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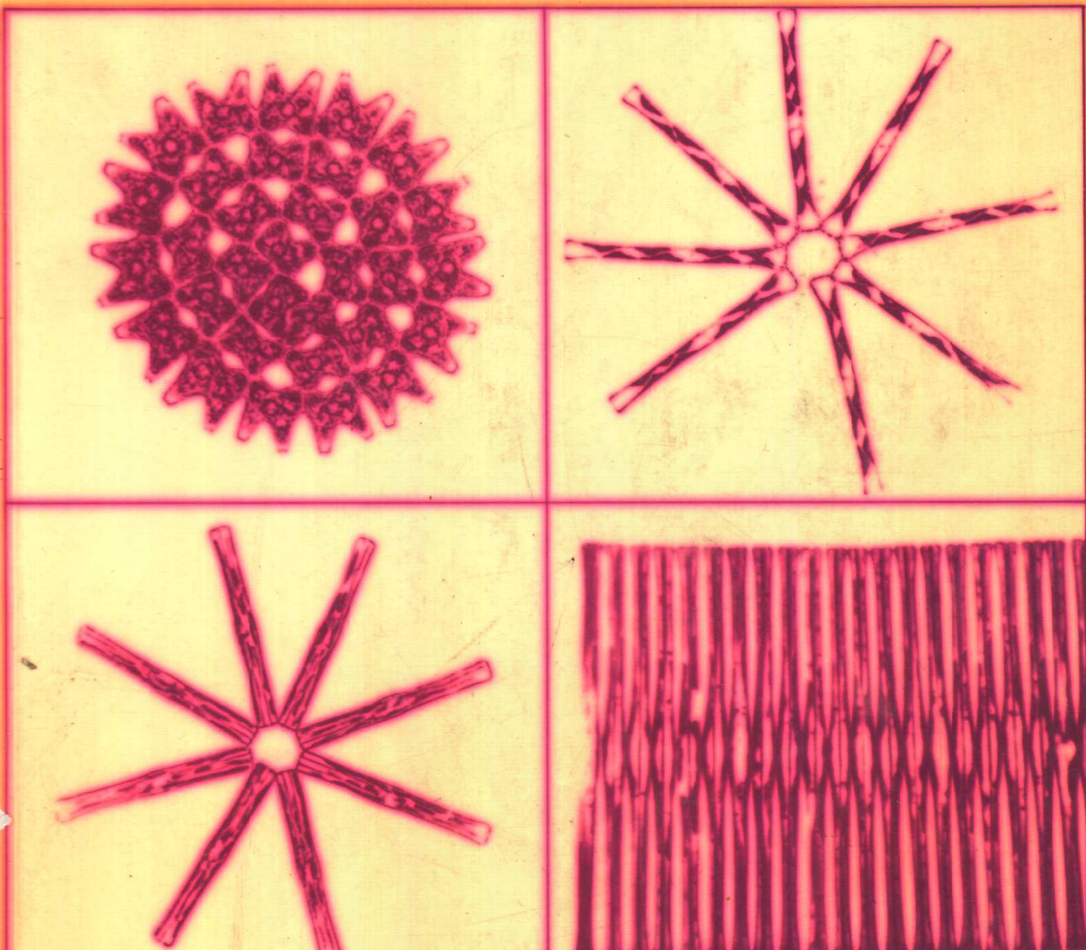
THE ECOLOGY OF FRESHWATER PHYTOPLANKTON

C. S. REYNOLDS



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Preface

The importance of phytoplankton is beyond question. Planktonic primary production provides the base upon which the aquatic food chains culminating in the natural fish populations exploited by man are founded, at the same time generating some 70% of the world's atmospheric oxygen supply. Excessive algal production in lakes and reservoirs presents expensive problems in the water industries, whilst deleterious effects upon fisheries and water-based recreation are fairly attributed to overabundance of phytoplankton. There is, therefore, a powerful economic and social need for as complete as practicable an understanding of the factors which regulate the spatial and temporal variations in the distribution and productivity of phytoplankton – or, in short, its ecology.

The volume of scientific literature devoted to phytoplankton biology is daunting and often bewildering. Many more titles are added each year. Fortunately, for both the beginner and the more seasoned student, there is a number of excellent general books and review papers describing fundamental features of plankton biology but there is a constant need for updating and revision as new principles and hypotheses become established.

I shall make no further attempt to justify the addition of yet another book to those already available. This volume is concerned mainly with the factors which determine the wax and wane of specific phytoplankton populations in standing freshwaters (lakes and reservoirs), though reference is made to marine plankton which is, generally, subject to similar controls. It is primarily intended for use by students, and I have therefore tended to oversimplify some of the more complex aspects of the subject, for the sake of ready comprehension, but further reading is recommended wherever suitable or relevant texts are available. I hope that I have adequately resisted the temptation to be unnecessarily encyclopaedic in referencing literature: there are many significant contributions that have not been cited.

Ecology is a complex science. There are probably almost as many definitions of 'ecology' as there are books on the subject. In framing this text, I have adopted the phrase to which I was introduced as a would-be ecology student: 'What lives where – and why'. Specifically, I have endeavoured to develop this theme through an overview of the structure of planktonic communities in which the functional adaptations of pelagic life are emphasised, building up to the dynamic aspects of production and seasonal periodicity. Biochemical aspects of phytoplankton are not specifically covered and I have included no more physiological information than I have found necessary. Again, appropriate further reading is referenced.

The text could not have been prepared without the considerable help of a great many friends and colleagues. I am grateful for advice on the presentation and discussion of subject matter (often outside my primary interests) freely contributed by Dr G. Fryer, F.R.S., Mr T. I. Furnass, Dr D. G. George, Dr G. H. Hall, Dr S. I. Heaney, Dr J. Hilton, Mr J. E. M. Horne, Mr G. H. M. Jaworski, Dr J. G. Jones, Dr J. W. G. Lund, F.R.S., Dr J. F. Talling, F.R.S. and Dr L. G. Willoughby. The excellence of the Freshwater Biological Association's comprehensive library facilities proved to be extremely beneficial to my background reading and literature searches; it is a pleasure to express my appreciation to the Council, Director and Library staff of the Association.

I should like to thank especially: Dr Hilda Canter-Lund F.R.P.S., not only for the selection of her excellent collection of algal photomicrographs but also for the enthusiastic and time-consuming trouble she took over their presentation; Sheila Wiseman, whose collaboration and support during the preparation of the book has been invaluable, and whose illustrative talents contributed most of the text figures herein; and Elisabeth Evans, upon whom fell the almost impossible task of turning my handwritten pages into a legible typescript.

Finally, special acknowledgements are also accorded to Mr Charles Sinker, O.B.E., M.A., and to Dr John W. G. Lund, C.B.E., F.R.S., both of whom deeply influenced my appreciation of ecology in general and of phytoplankton in particular, during my formative years. The most that I could wish for is that, through the pages of this text, I may in turn pass on the benefit of their teaching to others.

The Ferry House, Ambleside, Cumbria
January 1983

C. S. REYNOLDS

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What is phytoplankton?

'He prayeth best who loveth best all things both great and small.'
COLERIDGE, *The Ancient Mariner*

1.1 Terminology

Biology, and hydrobiology in particular, is littered with terms whose precise meanings, either through initial misconception or through later abuse, have evolved, degenerated or otherwise departed from their original definitions. 'Plankton' is no exception. It is therefore necessary at the outset to clarify its contemporary meaning and to distinguish it adequately from other, apparently overlapping terms.

The first use of the term 'plankton' is widely attributed to the German biologist, Viktor Hensen (Ruttner, 1953; Hutchinson, 1967), who, in the latter half of the nineteenth century, began a series of expeditions to gauge the distribution, abundance and composition of microscopic organisms in the open ocean.

The existence of such organisms, however, had been demonstrated some years earlier by another investigator, Johannes Müller. Using a fine-mesh silk net to concentrate the organisms, Müller opened the door on a hitherto unknown community, of quite uncontemplated richness and diversity. Müller called this community the 'Auftrieb'; but it was Hensen's name for the same community, 'plankton', which gained popular recognition.

According to Hensen's (1887) usage, 'plankton' included all organic particles '*which float freely and involuntarily in open water, independent of shores and bottom*'. The dependence of plankton upon water movements for maintenance and transport is accurately implied in this definition (*πλαηκτοσ* – wandering). It immediately excluded other, larger inhabitants (e.g. fish, mammals) of open water (the *pelagic* zone) having the ability to substantially regulate their own distribution, by swimming (the 'nekton'). Hensen's 'plankton' did not specifically exclude non-living particles, so it is therefore synonymous with '*seston*' in Kolkwitz's (1912) later terminology, that continues to command common acceptance. Seston thus applies to all particulate matter maintained in the pelagic zone: abioseston, or *tripton*, is the non-living fraction; bioseston, or plankton, comprises only discrete, living organisms.

There are two more serious criticisms of Hensen's definition of what we now understand to be 'plankton', but it has taken nearly a century of subsequent investigations to resolve these. One is simply that, in general, plankton does *not* float: there are few planktonic organisms which are consistently buoyant; on the contrary, most are often or always more dense than the water they inhabit. As will be pursued more exhaustively in Chapter 2, the specific adaptations of planktonic organisms for pelagic life seem largely directed towards prolonged *maintenance in suspension*. Moreover, there are occasions when it is beneficial for planktonic organisms to be able to avoid the immediate sub-surface water layers and when a positive sinking rate is actually advantageous. This leads directly to the second point, which is that many planktonic organisms are not exclusively confined to the pelagic zone but may spend part, or even most, of their life cycle on the sediments or in other (littoral) habitats. Put another way, many organisms present in open waters are only facultatively planktonic (or *meroplanktonic*).

For these reasons, it is perhaps more useful to regard plankton as 'the community of plants and animals *adapted to suspension* in the sea or in fresh waters and which is *liable to passive movement by wind and current*'. This definition does not exclude temporary inhabitants of the plankton or chance introductions to the pelagic (which is conceptually important in the context of the evolution of the planktonic habit) but it nevertheless lays stress upon morphological and behavioural adaptions to survive there.

Plankton is a potentially functional community, of similar organizational rank implicit in the terms 'forest-' or 'grassland-communities'. The plants and animals are conveniently segregated in the terms *phytoplankton* and *zooplankton* respectively, notwithstanding differences in opinion about where the dividing line is drawn. Botanists and zoologists still dispute their respective claims over organisms like dinoflagellates, which are simultaneously autotrophic (i.e. capable of elaborating their foods from inorganic substances dissolved in the water), phagotrophic (i.e. capable of ingesting other organisms, or parts thereof, and assimilating food therefrom) and motile. Here, autotrophy is considered sufficient qualification to be included in this treatment of 'phytoplankton'.

Before considering the taxonomic range of organisms represented in the phytoplankton of fresh waters and their specific adaptive features, it is convenient to mention some other methods of subdividing the phytoplankton involving the use of prefixes which may be encountered in the literature.

The first of these attempts to distinguish between the plankton of lakes (*limnoplankton*), ponds (*heleoplankton*) and rivers (*potamoplankton*). Whilst it is true that, qualitatively, the assemblages of planktonic organisms represented in these broad categories often comprise distinct elements (presumably in response to quite different sets of dominant environmental characteristics), there are sufficient species which are common to two or all three types of habitat to prevent the classification from having more than a very generalized application. Besides, the distinction between the two kinds of standing water (*lentic* habitats: ponds and lakes) has no clearly defined dividing line. Moreover, both habitats are, to a greater or lesser extent, simply extensions of flowing (*lotic*) habitats characterized by relatively protracted hydraulic residence times. Seasonal and spatial differences in the composition of their plankton are, in any case, of greater significance, and broadly similar cycles are reproduced in all three habitats (see Chapters 3 and 8).

Various authors have introduced prefixes to categorize the phytoplankton according to the individual sizes of the organisms: the terms *nannoplankton* (Rodhe, Vollenweider & Nauwerck, 1958), *nanoplankton* (Yentsch & Ryther, 1959), *ultraplankton* (Wetzel, 1964) and *μ-algae* (Fogg & Belcher, 1961) have been used to separate the lower size ranges of individuals from the larger ('*netplankton*') forms. The latter have a longer history of study, for it was not until the end of the nineteenth century that it was realized that the meshes of the first phytoplankton nets (apertures *ca.* 70 μm) allowed many smaller organisms to pass through. Lohmann (1911) introduced a centrifugation technique, which showed that the number of species in seawater that passed through nets often exceeded the number of species retained and that, sometimes, they accounted for the greater fraction of the total biomass present. Modifications to Lohmann's technique, devised by Kolkwitz (1911), Ütermohl (1931) and others, involving the fixation of intact water samples and the precipitation of planktonic organisms therefrom, have enabled routine direct estimations of the concentrations of planktonic organisms to be made and they still form the basis of many quantitative studies at the present time.

Few workers, however, continue to physically separate the larger algae from quantitative water samples with the result that there is no longer any agreed differentiation between 'netplankton' and 'nanoplankton'. Pavoni's (1963) nanoplankton generally measured < 30 μm in any plane; Nauwerck (1963) placed the limit at a nominal 80 μm, Kalff (1972) at 64 μm, and Gliwicz & Hillbricht-Ilkowska (1972) at 50 μm. Manny (1972) and Gelin (1975) adopted a critical limit of only 10 μm!

Nevertheless, the larger and smaller planktonic organisms do show differential morphological adaptations to planktonic life (see below) and are dissimilar in their susceptibility to loss processes (see Chapter 7). These differences are conveniently encapsulated within the terms 'netplankton' and 'nanoplankton'. Their continued use is desirable, provided it is qualified by the size ranges actually adopted.

Another set of terms relating to size is sometimes encountered. '*Microplankton*' corresponds roughly with nanoplankton, '*mesoplankton*' with the netplankton, whilst the meaning of *macroplankton* (occasionally '*megaloplankton*', or '*megaplankton*') embraces those aquatic angiosperms and pteridophytes that float freely on water surfaces. Such plants include the duckweeds (*Wolffia*, *Lemna* spp.), frogbit (*Hydrocharis*), the nororious Water Hyacinth (*Eichhornia*) and the water-ferns (*Azolla*). For at least part of the year, they do genuinely float on water and their distribution is subject to the effects of winds and currents. They are scarcely in suspension, however, and this fact excludes them from the definition of plankton adopted above. They are obviously adapted for a very different existence from that shared by the true plankton. Indeed, these terms hardly enhance anyone's understanding of plankton, and are best avoided.

Lastly, an important distinction must be drawn between plankton and the community of plants and animals which inhabits the surface film of quiet backwaters, the *neuston*. Though generally small, neustic organisms are specifically adapted to exploit the surface tension of water for maintenance. Few plant species are common to both communities, although some neustic crustaceans (e.g. the cladoceran *Scapholeberis* and the ostracod *Notodroma*) are able to move freely between the surface and the underlying water. Neither, however, is regarded as being truly planktonic.

1.2 Planktonic organisms

The planktonic community comprises both plants and animals. Unlike the case of marine zooplankton, few animal phyla are represented in the planktonic fauna. The most conspicuous of these are the Crustacea and Rotatoria, together with some rhizopods and ciliophorans. One family of Insecta (Arthropoda, class Hexapoda), the Chaoboridae, is represented, and there are a few freshwater planktonic genera drawn from elsewhere in the animal kingdom. These are set out in Table 1, with named examples; some of the more familiar genera, reference to which is made in later chapters, are also included. Some of the larger animals named (e.g. *Chaoborus*, *Mysis*) which swim sufficiently strongly to be able to alternate between open water and the bottom deposits could arguably be described as 'nektonic'; but the argument is academic and they are included here for completeness.

The phytoplankton of freshwaters includes representatives of several groups of algae and bacteria, as well as the infective stages of certain actinomycetes and fungi. Of these, the most conspicuous are undoubtedly the algae, but neither the biomass of bacteria nor the importance of their contribution to the functioning of aquatic ecosystems should be underestimated. Bacterial activities mediate many of the chemical processes which characterize aquatic habitats (e.g. the cycles involving carbon, nitrogen, iron and sulphur, and the consumption of dissolved oxygen), currently referred to as '*geochemical* cycling' (more correctly, 'biogeochemical cycling'). The subject matter of this book is directed largely towards planktonic 'algae', to the exclusion of the microbiological and mycological aspects of phytoplankton. For recent general account of the biology of aquatic bacteria, the reader is referred to Brock (1979).

One discrete and distinctive group of micro-organisms, however, is featured prominently in this work: the *Cyanobacteria.* Until relatively recently this group was variously referred to as the *Myxophyta* (*Cyanophyta*, *Schizophyta*), or, simply, 'blue-green algae', but they have been long recognized to be remote from any other algal group. (In any case, 'Algae' has ceased to have any real taxonomic meaning it should be regarded as a loose blanket term for 'primitive' cryptogamic photoautotrophs.) Specifically, 'blue-green algae' lack both the structural organization of chromosomes within a separate nucleus typical of cells and the discrete pigment-containing organelles (*plastids* or *chromatophores*) characteristic of many plants. In these features, the 'blue-green algae' share obvious affinities with the *prokaryotic* organization of bacterial cells. A protracted academic wrangle among botanists as to whether blue-greens should be regarded as bacteria or as algae was rejoined by the proposal to include an order Cyanobacteriales within the Procaryotae, class Photobacteria (Gibbons & Murray, 1978). It was immediately followed by the proposal (Stanier *et al.*, 1978) that cyanobacterial nomenclature, hitherto subject to the Botanical Code based on Linnaeus' original system of binomials, be brought under the rules of the Bacteriological Code (Lapage *et al.*, 1975). In essence, this change means that material must be related to cultured type-strains rather than to herbarium specimens, or to iconotypes, backed by latin diagnoses, as previously. There are considerable difficulties, however, in matching wild cyanobacteria to cultured material, whose morphology may alter so radically under laboratory conditions from that of the original isolate as to be scarcely recognizable. Thus, the ecologist is left with little practical alternative to the older, botanical names. Incorrect though they may be, these specific names and, indeed, the term 'blue-green algae', continue to be widely accepted; they at least have the virtue of being understood by bacteriologists, phycologists and other

Table 1. *Freshwater planktonic organisms*

Phytoplankton		
Bacteria[a]	Chemotrophs, including budding/appendaged forms which show morphological adaptations to pelagic life	e.g. *Planktomyces*, *Metallogenium*, *Ochrobium*
	Aerobic phototrophs	*Thiopedia*, *Chromatium*
	Oxidizing chemolithotrophs and organisms utilizing C_1 compounds	*Nitrosomonas*, *Methylomonas*, *Thiobacillus*
	Anaerobic chemo-organotrophs	*Desulfovibrio*
	Uncertain status	*Pelonema*, *Peloploca*
Cyanobacteria	See Table 2	
Actinomycetes	Presumably dispersed through open waters[b]	*Actinoplanes*
Fungi	Parasitic members of the Chytridales, Saprolegniales, dispersed through open water	*Rhizophydium*, *Blastocladiella*, *Zygorhizidium*, *Podochytrium*
Viruses[c]		
'Algae'	See Table 2	
Zooplankton		
Rhizopoda	A few planktonic amoeboids exist	*Pelomyxa*, *Asterocaelum*
Ciliophora	Ciliates, including holotrichs, oligotrichs and peritrichs	*Coleps*, *Ophryoglena*, *Tintinnidium*, *Vorticella*, *Epistylis*, *Metopus*, *Frontonia*
	Suctorians	*Acineta*
Mastigophora	The holozoic 'euglenoids'	*Peranema*
Coelenterata	One or two genera of trachyline hydrozoan polyps have planktonic medusae	*Craspedacusta*, *Limnocnida*
Rotatoria	About two dozen genera, almost wholly drawn from the Order Monogononta, are truly planktonic	*Brachionus*, *Keratella*, *Kellicottia*, *Notholca*, *Trichocerca*, *Ascomorpha*, *Asplanchna*, *Polyarthra*, *Filinia*, *Synchaeta*, *Conochilus*

Gastrotrichia	Occasional species reported from plankton	
Crustacea	Branchiopoda, Anostraca: some of the brine shrimps *may* be considered planktonic	*Artemia*
	Branchiopoda, Cladocera: includes several common and cosmopolitan genera	*Bosmina, Daphnia, Ceriodaphnia, Moina, Holopedium, Bythotrephes, Leptodora*
	Ostracoda: at least one tropical genus is planktonic	*Cypria*[d]
	Copepoda, Cyclopoidea: some free-living forms are entirely planktonic; certain parasites have planktonic larvae	*Mesocyclops, Ergasilus*
	Copepoda, Calanoidea	*Eudiaptomus, Limnocalanus* *Eurytemora*
	Branchiura. Ectoparasites, some of which are transmitted largely within pelagic zone.	*Argulus*
	Malacostraca, Mysidacea: mostly marine but a few species (believed relicts) enter pelagic zones of inland waters	*Mysis*
	Malacostraca, Amphipoda	*Macrohectopus*[e]
Arthropoda	Insecta, Diptera: one family has a larva adapted to pelagic life	*Chaoborus*
Mollusca	Lamellibranchiata: some representatives of predominantly marine families have a planktonic veliger larva	*Dreissensia*

(*a*) 'Functional' classification of the bacteria follows Buchanan & Gibbons (1974).
(*b*) See Willoughby (1976).
(*c*) Aquatic viruses are, as yet, almost unstudied, but several pathogens of phytoplankton 'algae' have been recognized (e.g. Safferman & Morris, 1963; Luftig & Haselkorn, 1967).
(*d*) *Cypria petenensis* and *C. javensis* are apparently planktonic in Laguma de Petén, Guatemala, and in several lakes in S.E. Asia respectively.
(*e*) *Macrohectopus branickii* is the endemic pelagic amphipod in L. Baykal.

biologists alike. Here, I intend to use 'algae' as meaning true, eukaryotic algae plus cyanobacteria.

1.3 Planktonic 'algae'

The 'algal' groups with planktonic representatives in freshwaters are listed separately in Table 2, together with notes on their diagnostic features and some of the generic names: all the freshwater genera mentioned in the subsequent chapters are noted at the appropriate point. There is no universally accepted phycological classification and alternative lists and group headings will be found elsewhere in the literature. None of these is necessarily correct but the variations are mainly ones of detail. The arrangement here mainly follows Christensen's (1962) scheme, although I have used alternative names for certain groupings (after Fott, 1959; Round, 1965; Bourrelly, 1966, 1968, 1970) where these have won more general acceptance. The finer points of taxonomy are not the concern of this book; the works cited should be consulted for more authoritative comments than mine!

It should be stressed that Table 2 merely conveys the diversity of planktonic representations. It should not be taken to imply that all genera occur simultaneously in all lakes or in equal quantities. The species structure of 'algal' assemblages is discussed in later chapters.

A final cautionary note might be added for the benefit of non-phycologists: in the same way that phytoplankton comprises organisms other than algae, so not all algae (or even very many) are planktonic or, for that matter, occur in freshwaters. A moment's thought is sufficient to exclude the large brown and red seaweeds, the waterside stoneworts or the green encrustations abhored by aquarists from anyone's understanding of plankton.

1.4 General features of planktonic 'algae'

Planktonic 'algae' are drawn from a diverse range of, at best, distantly related phylogenetic groups (Table 2). From an evolutionary standpoint, it may be postulated that the planktonic habit has arisen on several occasions, suggesting that adaptive radiation into pelagic environments has been backed by powerful selective pressures. That the 'algae' should have been relatively successful in exploiting the potential advantages offered by pelagic life has presumably depended upon a certain degree of pre-adaptation to a dispersed existence. Here, we may cite the generally low level of structural organization and morphological plasticity of 'algal' cells, the concomitant intracellular 'division of labour', which makes for considerable physiological and biochemical independence of individual

Table 2. *Groups of 'algae' represented in the freshwater phytoplankton and some selected genera*

KINGDOM: PROKARYOTA

CLASS: Photobacteria
CYANOBACTERIALES (blue-green bacteria/'algae')
(synonyms: CYANOPHYTA, MYXOPHYTA, SCHIZOPHYTA)
Prokaryotic 'algae' lacking typical membrane-bound nuclei and plastids

Order: *Chroococcales* Solitary or colonial coccoid 'blue-greens'

Includes: *Aphanocapsa, Aphanothece, Coelosphaerium, Gloeocapsa, Gloeothece, Gomphosphaeria, Microcystis, Synechococcus*

Order: *Nostocales* (= *Hormogonales, Oscillatoriales*) Filamentous blue greens, mostly capable of heterocyst- and akinete-formation

Includes: *Anabaena, Anabaenopsis, Aphanizomenon, Gloeotrichia, Lyngbya, Oscillatoria, Pseudanabaena, Spirulina, Trichodesmium*

KINGDOM: EUKARYOTA

Eucaryotic algae with typical nucleus and pigments localized within plastids (or chromatophores). Eight phyla (according to this treatment): two (**RHODOPHYTA** and **PHAEOPHYTA**) are without representatives in the freshwater phytoplankton

CRYPTOPHYTA
Naked, biflagellate algae, with one or two large plastids; division longitudinal; sexual reproduction unknown; assimilatory product of photosynthesis, starch. One class and one order

Order: *Cryptomonadales*

Includes: *Chilomonas, Chroomonas, Cryptomonas, Rhodomonas*

PYRRHOPHYTA (dinoflagellates)
Unicellular flagellates, rarely colonial; two flagella of different length and orientation; naked, or with cellulose cell wall, sometimes sculptured into plates. Numerous discoid plastids or colourless; assimilation products, starch or oil. Mostly marine

CLASS: Dinophyceae
Biflagellate cells, flagella located in transverse and longitudinal furrows. Planktonic representatives included within one order

Order: *Peridiniales*

Includes: *Ceratium, Glenodinium, Gonyaulax, Gymnodinium, Peridinium, Woloszynskia*

CLASS: Adinophyceae (= Desmophyceae)
Naked or cellulose-walled cells composed of two watchglass-shaped halves. One order represented in freshwater phytoplankton

Order: *Prorocentrales*

Includes: *Exuviella, Pyrocystis*

Table 2. (*cont.*)

RAPHIDOPHYTA (chloromonads)
Uniflagellate, cellulose-walled cells; numerous plastids, assimilatory product lipid. One class and one order

Order: *Raphidomonadales* (= *Chloromonadales*)

Includes: *Gonyostomum*

CHRYSOPHYTA
Unicellular, colonial, filamentous or siphonaceous algae, with a preponderance of carotenoid pigments; cell walls pectinaceous, often in two pieces, sometimes impregnated with silica (especially in the Bacillariophyceae); assimilatory products, chrysose, chrysolaminarin, leucosin, lipids but never starch. Five classes, all with planktonic representatives

CLASS: Chryosphyceae
Mainly unicellular or colonial; plastids brown, usually two; cell wall sometimes silicified or calcified; isogamous sexual reproduction; mainly freshwater. Three (out of eleven) orders represented in freshwater phytoplankton

Order: *Ochromonadales* (=*Chrysomonadales*) Unicellular and colonial Chrysophyceae, without a rigid cell wall, but often bearing siliceous scales

Includes: *Dinobryon*, *Mallomonas*, *Synura*, *Uroglena*

Order: *Chromulinales* Generally unicellular biflagellates without a rigid cell wall

Includes: *Chromulina*, *Chrysococcus*, *Kephyrion*, *Pseudopedinella*, *Stenocalyx*

Order: *Stichogloeales* Palmelloid colonial chrysophytes

Includes: *Stichogloea*

CLASS: Haptophyceae
Mainly unicellular flagellates most of which possess a rigid, flagellum-like haptonema. Mostly marine; class includes the (marine) coccolithophorids (chalk-forming algae). One (of at least two) orders represented in the plankton of fresh- (and brackish-) water forms

Includes: *Chrysochromulina*, *Prymnesium*

CLASS: Craspedophyceae (choanoflagellates)
Mostly epiphytic or epizoic chrysophytes with single flagellum, and distinctive periflagellar collar. One order: some planktonic representatives

Order: *Monosigales*

Includes: *Stylochromonas*

CLASS: Bacillariophyceae (diatoms)
Unicellular and colonial algae usually with numerous discoid plastids; pectinaceous cell wall, impregnated with silica, in two distinct halves (valves); assimilatory products, chrysose, oils. Never flagellate. Two large orders, both with planktonic representatives