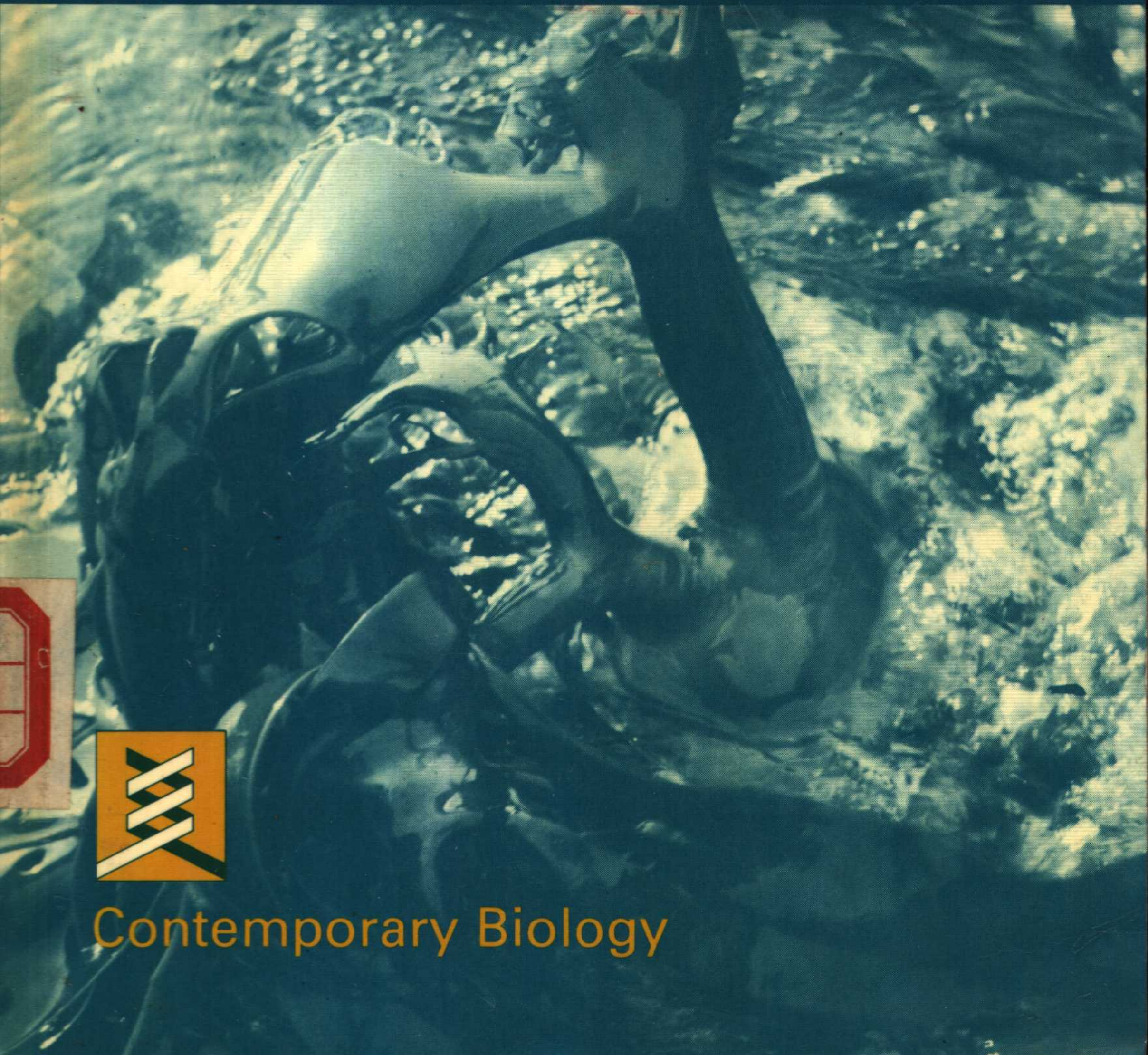
The Biology of Marine Plants

M. J. Dring



Contemporary Biology

The Biology of Marine Plants

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Preface

Marine plants have rarely been discussed as a distinct and self-contained group. They have traditionally been treated either as the poor relations of marine animals in courses and texts on Marine Biology, or as examples of particular groups of algae, where the essential 'marine-ness' of marine plants tends to disappear amongst the taxonomic and morphological parallels with freshwater algae. This book attempts to liberate marine plants from both of these traps by providing an introduction to recent analytical and experimental studies of plant growth in the sea. The physics and chemistry of the marine environment are examined with specific reference to the requirements of marine plants, and most of the book concentrates on those aspects of physiology which are unique to marine plants, or which help us to understand their ecology. This discussion emphasizes the importance of a good background knowledge of the environment for critical measurements of the most important factors, and the necessity for experimental work on marine plants to be well quantified, and to be conducted in ecologically relevant conditions.

Since over 90% of the species of marine plants are algae, most of the book is devoted to the marine representatives of this group, with examples from all oceans and coasts of the world, but there is no detailed morphological or taxonomic treatment. Phytoplankton and seaweeds are discussed together as far as possible, in spite of the obvious morphological and ecological contrasts between them, in order to obtain an integrated picture of the biology of marine plants in general. There is, however, a deliberate bias in certain chapters towards the seaweeds, since the physiology and ecology of these plants has not been so fully covered in books at this level as has the ecology of phytoplankton. Marine angiosperms are also discussed where appropriate alongside the autotrophic algae, and the ecological roles of bacteria and fungi in the sea are covered in a separate, final chapter.

A basic knowledge of plant biology — and especially plant physiology — is assumed, but sufficient background is provided for each topic to remind readers of the ideas and terms referred to in the text. It is hoped that the book will provide a stimulating and challenging text for second and third year undergraduate courses, as well as being of interest and value to postgraduate students and specialists in other areas of marine biology.

Acknowledgements

Most of the line drawings in this book are adaptations of previously published illustrations, and I wish to thank all authors and publishers for their permission to reproduce such material. Original prints of photographs were kindly provided by Robert Buggeln, Klaus Lüning, Betty Moss and Susan Waaland. Professor A.J. Willis has read every page of the manuscript with great care, and has provided valuable guidance and encouragement throughout the preparation of the book. Numerous other colleagues have kindly read and commented on parts of the manuscript, and I am particularly grateful for the detailed and constructive criticisms of Klaus Lüning, Graham Savidge, David Jewson and Philip Grime. Since I have not always accepted their advice, however, they are in no way responsible for the faults and errors that may remain.

1982 M.J.D.

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Marine Plants: taxonomic, morphological and ecological categories

It is generally accepted that life on earth began in the sea and that, until about 450 million years ago, all plants were marine plants. The next 400 million years witnessed the evolution of the land flora, including bryophytes, pteridophytes, gymnosperms and flowering plants. The story of this invasion of the land is usually told in terms of the developments in morphology and reproduction that made plants less and less dependent on the presence of free water, but one aspect that is often overlooked is that, in this process, plants lost their ability to live in sea water. Throughout the modern bryophytes, pteridophytes and gymnosperms, there is not a single marine species and, in the angiosperms, which have evolved more than 200 000 species adapted to almost every terrestrial and freshwater habitat, there is only one small group of seagrasses (about 50 species world-wide[89]) which can be described as truly marine. Even the fungi are poorly represented in the sea, since marine species account for only 1% of the total fungal flora.[125] Thus the sea remains — as it must have been in pre-Devonian times — the province of the algae, and today about 90% of all the species of marine plants belong to one or other of the groups of algae (Table 1.1).

TAXONOMIC CLASSIFICATION

Many of these algal groups are now themselves represented mainly by freshwater species, and only two groups — the brown (Phaeophyta) and the red algae (Rhodophyta) which predominate among attached marine plants — remain almost exclusively marine. These two groups are joined on the sea floor by a few distinct groups of macroscopic green algae (Chlorophyta: the Ulvales and the siphonaceous orders, see p. 8), which are again almost exclusively marine, in contrast to the microscopic green algae, which are predominantly freshwater or sub-aerial forms. The microscopic marine flora is dominated by two groups of brown-coloured algae, the diatoms (Chrysophyta) and the dinoflagellates (Pyrrhophyta). Of these two groups, the dinoflagellates are again predominantly marine, but the diatoms are more evenly divided, in terms of numbers of species, between marine and freshwater habitats (Table 1.1).

When considering the representation of different plant groups in the marine flora in terms of numbers of species, it is important to remember that species vary enormously in numbers of individuals and in the size of those individuals, and that the number of species described in any one group probably depends more on the amount of study that the group has received than on the actual diversity within the group. The absolute numbers listed in Table 1.1 should, therefore, be treated with caution, and the values for some of the groups could possibly be increased by 50 or even 100%. For example, some estimates place the total number of species of diatoms (which account for over 90% of the Chrysophyta in Table 1.1) at 12 000, of red algae at 3900, and of brown algae at 1500. Few of these recent estimates separate the numbers of marine and freshwater species, but it is probably reasonable to assume that the numbers of marine species will increase roughly in proportion to the increase in total numbers in any one group. There will probably, therefore, be little overall change in the percentage representation of different groups in the marine flora, and this approach to plant classification provides a clear indication of which groups are predominantly marine, and which are mainly or entirely confined to freshwater and terrestrial habitats.

The poor representation of so many major plant groups in the marine flora, and the virtual restriction of other groups to the sea, suggests that growth in the sea creates problems for plants that are quite different from those created by growth in fresh water or on land (where soil water is also 'fresh'). Few groups of plants have evolved that seem able to cope equally well with both environments — the diatoms being perhaps the only example (see Table 1.1). A major objective of the study of marine plants must clearly be to identify the critical differences between the sea and freshwater as an environment for plant growth.

Three of the groups of marine algae that have been mentioned so far — the brown, the red and the green algae — have been described simply on the basis of their colour. The colour of the thallus was introduced as a taxonomic character for the algae as long ago as 1836, and the modern classification of the algae still uses pigment composition as a primary character (Table 1.2). The 'green algae' (including Chlorophyta, Charophyta, Euglenophyta) have a similar pigmentation to the higher plants, and contain chlorophylls *a* and *b* and β-carotene. The remaining groups all contain chlorophyll *a* and β-carotene, but lack chlorophyll *b*. The brown-coloured algae (Phaeophyta, Chrysophyta, Pyrrhophyta and Cryptophyta) all contain chlorophyll *c* in addition to chlorophyll *a*, but derive their characteristic brown colour from a mixture of xanthophyll pigments, of which fucoxanthin is the most important in the Phaeophyta and the Chrysophyta, while peridinin is typical of dinoflagellates. Cryptomonads may be red, blue or green in colour, depending on the culture conditions, because of the

Table 1.1 Approximate number of marine species in each major plant group.

Plant group	Total species	Marine species	Marine spp. as percent of group	Contribution of group to marine flora (%)
Algae:	19300	8462	43.8	93.8
Chlorophyta	6500	900	13.8	10.0
Charophyta	250	0	0.0	–
Euglenophyta	450	15	3.3	0.2
Phaeophyta	1000	997	99.7	11.0
Chrysophyta	6000	3000	50.0	33.2
Pyrrhophyta	1000	900	90.0	10.0
Cryptophyta	100	50	50.0	0.6
Rhodophyta	2500	2450	98.0	27.1
Cyanophyta	1500	150	10.0	1.7
Fungi:	50000	500	1.0	5.5
Myxomycetes	500	0	0.0	–
Phycomycetes	1500	100	6.7	1.1
Ascomycetes	20000	210	1.1	2.3
Basidiomycetes	16000	10	0.06	0.1
Deuteromycetes	12000	180	1.5	2.0
Lichenes	15500	15	0.1	0.2
Bryophyta	22000	0	0.0	–
Pteridophyta	11000	0	0.0	–
Spermatophyta	220700	49	0.02	0.5
Gymnospermae	700	0	0.0	–
Angiospermae	220000	49	0.02	0.5
Monocotyledones	50000	49	0.10	0.5
Dicotyledones	170000	0	0.0	–
TOTAL	338500	9026	2.67	

Main sources: Smith, G.M. (1955) *Cryptogamic Botany*, Vol. 1, 2nd edition. McGraw-Hill, New York; Altman, P.L. and Dittmer, D.S. (1972) *Biology Data Book*, Vol. 1, 2nd edition. Federation of American Societies for Experimental Biology.

presence of phycobilin pigments, and these are also the major accessory pigments in red and blue-green algae. There are two basic types of phycobilin, and most species in these groups contain some of each. The red pigment, phycoerythrin, predominates in most red algae (Rhodophyta), and the blue-green pigment, phycocyanin, predominates in typical blue-green algae (Cyanophyta), but the balance between the pigments varies considerably within each group, so that some 'blue-green' algae (e.g. *Phormidium*) may be bright red in colour, whereas some 'red' algae may appear brown or olive-green (e.g. *Porphyra* spp.). The physiological and

Table 1.2 Primary classification of algae.

Division	Popular name	Major accessory pigments	Storage products	No., arrangement, type of flagella	Major marine representatives
Chlorophyta	Green algae	Chlorophyll *b*	Starch (amylose + amylopectin)	2, 4 or many equal, anterior, smooth	Siphonaceous orders, Ulvales
Charophyta	Charophytes	(as Chlorophyta, but distinguished by vegetative and reproductive morphology)			No marine representatives
Euglenophyta	Euglenoids	Chlorophyll *b*	Paramylon	1 anterior, tinsel	Few marine representatives
Phaeophyta	Brown algae	Chlorophyll $c_1 + c_2$, fucoxanthin	Laminaran	2 unequal, lateral, smooth + tinsel	Whole group marine
Chrysophyta	Yellow-brown or golden-brown algae	Chlorophyll $c_1 + c_2$, fucoxanthin	Chrysolaminaran	1 – 3 anterior, various	Diatoms, coccolithophorids, silicoflagellates
Pyrrhophyta	Dinoflagellates	Chlorophyll c_2, peridinin	Starch	2 equal, smooth	Dinoflagellates
Cryptophyta	Cryptomonads	Chlorophyll c_2, phycobilins	Starch	2 equal, lateral, both tinsel	Some cryptomonads
Rhodophyta	Red algae	Phycoerythrin ± phycocyanin	Floridean starch (amylopectin)	None	Nearly all species marine
Cyanophyta	Blue-green algae	Phycocyanin ± phycoerythrin	Myxophycean starch (glycogen-like)	None	Planktonic and benthic filaments

ecological implications of these variations in the pigment composition of marine algae are considered in Chapter 3.

Two other important characters in the primary classification of algae are the chemical nature of the storage products,[46] and the number, type and arrangement of the flagella in motile cells[19, 33] (Table 1.2). The three forms of starch that are found in the algae differ in the degree of branching and in the size of the polysaccharide molecule, but all three consist of glucose units linked in the same way as in higher plant starch (i.e. α-(1,4) linkages). The other storage products produced by algae (laminaran, chrysolaminaran and paramylon) also consist of glucose units, but are polymerized by β-(1,3) linkages. Almost all of these storage polysaccharides are synthesized by at least some marine species, and by some freshwater species. There seems to be no particular relationship, therefore, between the type of storage product and the marine habit.

With the important exception of the red and blue-green algae, all of the algal groups contain species which are flagellated for at least part of their life history. The number of flagella ranges from one (e.g. male gametes of centric diatoms, silicoflagellates) to many (e.g. zoospores of the siphonaceous green alga *Derbesia*), but is most commonly two, and these may be either equal or unequal in length. The flagella may be inserted at the anterior apex of the cell, as in most green algae and chrysophytes, or they may be inserted behind the apex or at the side of the cell (e.g. motile cells of brown algae, dinoflagellates and cryptomonads). The dinoflagellates are characterized by a flagellar arrangement that is peculiar to the group. Two flagella arise from the side of the cell, and one encircles the cell while the other is directed backwards from the point of insertion. Two distinct types of flagellum may occur: a smooth, 'whiplash' flagellum, and a 'flimmer' or 'tinsel' type which is covered in a series of short hairs. Almost all of the different combinations of these characters found among the algae can also be found in at least some marine species, but most also occur in freshwater and sub-aerial algae. The only arrangement that is really restricted to marine plants is that of the motile cells of brown algae, with two unequal flagella, one of each type, inserted at the side of a kidney-shaped cell. It is difficult to believe, however, that this arrangement imposes any particular disadvantage in fresh water, and its restriction to sea water is probably an evolutionary accident. The physiological and ecological characteristics of the vegetative thalli of brown algae seem more likely to be responsible for the restriction of these plants to the sea than does the flagellar arrangement of their reproductive cells.

MORPHOLOGICAL CLASSIFICATION

The primary classification of the algae presented in Table 1.2 aims to express the fundamental evolutionary or phylogenetic relationships between the different species, but it is possible, and often useful, to classify organisms according to different criteria, and for different purposes. Table 1.3 presents a morphological classification of marine plants (excluding fungi,

Table 1.3 Morphological classification of marine plants, with important or familiar examples of each category.

Type of thallus		CHLOROPHYTA	PYRRHOPHYTA	RHODOPHYTA	CHRYSOPHYTA
Unicells:	Flagellate	*Dunaliella*, *Chlamydomonas*	Dinoflagellates (cryptomonads)	—	Coccolithophorids, silicoflagellates
	Rhizopodial	—	'Marine amoebae'	(some spores)	'Marine amoebae'
	Protococcoidal	*Chlorella marina*	—	*Porphyridium*	Diatoms
Colonies:	Amorphous	(Mostly freshwater)	*Ceratium*	—	Colonial diatoms, *Phaeocystis*
	Coenobial	(Entirely freshwater)	—	—	—
		CYANOPHYTA			
Filaments:	Unbranched	*Ulothrix*, *Stichococcus*	*Oscillatoria*, *Lyngbya* *Phormidium*, *Calothrix*	—	*Diatoms (e.g. Melosira*, *Chaetoceros)*
	Branched	*Cladophora*	*Brachytrichia*	*Porphyra* (conchocelis)	—
			PHAEOPHYTA		
	Heterotrichous	*Phaeophila*	*Ectocarpus*	*Rhodochorton*	—
	Crustose	*Ulvella*	*Ralfsia*	*Lithothamnion*, *Petrocelis*	—
	Pseudo-parenchymatous	—	Desmarestia, *Leathesia*	Chondrus, *Eucheuma*, *Gigartina*, *Palmaria*	—
Coenocytes:	Simple	*Valonia*, *Acetabularia*	—	—	—
	Uniaxial	*Derbesia*, *Caulerpa*, *Bryopsis*			*Vaucheria*
	Multiaxial	Codium, *Udotea*, *Halimeda*	—	—	—
Parenchymatous thalli	2-dimensional	*Ulva*, *Monostroma*, *Enteromorpha*	*Scytosiphon*, *Petalonia*	*Porphyra*, *Delesseria*	—
	3-dimensional	—	*Dictyota*, *Fucus*, *Laminaria*	—	—
		SPERMATOPHYTA			
	Differentiated	Sea grasses	—	—	—

which are discussed in Chapter 9), and lists the most important and familiar examples of each category. The taxonomic position of each example is also indicated in order to show the relationship between this morphological classification and the primary taxonomy of the algae. It is clear that a substantial amount of parallel evolution must have occurred within the different groups of algae, since most of the morphological types are represented by algae from several different groups. Most of the different types of ***flagellate unicells*** (see above) are represented in the marine flora, but the dinoflagellates and the coccolithophorids are the most abundant. The latter group is named after the elaborate and varied scales, made of calcium carbonate (the 'coccoliths'), that totally cover the cell surface. The fine detail of the coccoliths is well preserved in marine sediments, and fossil forms dating back to the early Jurassic have great stratigraphic value (see p. 144), as well as testifying to the importance of these plants in the marine ecosystem. The fossil record is also rich in the siliceous remains of silicoflagellates, although these are rare in modern seas. Unicells exhibiting amoeboid movement are described as ***rhizopodial*** and a few species of 'marine amoebae', with or without chloroplasts, are attributed to the Pyrrhophyta and the Chrysophyta. The most important unicellular plants in the sea, however, are the diatoms, which are classed — together with the familiar and ubiquitous green alga *Chlorella* — as ***protococcoidal***. In these plants, the vegetative cells have no specialized organs for movement, such as flagella or pseudopodia, but they are not necessarily immobile. Benthic diatoms are often very active, gliding along a mucilage trail secreted from the underside of the cell.

In many species of diatoms, the daughter cells fail to separate completely after cell division; in other species, the daughter cells are held together by a mucilaginous matrix. As a result, ***unbranched filaments*** or ***amorphous colonies*** of diatoms may be formed, and equally simple multicellular thalli occur among green and blue-green algae, although these forms are less common in the sea than in freshwater habitats. Green algae also form more elaborate and complex colonies with a precise form and cell number (the ***coenobia*** of *Volvox*, *Pediastrum* and *Hydrodictyon*), but this type of thallus is not found in any marine species. Colonies or simple unbranched filaments may be either free-floating in the plankton or attached to a substrate, but the more complex types of thallus are seen only in attached, benthic plants. Irregularly ***branched filaments*** with an axis formed of single cells joined end to end (***uniseriate***) are found among green, red and blue-green algae, but even the simplest brown alga shows a differentiation of such a branched filamentous thallus into distinct prostrate filaments, which attach the plant to its substrate, and erect filaments, which grow away from the substrate. The relative development of the prostrate and erect systems in such a ***heterotrichous*** thallus is, however, often uneven; it may be difficult to identify the prostrate system in some species (e.g. the brown alga *Ectocarpus*), whereas in others the erect system may be completely lacking. The ***crustose*** thalli, that are frequently found on rocks in the intertidal zone, are formed by the fusion of the prostrate filaments in a heterotrichous thallus to produce a 2-dimensional plate of cells closely appressed to the substrate. Recent culture studies have shown that many of these crustose species are stages in the life history of an erect plant (e.g. *Ralfsia/Scytosiphon*; *Petrocelis/Gigartina*; see Chapter 5). This fusion and interweaving of filaments can also occur in erect systems to produce a coherent ***pseudo-parenchymatous*** thallus. This morphology is typical of most of the larger red algae, and is also found in some brown algae and in some siphonaceous green algae (see below), but the only other plants with such morphology are the fruiting bodies of higher fungi (i.e. 'toadstools'). These fungi are terrestrial, but pseudo-parenchymatous thalli are almost never found in photosynthetic plants outside the marine flora.

In truly ***parenchymatous*** thalli, cell division may occur in any plane, and a coherent 2- or 3-dimensional tissue is built up in this way. Parenchymatous sheets of cells, one or two cells thick, occur in green, red and brown algae, but thicker, 3-dimensional parenchymatous thalli are found only in brown algae, and all the very large seaweeds (kelps, wracks, rockweeds, etc.) have this morphology. Among the algae, therefore, this type of thallus is also confined to the sea. The largest and most complex green algae are ***coenocytic*** or siphonaceous forms, in which the thallus consists of tubular filaments that are not divided into cells. The simplest types are short, unbranched filaments or sacs, but larger thalli may be built up by the prolific branching of a single filament (***uniaxial***), or by weaving branched filaments together into a ***multiaxial*** pseudo-parenchymatous thallus. Again, almost all of these siphonaceous species are marine, so that this third type of macroscopic thallus construction is also largely confined to the sea.

Thus, the evolution of algal morphology has progressed considerably further in the sea than in freshwater or sub-aerial habitats. The most advanced form of thallus to be found in non-marine algae (apart from the Charophyta, which perhaps should not be considered as algae[19]) is the heterotrichous filamentous construction of the Chaetophorales (Chlorophyta). This contrast between algal morphology in marine and freshwater habitats raises another fundamental question for the marine botanist. Why are the more complex algal thalli found only among the seaweeds, whereas the more complex morphologies among other plant groups (vascular plants, Basidiomycetes) are confined to the land or to fresh water?

ECOLOGICAL CLASSIFICATION

The subject of this chapter — and indeed this whole book — is based on the idea that plants can be classified as 'marine' or 'non-marine' according to their ecological habitat. The boundaries between biological categories are never clear-cut, and the distinction between 'marine' and 'non-marine' plants is bound to be somewhat arbitrary. The plants which are considered to be marine in this book are those that have an absolute requirement for regular or continuous immersion in sea water. This definition excludes the many species of flowering plants which show a ***maritime*** distribution, or which can tolerate (but do not require) high concentrations of salt. The biology of such ***halophytes*** has been fully discussed in recent books by Waisel[256] and Reimold and Queen.[209] Our definition also excludes those algae which are characteristic of ***brackish water*** habitats (i.e. those with salt concentrations intermediate between fresh water and sea water), unless these species are also found in fully marine environments. Since very few species of plants, and relatively few of the larger taxa (see p. 2; Table 1.1), are able to grow in both freshwater or terrestrial habitats and under truly marine conditions, this definition appears to provide the most natural boundary between 'marine' and 'non-marine' plants.

Marine plants, then, are plants that characteristically grow in sea water but, since the vast majority of these plants are photosynthetic, they cannot grow *wherever* there is sea water. Photosynthetic marine plants are necessarily restricted to illuminated sea water, or the surface layer of the sea which is known as the ***photic zone.*** The depth of this zone depends on the degree of light penetration through the water; this is discussed in detail in Chapter 2, but an average depth for the photic zone is about 100 m. Since the mean depth of the world's oceans is close to 4000 m, photosynthetic plants are restricted to the upper 2.5% of the mean depth, and the majority of the primary productivity in the seas occurs in an even shallower surface layer (see Chapter 4). Heterotrophic plants, and especially fungi and bacteria, are not restricted to the photic zone, and they undoubtedly play an important ecological role as decomposers in sediments at all depths (see Chapter 9), but this book is primarily concerned with the illuminated one-fortieth of the seas.

These seas can be divided into two broad regions with contrasting physical conditions. About 10% of the total area of the sea overlies the shelves surrounding the major continents, and is relatively shallow (less than about 200 m). This region is described as ***'coastal'*** or 'neritic', whereas the deeper water beyond the continental shelves is described as ***'oceanic'*** (Fig. 1.1). Coastal waters receive run-off from the adjacent land-masses

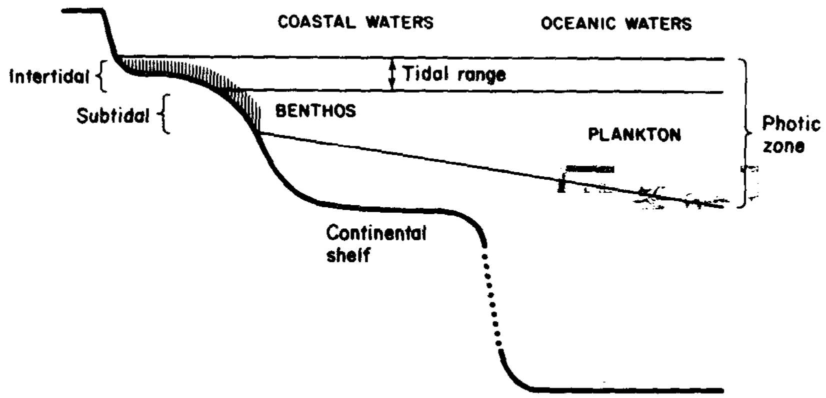

Fig. 1.1 The habitats occupied by marine plants (not to scale).

and, therefore, contain higher concentrations of inorganic nutrients than oceanic waters. This stimulates primary production, and the increased organic matter, combined with inorganic particles stirred up from shallow sediments by wave action, greatly increase the turbidity of the water. Thus, light penetration is reduced and photosynthesis may become impossible only 10 m below the surface. In oceanic waters, on the other hand, photosynthetic plants have been found growing at depths of nearly 200 m. The contrast between coastal and oceanic waters is most extreme in the vicinity of estuaries, where inorganic nutrient concentrations and turbidity tend to be highest, and reductions in salinity frequently add another dimension to the ecological variety.

Within each of these regions, two basic habitats can be recognized: ***planktonic*** and ***benthic*** (Fig. 1.1). The phytoplankton consists entirely of microscopic, free-floating plants (unicells, colonies or filaments) at the mercy, so far as their horizontal distribution is concerned, of the movement of the water in which they are suspended. Those organisms which are motile, such as the dinoflagellates and coccolithophorids, and those which can adjust the buoyancy of their cells (e.g. blue-green algae and some diatoms), may exert some control over their vertical distribution, and different species may thus become concentrated at different depths, but they can have little control over their horizontal distribution. Benthic plants are attached or sedentary forms ranging in morphology from non-flagellated unicells (mainly diatoms) through every morphological type listed in Table 1.3 to the massive parenchymatous seaweeds. Benthic habitats are frequently subdivided according to two criteria: the degree of exposure to the air that the plant receives, and the substrate to which the plant is attached. Habitats that are never completely submerged by the tides are described as ***supratidal***, while those that are never exposed to the air are ***subtidal***. The region in between, all of which is exposed to the air at some times and is submerged at others, is referred to as the ***intertidal*** (Fig. 1.1). The biological classification of the zonation patterns of rocky shores, mostly based on the term 'littoral', is discussed in Chapter 6, together with the physiology and ecology of intertidal plants.

The classification of benthic plants according to substrate utilizes a series of specific terms, which are largely self-explanatory but are, nevertheless, often misused. They make use of the prefixes *epi-* (on, upon) or *endo-* (inside, internal), and the terms most commonly encountered are shown in the table below.

Substrate	*Growing on surface*	*Growing within*
Mud, fine sediments	Epipelic	—
Sand grains	Epipsammic	—
Rocks	Epilithic	Endolithic
Plants	Epiphytic	Endophytic
Animals	Epizoic	Endozoic

Epipelic and ***epipsammic*** organisms are necessarily microscopic forms, and the most important algae in these habitats are benthic diatoms.