

# 1

## Morphology, life histories, and morphogenesis

### 1.1 Introduction: the plants and their environments

#### 1.1.1 Seaweeds

The term “seaweeds” traditionally includes only macroscopic, multicellular marine red, green, and brown algae. However, each of these groups has microscopic, if not unicellular, representatives. All seaweeds at some stage in their life cycles are unicellular, as spores or zygotes, and may be temporarily planktonic (Amsler & Searles 1980). Some remain small, forming sparse but productive turfs on coral reefs (Hackney et al. 1989). The blue-green algae are widespread on temperate rocky and sandy shores (Whitton & Potts 1982) and have occasionally been acknowledged in “seaweed” floras (e.g., Setchell & Gardner 1919; Newton 1931). They are particularly important in the tropics, where large macroscopic tufts of Oscillatoriaceae and smaller but abundant nitrogen-fixing Nostocaceae are major components of the reef flora (Hackney et al. 1989). Again, there are many unicellular blue-green algae. On the other hand, some benthic diatoms – normally not considered seaweeds – form large and sometimes-abundant tube-dwelling colonies that resemble seaweeds and presumably respond to the environment in much the same way (Lobban 1989). A deep-water green, *Palmoclatrus*, forms a morphologically complex thallus built from an apparently amorphous matrix with a nearly uniform distribution of cells (Womersley 1971; O’Kelly 1988), and a tropical chrysophyte, *Chrysonephos lewisii*, forms large, *Ectocarpus*-like thalli (Taylor 1960). On a smaller scale are the colonial filaments of some simple red algae, such as *Goniotrichum*. In this book we shall consider macroscopic and microscopic benthic environments and how algae respond to those environments.

Seaweeds are evolutionarily quite diverse. (In contrast, all vascular plants can be assigned to a single division, Tracheophyta.) The four traditional divisions

(or phyla) – Cyanophyta, Rhodophyta, Phaeophyta, and Chlorophyta – are assigned to two or more kingdoms, depending on the systematist. Cyanophyta are clearly placed in the Kingdom Eubacteria, but the others are either in Plantae (because they are basically multicellular) or in Protista (because they are closely related to unicellular algae). A new kingdom, Chromista, has recently been proposed to encompass the “brown-algal line,” namely, Phaeophyta, Chrysophyta, and Pyrrophyta (Cavalier-Smith 1986). Other authors would recognize this group at the level of a division (Chromophyta). Taxonomic opinion is also divided over the classes, especially within Chlorophyta. Green seaweeds have been split into Chlorophyceae (uninucleate; also including freshwater genera) and Bryopsidophyceae (multinucleate), but recent studies, using new criteria, suggest that virtually all marine green seaweeds belong together (with some freshwater genera as well) in the Class Ulvophyceae (Mattox & Stewart 1984; Floyd & O’Kelly 1984; also see van den Hoek et al. 1988; Sluiman 1989).

Ocean vegetation is dominated by evolutionarily primitive plants: the algae. No mosses, ferns, or gymnosperms are found in the oceans, and only a few diverse angiosperms (the seagrasses) occur in marine habitats (though the latter are scarcely known). The water column is chiefly the domain of the phytoplankton – unicellular or colonial plants, including classes not represented in the benthos – but populations of floating seaweeds are common (Norton & Mathieson 1983). Rocky shores are abundantly covered with a macrovegetation that is almost exclusively seaweeds; in western North America, surf grass (*Phyllospadix* spp.) is an exception. On and around the larger plants are many benthic microalgae, including early stages of seaweeds. Muddy and sandy areas have fewer seaweeds, because most species cannot anchor there, though some siphonous greens (e.g., some species of *Halimeda* and

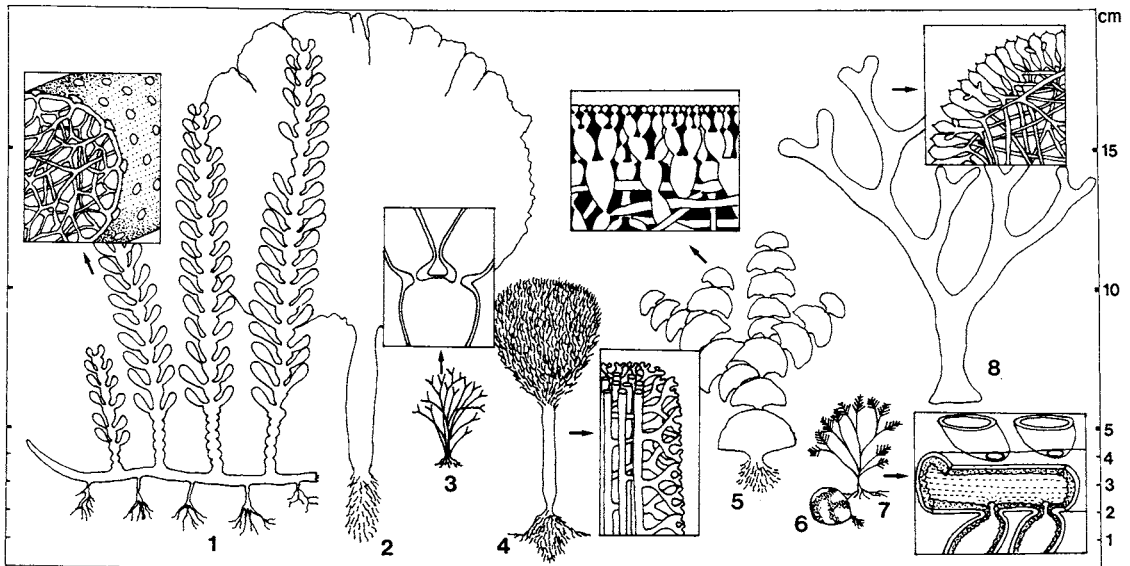


Figure 1.1. Thallus morphology and construction in siphonous green algae. Thalli drawn to scale; insets (not to scale) show principles of construction: (1) *Caulerpa cactoides* with network of trabeculae. (2) *Avrainvillea gardineri* (tightly woven felt of filaments). (3) *Chlorodesmis* sp.: bush of dichotomously branched siphons, constricted at the bases of the branches (inset). (4) *Penicillus capitatus*: calcified siphons form a multi-axial pseudotissue in the stem (inset), but separate to form bushy head. (5) *Halimeda tuna*: segmented, calcified thallus of woven medulla and cortical utricles (inset). (6) *Halicystis* stage of *Derbesia*, a single ovoid cell (shown at gametogenesis). (7) *Bryopsis plumosa* gametophyte: pinnately branched free siphons. (8) *Codium fragile*: interwoven uncalcified siphons form multi-axial branches. (From Menzel 1988, with permission of Springer-Verlag, Berlin.)

*Udotea*) produce penetrating, rootlike holdfasts that may also serve in nutrient uptake (Littler et al. 1988). In such areas, seagrasses become the dominant vegetation, particularly in tropical and subtropical areas (Helfferrich & McRoy 1980; Ferguson et al. 1980; Dawes 1981). There is also a paucity of freshwater macroalgae. Freshwater Rhodophyceae and Phaeophyceae are represented by relatively very few genera and species, and Ulvophyceae are also scarce, only a few genera (e.g., *Cladophora*) having penetrated fresh waters. That there are relatively few marine angiosperms may reflect the recent origin of the phylum and the problems of readaptation to the sea, including the physiological problems imposed by the osmotic strength of seawater and its quite different ion composition as compared with soil (King 1981). But why so few freshwater Rhodophyceae, Phaeophyceae, and Ulvophyceae? Or, to put it another way (Dring 1982), what features of these groups have led to their being largely restricted to the sea? Perhaps the answer lies not so much in the characteristics of marine or freshwater habitats but in the characteristics of the brackish waters that lie between.

Most seaweeds, in contrast to phytoplankters, are multicellular most of the time. What does this imply for physiological ecology? Multicellularity confers the advantage of allowing extensive development in the third dimension of the water column. Such development can be achieved in other ways, however. Siphonous green al-

gae form large multinucleate thalli that are at least technically single cells (acellular rather than unicellular), supported by turgor pressure (*Valonia*), ingrowths of the rhizome wall (trabeculae) in *Caulerpa*, or interweaving of numerous narrow siphons (*Codium*, *Avrainvillea*) (Fig. 1.1). Colonial diatoms, both tube-dwelling and chain-forming, also build three-dimensional structures, as do zooxanthellae in association with corals. Multicellular algae often grow vertically away from the substratum; this habit brings them closer to the light, enables them to grow large without extreme competition for space, and allows them to harvest nutrients from a greater volume of water. Of course, there are creeping filamentous algae, even endophytic and endolithic filaments (e.g., *Entocladia*), as well as crustose plants such as *Ralfsia* and *Porolithon*, that do not grow up into the water column. Support tissue usually is not necessary for this upward growth, because most small seaweeds are slightly buoyant, and the water provides support. Support tissue is metabolically expensive, because it is nonphotosynthetic. However, strength and resilience are required to withstand water motion. Some of the larger seaweeds (e.g., *Pterygophora*) have stiff, massive stipes, but others (e.g., *Hormosira*) employ flotation to keep them upright. Many of the kelps and fucoids have special gas-filled structures, pneumatocysts; but in other seaweeds (e.g., erect species of *Codium*; Dromgoole 1982), gas trapped among the filaments achieves the

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same effect. (*Codium fragile* subsp. *tomentosoides* has become a nuisance in New England because it becomes buoyant enough to carry off the cultivated shellfish to which they have attached; Wassman & Ramus 1973.)

A second important feature of multicellularity is that it allows division of labor between tissues; such division is developed to various degrees in seaweeds. Nutrient (and water) uptake and photosynthesis take place over virtually the entire surface of the seaweed thallus, in contrast to the case for vascular land plants. Differentiation and specialization among the vegetative cells of algal thalli range from virtually nil (as in *Ulothrix*, where all cells except the rhizoids serve both vegetative and reproductive functions), through the simple but somewhat differentiated thalli seen in *Porphyra* blades (e.g., Kaska et al. 1988), to the highly differentiated photosynthetic, storage, and translocation tissues in a variety of organs, including stipe, blades, and pneumatocysts, that occur in fucoids and kelps (Fagerberg et al. 1979; Kilar et al. 1989) (see Fig. 1.5). Of course, no seaweed shows the degrees of differentiation seen in vascular plants. Even in vascular plants, the cells are biochemically more general than are animal cells: The organs of vascular plants (stems, leaves, roots, flowers) all contain much the same mix of cells, whereas animal organs each contain only a few specialized cell types. The low diversity of cells in an algal thallus means that each cell is physiologically and biochemically even more general than vascular-plant cells.

#### 1.1.2 Environmental-factor interactions

Benthic algae interact with other marine organisms, and all interact with their physicochemical environment. As a rule, they live attached to the seabed between the top of the intertidal zone and the maximum depth to which adequate light for growth can penetrate. Among the major environmental factors affecting seaweeds are light, temperature, salinity, water motion, and nutrient availability. Among the biological interactions are relations between seaweeds and their epiphytic bacteria, fungi, algae, and sessile animals; interactions between herbivores and plants (both macroalgae and epiflora); and the impact of predators, including humans. Individual patterns of growth, morphology, and reproduction are overall effects of all these factors combined (Fig. 1.2).

An organism's physicochemical environment, consisting of all the external abiotic factors that influence the organism, is very complex and constantly varying. In order for us to discuss or study it, we need to reduce it to smaller parts, to think about one variable at a time. And yet, each of the environmental "factors" that we might consider – temperature, salinity, light, and so forth – is really a composite of many variables, and they tend to interact. The following paragraphs are intended to paint the whole picture, before we go on to study it pixel by pixel.

Factor interactions can be grouped into four categories: (1) multifaceted factors, (2) interactions between environmental variables, (3) interactions between environmental variables and biological factors, and (4) sequential effects.

Many environmental factors have several components that do not necessarily change together. Light quality and quantity, which are important in photosynthetic responses and metabolic patterns, both change with depth, but the changes depend on turbidity and the nature of the particles. In submarine caves, light quantity diminishes with little change in quality. Natural light has the further important component of day length, which influences reproductive states. Salinity is another complex factor, of which the two chief components are the osmotic potential of the water and the ionic composition. Osmotic potential affects water flow in and out of the cell, turgor pressure, and growth, while the concentrations of  $\text{Ca}^{2+}$  and  $\text{HCO}_3^-$  affect membrane integrity and photosynthesis, respectively. The hydrodynamic aspects of water motion are critical to thallus survival on wave-swept shores and to spore settling, and water motion also has important effects on the boundary layers over plant surfaces and thus on nutrient uptake and gas exchange. Nutrients must be considered not simply in their absolute concentrations but also in the amounts present in biologically available forms; concentrations of trace metals may create toxicity problems, particularly in polluted areas. Pollution, as a factor, may include not only the toxic effects of component chemicals but also an increase in turbidity, hence a reduction in irradiance. Emersion often involves desiccation, heating or chilling, removal of most nutrients (carbon can be an exception), and, frequently, changes in the salinity of the water in the surface film on the plants and in the free space between cells.

Interactions among environmental variables are the rule rather than the exception. Bright light is often associated with increased heating, particularly of plants exposed at low tide. Light, especially blue light, regulates the activities of many enzymes, including some involved in carbon fixation and nitrogen metabolism. Temperature and salinity affect the density of seawater, hence the mixing of nutrient-rich bottom water with nutrient-depleted surface water. Thermoclines can affect plankton movements, including migration of the larvae of epiphytic animals. Temperature also affects cellular pH and hence some enzyme activities. The carbonate equilibrium and especially the concentration of free  $\text{CO}_2$  are greatly affected by pH, salinity, and temperature, while the availability of  $\text{NH}_4^+$  is pH-dependent, because at high pH the ion escapes as free ammonia. Water motion can affect turbidity and siltation as well as nutrient availability. These are examples of one environmental variable affecting another. There are also examples of two environmental variables acting synergistically on plants; for instance, the combination of low

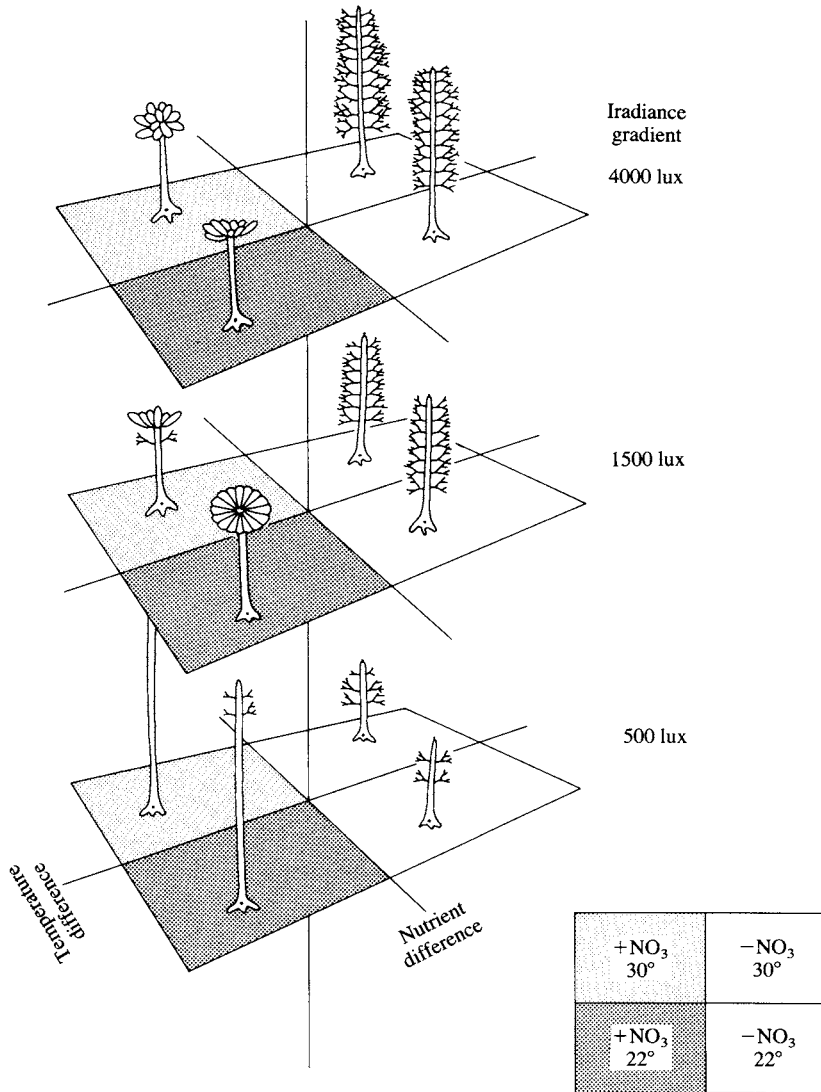


Figure 1.2. Interacting factors in *Acetabularia* growth and reproduction. Each matrix shows four conditions of nitrate availability and temperature; the matrices are arranged vertically along the irradiance gradient. (Original data for *A. calyculus* in illuminance units.) (Redrawn from Shihira-Ishikawas, in Bonotto 1988.)

salinity and high temperature can be harmful at levels where each alone would be tolerable. In several seaweeds, the combined effects of temperature and photoperiod regulate development and reproduction. Interactions between physicochemical and biological factors are also the rule rather than the exception. The environment of a given plant includes other organisms, as we have seen, with which the plant interacts through intraspecific and interspecific competition, predator-prey relationships, and basiphyte-epiphyte relationships. These other organisms are also affected by the environment, as are their effects on other organisms. Moreover, other organisms may greatly modify the physicochemical environment of a given individual. Protection from

strong irradiance and desiccation by canopy seaweeds is important to the survival of understory algae, including germlings of the larger species. Organisms shade each other (and sometimes themselves) and have large effects on nutrient concentrations and water flow. Other interactions stem from the way the biological parameters, such as age, phenotype, and genotype, affect a plant's response to the abiotic environment, as well as the effects that organisms have on the environment. The chief biological parameters that condition a given plant's response to its environment are age, reproductive condition, nutrient status (including stores of N, P, and C), and past history. By "past history" is meant the effects of past environmental conditions on plant development.

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Genetic differentiation within populations leads to different responses in plants from different parts of a population. The seasons can also affect certain physiological responses, aside from those involved in life-history changes; these responses include acclimation of temperature optima and tolerance limits.

Finally, there are factor interactions through sequential effects. Nitrogen limitation may cause red algae to catabolize some of their phycobiliproteins, which will in turn reduce their light-harvesting ability. In general, any factor that alters the growth, form, or reproductive or physiological condition is apt to change the responses of the plant to other factors both currently and in the future. A good example of a sequential effect, and also biotic–abiotic interaction, was seen by Littler and Littler (1987) following an unusual flash flood in southern California. Intertidal urchins (*Strongylocentrotus purpuratus*) were almost completely wiped out, but the persistent macroalgae suffered little damage from the fresh water. Subsequently, however, there was a great increase in ephemeral algae (*Ulva*, *Enteromorpha*, Ectocarpaceae) because of the reduction in grazing pressure.

The complexity of the interactions of variables in nature often confounds interpretation of the effects even of “major” events, such as the recent El Niño warm-water period (Paine 1986). In laboratory experiments, usually one variable is tested at a time, and all other factors are held constant, or at least equal in all treatments. Variations in additional factors can confound the results. For example, Underwood (1980) criticized some field experiments designed to determine the effects of grazer exclusion because the fences and cages used to keep out grazers also affected the water motion over the rock surface and provided some shade. Reed et al. (1991) pointed out the potential for density effects to confound studies of abiotic factors. Schiel and Foster (1986) criticized many studies of subtidal ecology for methodological problems, including inadequate experimental design, use of pseudoreplicates, and lack of any measure of variance. They commented that “correlations between algal abundances and various physical and biological factors have been cited in dozens of studies, often with poor quantitative assessments. The existence of patterns and abundance of species constitutes evidence that these physical factors and biological interactions may affect the structure of these communities. They do not at the same time, however, demonstrate the importance or unimportance of these factors in producing observed patterns” (Schiel & Foster 1986, p. 273; see also Norton et al. 1982). The statistical designs of experiments are considerably more complicated when more than one variable is being assessed at a time; practical reviews in this area have been provided by Box et al. (1978), Green (1979), and Underwood (1981b).

Moreover, because plants are so different from humans and from the animals with which we are most familiar, any assumption made about plants needs to be

checked by observation and experiment (Evans 1972). Drawing conclusions by analogy with other plants, or even with other algal groups, is no less fraught with potentially invalid assumptions. For instance, the planktonic stages of seaweeds are scarcely known, and one might be tempted to fill in missing information by making comparisons with other unicellular algae: phytoplankton. Yet, from the little we do know, there evidently are limits to the analogies, and not only because of differences between divisions: Seaweed propagules do not behave like phytoplankton, inasmuch as they have incomplete or inefficient photosynthetic systems and do not live long unless they settle (Santelices 1990b).

#### 1.1.3 Culture versus nature

Several considerations confound the interpretation of field reality via laboratory studies. First, while laboratory studies can provide much more controlled conditions than are found in nature, they are limited in some important ways and contain some implicit assumptions, such as the following: (1) High nutrient levels do not alter the plants’ responses to the factor under study. (2) The reactions of plants to uniform conditions (including the factor under study) are not different from their responses to the factor(s) under fluctuating conditions. To a certain extent these assumptions are valid. Culture media are very rich in nutrients, to compensate for lack of water movement and exchange, but that such substitution can give precisely the same results with all parameters is doubtful. Other culture conditions are also generally optimal, except for the variable under study, and the results may not elucidate the behavior of plants in the field, which are subject to competition and often suboptimal conditions (Neushul 1981). Another important difference between culture and nature is that in culture, species usually are tested in isolation, away from interspecific competition and grazing. Furthermore, culture conditions are uniform (at least on a large scale), whereas in nature there often are large and unpredictable fluctuations in the environment (Fréchette & Legendre 1978; Turpin et al. 1981). Microscale heterogeneity in culture conditions should not be overlooked (Allen 1977; Norton & Fetter 1981). In the culture flask, one cell may shade another, and cells form nutrient-depleted zones around them, creating a mosaic of nutrient concentrations through which cells pass. On the other hand, scale also needs to be considered at the large end – for instance, the amount of space needed for a patch of a given alga to establish itself (Schiel & Foster 1986).

Second, the use of taxonomic species to define ecological entities is a handicap:

The criteria used by the taxonomist for the delineation of taxa are chosen deliberately from the conservative and stable features of morphology that are not subject to marked genetic variation, polymorphism or phenotypic

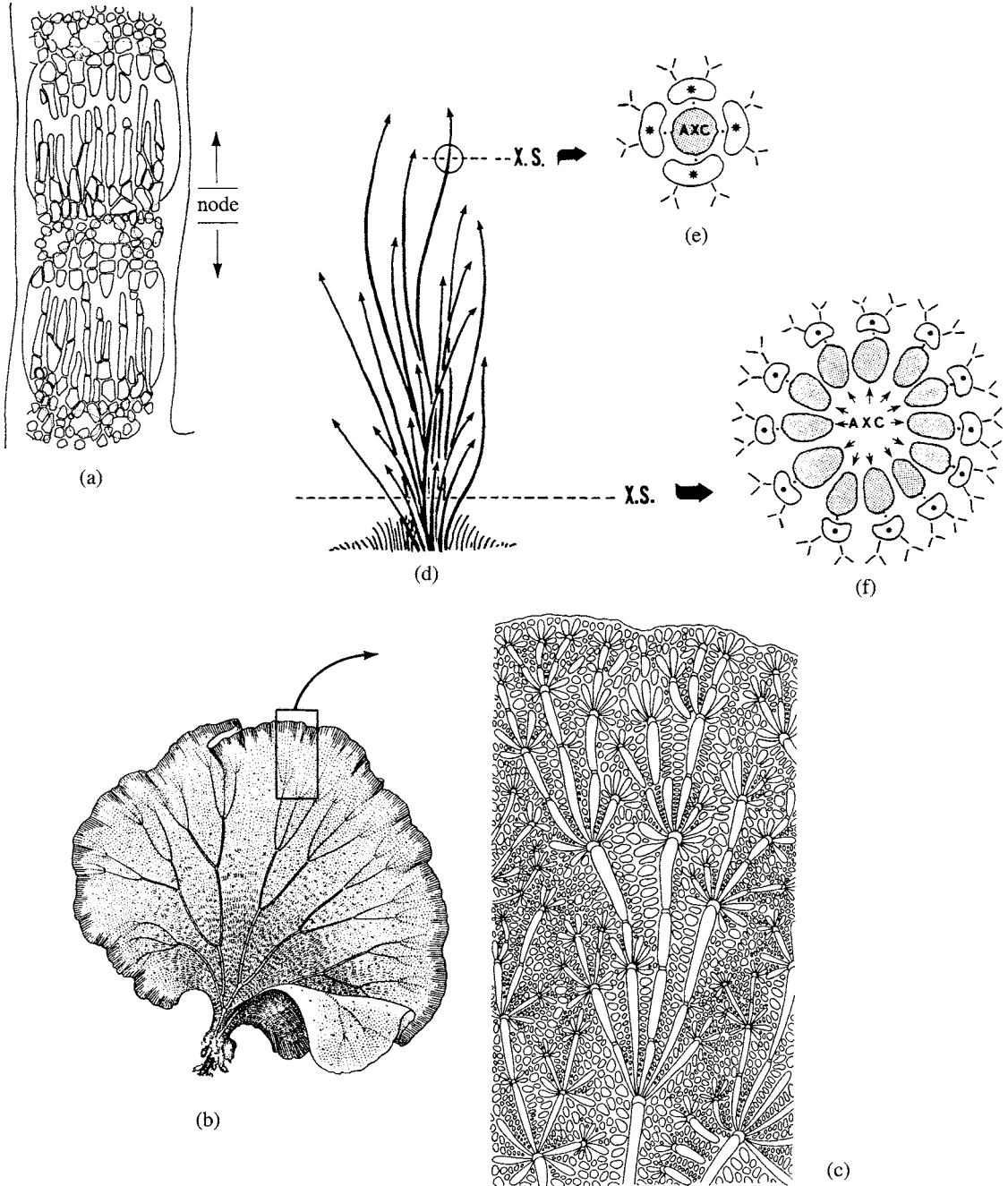
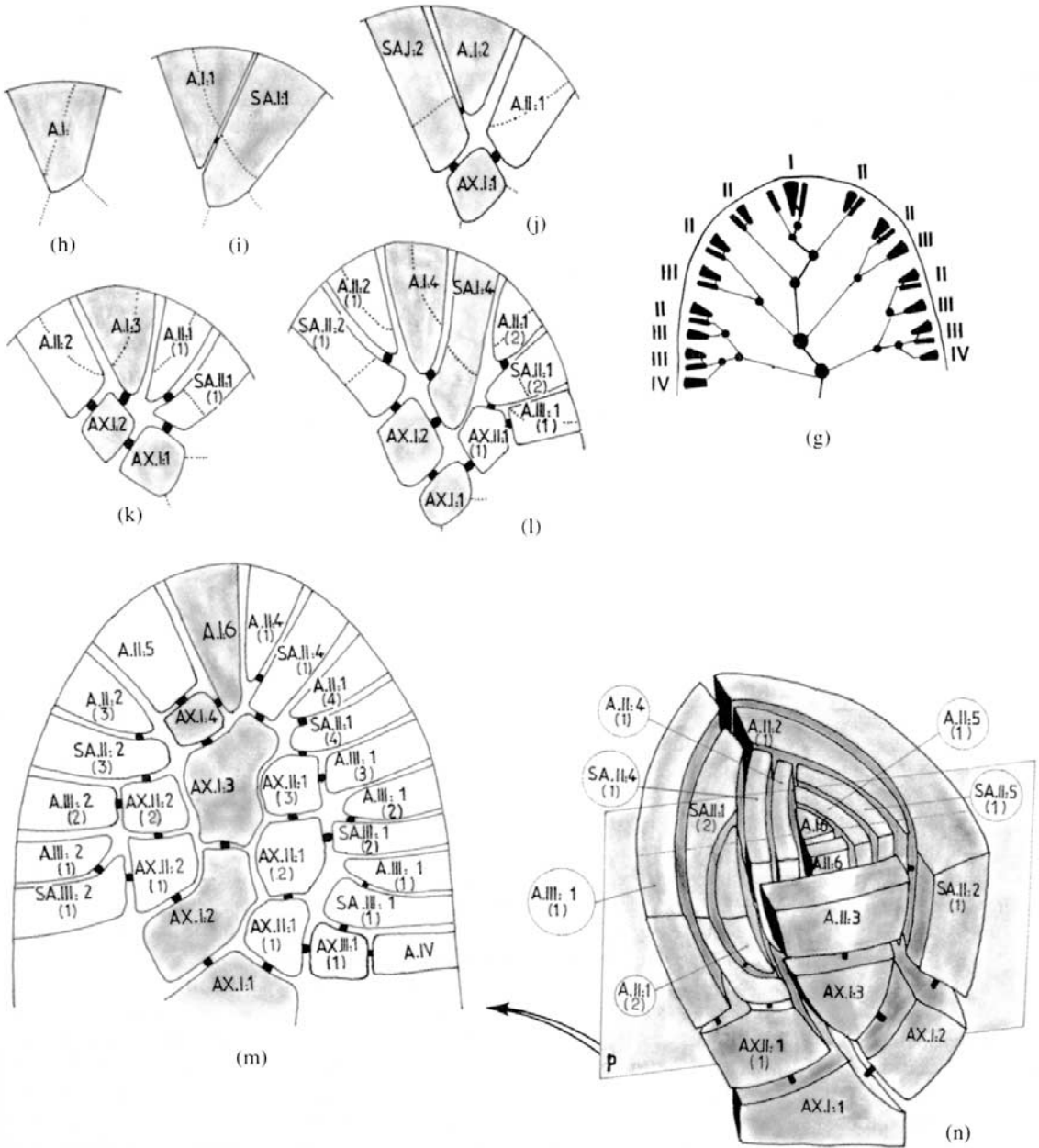


Figure 1.3. Filamentous thallus construction. (a) Small portion of a *Ceramium* axis with cortication growing upward and downward from a node between axial cells. (b, c) Formation of bladelike thallus from filaments in *Anadyomene stellata* (b,  $\times 1.82$ ; c,  $\times 13.65$ ). (d–f) Growth of *Dumontia incrassata* showing schematically the axial filaments and apical cells (arrows); cross-section in the uniaxial part of the thallus near the tip (e) shows a single axial cell (AXC) surrounded by four pericentral cells (\*) that have in turn produced cortical cells; (f) cross section through base shows multiaxial construction with a core of axial cells, each with one pericentral cell. (g–n) Apical growth of *Gracilaria verrucosa*. (g) A primary apical cell (I) occurs at the tip of the main axis, and secondary apical cells (II, III, etc.) occur at the tips of lateral filaments. (h–m) Division of the apical cell (A.I), shown by dotted line in (h), gives rise to a subapical cell (SA.I:1) and a new apical cell (A.I:1)(i). In (i–j), the subapical cell is shown dividing to form an axial

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cell (AX.I:1) and a secondary apical cell (A.II:1), while the new apical cell (A.I:1) cuts off another subapical cell (SA.I:2) and becomes A.I:2. The lineages can be traced further with the help of the pit connections (represented as dark bars between cells). (n) The three-dimensional arrangement is complex because the apical cell divides on three faces. P is the plane of the vertical section in (m). (Part a from Taylor 1957; b and c from Taylor 1960, with permission of University of Michigan Press; d–f from Wilce & Davis 1984, with permission of *Journal of Phycology*; g–n from Kling & Bodard 1986, with permission of *Cryptogamie: Algologie*.)

change. These same criteria . . . may be quite inappropriate for describing the ecologically relevant differences between individuals, populations and communities. . . . The failure of taxonomic categories to fit as ecological categories is not surprising . . . yet it may be just the taxonomically useless characters that are mainly

responsible for determining the precise ecologies of organisms [Harper 1982, p. 12]

See also Russell (1988). The taxonomy of widespread organisms must be approached with particular caution. When what appears to be a single species occurs in

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widely different latitudes or longitudes, its physiological and ecological parameters may be quite different (and the taxonomy may change as information accumulates). Incisive studies on the species concept have been published by Mann (1984) for diatoms and by Blackburn and Tyler (1987) for desmids.

For many topics, only one study or a few studies have been done, and a phenomenon demonstrated in a particular alga under certain conditions will not necessarily turn out to be the same in other algae or under other conditions. Lewin (1974, p. 2) commented about laboratory studies that “there is still a tendency . . . to over-generalize on the basis of investigations on no more than one or two examples.” Equally, very few natural populations or communities have been studied often enough to assess how much variability is present from place to place (ecotypic variation). The kelp beds of southern California are exceptional in that they have been repeatedly analyzed by different people along the coast for over 25 years. The impression now emerging is that there is no typical kelp bed; environmental parameters differ from one kelp bed to another, and parameters such as specific growth rate versus nitrogen supply vary among *Macrocystis* populations, which have limited dispersal and genetic mixing (Kopczak et al. 1991).

Eventually, the isolated pixels have to be reassembled into models of nature. This can be done in part by experimentally assessing factor combinations, and in part through mathematical modeling (Newell 1979; McQuaid & Branch 1984; Kooistra et al. 1989). Alderdice (1972) and Newell (1979) suggested that an organism has a multidimensional “zone of tolerance,” the boundaries of which are defined by its tolerance to all environmental variables. These boundaries depend not only on the species and genotype of the organism but also on its size, age, stage of life history, and previous environmental experience; the boundaries change as these change. Within the overall zone of tolerance there are smaller multidimensional zones that are defined by the local conditions under which the organism is operating; acclimation to other conditions, such as during seasonal changes, involves changes in the boundaries of these smaller zones. These zones can be visualized on paper as far as three axes (see Fig. 6.21), but computers can manipulate data along many axes.

In this first chapter we shall review the foundation of structures and life histories on which any understanding of seaweed physiological ecology must rest, and then trace events involved in the development of seaweed thalli from gametes or spores to reproductive individuals.

### 1.2 Seaweed morphology and anatomy

#### 1.2.1 Thallus construction

Diversity of thallus construction in algae contrasts strongly with uniformity in vascular plants. In the latter, parenchymatous meristems (e.g., at the shoot

and root apices) produce tissue that differentiates in a wide variety of shapes. Among the algae, parenchymatous development is found in kelps, fucoids, Ulvales, Dictyotales, and others. However, the great majority of seaweeds either are filamentous or are built up of united or corticated filaments. Large and complex structures can be built up this way (e.g., *Codium magnum*; see photo by Dawson 1966). Cell division may take place throughout the plant, or the meristematic region may be localized. If localized, it is most commonly at the apex, but may be at the base or somewhere in between (intercalary).

A simple filament consists of an unbranched chain of cells attached by their end walls and results from cell division only in the plane perpendicular to the axis of the filament. Unbranched filaments are uncommon among seaweeds, except the blue-green algae (Oscillatoriaceae); two eukaryotic genera are *Ulothrix* and *Chaetomorpha*. Usually, some cell division takes place parallel to the filament axis to produce branches (*Cladophora*, *Antithamnion*) (see Fig. 1.15). Filaments consisting of a single row of cells (branched or not) are called uniseriate. Pluriseriate filaments, in genera such as *Percursaria*, *Bangia*, and *Sphacelaria* (Fig. 1.4a), are formed by vertical cell divisions in which the daughter cells do not grow out into branches but remain as compact parenchyma. Branches need not grow out free, but may creep down the main filament, forming cortication, as seen in *Ceramium* (Fig. 1.3a) and *Desmarestia*. In some of the more massive Rhodomeleaceae, such as *Laurencia* and *Acanthophora*, the cortication becomes so extensive that the origin of the structure is obscured. A detailed study by Kling and Bodard (1986) of axis development in *Gracilaria verrucosa* (uniaxial) showed how complex – and difficult to interpret – pseudoparenchymatous growth can be (Fig. 1.3g–n; compare with Fig. 1.4d–m).

Many of the more massive seaweed thalli are multiaxial, produced by the adhesion of several filaments. This is common among the red algae (Fig. 1.3d–f; also see Fig. 1.44a,b) (Coomans & Hommersand 1990). Multiaxial construction is most readily seen in the less tightly compacted thalli of *Nemalion* or *Liagora*. The contrast between multiaxial and uniaxial growth can be seen within thalli of *Dumontia incrassata* (Fig. 1.3d–f), in which bases are multiaxial, but upper branches are uniaxial (Wilce & Davis 1984). Conversely, *Weeksia fryeana* is uniaxial at first and later becomes multiaxial (Norris 1971). The adhesion of filaments can also produce a pseudoparenchymatous crust (*Peyssonnelia*, *Ralfsia*) or blade (*Anadyomene*; Fig. 1.3b,c). Many siphonous green algae, including *Halimeda* and *Codium*, are formed by the interweaving of numerous filaments (Fig. 1.1). In the Corallinaceae, multiaxial apical growth forms the hypothallus (in crusts) or central medulla (in erect forms), while intercalary meristems on the lateral branches form the epithallus and perithallus (cortex in



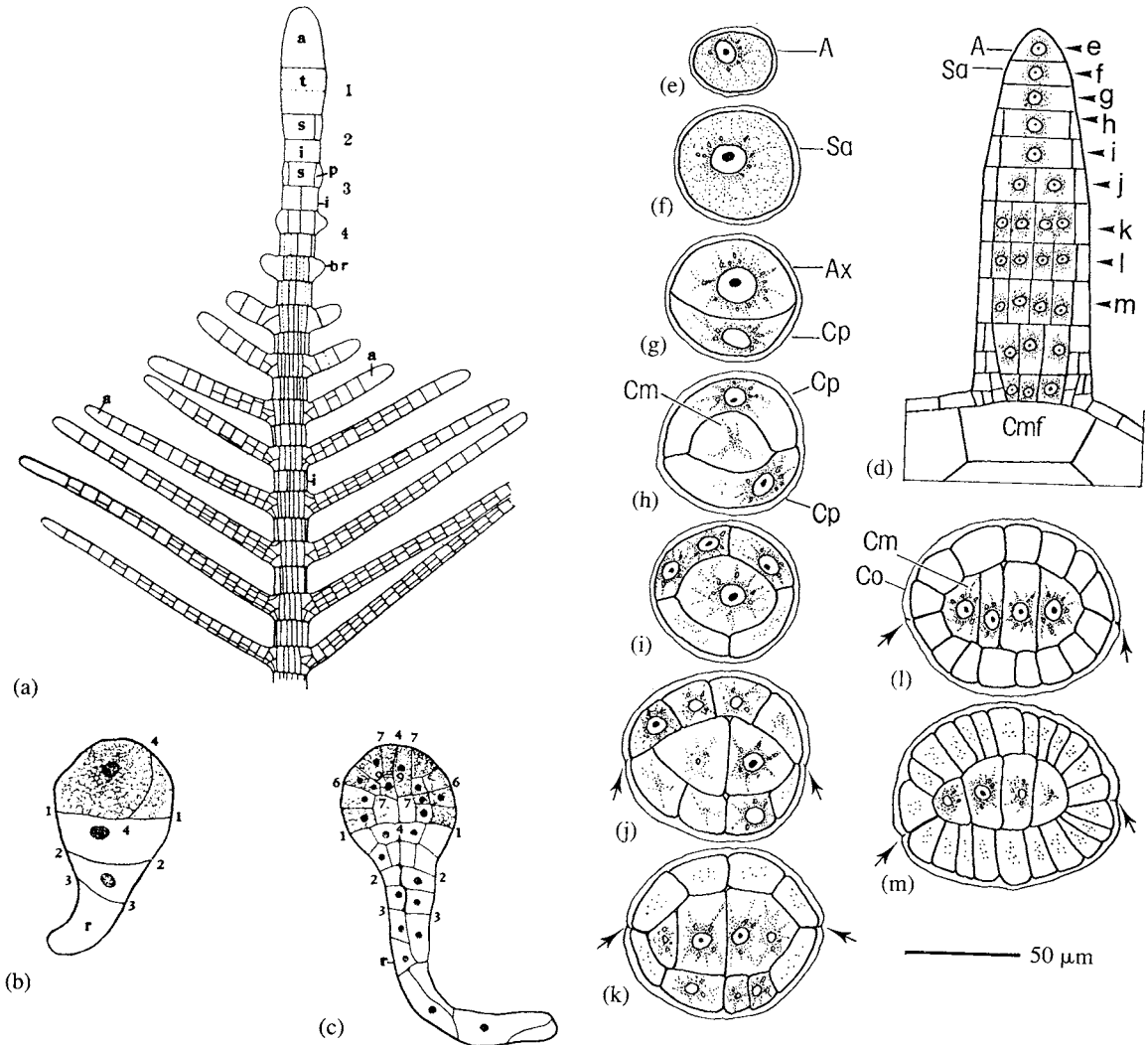


Figure 1.4. Parenchymatous development in seaweeds. (a) *Sphacelaria plumula* apex showing first transverse division (t), followed by pairs of cells (i, s), of which s forms branches, but i does not. (b, c) *Fucus vesiculosus* germination showing successive cell divisions (numbered) (divisions 5 and 8 in the plane of the page). (Parts a–c from Fritsch 1945, based on classical literature.) (d–m) *Dictyota*: development of parenchyma; (d) long section through adventive branch, showing locations of cross sections at each level (diagrammatic); (e–m) serial cross sections to show sequence of periclinal divisions. Arrows indicate junction between original two pericentral cells (first shown in h). For the sake of clarity, the proportions of the cells were changed; the adventive branch is actually half as long and twice as wide as shown. A, apical cell; Sa, subapical cell; Ax, axial cell; Cp, pericentral cell, Cm, medullary cell; Co, cortical cell. (Parts d–m from Gaillard & L'Hardy-Halos 1990, with permission of Blackwell Scientific Publications.)

erect axes) (Cabiocch 1988). [Woelkerling (1988) provides new terminology for (crustose) corallines, emphasizing their filamentous development.] A potential disadvantage of pseudoparenchymatous growth is lack of cytoplasmic contact between adjacent cells in different filaments, a problem that red algae overcome (perhaps) through secondary pit connections (Raven 1986).

Cell division in two planes can alternatively result in a monostromatic sheet of cells, as in *Monostroma*

and some species of *Porphyra*. In the Delesseriaceae, marginal meristems produce the wings, while apical cells produce the axial filaments. Such solid tissues are called parenchyma and may become thicker through cell division in a third plane, as in *Ulva* and distromatic *Porphyra*, and in the kelps and fucoids (Fig. 1.4; also see Figs. 1.43 and 1.45). The ontogeny of the parenchyma in Dictyotales (Fig. 1.4d–m) has been followed in detail by Gaillard and L'Hardy-Halos (1990), who cite many sources, and by Katsaros and Galatis (1988).

Table 1.1. Functional-form groups of macroalgae

| Functional-form group    | External morphology                    | Internal anatomy   | Texture          | Sample genera   |
|--------------------------|--|--|------------------|---|
| Sheet group              | Thin, tubular, and sheetlike (foliose) | Uncorticated, one to several cells thick                           | Soft             | <i>Ulva</i> , <i>Enteromorpha</i> , <i>Dictyota</i>   |
| Filamentous group        | Delicately branched (filamentous)      | Uniseriate, multiseriate, or lightly corticated                    | Soft             | <i>Centroceras</i> , <i>Polysiphonia</i> , <i>Chaetomorpha</i> , <i>Microcoleus</i>           |
| Coarsely branched group  | Coarsely branched, upright             | Corticated   | Fleshy-wiry      | <i>Laurencia</i> , <i>Chordaria</i> , <i>Caulerpa</i> , <i>Penicillus</i> , <i>Gracilaria</i> |
| Thick, leathery group    | Thick blades and branches              | Differentiated, heavily corticated, thick-walled                   | Leather, rubbery | <i>Laminaria</i> , <i>Fucus</i> , <i>Udotea</i> , <i>Chondrus</i>                             |
| Jointed calcareous group | Articulated, calcareous, upright       | Calcified genicula, flexible intergenicula with parallel cell rows | Stony            | <i>Corallina</i> , <i>Halimeda</i> , <i>Galaxaura</i>   |
| Crustose group           | Prostrate, encrusting                  | Calcified or uncalcified parallel rows of cells                    | Stony or tough   | <i>Lithothamnion</i> , <i>Ralfsia</i> , <i>Hildenbrandia</i>                                  |

Source: Littler et al. (1983b), with permission of *Journal of Phycology*.

Incomplete cytokinesis during tetraspore formation occurs in *Gracilaria tikvahiae*, leading to two-, three-, and four-nucleate spores. These give rise to chimeric germings, detectable in crosses of color mutants because of different color segments (van der Meer 1977). The existence of chimeric plants – having several genotypes within one thallus – is a recently recognized phenomenon that has implications for understanding morphogenesis. Several cogerming zygotes can become interwoven in *Codium fragile* (Friedmann & Roth 1977), *Dumontia incrassata* (Rietema 1984), and potentially in any multiaxial thallus, as well as in the parenchymatous *Smithora naiadum* (McBride & Cole 1972).

### 1.2.2 The Littler functional-form model

The construction of the thallus has importance for developmental physiology. Similar morphologies can be constructed in different ways; the overall morphology is important to ecological physiology. Among different algal classes, certain morphologies are repeated, which, as noted by Littler et al. (1983a), indicates convergent adaptations to critical environmental factors. On the other hand, species face divergent selection pressures: those favoring more productive, reproductive, and competitive thalli, versus those favoring longevity and environmental resistance (Littler & Kauker 1984; Russell 1986; Norton 1991). Many sea-

weeds show a variety of morphologies within one life history (see sec. 1.5). Heterotrichous plants with crustose bases and erect fronds within one generation (e.g., *Corallina*) and heteromorphic plants with crustose/filamentous and frondose generations (e.g., *Scytosiphon*) (Fig. 1.24) are both common. How can we assess the significance of morphology when we are faced with convergence between classes on the one hand and diversification within species on the other hand?

The functional-form model advanced by Littler and Littler in 1980, and subsequently tested extensively by them and by others, holds that the functional characteristics of plants, such as photosynthesis, nutrient uptake, and grazer susceptibility, are related to form characteristics, such as morphology and surface-area : volume (SA : V) ratios (Table 1.1). One can thus set up predictions of function from an examination of form. For example, a negative side of multicellularity is a reduced SA : V ratio for the organism. The effect of multicellularity is small in uniseriate filaments (where only the end walls adjoin other cells), and larger in massive parenchymatous forms. Rosenberg and Ramus (1984) demonstrated the predicted correlation with nutrient uptake: *Ulva curvata* (SA : V = 165 cm<sup>2</sup> cm<sup>-3</sup>) had the highest uptake, *Fucus evanescens* and *Gracilaria tikvahiae* had about equal SA : V ratios and uptake rates, and *Codium decortatum* (SA : V = 8.9 cm<sup>2</sup> cm<sup>-3</sup>) had the lowest uptake rate. The decrease in