Chapter 1

Phytoplankton

1.1 Definitions and terminology

The correct place to begin any exposition of a major component in biospheric functioning is with precise definitions and crisp discrimination. This should be a relatively simple exercise but for the need to satisfy a consensus of understanding and usage. Particularly among the biological sciences, scientific knowledge is evolving rapidly and, as it does so, it often modifies and outgrows the constraints of the previously acceptable terminology. I recognised this problem for plankton science in an earlier monograph (Reynolds, 1984a). Since then, the difficulty has worsened and it impinges on many sections of the present book. The best means of dealing with it is to accept the issue as a symptom of the good health and dynamism of the science and to avoid constraining future philosophical development by a redundant terminological framework.

The need for definitions is not subverted, however, but it transforms to an insistence that those that are ventured are provisional and, thus, open to challenge and change. To be able to reveal something also of the historical context of the usage is to give some indication of the limitations of the terminology and of the areas of conjecture impinging upon it.

So it is with 'plankton'. The general understanding of this term is that it refers to the collective of *organisms* that are *adapted* to spend part or all of their lives in apparent *suspension* in the *open water* of the sea, of lakes, ponds and rivers. The italicised words are crucial to the concept and are not necessarily contested. Thus, 'plankton' excludes other suspensoids that are either non-living, such as clay particles and precipitated chemicals, or are fragments or cadavers derived from biogenic sources. Despite the existence of the now largely redundant subdivision *tychoplankton* (see Box 1.1), 'plankton' normally comprises those living organisms that are only fortuitously and temporarily present, imported from adjacent habitats but which neither grew in this habitat nor are suitably adapted to survive in the truly open water, ostensibly independent of shore and bottom. Such locations support distinct suites of surface-adhering organisms with their own distinctive survival adaptations.

'Suspension' has been more problematic, having quite rigid physical qualifications of density and movement relative to water. As will be rehearsed in Chapter 2, only rarely can plankton be *isopycnic* (having the same density) with the medium and will have a tendency to *float* upwards or *sink* downwards relative to it. The rate of movement is also size dependent, so that 'apparent suspension' is most consistently achieved by organisms of small (<1 mm) size. Crucially, this feature is mirrored in the fact that the intrinsic movements of small organisms are frequently too feeble to overcome the velocity and direction of much of the spectrum of water movements. The inability to control horizontal position or to swim against significant currents in open waters separates 'plankton' from the 'nekton' of active swimmers, which include adult fish, large cephalopods, aquatic reptiles, birds and mammals.

Box 1.1 Some definitions used in the literaure on plankton

seston	the totality of particulate matter in water; all material not in solution
tripton	non-living seston
plankton	living seston, adapted for a life spent wholly or partly in quasi-suspension in open water, and whose powers of motility do not exceed turbulent entrainment (see Chapter 2)
nekton	animals adapted to living all or part of their lives in open water but whose intrinsic movements are almost independent of turbulence
euplankton	redundant term to distinguish fully adapted, truly planktic organisms from other living organisms fortuitously present in the water
tychoplankton	non-adapted organisms from adjacent habitats and present in the water mainly by chance
meroplankton	planktic organisms passing a major part of the life history out of the plankton (e.g. on the bottom sediments)
limnoplankton	plankton of lakes
heleoplankton	plankton of ponds
potamoplankton	plankton of rivers
phytoplankton	planktic photoautotrophs and major producer of the pelagic
bacterioplankton	planktic prokaryotes
mycoplankton	planktic fungi
zooplankton	planktic metazoa and heterotrophic protistans

Some more, now redundant, terms

The terms *nannoplankton, ultraplankton, μ-algae* are older names for various smaller size categories of phytoplankton, eclipsed by the classification of Sieburth *et al.* (1978) (see Box 1.2).

In this way, plankton comprises organisms that range in size from that of viruses (a few tens of nanometres) to those of large jellyfish (a metre or more). Representative organisms include bacteria, protistans, fungi and metazoans. In the past, it has seemed relatively straightforward to separate the organisms of the plankton, both into broad phyletic categories (e.g. bacterioplankton, mycoplankton) or into similarly broad functional categories (photosynthetic algae of the phytoplankton, phagotrophic animals of the zooplankton). Again, as knowledge of the organisms, their phyletic affinities and physiological capabilities has expanded, it has become clear that the divisions used hitherto do not precisely coincide: there are photosynthetic bacteria, phagotrophic algae and flagellates that take up organic carbon from solution. Here, as in general, precision will be considered relevant and important in the context of organismic properties (their names, phylogenies, their morphological and physiological characteristics). On the other hand, the generic contributions to systems (at the habitat or ecosystem scales) of the photosynthetic primary producers, phagotrophic consumers and heterotrophic decomposers may be attributed reasonably but imprecisely to phytoplankton, zooplankton and bacterioplankton.

The defintion of phytoplankton adopted for this book is the collective of photosynthetic microorganisms, adapted to live partly or continuously in open water. As such, it is the photoautotrophic part of the plankton and a major primary producer of organic carbon in the pelagic of the seas and of inland waters. The distinction of phytoplankton from other categories of plankton and suspended matter are listed in Box 1.1.

It may be added that it is correct to refer to phytoplankton as a singular term ('phytoplankton is' rather than 'phytoplankton are'). A single organism is a *phytoplanktont* or (more ususally) *phytoplankter*. Incidentally, the adjective 'planktic' is etymologically preferable to the more commonly used 'planktonic'.

1.2 Historical context of phytoplankton studies

The first use of the term 'plankton' is attributed in several texts (Ruttner, 1953; Hutchinson, 1967) to Viktor Hensen, who, in the latter half of the nineteenth century, began to apply quantitative methods to gauge the distribution, abundance and productivity of the microscopic organisms of the open sea. The monograph that is usually cited (Hensen, 1887) is, in fact, rather obscure and probably not well read in recent times but Smetacek *et al*. (2002) have provided a probing and engaging review of the original, within the context of early development of plankton science. Most of the present section is based on their article.

The existence of a planktic community of organisms in open water had been demonstrated many years previously by Johannes Müller. Knowledge of some of the organisms themselves stretches further back, to the earliest days of microscopy. From the 1840s, Müller would demonstrate net collections to his students, using the word *Auftrieb* to characterise the community (Smetacek *et al*., 2002). The literal translation to English is 'up drive', approximately 'buoyancy' or 'flotation', a clear reference to Müller's assumption that the material floated up to the surface waters − like so much oceanic dirt! It took one of Müller's students, Ernst Haeckel, to champion the beauty of planktic protistans and metazoans. His monograph on the Radiolaria was also one of the first to embrace Darwin's (1859) evolutionary theory in order to show structural affinities and divergences. Haeckel, of course, became best known for his work on morphology, ontogeny and phylogeny. According to Smetacek *et al*. (2002), his interest and skills as a draughtsman advanced scientific awareness of the range of planktic form (most significantly, Haeckel, 1904) but to the detriment of any real progress in understanding of functional differentiation. Until the late 1880s, it was not appreciated that the organisms of the *Auftrieb*, even the algae among them, could contribute much to the nutrition of the larger animals of the sea. Instead, it seems to have been supposed that organic matter in the fluvial discharge from the land was the major nutritive input. It is thus rather interesting to note that, a century or so later, this possibility has enjoyed something of a revival (see Chapters 3 and 8).

If Haeckel had conveyed the beauty of the pelagic protistans, it was certainly Viktor Hensen who had been more concerned about their role in a functional ecosystem. Hensen was a physiologist who brought a degree of empiricism to his study of the perplexing fluctuations in North Sea fish stocks. He had reasoned that fish stocks and yields were related to the production and distribution of the juvenile stages. Through devising techniques for sampling, quantification and assessing distribution patterns, always carefully verified by microscopic examination, Hensen recognised both the ubiquity of phytoplankton and its superior abundance and quality over coastal inputs of terrestrial detritus. He saw the connection between phytoplankton and the light in the near-surface layer, the nutritive resource it provided to copepods and other small animals, and the value of these as a food source to fish.

Thus, in addition to bequeathing a new name for the basal biotic component in pelagic ecosystems, Hensen may be regarded justifiably as the first quantitative plankton ecologist and as the person who established a formal methodology for its study. Deducing the relative contributions of Hensen and Haeckel to the foundation of modern plankton science, Smetacek *et al.* (2002) concluded that it is the work of the latter that has been the more influential. This is an opinion with which not everyone will agree but this is of little consequence. However, Smetacek *et al.* (2002) offered a most profound and resonant observation in suggesting that Hensen's general understanding of the role of plankton ('the big picture') was essentially correct but erroneous in its details, whereas in Haeckel's case, it was the other way round. Nevertheless, both have good claim to fatherhood of plankton science!

1.3 The diversification of phytoplankton

Current estimates suggest that between 4000 and 5000 legitimate species of marine phytoplankton have been described (Sournia *et al.* 1991; Tett and Barton, 1995). I have not seen a comparable estimate for the number of species in inland waters, beyond the extrapolation I made (Reynolds, 1996a) that the number is unlikely to be substantially smaller. In both lists, there is not just a large number of mutually distinct taxa of photosynthetic microorganisms but there is a wide variety of shape, size and phylogenetic affinity. As has also been pointed out before (Reynolds, 1994a), the morphological range is comparable to the one spanning forest trees and the herbs that grow at their base. The phyletic divergence of the representatives is yet wider. It would be surprising if the species of the phytoplankton were uniform in their requirements, dynamics and susceptibilities to loss processes. Once again, there is a strong case for attempting to categorise the phytoplankton both on the phylogeny of organisms and on the functional basis of their roles in aquatic ecosystems. Both objectives are adopted for the writing of this volume. Whereas the former is addressed only in the present chapter, the latter quest occupies most of the rest of the book. However, it is not giving away too much to anticipate that systematics provides an important foundation for species-specific physiology and which is itself part-related to morphology. Accordingly, great attention is paid here to the differentiation of individualistic properties of representative species of phytoplankton.

However, there is value in being able simultaneously to distinguish among functional categories (trees from herbs!). The scaling system and nomenclature proposed by Sieburth *et al.* (1978) has been widely adopted in phytoplankton ecology to distinguish functional separations within the phytoplankton. It has also eclipsed the use of such terms as *μ-algae* and *ultraplankton* to separate the lower size range of planktic organisms from those (*netplankton*) large enough to be retained by the meshes of a standard phytoplankton net. The scheme of prefixes has been applied to size categories of zooplankton, with equal success. The size-based categories are set out in Box 1.2.

At the level of phyla, the classification of the phytoplankton is based on long-standing criteria, distinguished by microscopists and biochemists over the last 150 years or so, from which there is little dissent. In contrast, subdivision within classes, orders etc., and the tracing of intraphyletic relationships, affinities within and among families, even the validity of supposedly well-characterised species, has become subject to massive reappraisal. The new factor that has come into play is the powerful armoury of the molecular biologists, including the methods for reading gene sequences and for the statistical matching of these to measure the closeness to other species.

Of course, the potential outcome is a much more robust, genetically verified family tree of authentic species of phytoplankton. This may be some years away. For the present, it seems pointless to reproduce a detailed classification of the phytoplankton that will soon be made redundant. Even the evolutionary connectivities among the phyla and their relationship to the geochemical development of the planetary structures are undergoing deep re-evaluation (Delwiche, 2000; Falkowski, 2002). For these reasons, the

Box 1.2 | The classification of phytoplankton according to the scaling nomenclature of Sieburth *et al.* (1978)

Maximum linear dimension	*Name*[a]
0.2–2 μm	picophytoplankton
2–20 μm	nanophytoplankton
20–200 μm	microphytoplankton
200 μm–2 mm	mesophytoplankton
>2 mm	macrophytoplankton

[a] The prefixes denote the same size categories when used with '-zooplankton', '-algae', '-cyanobacteria', 'flagellates', etc.

taxonomic listings in Table 1.1 are deliberately conservative.

Although the life forms of the plankton include acellular microorganisms (viruses) and a range of well-characterised Archaea (the halobacteria, methanogens and sulphur-reducing bacteria, formerly comprising the Archaebacteria), the most basic photosynthetic organisms of the phytoplankton belong to the Bacteria (formerly, Eubacteria). The separation of the ancestral bacteria from the archaeans (distinguished by the possession of membranes formed of branched hydrocarbons and ether linkages, as opposed to the straight-chain fatty acids and ester linkages found in the membranes of all other organisms: Atlas and Bartha, 1993) occurred early in microbial evolution (Woese, 1987; Woese *et al.*, 1990).

The appearance of phototrophic forms, distinguished by their crucial ability to use light energy in order to synthesise adenosine triphosphate (ATP) (see Chapter 3), was also an ancient event that took place some 3000 million years ago (3 Ga BP (before present)). Some of these organisms were photoheterotrophs, requiring organic precursors for the synthesis of their own cells. Modern forms include green flexibacteria (Chloroflexaceae) and purple non-sulphur bacteria (Rhodospirillaceae), which contain pigments similar to chlorophyll (bacteriochlorophyll *a*, *b* or *c*). Others were true photoautotrophs, capable of reducing carbon dioxide as a source of cell carbon (photosynthesis). Light energy is used to strip electrons from a donor substance. In most modern plants, water is the source of reductant electrons and oxygen is liberated as a by-product (oxygenic photosynthesis). Despite their phyletic proximity to the photoheterotrophs and sharing a similar complement of bacteriochlorophylls (Béjà *et al.*, 2002), the Anoxyphotobacteria use alternative sources of electrons and, in consequence, generate oxidation products other than oxygen (anoxygenic photosynthesis). Their modern-day representatives are the purple and green sulphur bacteria of anoxic sediments. Some of these are planktic in the sense that they inhabit anoxic, intensively stratified layers deep in small and suitably stable lakes. The trait might be seen as a legacy of having evolved in a wholly anoxic world. However, aerobic, anoxygenic phototrophic bacteria, containing bacterichlorophyll *a*, have been isolated from oxic marine environments (Shiba *et al.*, 1979); it has also become clear that their contribution to the oceanic carbon cycle is not necessarily insignificant (Kolber *et al.*, 2001; Goericke, 2002).

Nevertheless, the oxygenic photosynthesis pioneered by the Cyanobacteria from about 2.8 Ga before present has proved to be a crucial step in the evolution of life in water and, subsequently, on land. Moreover, the composition of the atmosphere was eventually changed through the biological oxidation of water and the simultaneous removal and burial of carbon in marine sediments (Falkowski, 2002). Cyanobacterial photosynthesis is mediated primarily by chlorophyll *a*, borne on thylakoid membranes. Accessory

Table 1.1 Survey of the organisms in the phytoplankton

Domain: BACTERIA

Division: **Cyanobacteria** (blue-green algae)

Unicellular and colonial bacteria, lacking membrane bound plastids. Primary photosynthetic pigment is chlorophyll a, with accessory phycobilins (phycocyanin, phycoerythrin). Assimilation products, glycogen, cyanophycin. Four main sub-groups, of which three have planktic representatives.

Order: CHROOCOCCALES

Unicellular or coenobial Cyanobacteria but never filamentous. Most planktic genera form mucilaginous colonies, and these are mainly in fresh water. Picophytoplanktic forms abundant in the oceans.

Includes: *Aphanocapsa, Aphanothece, Chroococcus, Cyanodictyon, Gomphosphaeria, Merismopedia, Microcystis, Snowella, Synechococcus, Synechocystis, Woronichinia*

Order: OSCILLATORIALES

Uniseriate–filamentous Cyanobacteria whose cells all undergo division in the same plane. Marine and freshwater genera.

Includes: *Arthrospira, Limnothrix, Lyngbya, Planktothrix, Pseudanabaena, Spirulina, Trichodesmium, Tychonema*

Order: NOSTOCALES

Unbranched–filamentous Cyanobacteria whose cells all undergo division in the same plane and certain of which may be facultatively differentiated into heterocysts. In the plankton of fresh waters and dilute seas.

Includes: *Anabaena, Anabaenopsis, Aphanizomenon, Cylindrospermopsis, Gloeotrichia, Nodularia*

Exempt Division: **Prochlorobacteria**

Order: PROCHLORALES

Unicellular and colonial bacteria, lacking membrane-bound plastids. Photosynthetic pigments are chlorophyll *a* and *b*, but lack phycobilins.

Includes: *Prochloroccus, Prochloron, Prochlorothrix*

Division: **Anoxyphotobacteria**

Mostly unicellular bacteria whose (anaerobic) photosynthesis depends upon an electron donor other than water and so do not generate oxygen. Inhabit anaerobic sediments and (where appropriate) water layers where light penetrates sufficiently. Two main groups:

Family: Chromatiaceae (purple sulphur bacteria) Cells able to photosynthesise with sulphide as sole electron donor. Cells contain bacteriochlorophyll *a*, *b* or *c*.

Includes: *Chromatium, Thiocystis, Thiopedia.*

Family: Chlorobiaceae (green sulphur bacteria) Cells able to photosynthesise with sulphide as sole electron donor. Cells contain bacteriochlorophyll *a*, *b* or *c*.

Includes: *Chlorobium, Clathrocystis, Pelodictyon*.

Domain: EUCARYA

Phylum: **Glaucophyta**

Cyanelle-bearing organisms, with freshwater planktic representatives.

Includes: *Cyanophora, Glaucocystis*.

Phylum: **Prasinophyta**

Unicellular, mostly motile green algae with 1–16 laterally or apically placed flagella, cell walls covered with fine scales and plastids containing chlorophyll *a* and *b*. Assimilatory products mannitol, starch.

(cont.)

Table 1.1 (cont.)

CLASS: Pedinophyceae
Order: PEDINOMONADALES
Small cells, with single lateral flagellum.
Includes: *Pedinomonas*
CLASS: Prasinophyceae
Order: CHLORODENDRALES
Flattened, 4-flagellated cells.
Includes: *Nephroselmis, Scherffelia* (freshwater); *Mantoniella, Micromonas* (marine)
Order: PYRAMIMONADALES
Cells with 4 or 8 (rarely 16) flagella arising from an anterior depression. Marine and freshwater.
Includes: *Pyramimonas*
Order: SCOURFIELDIALES
Cells with two, sometimes unequal, flagella. Known from freshwater ponds.
Includes: *Scourfieldia*
Phylum: **Chlorophyta** (green algae)
Green-pigmented, unicellular, colonial, filamentous, siphonaceous and thalloid algae. One or more chloroplasts containing chlorophyll *a* and *b*. Assimilation product, starch (rarely, lipid).
CLASS: Chlorophyceae
Several orders of which the following have planktic representatives:
Order: TETRASPORALES
Non-flagellate cells embedded in mucilaginous or palmelloid colonies, but with motile propagules.
Includes: *Paulschulzia, Pseudosphaerocystis*
Order: VOLVOCALES
Unicellular or colonial biflagellates, cells with cup-shaped chloroplasts.
Includes: *Chlamydomonas, Eudorina, Pandorina, Phacotus, Volvox* (in fresh waters); *Dunaliella, Nannochloris* (marine)
Order: CHLOROCOCCALES
Non-flagellate, unicellular or coenobial (sometimes mucilaginous) algae, with many planktic genera.
Includes: *Ankistrodesmus, Ankyra, Botryococcus, Chlorella, Coelastrum, Coenochloris, Crucigena, Choricystis, Dictyosphaerium, Elakatothrix, Kirchneriella, Monorophidium, Oocystis, Pediastrum, Scenedesmus, Tetrastrum*
Order: ULOTRICHALES
Unicellular or mostly unbranched filamentous with band-shaped chloroplasts.
Includes: *Geminella, Koliella, Stichococcus*
Order: ZYGNEMATALES
Unicellular or filamentous green algae, reproducing isogamously by conjugation. Planktic genera are mostly members of the Desmidaceae, mostly unicellular or (rarely) filmentous coenobia with cells more or less constricted into two semi-cells linked by an interconnecting isthmus. Exclusively freshwater genera.
Includes: *Arthrodesmus, Closterium, Cosmarium, Euastrum, Spondylosium, Staurastrum, Staurodesmus, Xanthidium*

(cont.)

Table 1.1 (cont.)

Phylum: **Euglenophyta**

Green-pigmented unicellular biflagellates. Plastids numerous and irregular, containing chlorophyll *a* and *b*. Reproduction by longitudinal fission. Assimilation product, paramylon, oil. One Class, Euglenophyceae, with two orders.

Order: EUTREPTIALES

Cells having two emergent flagella, of approximately equal length. Marine and freshwater species.

Includes: *Eutreptia*

Order: EUGLENALES

Cells having two flagella, one very short, one long and emergent.

Includes: *Euglena, Lepocinclis, Phacus, Trachelmonas*

Phylum: **Cryptophyta**

Order: CRYPTOMONADALES

Naked, unequally biflagellates with one or two large plastids, containing chlorophyll *a* and c_2 (but not chlorophyll *b*); accessory phycobiliproteins or other pigments colour cells brown, blue, blue-green or red; assimilatory product, starch. Freshwater and marine species.

Includes: *Chilomonas, Chroomonas, Cryptomonas, Plagioselmis, Pyrenomonas, Rhodomonas*

Phylum: **Raphidophyta**

Order: RAPHIDOMONADALES (syn. CHLOROMONADALES)

Biflagellate, cellulose-walled cells; two or more plastids containing chlorophyll *a*; cells yellow-green due to predominant accessory pigment, diatoxanthin; assimilatory product, lipid. Freshwater.

Includes: *Gonyostomum*

Phylum: **Xanthophyta** (yellow-green algae)

Unicellular, colonial, filamentous and coenocytic algae. Motile species generally subapically and unequally biflagellated; two or many more discoid plastids per cell containing chlorophyll *a*. Cells mostly yellow-green due to predominant accessory pigment, diatoxanthin; assimilation product, lipid. Several orders, two with freshwater planktic representatives.

Order: MISCHOCOCCALES

Rigid-walled, unicellular, sometimes colonial xanthophytes.

Includes: *Goniochloris, Nephrodiella, Ophiocytium*

Order: TRIBONEMATALES

Simple or branched uniseriate filamentous xanthophytes.

Includes: *Tribonema*

Phylum: **Eustigmatophyta**

Coccoid unicellular, flagellated or unequally biflagellated yellow-green algae with masking of chlorophyll *a* by accessory pigment violaxanthin. Assimilation product, probably lipid.

Includes: *Chlorobotrys, Monodus*

Phylum: **Chrysophyta** (golden algae)

Unicellular, colonial and filamentous. often uniflagellate, or unequally biflagellate algae. Contain chlorophyll *a*, c_1 and c_2, generally masked by abundant accessory pigment, fucoxanthin, imparting distinctive golden colour to cells. Cells sometimes naked or or enclosed in an urn-shaped lorica, sometimes with siliceous scales. Assimilation products, lipid, leucosin. Much reclassified group, has several classes and orders in the plankton.

(cont.)

Table 1.1 (cont.)

CLASS: Chrysophyceae
Order: CHROMULINALES
Mostly planktic, unicellular or colony-forming flagellates with one or two unequal flagella, occasionally naked, often in a hyaline lorica or gelatinous envelope.
Includes: *Chromulina, Chrysococcus, Chrysolykos, Chrysosphaerella, Dinobryon, Kephyrion, Ochromonas, Uroglena*
Order: HIBBERDIALES
Unicellular or colony-forming epiphytic gold algae but some planktic representatives.
Includes: *Bitrichia*
CLASS: Dictyochophyceae
Order: PEDINELLALES
Radially symmetrical, very unequally biflagellate unicells or coenobia.
Includes: *Pedinella* (freshwater); *Apedinella, Pelagococcus, Pelagomonas, Pseudopedinella* (marine)
CLASS: Synurophyceae
Order: SYNURALES
Unicellular or colony-forming flagellates, bearing distinctive siliceous scales.
Includes: *Mallomonas, Synura*

Phylum: **Bacillariophyta** (diatoms)
Unicellular and coenobial yellow-brown, non-motile algae with numerous discoid plastids, containing chlorophyll *a*, c_1 and c_2, masked by accessory pigment, fucoxanthin. Cell walls pectinaceous, in two distinct and overlapping halves, and impregnated with cryptocrystalline silica. Assimilatory products, chrysose, lipids. Two large orders, both conspicuously represented in the marine and freshwater phytoplankton.
CLASS: Bacillariophyceae
Order: BIDDULPHIALES (centric diatoms)
Diatoms with cylindrical halves, sometimes well separated by girdle bands. Some species form (pseudo-)filaments by adhesion of cells at their valve ends.
Includes: *Aulacoseira, Cyclotella, Stephanodiscus, Urosolenia* (freshwater); *Cerataulina, Chaetoceros, Detonula, Rhizosolenia, Skeletonema, Thalassiosira* (marine)
Order: BACILLARIALES (pennate diatoms)
Diatoms with boat-like halves, no girdle bands. Some species form coenobia by adhesion of cells on their girdle edges.
Includes: *Asterionella, Diatoma, Fragilaria, Synedra, Tabellaria* (freshwater); *Achnanthes, Fragilariopsis, Nitzschia* (marine)

Phylum: **Haptophyta**
CLASS: Haptophyceae
Gold or yellow-brown algae, usually unicellular, with two subequal flagella and a coiled haptonema, but with amoeboid, coccoid or palmelloid stages. Pigments, chlorophyll *a*, c_1 and c_2, masked by accessory pigment (usually fucoxanthin). Assimilatory product, chrysolaminarin. Cell walls with scales, sometimes more or less calcified.
Order: PAVLOVALES
Cells with haired flagella and small haptonema. Marine and freshwater species.
Includes: *Diacronema, Pavlova*

(cont.)

Table 1.1 (cont.)

Order: PRYMNESIALES
Cells with smooth flagella, haptonema usually small. Mainly marine or brackish but some common in freshwater plankton.
Includes: *Chrysochromulina, Isochrysis, Phaeocystis, Prymnesium*

Order: COCCOLITHOPHORIDALES
Cell suface covered by small, often complex, flat calcified scales (coccoliths). Exclusively marine.
Include: *Coccolithus, Emiliana, Florisphaera, Gephyrocapsa, Umbellosphaera*

Phylum: **Dinophyta**
Mostly unicellular, sometimes colonial, algae with two flagella of unequal length and orientation. Complex plastids containing chlorophyll a, c_1 and c_2, generally masked by accessory pigments. Cell walls firm, or reinforced with polygonal plates. Assimilation products: starch, oil. Conspicuously represented in marine and freshwater plankton. Two classes and (according to some authorities) up to 11 orders.

CLASS: Dinophyceae
Biflagellates, with one transverse flagellum encircling the cell, the other directed posteriorly.

Order: GYMNODINIALES
Free-living, free-swimming with flagella located in well-developed transverse and sulcal grooves, without thecal plates. Mostly marine.
Includes: *Amphidinium, Gymnodinium, Woloszynskia*

Order: GONYAULACALES
Armoured, plated, free-living unicells, the apical plates being asymmetrical. Marine and freshwater.
Includes: *Ceratium, Lingulodinium*

Order: PERIDINIALES
Armoured, plated, free-living unicells, with symmetrical apical plates. Marine and freshwater.
Includes: *Glenodinium, Gyrodinium, Peridinium*

Order: PHYTODINIALES
Coccoid dinoflagellates with thick cell walls but lacking thecal plates. Many epiphytic for part of life history. Some in plankton of humic fresh waters.
Includes: *Hemidinium*

CLASS: Adinophyceae

Order: PROROCENTRALES
Naked or cellulose-covered cells comprising two watchglass-shaped halves. Marine and freshwater species.
Includes: *Exuviella, Prorocentrum*

pigments, called phycobilins, are associated with these membranes, where they are carried in granular phycobilisomes. Life forms among the Cyanobacteria have diversified from simple coccoids and rods into loose mucilaginous colonies, called coenobia, into filamentous and to pseudotissued forms. Four main evolutionary lines are recognised, three of which (the chroococcalean, the oscillatorialean and the nostocalean; the stigonematalean line is the exception) have major planktic representatives that have diversified greatly among marine and freshwater systems. The most ancient group of the surviving groups of photosynthetic organisms is, in