Introduction to the ALGAE

STRUCTURE AND REPRODUCTION

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Preface

It seems to the authors, from their own experience in offering a semester-long introductory course in general phycology, that there has been a need for a teachable textbook in the field. The great syntheses of Smith (1950) and Fritsch (1935, 1945) contain much useful information, but they are too encyclopedic in scope for an introductory course, and phycology has advanced greatly on a number of fronts since they were published.

The authors have emphasized the structure and reproduction of representative algae in the present volume and have omitted in-depth coverage of algal physiology and biochemistry because of their special competence in the areas emphasized. The excellent volume edited by Stewart (1974) has quite adequately summarized algal physiology and biochemistry and, furthermore, a volume on algal genetics (Lewin, 1976) has been published recently.

No effort has been spared in citing *relevant* literature regarding the organisms and phenomena included in this volume, but the authors have not attempted to be comprehensive in their coverage. In general, it has been their purpose to include references to significant phycological literature that appeared since Smith's and Fritsch's volumes were published.

A special effort has been made in choosing representative types of algae for discussion to include as many as possible that the reader might hopefully be able to observe in the living condition in the laboratory. The ease with which many species of algae can be grown and maintained in laboratory culture, collected in the field, or procured from biological supply houses or culture collections should shame those who provide introductory students only with specimens bleached in preservative. A brief summary of methods of cultivating algae is included in the Appendix. It is hoped that both students and instructors will engage in cultivating algae in the laboratory. A glossary has been included to assist the reader in mastering phycological terminology.

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1

Introduction to the Algae[1]

Definition

The term *algae* (sing. *alga*) means different things to different people, and even the professional botanist and biologist find algae embarrassingly elusive of definition. Thus, laymen have given them such names as "pond scums," "frog spittle," "water mosses," and "seaweeds," while some professionals shrink from defining them. The reasons for this are that algae share their more obvious characteristics with other plants, while their really unique features are more subtle. There are a number of liverworts, mosses, ferns, and angiosperms that live in aquatic habitats with freshwater algae, and even marine environments contain angiosperms ("seagrasses," which are *not* members of the grass family!) as well as algae. There are also a great many terrestrial and subterranean algae, so that aquatic habitat is an untrustworthy criterion on which to base a distinction. A delightfully written and informal account of the algae has been published by Tiffany (1958).

How then does one distinguish algae from other chlorophyllous plants? The distinguishing characteristics reside in the phenomenon of sexual reproduction as it occurs in algae in which it differs from that in other green plants as follows: (1) In unicellular algae, the organisms themselves may function as gametes (Fig. 1.1*a*); (2) in some multicellular algae, the gametes may be produced in special *unicellular* containers or gametangia (Fig. 1.1*b*); or (3) in others, the gametangia are *multicellular* (Fig. 1.1*c*), every gametangial cell being fertile, that is, producing a gamete. None of these characteristics occurs in liverworts (Fig. 1*d*, *e*), mosses, ferns, or angiosperms. In their asexual reproduction, many algae produce flagellated spores and/or nonmotile spores in unicellular sporangia, or if the latter are multicellular, every cell is fertile.

[1]The blue-green algae are very similar to bacteria and by some biologists (e.g., Stanier, et al., 1971) said to be bacteria. See, however, p. 31.

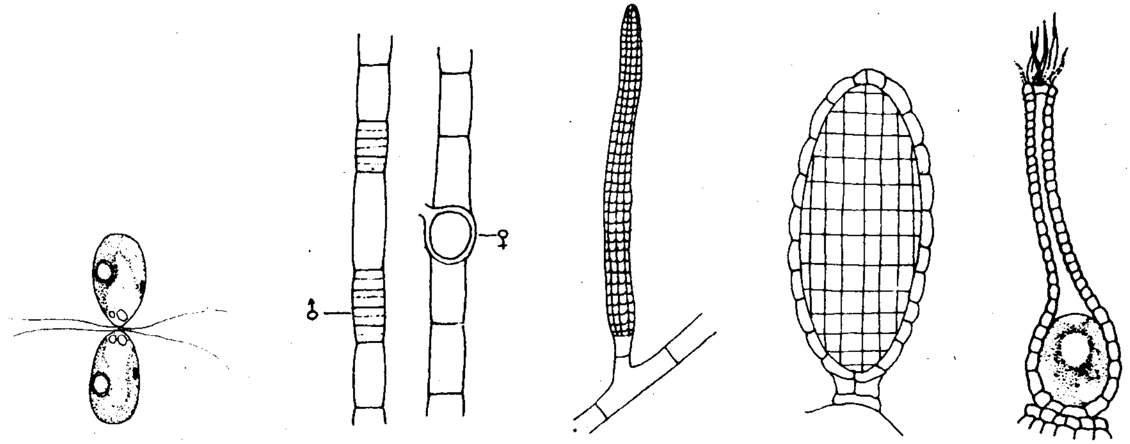

Fig. 1.1 Characteristics of the sexual reproduction of algae (*a*)–(*c*) and nonalgal plants (*d*), (*e*). (*a*) Uniting gametes of a unicellular alga, *Chlamydomonas*. (*b*) Unicellular gametangia of a filamentous alga, *Oedogonium*. (*c*) Multicellular gametangium of *Ectocarpus*. Note that every cell is gametogenous. (*d*) Archegonium and (*e*) Antheridium of a liverwort, a representative nonalgal plant. Sex organs multicellular and consisting of both gametic and sterile (vegetative) cells.

The Occurrence and Distribution of Algae[2]

When it is said that algae are ubiquitous, as in fact they are, such a statement might seem to tax credulity by one, for example, who was observing a desert scene or a permanent snowfield, but even in such diverse habitats algae are present.

Algae are aquatic or subaerial. By the latter is meant that they are exposed to the atmosphere rather than being submerged in water. Aquatic algae grow in waters of low salinity (as low as 10 ppm),[3] called *freshwater*, and in marine waters where the solutes are usually 33–40‰[4], although some algae occur in such locations as the Laguna Madre of Texas where the salinity may rise to 100‰ in dry seasons; this is in contrast to such an algal habitat as Mountain Lake, Virginia, in which the solutes total only 3.6 ppm. Some algae are remarkably tolerant to varying salinities such as those (e.g., *Enteromorpha*, p. 171) that live on ships that ply both freshwater and oceans. A number of algae live in brackish water; the latter is unpalatable for drinking but contains less salts than ocean water; for such algae the salinity optimum is less than that of seawater.

[2]No attempt has been made here to present a comprehensive account of algal ecology in view of the availability of such in-depth treatments of it as those of Dawson (1966), Boney (1966), Prescott (1968), and Round (1973).

[3]Parts per million.

[4]Parts per thousand.

With respect to their solutes, lakes are sometimes classified as **oligotrophic** or **eutrophic**. The former have been defined as those having less than 100 ppm of solutes, while the latter may have considerably higher concentrations. Oligotrophic lakes, as would be expected, support a sparser algal flora, with respect to numbers of organisms, than eutrophic lakes, but the number of species may be greater. Bodies of freshwater have also been classified as alkaline, hard-water lakes (with pH > 7) and as acid, soft-water lakes (with pH < 7), and their floras differ. Some species of algae can tolerate a broad range of pH, while others are more restricted. Bodies of water in which algae grow differ also in the concentration of dissolved oxygen and carbon dioxide and that of many other substances, as well as in temperature and turbidity (which affects depth of light penetration and hence photosynthesis and algal growth). All these factors have been examined carefully by many investigators as they affect algal growth, and these data have been summarized in part by Dawson (1966), Boney (1966), Prescott (1968), and Round (1973), among others.

Aquatic algae may be suspended (planktonic) or attached and living on the bottom (benthic). The **plankton** consists of a flora and fauna, together with bacteria and often fungi, of suspended organisms, while the **benthos** is composed of attached and bottom-dwelling organisms. A few algae are **neustonic**; that is, they live at the interface of water and the atmosphere.

Planktonic algae may be collected by drawing a plankton net through the water. Plankton nets are composed of silk with finely woven meshes, commonly 180 pores to the square inch. This serves as a strainer that filters out and concentrates many planktonic algae and other microorganisms. Planktonic algae may also be concentrated for microscopic study by centrifugation. Planktonic algae under certain combinations of nutrition favorable to them increase enormously in number and form **water blooms** (Fitzgerald, 1971). Diatoms, green algae, *Euglena* (p. 258), and blue-green algae (Fig. 2.1) are most frequently present in blooms.

Benthic algae grow attached to various substrates and may be classified as **epilithic** (living on stones), **epipelic** (attached to mud or sand), **epiphytic** (attached to plants), and **epizoic** (attached to animals). Examples of algae growing on all of these substrates are included in later pages.

In addition to the classification of algal habitats above, certain other categories have been erected to describe growth habits of marine algae. Some are **subaerial** or said to be **supralittoral**, since they grow above the water level and in the spray zone (e.g., *Gloeocapsa*, p. 45; *Calothrix*, p. 61; and *Prasiola*, p 177). Others are **intertidal** in that they are exposed periodically in accordance with variations in water level due to tides. Still others are **sublittoral**; that is, they are constantly submerged and, depending on turbidity, may grow at depths as great as 100–200 m, the latter in clear tropical waters. Subaerial algae may be **edaphic** (growing in and on soil), epilithic, epiphytic, epizoic, and corticolous (growing on tree bark) and a few are parasitic (see p. 535).

The presence of algae on moist rocks, wood, living trees, and the surface of moist soil is readily observable, but the occurrence of algae beneath the surface of the soil is not so obvious. To educe evidence of their presence it is only necessary to moisten soil and to keep it under illumination or to introduce soil into sterile nutrient solutions

(p. 572) under illumination (Starr, 1973). Shtina (1974) recorded that 1410 species and forms of algae had been reported to be present in Russian soils.

Many of the blue-green algae, like certain bacteria, in soil fix gaseous nitrogen into a combined form and are thus of great importance in improving soil fertility (see p. 34). The role of other algae in the soil is less clear, although it is certain that they are involved in various types of relationships, either stimulatory or inhibitory, with other soil organisms (Parker and Bold, 1961). Bailey, et al. (1973) suggested, on the basis of their experiments, that algae are important in stabilizing and in improving the physical properties of soil by aggregating particles and by adding organic matter.

Some, but not all, subterranean algae have been proved to be facultatively heterotrophic in darkness (Parker, 1961, 1971D; Parker, et al., 1961), but the nature of the nutrition of the others remains an enigma.

Algae have been found in desert soils when they were not always obvious macroscopically (Chantanachat and Bold, 1962; Friedmann, et al., 1967; Friedmann, 1971), although they are important as primary producers (Friedmann and Ocampo, 1976). Friedmann and his associates found that although the macroenvironment may be hostile to algae, a surprising variety is present in the desert, their source of water probably being dew. These authors have classified desert soil algae as **endedaphic** (living in soil), **epidaphic** (living on the soil surface), **hypolithic** (on the lower surface of stones on soil)—and as rock algae, including **chasmolithic** algae (in rock fissures) and **endolithic** algae (rock penetrating). Trainor (1970) reported that algae survived in desiccated soils for more than 10 years in his laboratory. Booth (1941) reported that several filamentous blue-green algae are pioneers in plant succession on bare soil, where they form crusts that cut down on evaporation from the soil and also prevent erosion.

It is of interest that Brook (1968) reported the discoloration of roofs in the United States and Canada by certain blue-green and green algae, and the authors have observed discoloration of buildings by algae.

Corticolous or tree bark-inhabiting algae have been studied by Edwards (1968), Cox and Hightower (1972), and Wylie and Schlichting (1973), who reported a considerable number of algae from such habitats. A number of algae, both blue-green and green, grow as members of lichen associations (Ahmadjian, 1967); of these, *Trebouxia* is one of the most frequently encountered.

Some algae live **endozoically** in various protozoa, coelenterates, molluscs, and worms. *Chlorella*-like algae are present within *Paramecium*, *Hydra*, molluscs (Cooke, 1975), and some freshwater sponges. Others, zooxanthellae (division Pyrrhophycophyta), live in intimate association with corals, where their photosynthetic activity is of primary importance to the reef community (Benson and Muscatine, 1974). Trench (1971) demonstrated that ^{14}C-labeled products of algae rapidly appear in the lipids and proteins of the host animals; these extracellular products range between 20 and 50% of the algal photosynthate. Pearse (1974) demonstrated that sea anemones containing algae were phototactic, while those lacking them did not move to or from light of varying intensity. A rather comprehensive review of algal associations with animals has been prepared by D. Smith, et al., (1969). Much of the literature on endosymbionts of *Hydra* has been summarized by Pardy (1974). Other reports on this subject are those of Droop (1963), Karakashian and Karakashian (1965), Oschman (1967), and Trench (1971). Of considerable interest is the association of the green alga *Platymonas* with the flatworm *Convoluta roscoffensis;* the latter seemingly is dependent for its development on the presence within it of the alga (Oschman, 1966; Provasoli, et al., 1968). Muscatine, et al. (1974) reported that the alga releases amino acids to the animal that is not holozoic and entirely dependent on the alga. Muscatine, et al. (1975) have reviewed the host-symbiont interfaces in various algal-invertebrate associations. The cell walls of the symbionts may be modified, unmodified, or lacking. Several algae grow as endophytes within other plants. Here may be mentioned the blue-green alga *Anabaena azollae*, which grows within the water fern *Azolla*, and the species of *Anabaena* or *Nostoc*, which live within the thalli of the hornwort *Anthoceros* and in the roots of cycads (Grilli, 1974) and those of *Gunnera*, an angiosperm. Lewin and Cheng (1975) have reported the consistent association of a marine *Synechocystis* (a blue-green alga) with ascidians and its occurrence on mangrove roots. The organism is remarkable in that, although it is prokaryotic in organization, it lacks phycobilin pigments (Lewin, 1975) and contains *both* chlorophylls *a* and *b*. D. Smith (1973) has summarized our knowledge of some cases of algal-animal symbiosis.

In this discussion of algal habitats, mention must be made of some of the effects of the algae on their environment. It has been demonstrated that algae secrete a number of substances from their cells (Hellebust, 1974). For example, Aaronson, et al. (1971) have reported that the unicellular *Ochromonas* (p. 363) contributes DNA, RNA, carbohydrates, vitamins, and proteins (including enzymes) to the surrounding medium. Other evidences of such extracellular secretion are presented in the reports of Lefevre (1964), Nalewajko (1966), Fogg (1971), Nalewajko and Lean (1972), Huntsman (1972), Belly, et al. (1973), W. Smith (1974), and Walsby (1974A, B). That transfer of these substances between algae and algae and between algae and other organisms occurs has been demonstrated by Lange (1970), Harlin (1973), and Bauld and Brock (1974). It has also been demonstrated in laboratory cultures that stimulatory and inhibitory effects occur between algae and algae and among algae, bacteria, and fungi (Parker and Bold, 1961; Fitzgerald, 1969; and Kroes, 1971, among others). It is probable that similar mutualistic effects occur among algae and other organisms in nature. Some of the secreted substances have antibiotic effects (Burkholder, et al. 1960; Berland, et al., 1972; and Khaleafa, et al., 1975). Of particular interest are recent observations (Deig, et al., 1974) that liquid extracts from a number of common red seaweeds were effective in halting replication of herpes virus types I and II, the agents responsible for such ailments as cold sores and sores in the genital area.

Finally, a number of algae or their products are toxic to various animals (Gorham, 1964; Harris and James, 1974). The most notable in this respect are the blue-green algae (see p. 47) and dinoflagellates (p. 417), although one member of the Prymnesiophyceae (*Prymnesium parvum*) is responsible for the death of fish.

The question also arises regarding the distribution of algae and the vectors that accomplish it. In aquatic habitats, vectors such as tides, currents, and agitation by wind are obvious factors, as are movements of animals and of ships. Milliger, et al.

(1971) have reported that beetles are active in dispersing algae, having recovered species of 101 different algal genera from 23 species of beetles. Proctor (1966) and Atkinson (1972) have demonstrated the role of aquatic birds as vectors in algal distribution. Schlichting's (1970, 1971) reports suggest that aquatic algae might be transported by bursting bubbles and air currents.

Edaphic algae and those present in drying ditches and pond margins are distributed by air currents, some of the literature on this topic and in algal survival having been summarized by Schlichting (1964, 1970, 1974A, B). McElhenney, et al. (1962) and McGovern, et al. (1966) reported that some of such airborne algae were allergenic. In this connection, Bernstein and Safferman (1970) found viable algae in house dusts. R. Brown (1971) studied dispersal of airborne algae in Hawaii. Schwimmer and Schwimmer (1964) and Schlichting and James (1972) have reviewed the relation of algae to medicine.

Finally, among algae of extreme habitats must be mentioned those that thrive on long-persistent snows (Stein and Brooke, 1964; Stein and Amundsen, 1967; Kol, 1968; Thomas, 1972; Gerrath and Nicholls, 1974; Hoham, 1973; 1974A, B; 1975A, B; 1976; Hoham and Mullet, 1977; and Fjeringstad, et al., 1974) and, by contrast, those thermophilic algae that inhabit hot springs. The latter, mostly blue-green algae, grow at temperatures between 50 and 73°C (Bauld and Brock, 1974). Castenholz (1969) has reviewed the occurrence of these algae and their environment.

Place of Algae in the Plant Kingdom

In surveys of the plant kingdom, the algae are usually studied first for several reasons. First, the fossil record indicates that the most ancient organisms that contained chlorophyll *a* were probably blue-green algae[5] with a fossil record extending back possibly 3 billion years into the Precambrian (Schopf, 1970). There are suggestions that these were followed in later Precambrian times by the several groups of eukaryotic algae (Schopf and Blacic, 1971). Thus, the antiquity of algae in the history of living organisms argues for their primacy in the plant kingdom. A second reason for this primacy is the relative simplicity of organization of most algal plant bodies, as compared with other groups of plants, especially the vascular plants, although in this connection, the kelps (p. 317) suggest caution. A third reason is that algae illustrate so elegantly and with great clarity many important biological phenomena (e.g., sexual reproduction) that in other plants are complicated by secondary characteristics. Most botanists, accordingly, view the algae, especially the green algae, as likely progenitors for the remaining members of the plant kingdom (other than algal groups) because they are similar in pigmentation (having chlorophyll *a* and *b*) and in the nature of their storage reserves (starch).

Form of the Algal Plant Body

The form of the plant body of algae (Fig. 1.2) varies from the *relative* simplicity of the single cell to the complexity exhibited by the giant kelps and the rockweeds.

[5]Cyanochloronta, Chapter 2, p. 31; see, however, Schopf (1976.)

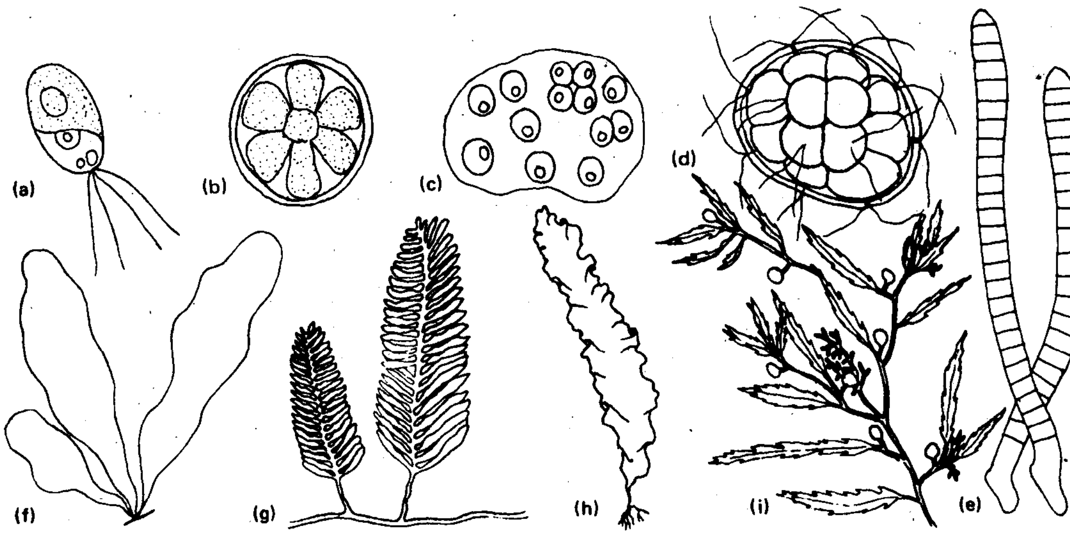

Fig. 1.2 Types of algal plant body, diagrammatic. (*a*) Unicellular, motile. (*b*) Unicellular, nonmotile. (*c*) Colonial, noncoenobic. (*d*) Colonial, coenobic. (*e*) Filamentous. (*f*) Membranous or foliar. (*g*) Tubular, coenocytic. (*h*) Blade-like, kelp. (*i*) Leafy axis.

While small algae like *Micromonas pusilla* (1 × 1.5 μm) and species of *Chlorella* (5–8 μm) are in the range of bacterial size, although eukaryotic, kelps, some of which are the largest of algae, may attain a length of 60 m.

Unicellular[6] (Fig. 1.2*a*, *b*), colonial (Fig. 1.2*c*, *d*), filamentous (Fig. 1.2*e*), membranous or foliose (Fig. 1.2*f*), and tubular (Fig. 1.2*g*) types of algal plant body occur, together with more highly differentiated blade-like types (Fig. 1.2*h*) and those that have rootlike organs, stems, and leaves (Fig. 1.2*i*), albeit these organs are lacking in vascular tissue, although phloem-like conducting cells occur in some (see p. 320). Two types of colonial algae are known. In the first (Fig. 1.2*c*), the aggregate is indefinite in cellular number, continues to grow by cell division of its components, and reproduces by fragmentation. The second type of colony, called a **coenobium** (Fig. 1.2*d*), has a fixed number of cells at its origin, and this number is not augmented during the individual's existence, even if some cells are accidentally lost or destroyed.

Growth of the various multicellular algae may be diffuse or generalized or it may be localized. In **generalized growth**, all of the cells may undergo division, so that the organism undergoes overall increase in size as in *Ulva*, the sea lettuce (Fig. 1.2*f*). In **localized growth**, cell multiplication is restricted to certain parts of the organism. Localized growth may be apical, basal, or intercalary. **Apical growth** is that which is restricted to the extremities of the organism or at its tips and occurs, for example, in *Cladophora* (Fig. 3.113), *Fucus* (Fig. 6.75), and *Dictyota* (Fig. 6.36), among other

[6]May be motile by means of flagella (see Fig. 3.2, p. 66) or nonmotile; the basal holdfast cell of some filamentous algae excluded.