Algal Ecology

Secondary article

Robert E DeWreede, *University of British Columbia, Vancouver, Canada*

Algal ecology is the study of the distribution and abundance of algae, of the environment in which they exist, and of the interactions between the algae and with other organisms.

Article Contents

Introduction

The eukaryotic algae are, in general, aquatic, photosynthetic organisms with a simple morphology (lacking the complex tissues of vascular plants), and with reproductive structures in which all cells form spores or gametes. Both unicellular and multicellular species exist, and they may or may not be flagellated. The distribution and abundance of algae is determined by physical factors such as light, temperature, salinity and water motion, and by biological factors such as herbivory and competition, and by complex interactions between these variables.

Habitats and Adaptations (Eukaryotic Algae)

Algae have been found in almost all environments where humans have been able to explore. In extreme environments such as hot thermal springs and deserts, prokaryotic 'algae' (now classified with the bacteria) are present. Less extreme environments, e.g. snow fields, underneath polar ice, cooler hot spring waters and aerial environments, support some eukaryotic algae.

Algae cope with environmental stress in many ways. Some green algae such as *Chlamydomonas nivalis* (Chlorophyta, snow algae) produce protective pigments to shield the chloroplasts from intense sunlight. The giant kelp *Macrocystis* (a brown alga; Heterokontophyta), which can attain lengths of over 30 m, has specialized tissues for moving energy-rich compounds from the light-saturated blades to the basal parts that may lack sufficient light for photosynthesis.

Even in less extreme habitats algae cope with a variety of physical stresses. In late summer in temporary ponds and small lakes desiccation may occur. Here, some members of the Volvocales (Chlorophyta) produce resistant stages, which can survive drying until water once more accumulates. In marine waters, high intertidal species of *Porphyra* (Rhodophyta; red algae), often dry out so much that they crumble to the touch; yet, once rewetted by the incoming tide, they resume normal metabolic processes within 20–30 minutes.

Biological factors are also important determinants of algal abundance. Some tropical algae such as species of *Halimeda* (Chlorophyta) produce toxic compounds which reduce grazing by fish (Paul and van Alstyne, 1988). Many of the larger brown algae produce phloroglucinol-like compounds which deter grazing by sea urchins and chitons (Paul, 1992). Some algae are thought to have evolved complex life histories in order to avoid excessive herbivory. For example, red algae such as *Mastocarpus* alternate between a bladed phase which produces gametes and a crustose phase producing spores. The crustose phase is more resistant to some herbivores such as chitons, but the blades are better suited for the dissemination of reproductive structures.

Marine versus Freshwater

Algae exist in freshwater and marine habitats, both in constantly submerged sites and in areas periodically covered by water. In freshwater habitats such periodic emersion may occur as a result of seasonal drought; in marine waters it is due to tidal cycles. Freshwater habitats are usually the domain of smaller algae, such as microscopic green algae, euglenophytes, diatoms, chrysophytes and dinoflagellates; brown and red algae are rare. In contrast, in marine habitats, larger algae (seaweeds) such as brown and red algae are very common, as are the larger green algae; euglenoids, diatoms, dinoflagellates and haptophytes can also be found there.

In green algae inhabiting freshwater, environmental cues such as falling water levels in a drying pond may initiate the production of soluble organic chemicals called pheromones by some individuals. These pheromones trigger the formation of reproductive structures and eventually gametes, and also attract flagellated sperm cells to the nonmotile egg. The product of sexual reproduction is often a resistant stage, a stage usually lacking in marine green algae.

Euglenophytes (Euglenophyta) may occur in ponds on agricultural lands, and as sand-dwelling species on some marine beaches. Euglenophytes have 'eyespots' which, in conjunction with a light-sensitive site at the base of one of the flagella, enable them to move in response to light direction.

Diatoms (Heterokontophyta) are single-celled algae with a wall of silica. There are two distinct diatom groups: pennate diatoms are generally symmetric about a central line and usually attached to a substratum; centric diatoms are symmetrical about a central point and usually free floating. Diatoms mostly lack flagella but movement can occur in those pennate diatoms that are attached to a substratum and possess a raphe. Centric diatoms are planktonic and are a major contributor to open ocean productivity.

Chrysophytes (Heterokontophyta) and dinoflagellates (Dinophyta) occur in both freshwater and marine habitats. Chrysophytes are flagellated unicells, often a golden-brown colour due to pigments such as xanthophylls and carotenoids. Some are the predominant species in nutrient-poor alpine lakes. Dinoflagellates are responsible (in part or entirely) for a multitude of phenomena, including bioluminescence, red tides, shellfish poisoning and ciguatera. Dinoflagellates also occur in corals, where they contribute significantly to their growth. The colour of dinoflagellates varies from greenish hues to shades of red, and many species lack chloroplasts. In these latter, feeding often occurs by ingesting small cells, or by liquefying the flesh of prey (see *Pfiesteria*, below).

Bioluminescence occurs in some dinoflagellates (e.g. *Noctiluca* and *Pyrocystis*) by means of the same chemicals (luciferan and luciferase) used by some other organisms with bioluminescent organs, such as fish (Sweeney, 1987). Bioluminescence may be a means of startling herbivores. Many dinoflagellates produce toxins, although the purpose of this is unclear since the immediate consumer of the toxic cell, e.g. a filter feeder such as a clam or mussel, is not affected.

As mentioned above, red algae (Rhodophyta) are rare in freshwater habitats, and common in marine ones. They have no flagella at any stage of their life history, and thus do not make use of pheromones in sexual reproduction. The life history of many red algae, with alternating gametophyte (haploid) and sporophyte (diploid) stages, is made more complex in many of its species by an additional life history stage, the carposporophyte which forms diploid spores. This is one way in which red algae apparently maximize the production of offspring whenever sexual fusion occurs. Many red algae also produce phycolloids (e.g. carrageenans and agars) as part of their cell walls. These chemicals are complex, sulfated, long-chain carbohydrates used widely in the food, chemical, and pharmaceutical industry. The function of phycocolloids in these algae is not known, but they may facilitate the retention of water during low tide, and discourage the settlement of epiphytes.

Brown algae are also rare in freshwater, but often are the most visible algae in temperate and tropical seas. Brown algae lack any unicellular individuals, except for the spores and gametes. Pheromones play an important role in promoting successful sexual reproduction for some brown algae. Chemical analyses of brown algal pheromones have shown that each algal species (e.g. kelps such as species of *Laminaria* and *Alaria*) secretes several pheromones (a ‘bouquet’; Maier and Müller, 1986) which are not always species specific. Hence a sperm cell of one species may be attracted by the pheromones secreted by the egg of another species. In this case, species specificity is ensured by proteins that coat the egg, and which must be ‘recognized’ by the sperm cell.

The haptophytes (Haptophyta) are a group of unicellular algae with two flagella and a haptonema (an extensible structure between the two flagella) which may facilitate feeding or attach the organism to a substrate. Some haptophytes form immense open ocean blooms.

Subaerial Algae

Subaerial algae may be found on leaves, tree trunks, muddy banks, on or beneath the surface of soil, and on brick walls. On walls and tree trunks these algae form dusty green streaks of colour difficult to distinguish from lichens and bryophytes. Species of the green algal family Chlorococcaceae, and specifically the genus *Chlorococcum*, are common in these habitats. Species of *Chlorococcum* are simple, round cells capable of reproducing both asexually (by zoospores) and sexually. Some species are remarkably resistant to desiccation, possibly due to their thick cell walls which form under dry conditions. A green soil alga, *Zygogonium ericetorum*, produces a purple pigment which colours the soils of heaths in parts of the UK.

Extreme Environments

Despite their fragility, algae also occur in extreme environments. One green algae that thrives in highly saline habitats, e.g. salt ponds (normal salinity in seawater ranges from 2.8 to 36‰; salt ponds may even form a brine (a saturated salt solution)), is *Dunaliella salina*. This species produces both β-carotene (a yellow-orange pigment), to shield the alga from excess light, and glycerol, which counteracts the osmotic potential of the highly saline water. Industrial production of this alga occurs, for example in Australia, where both the pigment and the glycerol are extracted from cultured *Dunaliella* (Borowitzka *et al.*, 1986).

Another extreme environment is found in mine tailings, or the areas affected by the drainage from some mine sites, which may contain high concentrations of copper, cadmium, iron, etc. In addition, acids may form if the tailings contain sulfated minerals; these acids in turn leach more heavy metals from the rock. Freshwater organisms in such environments suffer from both the low pH and the metals. Low pH does not affect marine waters as much, due to their buffering capacity, and heavy metals may flocculate by complexing with organic particles. One study of acid mine drainage (AMD), at Britannia Mines in British Columbia, Canada, reported that an area up to some 500 m on either side of a creek carrying the AMD was devoid of algae. Further away, some unicellular green algae appeared, then a multicellular green seaweed *Enteromorpha*, followed by the brown seaweed *Fucus*. Transplant studies of *Fucus* from nonaffected sites to sites impacted by AMD showed an increase in copper concentration from $<$ 500 ppm Cu (dry weight) at day 0 to 2400 ppm at day 40 (Marsden, 1999). The ability of *Enteromorpha* to tolerate some heavy metals was also noted in studies on AMD in Chile.

Some algae tolerate metals by avoiding them, e.g. the diatom *Achnanthes* sp., which grows on a gelatinous stalk and hence away from such high copper content materials as antifouling paints on ships. Other diatoms, *Navicula* and *Amphora*, apparently detoxify copper internally by complexing it with organic compounds. The brown alga *Ectocarpus siliculosus* has both copper tolerant and resistant strains; the resistant strains exclude more copper than nonresistant strains.

Thermal Springs

The location and abundance of algae in thermal springs are determined predominantly by temperature and dissolved mineral gradients. Higher water temperatures (over 60°C) favour cyanobacteria, whereas eukaryotic algae such as *Cyanidium caldarium* have upper temperature limits around 55–57°C (Darley, 1982). Tolerance to such high temperatures is due in part to the high melting point of algal membrane lipids, and the increased thermal stability of algal proteins. Diatoms also occur in hot springs, especially at temperatures between 30 and 40°C; *Achnanthes exigua* has a temperature maximum of 44°C, and a minimum at 10°C. At lower temperatures (20–30°C) the green alga *Zygogonium* may form purple bands of colour (due to an iron–tannin complex stored in vacuoles) in some springs. This species also prefers acid waters, tolerating a pH from 1 to 5.

Snow and Ice

Some algae make their home on snow and ice. Patches of red, orange, yellow and green colours on alpine snow are often caused by algae such as *Chlamydomonas nivalis*, and species of *Chloromonas* and *Chlainomonas*, all green algae (Hoham, 1980) growing in the meltwater on top of snow or ice. Similar to their salt-tolerant relative *Dunaliella*, many of these algae produce carotenoid pigments, e.g. astaxanthin, reducing photodegradation of the chlorophyll pigments. Snow algae are present as dormant zygotes for most of the year and only reproduce sexually in the meltwater. *C. nivalis* has a growth optimum at $<$ 10°C, and can photosynthesize at 0°C.

Zonation

Zonation refers to the existence of zones of organisms in marine intertidal and subtidal environments. Zonation is sometimes obvious in intertidal habitats, but often much less so subtidally. Various theories have been proposed to account for zonation, ranging from physical causes such as 'tide factors', to biological ones such as herbivory.

The tide factor hypothesis, and its variants, proposes that zonation results from differential tolerances of marine organisms to desiccation and temperature, generated by the rise and fall of the tides. Tidal patterns differ around the world, and can be diurnal, semidiurnal or mixed semidiurnal. Since the extent of the intertidal area covered by any tide can vary from day to day, especially where mixed semidiurnal tides occur (as in the Eastern Pacific), any given elevation may be exposed to air from minutes to hours on different days, and from hours to weeks over a month. Thus, elevations only a few centimetres higher than another site could be subjected to additional hours of exposure to air over a 24-hour period. However, the correlation between such 'breaks' in times of air exposure and actual zonal boundaries is poor.

Factors such as competition and herbivory have also been proposed to account for zonation. Since biological diversity increases in the lower intertidal zone (compared to the higher intertidal) biological factors may increase in importance in lower elevation sites. Experiments manipulating the numbers of herbivores or predators have shown that some of these have a significant impact on the extent of a particular zone. For example, removal of *Pisaster*, a predatory starfish, results in extending the lower limit of the zone of mussels (*Mytilus calfornianus*); the mussels in turn overgrow the algae, thus lowering the upper extent of the algal zone.

The physiological properties of algae clearly play a central role in their tolerance to desiccation. The ability of some *Porphyra* species to tolerate extreme desiccation has already been mentioned. A green alga, *Prasiola meridionalis*, which exists higher in the intertidal zone than *Porphyra*, can tolerate days of desiccation and high temperatures. Some species, e.g. *Fucus gardneri*, a brown seaweed found high in the intertidal zone, can photosynthesize in air (Quadir *et al*., 1979), although eventually nutrient stores are depleted, as these cannot be obtained from air. For some desiccated algae (e.g. *Fucus*, *Ulva* and *Gracilaria*), it has been found that nutrient uptake rates upon reimmersion in seawater are positively related to increasing elevation in the intertidal zone (Thomas *et al.*, 1987). Thus, some higher elevation algae not only can have a positive net photosynthesis in air but also are capable of replenishing nutrient pools quickly.

Subtidal zonation has also been described. The cause of zonation here has been attributed to at least two possible factors: the change in the composition of available light and the change in light intensity with increased depth. Because of the materials dissolved in seawater, red light is generally absorbed within the first few metres from the surface; blue light penetrates deepest. Since the different groups of algae have different pigments and thus utilize different portions of the visible spectrum optimally, one theory explained the alleged deep occurrence of red algae by their ability to make use of blue light, and the apparent absence of green algae at such depths by their inability to utilize this part of the spectrum as efficiently. The second theory attributed the presence of algae at deeper depths to their ability to simply absorb light, i.e. some algae were argued to function better or worse as a 'black body'. More recent experiments have supported the latter theory (Ramus, 1983). That light absorption capacity controls depth of occurrence was given further credence by more detailed studies of deep water collections; there is a much less clear pattern of zonation by pigment group than had been alleged, and deep algae can be green, red or brown.

Intertidal zone

The abundance and distribution of intertidal algae are determined by a mix of physical and biological factors, and by the physiological properties of the individual species of algae. Some of the physical factors that are important in this respect have been mentioned above, e.g. desiccation, temperature and salinity. Higher temperatures (27–30°C) can result in higher rates of respiration and a breakdown of photosynthetic mechanisms. Specifics depend of course on the individual species. Both increased and decreased salinity (relative to the normal range the species encounters, usually 25–36‰) also results in increased rates of respiration. Thus, the combination of higher temperatures and lower salinity can be particularly stressful to marine algae. Another physical factor is the effect of wave impact on seaweed distribution. The relationship between the drag and acceleration forces generated by moving water, and a seaweed's morphology, physical strength and the force of attachment, has been shown to affect thallus shape, surface area and abundance. Some seaweeds cope with the impact of increased water movement by reducing surface area, and increasing elasticity; for example, a species with wide blades, *Mazaella splendens* (a red seaweed), was replaced by a closely related species with narrower blades, *M. linearis*, in sites of relatively higher wave impact (Shaughnessy *et al.*, 1996).

Subtidal zone

Some of the same biological factors that influence the abundance and distribution of intertidal seaweeds also act in the subtidal zone, e.g. competition and herbivory. Competition may occur for substrate and light; common herbivores in the subtidal zone are sea urchins and, in tropical seas, also herbivorous fish. Sea urchin food preference studies have shown an avoidance of some algae, and a preference for others. Avoidance is usually attributed to comparative toughness and to unpalatable chemicals. For example, temperate water genera of brown algae such as *Agarum* and *Laminaria*, and tropical green seaweeds such as *Halimeda*, produce compounds (usually phlorotannins in brown algae and other complex organic compounds in *Halimeda*) which are strong deterrents to herbivores (Paul and van Alstyne, 1988). Some of these algae are recognized by fish as unpalatable; this benefits adjacent palatable species of algae which are also avoided by grazing fish; an example of a positive interaction. Extensive studies of *Halimeda* have shown that this species has a mix of stored antiherbivore compounds, and that the act of herbivory can result in the conversion of a less toxic compound into a more toxic one. It is not clear whether herbivory itself induces the formation of antiherbivore compounds. Studies on *Fucus* indicate that such compounds do form in response to herbivory (van Alstyne, 1988), but similar studies using other algae have not found this to be the case (Steinberg, 1994).

As already indicated, different physical factors differ in ecological importance in the intertidal and subtidal zones. Desiccation is absent in the subtidal, and the marked variations in salinity and temperature that can occur in the intertidal zone are much less likely to occur subtidally. Light plays a role in limiting the depth at which different species of algae occur in the subtidal, and excess light limits some intertidal seaweeds. In the shallow subtidal, wave action is important, as it is in the intertidal zone.

Blooms

Algal blooms are concentrations of (usually) unicellular algae, well above their normal concentrations (e.g. 210 000 cells L^{-1} in a bloom of the dinoflagellate *Gymnodinium mikimotoi*). Blooms may consist of primarily a single species of algae, or of several; some blooms consist of different species over time as species succession occurs. Bloom-forming species are diverse, e.g. *Gyrodinium* spp., *Alexandrium* spp., *Gonyaulax* spp., *Gymnodinium* spp. (dinoflagellates), *Heterosigma akashiwo* (Raphidophyta), *Emiliana huxleyi* and *Prymnesium* (*parvum*?)

(Haptophyta), *Pseudonitzschia australis* (Bacillariophyceae), and *Aureococcus anaphagefferens* (Chrysophyceae). Conditions that favour the formation of blooms are relatively calm, clear waters, and increasing light and nutrient levels. Such conditions are more likely in springtime, following the activities of winter and early spring storms.

Blooms are often described on the basis of colour. White blooms caused by *Emiliana huxleyi* have occurred over immense areas of the North Atlantic south of Iceland and elsewhere (van den Hoek *et al*., 1995). The white colour is caused by the alga's calcium carbonate scales, which have also been identified as an important sink for carbon dioxide. Some dinoflagellates, e.g. *Gymnodinium* sp., create olive-green blooms, and produce a toxin that causes stinging in the eyes and respiratory discomfort. Other dinoflagellates, e.g. *Gonyaulax catenella* and *G. tamarensis*, are responsible in part for 'red tides', and various species cause paralytic or diarrhoetic shellfish poisoning. Ciguatera (the accumulation of toxins by fish) is also attributed to dinoflagellates, in this case a species associated with tropical algae eaten by herbivorous fish. Brown tides are often the result of diatom blooms; domoic acid, a toxic chemical produced by *Pseudonitzschia australis*, has been a threat in the northeastern USA, where it was responsible for brain damage and human deaths. Apart from direct effects on humans, algal blooms also cause immense harm to shellfish and fin-fish aquaculture operations. Some diatom species (e.g. *Chaetoceros* sp.) damage the gills of fish with their silicon spines. In 1998, blooms of the dinoflagellate *Gymnodinium mikimotoi* resulted in the death of at least 1500 tonnes of fish in Hong Kong, about half the amount of fish produced there in 1997. Estimates of financial losses ranged from US$10.3 million (government estimate) to US$30 million (farmer's estimate) (Lu and Hodgkiss, 1999).

Harmful blooms are seen more frequently today, and in places where they have been rarely seen in the past. Factors held responsible for this are increased awareness, eutrophication from agriculture, transfer of toxic organisms around the globe by ship's ballast water, and possibly increased run-off due to deforestation. Desertification in the Sahara may be contributing to blooms of *Emiliana huxleyi* in the Mediterranean, as desert dust provides minerals required by this algae.

Fish-eating Dinoflagellates (*Pfiesteria*)

The 'cell from Hell' is the term that has been used to describe the dinoflagellate *Pfiesteria piscicida*. In 1991 it is estimated that at least a billion (1×10^9) fish were lost on the east coast of the USA, and in 1995 perhaps 10 million, due to *Pfiesteria*. The toxin it produces is lethal to fish (causing severe lesions and death) and to humans (causing nausea and memory loss so severe it mimics Alzheimer disease).

Pfiesteria has an unusually complex life history of some 24 different stages varying from a cyst which lies on the mud, to amoeboid stages, predatory forms which release toxins that can result in ulcerating sores on fish, and other forms capable of consuming the flesh of the dead fish (Burkholder and Glasgow, 1997). An added feature is that one of the stages, a nontoxic zoospore, grazes on other algae and is able to retain the prey chloroplasts for some time as functional organelles. Thus, this normally nonphotosynthetic organism can have at least one photosynthetic stage, apparently making it less dependent on prey (Lewitus *et al*., 1999). Actions have been initiated to reduce effluents which, it is hoped, will reduce the incidence of such blooms in areas such as Chesapeake Bay, USA.

References

Borowitzka LJ, Moulton TP and Borowitzka MA (1986) Salinity and the commercial production of beta-carotene from *Dunaliella salina*. In: Barclay WR and McIntosh RP (eds) *Algal Biomass Technologies, an Interdisciplinary Perspective*. *Nova Hedwigia* **83**: 224–229.

Burkholder JM and Glasgow HB Jr (1997) The ichthyotoxic dinoflagellate, *Pfiesteria piscicida*: behaviour, impacts, and environmental controls. *Limnology and Oceanography* **42**: 1052–1075.

Darley WM (1982) Algal Biology: A Physiological Approach. In: Wilkinson JF (ed) *Basic Microbiology*. Oxford: Blackwell Science.

Hoham RW (1980) Unicellular chlorophytes – snow algae. In: Cox ER (ed) *Phytoflagellates*, pp. 61–84. Amsterdam: Elsevier.

Lewitus AJ, Glasgow HB Jr and Burkholder JM (1999) Kleptoplastidy in the toxic dinoflagellate *Pfiesteria piscicida* (Dinophyceae). *Journal of Phycology* **35**: 303–312.

Lu Songhui and Hodgkiss IJ (1999) A *Gymnodinium mikimotoi* occurrence spring 1998. *Harmful Algae News* **18**: 2-3.

Maier I and Müller DG (1986) Sexual pheromones in algae. *Biological Bulletin (Woods Hole)* **170**: 145–175.

Marsden AD (1999) The effects of acid mine drainage at Britannia Beach, B.C. on *Fucus gardneri* and associated intertidal algae. MSc thesis, Department of Botany, The University of British Columbia, Vancouver, Canada.

Paul VJ (1992) *Ecological Roles of Marine Natural Products*. Ithaca, NY: Comstock Publishing.

Paul VJ and van Alstyne K (1988) Antiherbivore defenses in *Halimeda*. *Proceedings of the 6th International Coral Reef Symposium*, pp. 133–138. Australia.

Quadir A, Harrison PJ and DeWreede RE (1979) The effects of emergence and submergence on the photosynthesis and respiration of marine macrophytes. *Phycologia* **18**: 83–88.

Ramus J (1983) A physiological test of the theory of complementary chromatic adaptation. II. Brown, green, and red seaweeds. *Journal of Phycology* **19**: 173–178.

Shaughnessy FJ, DeWreede RE and Bell EC (1996) Consequences of morphology and tissue strength to blade survivorship of two closely related Rhodophyta species. *Marine Ecology Progress Series* **136**: 257–266.

Steinberg PD (1994) Lack of short-term induction of phlorotannins in the Australian brown algae *Sargassum vestitum* and *Ecklonia radiata*. *Marine Ecology Progress Series* **121**: 129–133.

Sweeney BM (1987) Bioluminescence and circadian rhythms. In: Taylor FJR (ed) *The Biology of Dinoflagellates*, pp. 269–281. Oxford: Blackwell.

Thomas TE, Turpin DH and Harrison PJ (1987) Desiccation enhanced nitrogen uptake rates in intertidal seaweeds. *Marine Biology* **94**: 293–298.

van Alstyne KL (1988) Herbivore grazing increases polyphenolic defenses in the intertidal brown algae *Fucus distichus*. *Ecology* **96**: 655–663.

van den Hoek C, Mann DG and Jahns HM (1995) *Algae: An Introduction to Phycology*. Cambridge: Cambridge University Press.

Further Reading

Anderson DM (1995) Toxic red tides and harmful algal blooms: a practical challenge in coastal oceanography. *Review of Geophysics* **33** (suppl.): 1189–1200.

Kingsford M and Battershill C (eds) (1998) *Studying Temperate Marine Environments: A Handbook for Ecologists*. Christchurch, New Zealand: Canterbury University Press.

Van den Hoek C, Mann DG and Jahns HM (1995) *Algae: An Introduction to Phycology*. Cambridge: Cambridge University Press.