>Tetrastrum</i>		J
	<i>Cryptomonas / Rhodomonas</i>		X
	<i>Planktothrix agardhii / Limnothrix</i>		Y
			S

Fig. 2. Associations of phytoplankton selected under conditions of energy limitation (as in the vernal period of temperate lakes), nutrient limitation (late summer) and an intermediate period of relative repletteness, in lakes of different trophic types. Figure based on diagram of REYNOLDS (1984).

with mucilaginous colonies, such as *Sphaerocystis*, may actually pass through the gut of zooplankton and benefit from the nutrient bath on the way.

Some filter feeders (e.g. some cladocerans) may be relatively non-discriminating. However, many or perhaps most zooplankton display distinct preferences among the available algal cells. Lampert and Sommer present some sample data for *Daphnia magna*. It is clear from these results that *D. magna* prefers small spherical cells over large or elongate cells.

Figure 6.15 The effect of zooplankton biomass on the phytoplankton in Schöhsee. (a) Particulate organic carbon (POC, includes both phytoplankton and detritus), particle sizes <250 and <35 μm . Particles under 35 μm are considered edible. (b) Water transparency. (c) Photosynthetic rates of phytoplankton (dashed line) and the feeding rates of the zooplankton (solid line). Periods where the grazing rates of the zooplankton exceed the production rates of phytoplankton are shaded. The clear-water phase occurs in mid-May (from Lampert 1989).



Selectivity coefficient ($W_i = \text{grazing rate on species } x / \text{grazing rate on most edible species}$)

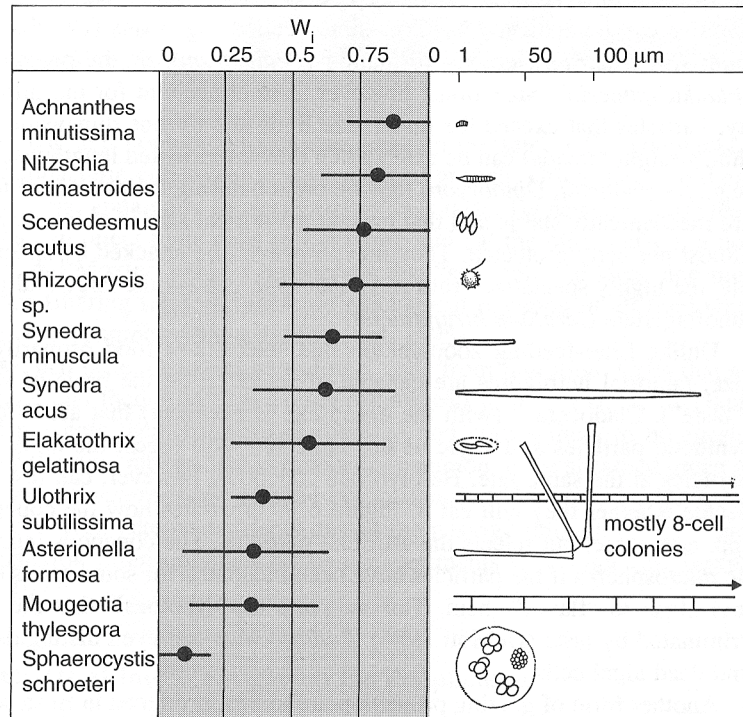


Figure 6.16 Selectivity coefficients (W_1 , mean value and standard deviation) for various phytoplankton species in microcosm experiments with *Daphnia magna* as the grazer. The sketches of the algal species are scaled according to actual size; large and species with gelatinous sheaths are grazed poorly. (Data from Sommer 1988c.)