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Seaweed thalli and cells

1.1 Introduction: the algae and their environments

1.1.1 Seaweeds

The term "seaweed" 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 gametes and zygotes, and may be temporarily planktonic (Amsler and Searles 1980; Maximova and Sazhin 2010). Some remain small, forming sparse but productive turfs on coral reefs (Hackney *et al.* 1989) while others, such as the "kelps" of temperate reefs, can form extensive underwater forests (Graham *et al.* 2007a). Siphonous algae such as *Codium*, *Caulerpa* and *Bryopsis* that form large thalli are, in fact, acellular. The prokaryotic Cyanobacteria have occasionally been acknowledged in "seaweed" floras (e.g. Setchell and Gardner 1919; Littler and Littler 2011a). They are widespread on temperate rocky and sandy shores (Whitton and Potts 1982) and 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 (Littler and Littler 2011a, b; Charpy *et al.* 2012). Benthic diatoms also form large and sometimes abundant tube-dwelling colonies that resemble seaweeds (Lobban 1989). An ancient lineage of (mostly) deep-water green algae, the Palmophyllales, that includes *Verdigellas* and *Palmophyllum*, have a palmelloid organization with complex thalli built from an amorphous matrix with a nearly uniform distribution of spherical cells (Womersley 1971; Zechman *et al.* 2010). On a smaller scale are the colonial filaments of some simple red algae, such as *Stylonema* (previously *Goniotrichum*). A "seaweed" is therefore problematic to precisely define: here "seaweed" refers to algae from the red, green, and brown lineages that, at some stage of their life cycle, form multicellular or siphonous macrothalli. In this book we shall consider macroscopic and microscopic marine benthic environments and how seaweeds respond to those environments.

The algae are evolutionarily diverse, but are related to one another through the endosymbiotic events that gave rise to plastids. The traditional classification of seaweeds as "red", "green", and "brown" is still fitting, but our understanding of how these groupings arose and their relatedness to each other and other eukaryotes has been transformed over the past 20 years as our understanding of endosymbiosis has grown (e.g. Walker *et al.* 2011). The evolutionary origin of the algae continues to be the subject of considerable research effort and debate (e.g. Brodie and Lewis 2007; Archibald 2009; Keeling 2010; Yoon *et al.* 2010; Burki *et al.* 2012; Collén *et al.* 2013). The taxonomic position of a species can be viewed as a "working hypothesis", and as such is subject to change as new information arises (Cocquyt *et al.* 2010). Unraveling algal evolution is complex because, in addition to the multiple endosymbiotic events, there are other complicating events such as horizontal (lateral) gene transfer (HGT; see Brodie and Lewis 2007). Knowledge of the relatedness of the different seaweed groups, and their relations to

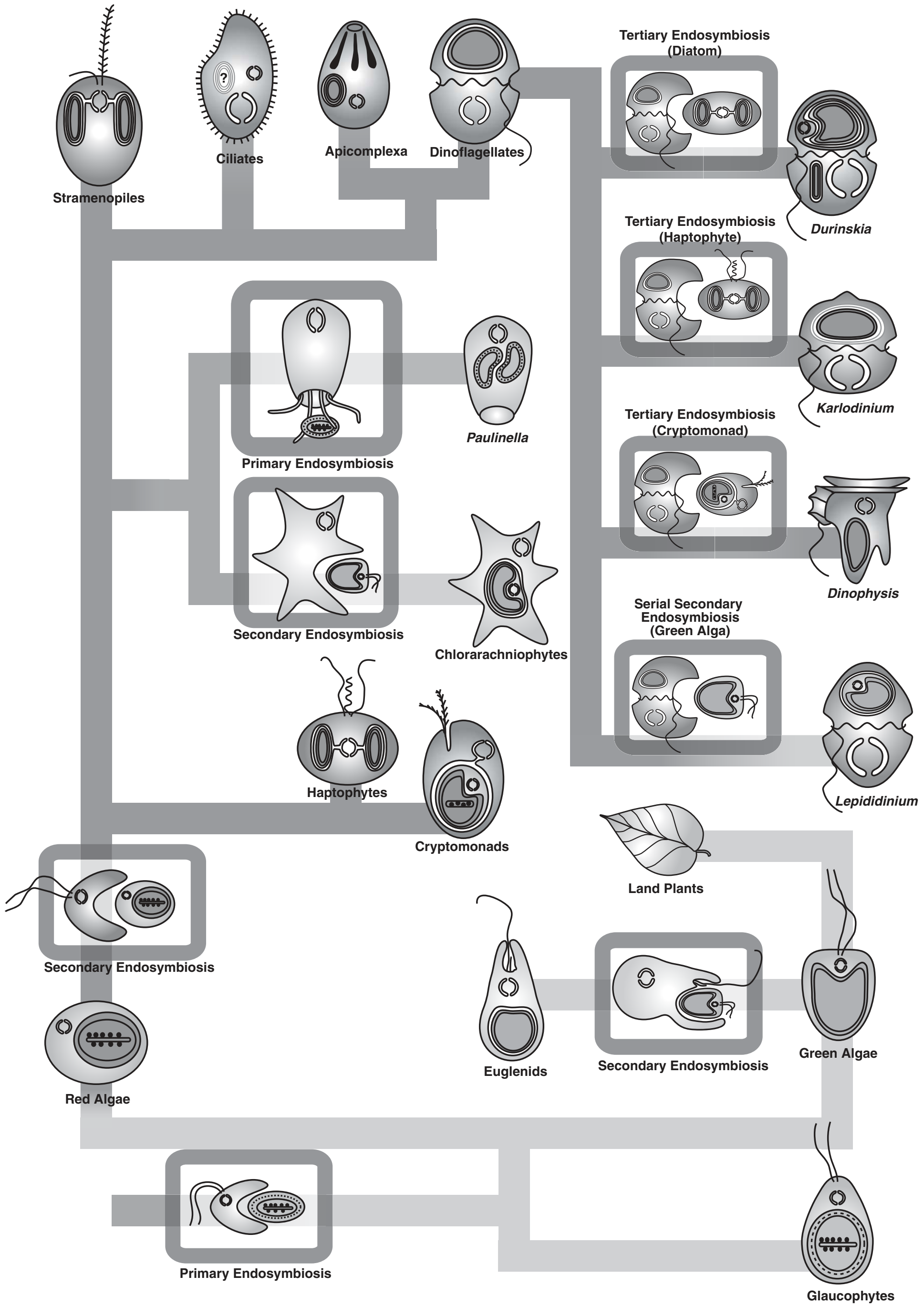

Figure 1.1 Schematic view of plastid evolution in the history of eukaryotes. The various endosymbiotic events that gave rise to the current diversity and distribution of plastids involve divergences and reticulations whose complexity has come to resemble an

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other eukaryotes, is helpful in predicting aspects of their physiology and ecology.

There are several hypotheses on how algal plastids have arisen. A leading hypothesis is that a primary endosymbiotic event (~1.5 billion years ago), in which a free-living cyanobacterium was engulfed and incorporated within a heterotrophic eukaryote, gave rise to three major lineages: (1) the glaucophytes, (2) the green lineage in which the green algae are ancestral to the terrestrial plants, and (3) the red lineage which includes the red seaweeds (Yoon *et al.* 2004; Keeling 2010; Fig. 1.1). But there may have been more than one primary event, and the glaucophytes could have arisen separately from the green and red lineages (see Graham *et al.* 2009). At least three secondary endosymbiotic events (eukaryote + eukaryote) have occurred. It is fairly certain that two separate secondary events involving unicellular green algae gave rise to the euglenoids and chlorarachniophytes (reviewed by Keeling 2009, 2010; Fig. 1.1). Less clear, however, are the secondary endosymbiotic event(s) involving unicellular red algae (Burki *et al.* 2012). The chromalveolate hypothesis proposed by T. Cavalier-Smith (1999) suggests that a single secondary endosymbiotic event involving a red alga gave rise to six lineages (Fig. 1.1): ciliates, dinoflagellates, apicomplexa, haptophytes, cryptomonads, and the stramenopiles (heterokonts), with the first three belonging to the Alveolata. The chromalveolate hypothesis is "highly contentious" but considered by Keeling (2009) and others as the "hypothesis to beat". At the time of writing (2013), the consensus is that the stramenopiles and Alveolata group with Rhizaria, forming the "SAR" clade; the haptophytes form a closely related sister group to the SAR clade, and the position of the cryptomonads is equivocal (Walker *et al.* 2011; Burki *et al.* 2012). Within the stramenopiles, the unicellular diatoms share a common ancestor with the multicellular brown seaweeds (Phaeophyceae; Patterson 1989a; Andersen 2004). However, phylogenies based on carbon storage and cell wall polysaccharides suggest that the stramenopiles arose separately from the Alveolates, and that a related, but distinct, red algal plastid was incorporated into an ancestral stramenopile in a second endosymbiotic event (Michel *et al.* 2010a, b). The dinoflagellates arose from tertiary or serial secondary endosymbioses (Fig. 1.1). As new information arises, and new molecular and bioinformatic techniques are added to the existing repertoire, hypotheses on eukaryotic evolution and speciation will continue to develop.

Ocean vegetation is dominated by the algae. No mosses, ferns, or gymnosperms are found in the oceans, and only a few angiosperms (the seagrasses) occur in marine habitats. That there are relatively few marine angiosperms may reflect the problems of adaptation to the sea, including ion regulation and pollination (Ackerman 1998). The water column is chiefly the domain of the phytoplankton, but populations of floating seaweeds that have been detached from the substratum are common and provide an important mechanism of dispersal (sec. 3.3.7). Intertidal rocky shores are abundantly covered with a macrovegetation

Caption for Figure 1.1 (*cont.*) electronic circuit diagram. Endosymbiosis events are boxed, and the lines are shaded to distinguish lineages with no plastid (dark gray), plastids from the green algal lineage (light gray) or the red algal lineage (mid-gray). At the bottom is the single primary endosymbiosis leading to three lineages (glaucophytes, red algae, and green algae). On the lower right, a discrete secondary endosymbiotic event within the euglenids led to their plastid. On the lower left, a red alga was taken up in the ancestor of chromalveolates. From this ancestor, haptophytes and cryptomonads (as well as their non-photosynthetic relatives such as katablepharids and telonemids) first diverged. After the divergence of the rhizarian lineage, the plastid appears to have been lost, but in two subgroups of Rhizaria, photosynthesis was regained: in the chlorarachniophytes by secondary endosymbiosis with a green alga, and in *Paulinella* by taking up a cyanobacterium (many other rhizarian lineages remain non-photosynthetic). At the top left, the stramenopiles diverged from alveolates, where plastids were lost in ciliates and predominantly became non-photosynthetic in the apicomplexan lineage. At the top right, four different events of plastid replacement are shown in dinoflagellates, involving a diatom, haptophyte, cryptomonad (three cases of tertiary endosymbiosis) and green alga (a serial secondary endosymbiosis). Most of the lineages shown have many members or relatives that are non-photosynthetic, but these have not all been shown for the sake of clarity. (From Keeling, 2010, reproduced with permission.)

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that is almost exclusively seaweeds, although in western North America surf grass *(Phyllospadix* spp.) is an exception. Seaweed surfaces themselves are colonized by benthic microalgae and bacteria, with which they may have intimate ecological relationships, and seaweed microstages grow on and within larger seaweeds. Muddy and sandy areas have fewer seaweeds, because most species cannot anchor there, though some siphonous greens (e.g. some species of *Halimeda*, *Caulerpa*, and *Udotea*) produce penetrating, root-like holdfasts that also serve in nutrient uptake (Littler *et al.* 1988). In such areas, seagrasses become the dominant vegetation, particularly in tropical and subtropical areas (Larkum *et al.* 2006). There is also a paucity of freshwater macroalgae. Freshwater red and brown algae are represented by relatively few genera and species, and Ulvophyceae are also scarce with only a few genera (e.g. *Cladophora*) having penetrated fresh waters (Wehr and Sheath 2003).

Most seaweeds 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 algae 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. 1.2). Colonial diatoms, both tube-dwelling and chain-forming, also build three-dimensional structures, as do zooxanthellae (dinoflagellates) 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

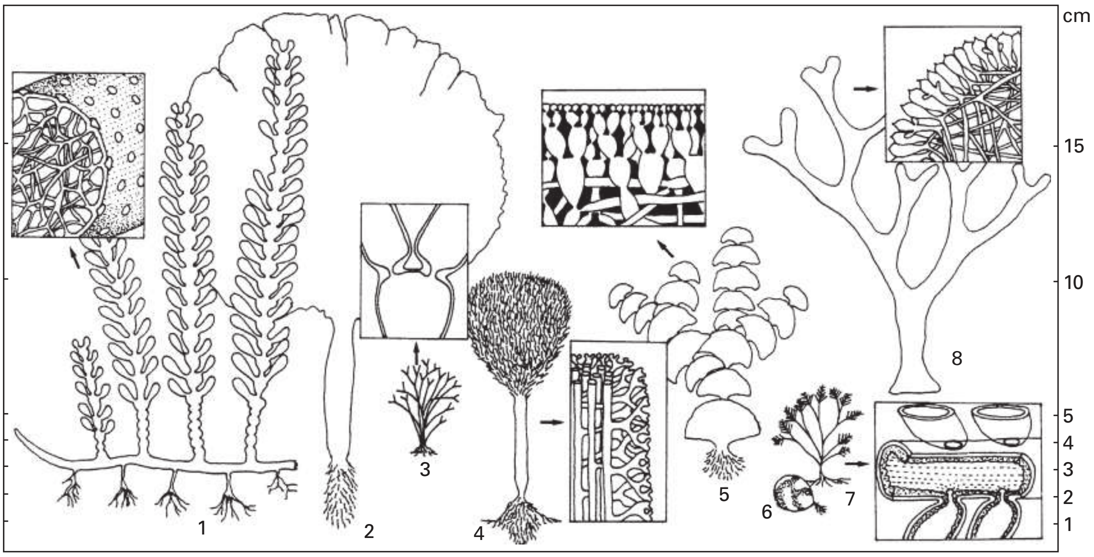

Figure 1.2 Thallus morphology and construction in siphonous green algae. Thalli drawn to scale; insets (not to scale) show principles of construction: (1) *Caulerpa cactoides*: network of trabeculae. (2) *Avrainvillea gardineri*: tightly woven felt of filaments. (3) *Chlorodesmis* sp.: bush of dichotomously branched siphons, constricted at the bases of the branches (inset). (4) *Penicillus capitus*: calcified siphons form a multiaxial 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 multiaxial branches. (From Menzel 1988, with permission of Springer-Verlag, Berlin.)

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water. On the other hand, there are creeping filamentous algae, even endophytic and endolithic filaments (e.g. *Entocladia*), as well as crustose algae 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, 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 (Dromgoole 1990; Raven 1996), whereas in other seaweeds (e.g. erect species of *Codium*) gas trapped among the filaments achieves the same effect (Dromgoole 1982).

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 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 to *Porphyra* [many species of this genus are now treated in other genera, with most being in *Pyropia;* Sutherland *et al.* 2011; see sec. 10.2] and *Ulva* whose blades are morphologically simple but are differentiated into regions with distinct physiologies (e.g. Hong *et al.* 1995; Han *et al.* 2003), 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 (Graham *et al.* 2009). Of course, no seaweed shows the degrees of differentiation seen in vascular plants. Even in vascular plants, the cells are biochemically more general than 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 a seaweed thallus means that each cell is physiologically and biochemically even more general than vascular plant cells.

The evolution of multicellularity entails the coordinated growth of cells, which, in turn, requires cell-to-cell communication. The detection of genes coding for receptor kinases (signaling molecules that are found in all multicellular eukaryotes) in *Ectocarpus*, and their absence in the related unicellular diatoms, suggests that these molecules were a prerequisite for multicellularity. Another pre-requisite is cell–cell adhesion via a sticky extracellular matrix. Integrin-related proteins that have a key role in cell adhesion in animals are also present in *Ectocarpus*, but not in diatoms (Cock *et al.* 2010a). In the red seaweeds, pit plugs are considered a vital step in the evolution of multicellularity, by providing structural integrity within the otherwise loosely packaged cells of pseudoparenchymatous construction (Graham *et al.* 2009, p. 319; Gantt *et al.* 2010).

1.1.2 Environmental-factor interactions

Benthic algae interact with other marine organisms, and all interact with their physico-chemical 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 (abiotic) factors affecting seaweeds are light, temperature, salinity, water motion, and nutrient availability. Among the biological (biotic) interactions are relations between seaweeds and their epiphytic bacteria, fungi, algae, and sessile animals; interactions between herbivores and seaweeds (both macroalgae and epiphytes); and the impact of predators, including humans. Each propagule contains the genetic information that will allow the maturing seaweed to develop a phenotype that is suited to its environment: in fact, there can be a high degree of phenotypic plasticity even within a genetically uniform population grown under the same environmental conditions (Fig. 1.3). Individual patterns of growth, morphology, and reproduction are overall effects of all these factors combined.

An organism's physico-chemical 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

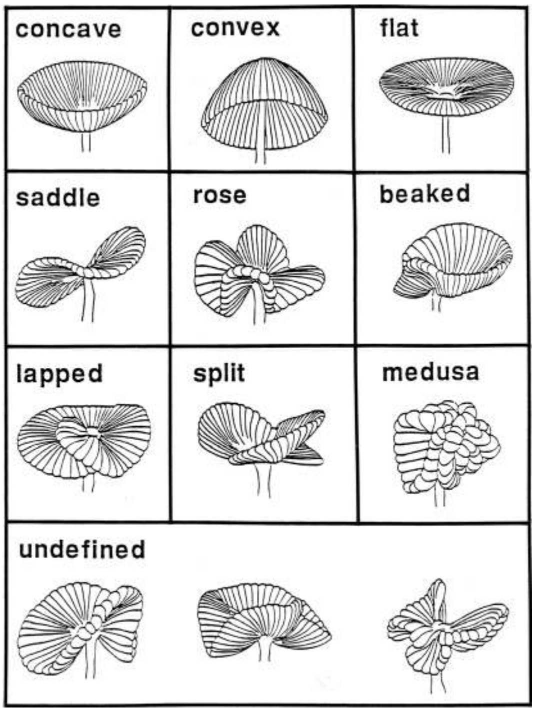

Figure 1.3 Variation in cap morphologies of *Acetabuaria acetabulum*, the progeny of which were raised in the same experimental conditions. "Concave" included a minor variant ("concave-bell") in which the rim of a concave cap was flattened. "Convex" are mirror images of concave. "Flat" caps are usually perpendicular to the stalk. "Saddles" have two opposing quadrants of the cap curved up and the other two down. In "beaked", one or both halves of the cap are adpressed and parallel to the stalk. "Split" caps have rays that are not all fused so that the cap is divided into halves, quarters or sixths. In "lapped", the rays adjacent to the two that had not fused overlap each other. "Rose" and "medusas" are the most convoluted cap shapes. "Undefined" are caps which combine two or more of the above morphologies. (From Nishimura and Mandoli 1992, reproduced with permission.)

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. Most importantly, the organization of life is now best understood as constitutive hierarchies (Mayr 1982, p. 65), in which at each new level or system there are emergent properties that are not predictable from study of the component parts. This is most evident in comparing the properties of individuals (say, humans) to the properties of the next level of components (organ systems, e.g. nervous system), but it also works upward from the individual through populations, communities, ecosystems, and the biosphere. It has major implications when we attempt to predict community or ecosystem properties from studies at the species (population) level, as we usually must. The following paragraphs are intended to paint the big 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.

1. Many environmental factors have several components that do not necessarily change together (i.e. multifaceted factors). 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 additional 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 Ca^{2+} and HCO_3^- affect membrane integrity and photosynthesis, respectively. Hydrodynamic forces affect thallus survival and spore settlement on wave-swept shores, and water motion also has important effects on the boundary layers over seaweed 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

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turbidity, hence a reduction in irradiance. Emersion often involves desiccation, heating, or chilling, removal of most nutrients (except CO_2), and, frequently, changes in the salinity of the water in the surface film on the seaweeds and in the free space between cells.

2. Interactions among environmental variables are the rule rather than the exception. Bright light is often associated with increased heating, particularly of seaweeds 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 seawater carbonate system and especially the concentration of free CO_2 are greatly affected by pH, salinity, and temperature, while the availability of ammonium 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 seaweed; for instance, the combination of low salinity and high temperature can be harmful at levels where each alone would be tolerable. In some seaweeds, the combined effects of temperature and photoperiod regulate development and reproduction.
3. Interactions between physico-chemical and biological factors are also the rule rather than the exception. The environment of a given seaweed includes other organisms, as we have seen, with which the seaweed interacts through intraspecific and interspecific competition, predator–prey relationships, associations with parasites and pathogens, 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 physico-chemical 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 seaweed'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 seaweed'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 seaweed development. Genetic differentiation within populations leads to different responses in seaweeds 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.
4. 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 seaweed 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 freshwater. Subsequently, however, there was a great increase in ephemeral algae (*Ulva*, 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 El Niño warm-water periods (Paine 1986; sec. 7.3.7).

Testing the effects of the various factor interactions described above requires a multifaceted approach that includes quantitative field observations, field manipulations and targeted laboratory experiments; for each approach a rigorous experimental design is essential so that the appropriate statistical analyses can be applied to detect differences among experimental treatments. 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. Experiments in which two (or occasionally three) factors are varied are possible but the number of culture vessels required for independent replication of treatments can be technically difficult to achieve especially with large seaweeds: it is important to avoid pseudoreplication in both laboratory and field experiments (Hurlbert 1984). It is also important to understand how field manipulations can confound results, and to include appropriate controls. 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. Furthermore, field studies that use correlation analyses to elucidate whether an environmental factor causes a specific biological pattern (e.g. growth, onset of reproduction) can be misleading because the key environmental factors that regulate seaweed biological processes are themselves tightly correlated, for example light, temperature, and nitrate concentration. As Schiel and Foster (1986, p. 273) explain “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.”

1.1.3 Laboratory culture versus field experiments

Several considerations confound the interpretation of field reality via laboratory studies. First, while laboratory studies 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 common in lab experiments do not alter the seaweeds’ responses to the factor under study. (2) The reactions of seaweeds 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 can be very rich in nutrients, to compensate for lack of water movement and exchange, but it is unlikely that this substitution can give precisely the same results. Other culture conditions are also generally optimal, except for the variable under study, and the results may not elucidate the behavior of seaweeds in the field, which are subject to competition and often suboptimal conditions (Neushul 1981). Another important difference between laboratory and field 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 (e.g. Gorospec and Karl 2011). Microscale heterogeneity in culture conditions should not be overlooked (Allen 1977; Norton and 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. In the field, 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 and Foster 1986). In essence, for both field and laboratory experiments, informed decisions must be made on the experimental conditions that are provided, and it is important to be aware that these conditions will affect the outcome and interpretation of the results.

Second, the timescale over which an experiment is conducted affects the interpretation of the data (Raven and Geider 2003). In short-term physiological experiments (seconds to minutes), a single factor can be varied (e.g. different levels of UV-B radiation) and a response (e.g. the production of reactive oxygen species) is measured. This physiological response is at the level of *regulation* i.e. the up- or down-regulation

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of pre-existing enzymes, and reveals the physiological potential of that organism to respond to an immediate environmental change. In medium-term experiments (hours to days) *acclimation* to new environmental conditions may occur. Acclimation involves gene expression, and the synthesis of new proteins such as enzymes. *Adaptation* to particular environmental factors occurs over a longer timescale (up to millennia) and is a mechanism for speciation (sec. 7.1).

Third, when a single species occurs in widely different latitudes or longitudes, its physiology and ecology may be quite different. 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. In Australia, for example, the kelp *Ecklonia radiata* dominates across 3000 km of coastline, from the southeast to southwest. However, the morphology and ecology of *Ecklonia* on the east coast is very different to *Ecklonia* on the west and south coasts, with the result that different coastal management plans are required for these different regions (Connell and Irving 2009). 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 since the 1960s (Steneck *et al.* 2002; Graham *et al.* 2007a). For *Macrocystis*, 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 populations (Kopczak *et al.* 1991).

In this first chapter we shall review the foundations of seaweed construction, cell biology, molecular biology and genetics on which any understanding of seaweed physiological ecology must rest. In Chapter 2, we continue this review by tracing the development of seaweed thalli from gametes and spores to reproductive individuals. In both these chapters, we build upon the fundamental information on seaweed anatomy and development that is described in algal text books, particularly van den Hoek *et al.* (1995) and Graham *et al.* (2009).

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. For seaweeds, parenchymatous construction is prevalent only in the brown orders. For example, in kelps, fucoids, and Dictyotales, this mode of construction has given rise to internal and morphological complexity (Fig. 1.4). The larger seaweeds, especially Laminariales and Fucales, have several different tissue and cell types, including photosynthetic epidermis, cortex, medulla, sieve tubes, and mucilage ducts (Graham *et al.* 2009). The ontogeny of the parenchyma in the 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). 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, for example *Codium amplivesiculatum* (previously *C. magnum)* can reach several meters long (Dawson 1950). Cell division may take place throughout the alga, 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; examples are *Ulothrix* and *Chaetomorpha*. Usually, some cell division takes place parallel to the filament axis to produce branches *(Cladophora*, *Ectocarpus*, *Antithamnion*; see Fig. 1.17). Filaments consisting of a single row of cells (branched or not) are called uniseriate. Pluriseriate filaments, i.e. two or more rows of cells, are seen in genera such as *Blidingia*, *Bangia*, and *Sphacelaria* (Fig. 1.4a; Graham *et al.* 2009). Branches need not grow out free, but may creep down the main filament, forming cortication, as seen in *Ceramium* (Fig. 1.5a) and *Ballia*. In some of the

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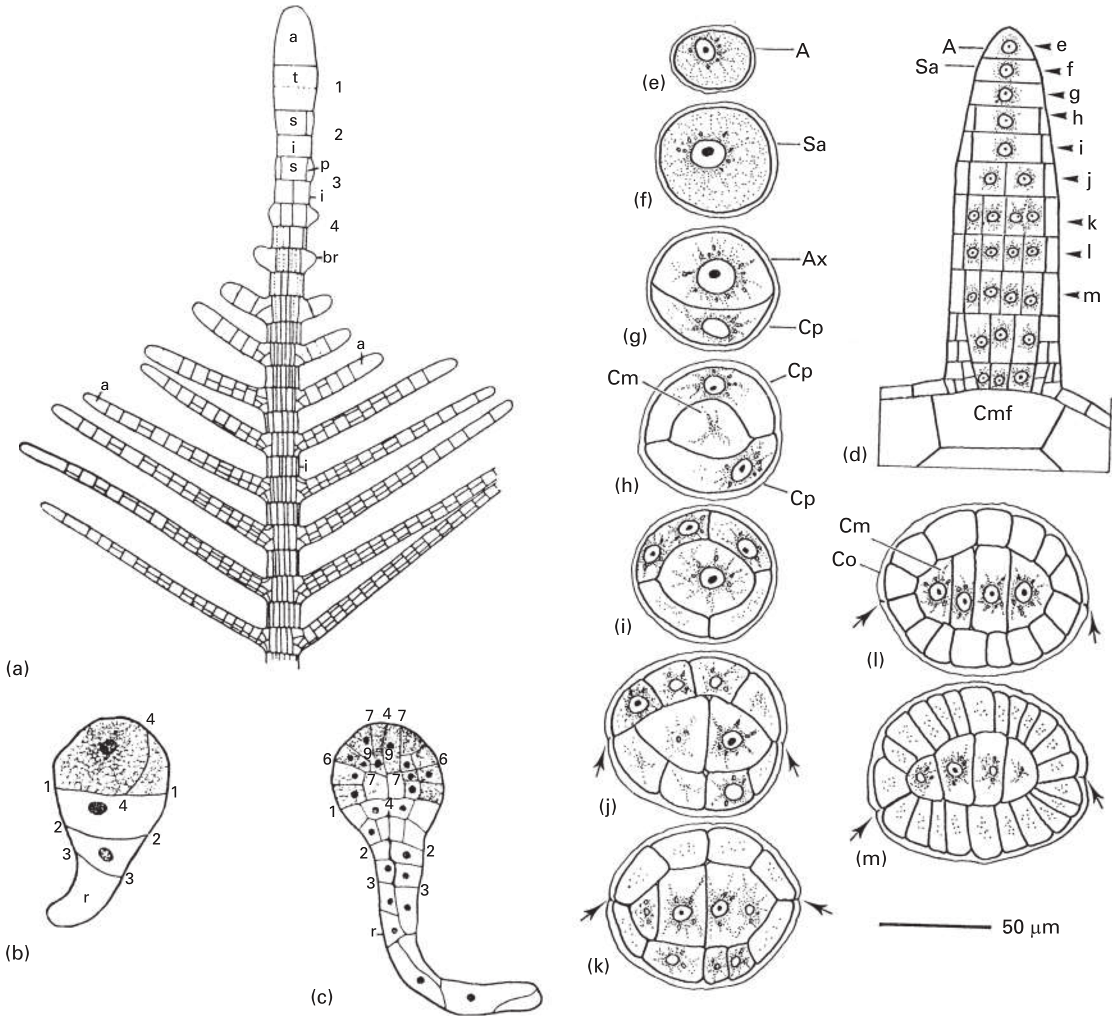

Figure 1.4 Parenchymatous development in seaweeds. (a) *Sphacelaria plumula* apex showing first transverse division (t), followed by pairs of cells (i, s), of which s forms branches, but i does not. (b, c) *Fucus vesiculosus* germination showing successive cell divisions (numbered) (divisions 5 and 8 in the plane of the page). (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 a–c from Fritsch 1945, based on classical literature; d–m from Gaillard and L'Hardy-Halos 1990, with permission of Blackwell Scientific Publications.)