Algal Ecology

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.

Harmful algae are not a homogenous group of organisms that can be classified as a taxonomic unit. In fact, algae are not even a natural taxonomic grouping. We define eukaryotic algae as organisms that have a permanent plastid, chlorophyll-a as their primary photosynthetic pigment and that lack a sterile covering of cells around the reproductive cells (Lee 1999) and "prokaryotic algae" as cyanobacteria (blue-green algae). The taxa considered in this chapter are primarily the species listed by th Intergovernmental Oceanographic Commission (IOC). To be consistent with the list, only planktonic species are included here. It is sometimes hard to delineate species that are typically harmful from those that are not. Therefore, we use genera as the primary taxonomic unit and combine closely related species where their harmful status is uncertain. The taxonomy of harmful algae has recently been reviewed in several chapters in the volume edited by Hallegraeff et al. (2003). The present chapter focuses on molecular taxonomy, especially the relationships between observed morphological features and genetic characters. The molecular taxonomy of all harmful algae cannot be covered in this chapter, so we highlight examples from three main groups, the dinoflagellates, cyanobacteria, and diatoms. Molecular data for these organisms and other species can be retrieved from www.ncbi.nlm. nih.gov.

Analysis of molecular sequences can be used to resolve the evolutionary relationships and taxonomic position for species that have few distinct morphological characteristics. Since the pioneering work on bacteria by Woese (1987), the analysis of ribosomal RNA genes has revolutionized our understanding of the phylogeny and taxonomy of morphologically depauperate organisms. The small subunit ribosomal RNA gene (ssu rDNA) is still the most commonly used sequence for molecular taxonomy: here we will use the term 18S rDNA for the eukaryotic and 16S rDNA for the prokaryotic ssu rDNA, respectively. The sequence for the gene encoding of the large subunit ribosomal RNAs from eukaryotes is collectively called 28S rDNA here. The 28S rDNA has higher information content than the 18S rDNA and is therefore preferred for many taxonomic studies. The 5.8S rDNA is located in the region between the 18S and 28S rDNAs. There are two apparently non-coding regions that are transcribed together with the three rRNA encoding genes; they are called intergenic transcribed spacers (ITS). The ITS regions are generally less conserved and thus allow better resolution between closely related species, or different strains in one species, than do either the 18S or the 28S rDNA, and they are often used at the population level. There are other genes or loci that can be useful in taxonomy. Comparison of protein coding genes can provide valuable information, but generally only if they are homologous genes, i.e., they share the same evolutionary history. Comparisons of different genes, and the use of different methods of analysis, can give conflicting results (see for example Taylor 2004) and some loci may be inappropriate for use as taxonomic markers, for example, genes encoding proteins under strong directional selection.When distinguishing taxa among algae, plastid gene sequences have been used less than has been the case for higher plants. The pigmentation of the plastid, however, has been used extensively to classify algae and is still considered a valid character (Daugbjerg et al. 2000; de Salas et al. 2003). One complication with using plastid sequences in one major group of harmful algae, the dinoflagellates, is the high evolutionary rate in peridinin-containing plastids (Zhang et al. 2000), which makes it difficult to align sequences and thus to perform valid phylogenetic analyses. Another complication is that plastid sequences, e.g., both 16S rDNA and the protein-coding *psbA* gene sequences, from different species can be identical (Takishita et al. 2002).

Habitats and Adaptations (Eukaryotic Algae

Algae have been found in almost all environments wherehumans have been able to explore. In extreme environmentssuch as hot thermal springs and deserts, prokaryotic‘algae’ (now classified with the bacteria) are present. Lessextreme environments, e.g. snow fields, underneath polarice, cooler hot spring waters and aerial environments,support some eukaryotic algae.Algae cope with environmental stress in many ways.

Some green algae such as Chlamydomonasnivalis (Chlorophyta, snow algae) produce protective pigments to shieldthe chloroplasts from intense sunlight. The giant kelp Macrocystis (a brown alga; Heterokontophyta), which canattain lengths of over 30 m, has specialized tissues formoving energy-rich compounds from the light-saturated blades to the basal parts that may lack sufficient light forphotosynthesis.Even in less extreme habitats algae cope with a variety ofphysical stresses. In late summer in temporary ponds andsmall 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 theycrumble to the touch; yet, once rewetted by the incomingtide, they resume normal metabolic processes within 20]30 minutes.

Biological factors are also important determinants ofalgal abundance. Some tropical algae such as species of Halimeda (Chlorophyta) produce toxic compounds which reduce grazing by fish (Paul and van Alstyne, 1988). Manyof the larger brown algae produce phloroglucinol-likecompounds which deter grazing by sea urchins and chitons(Paul, 1992). Some algae are thought to have evolvedcomplex life histories in order to avoid excessive herbivory.

For example, red algae such as Mastocarpus alternatebetween a bladed phase which produces gametes and acrustose phase producing spores. The crustose phase ismore resistant to some herbivores such as chitons, but theblades are better suited for the dissemination of reproductivestructures.

Marine versus Freshwater

Algae exist in freshwater and marine habitats, both inconstantly submerged sites and in areas periodicallycovered by water. In freshwater habitats such periodicemersion may occur as a result of seasonal drought; inmarine waters it is due to tidal cycles. Freshwater habitatsare usually the domain of smaller algae, such as microscopicgreen algae, euglenophytes, diatoms, chrysophytesand dinoflagellates; brown and red algae are rare. Incontrast, in marine habitats, larger algae (seaweeds) suchas brown and red algae are very common, as are the largergreen algae; euglenoids, diatoms, dinoflagellates andhaptophytes can also be found there.In green algae inhabiting freshwater, environmental cuessuch as falling water levels in a drying pond may initiate theproduction of soluble organic chemicals called pheromonesby some individuals. These pheromones trigger the formationof reproductive structures and eventually gametes, andalso attract flagellated sperm cells to the nonmotile egg. Theproduct of sexual reproduction is often a resistant stage, astage usually lacking in marine green algae.Euglenophytes (Euglenophyta) may occur in ponds onagricultural lands, and as sand-dwelling species on somemarine beaches. Euglenophytes have ‘eyespots’ which, inconjunction 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 centralline and usually attached to a substratum; centric diatomsare symmetrical about a central point and usually freefloating. Diatoms mostly lack flagella but movement canoccur in those pennate diatoms that are attached to asubstratum 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 goldenbrowncolour due to pigments such as xanthophylls andcarotenoids. Some are the predominant species in nutrientpooralpine lakes. Dinoflagellates are responsible (in partor entirely) for a multitude of phenomena, including bioluminescence, red tides, shellfish poisoning and ciguatera.

Dinoflagellates also occur in corals, where they contributesignificantly to their growth. The colour ofdinoflagellates varies from greenish hues to shades of red,and many species lack chloroplasts. In these latter, feedingoften occurs by ingesting small cells, or by liquefying theflesh 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 organismswith bioluminescent organs, such as fish (Sweeney, 1987).

Bioluminescence may be a means of startling herbivores.Many dinoflagellates produce toxins, although the purposeof this is unclear since the immediate consumer of thetoxic cell, e.g. a filter feeder such as a clam or mussel, is notaffected.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 thusdo 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 anadditional life history stage, the carposporophyte whichforms diploid spores. This is one way in which red algaeapparently maximize the production of offspring wheneversexual fusion occurs. Many red algae also produce phycolloids (e.g. carrageenans and agars) as part of their cell walls. These chemicals are complex, sulfated, longchaincarbohydrates used widely in the food, chemical, and pharmaceutical industry. The function of phycocolloids inthese algae is not known, but they may facilitate the retention of water during low tide, and discourage thesettlement of epiphytes.Brown algae are also rare in freshwater, but often are themost visible algae in temperate and tropical seas. Brownalgae lack any unicellular individuals, except for the sporesand gametes. Pheromones play an important role inpromoting successful sexual reproduction for some brownalgae. 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 Mu¨ller, 1986) which are notalways species specific. Hence a sperm cell of one speciesmay be attracted by the pheromones secreted by the egg ofanother species. In this case, species specificity is ensuredby proteins that coat the egg, and which must be‘recognized’ by the sperm cell. The haptophytes (Haptophyta) are a group of unicellularalgae with two flagella and a haptonema (anextensible structure between the two flagella) which mayfacilitate 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 lichensand 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 areremarkably resistant to desiccation, possibly due to theirthick 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 theUK.

Extreme Environments

Despite their fragility, algae also occur in extremeenvironments. One green algae that thrives in highly salinehabitats, e.g. salt ponds (normal salinity in seawater rangesfrom 2.8 to 36%; salt ponds may even form a brine (a saturated salt solution)), is *Dunaliella salina*. This species produces both b-carotene (a yellow-orange pigment), to shield the alga from excess light, and glycerol, which counteracts the osmotic potential of the highly salinewater. Industrial production of this alga occurs, for example in Australia, where both the pigment andthe 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 theAlgal Ecologytailings contain sulfated minerals; these acids in turn leachmore heavy metals from the rock. Freshwater organisms insuch environments suffer from both the low pH and themetals. Low pH does not affect marine waters as much, dueto their buffering capacity, and heavy metals mayflocculate by complexing with organic particles. One studyof acid mine drainage (AMD), at Britannia Mines inBritish Columbia, Canada, reported that an area up tosome 500mon 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 non-affected sites to sitesimpacted by AMD showed an increase in copperconcentration from 5 500 ppm Cu (dry weight) at day 0to 2400 ppm at day 40 (Marsden, 1999). The ability of *Enteromorpha* to tolerate some heavy metals was alsonoted in studies on AMD in Chile.Some algae tolerate metals by avoiding them, e.g. the diatom *Achnanthes* sp., which grows on a gelatinous stalkand 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 andresistant strains; the resistant strains exclude more copperthan nonresistant strains.

Thermal Springs

The location and abundance of algae in thermal springs are determined predominantly by temperature and dissolvedmineral gradients. Higher water temperatures (over 608C) favour cyanobacteria, whereas eukaryotic algae such as Cyanidium caldarium have upper temperature limitsaround 55]578C (Darley, 1982). Tolerance to such hightemperatures is due in part to the high melting point ofalgal membrane lipids, and the increased thermal stabilityof algal proteins. Diatoms also occur in hot springs, especially at temperatures between 30 and 408C;

Achnanthes exigua has a temperature maximum of 448C, and aminimum at 108C. At lower temperatures (20]308C) the green alga *Zygogonium* may form purple bands of colour (due to an iron]tannin complex stored in vacuoles) in somesprings. This species also prefers acid waters, tolerating apH from 1 to 5.

Snow and Ice

Some algae make their home on snow and ice. Patches ofred, orange, yellow and green colours on alpine snow areoften 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 orice. Similar to their salt-tolerant relative Dunaliella, many of these algae produce carotenoid pigments, e.g. *astaxanthin*, reducing photodegradation of the chlorophyllpigments. Snow algae are present as dormant zygotes formost of the year and only reproduce sexually in themeltwater. *C. nivalis* has a growth optimum at 5108C,and can photosynthesize at 08C.

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 muchless so subtidally. Various theories have been proposed toaccount 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 bythe rise and fall of the tides. Tidal patterns differ around theworld, and can be diurnal, semidiurnal or mixed semidiurnal.Since the extent of the intertidal area covered byany tide can vary from day to day, especially where mixedsemidiurnal tides occur (as in the Eastern Pacific), anygiven elevation may be exposed to air from minutes to hours on different days, and from hours to weeks over amonth. Thus, elevations only a few centimetres higher thananother site could be subjected to additional hours ofexposure to air over a 24-hour period. However, thecorrelation between such ‘breaks’ in times of air exposureand actual zonal boundaries is poor.Factors such as competition and herbivory have alsobeen proposed to account for zonation. Since biologicaldiversity increases in the lower intertidal zone (comparedto the higher intertidal) biological factors may increase inimportance in lower elevation sites. Experiments manipulatingthe numbers of herbivores or predators have shown that some of these have a significant impact on the extent ofa particular zone. For example, removal of Pisaster, apredatory starfish, results in extending the lower limit of the zone of mussels (Mytiluscalfornianus); the mussels inturn overgrow the algae, thus lowering the upper extent ofthe algal zone.The physiological properties of algae clearly play acentral role in their tolerance to desiccation. The ability ofsome

Porphyra species to tolerate extreme desiccation hasalready been mentioned. A green alga, *Prasiolameri dionalis*, which exists higher in the intertidal zone than Porphyra, can tolerate days of desiccation and hightemperatures. Some species, e.g. *Fucus gardneri*, brown seaweed found high in the intertidal zone, can photosynthesizein air (Quadir et al., 1979), although eventuallynutrient stores are depleted, as these cannot be obtainedfrom 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 toincreasing elevation in the intertidal zone (Thomas et al.,1987). Thus, some higher elevation algae not only can havea positive net photosynthesis in air but also are capable of replenishing nutrient pools quickly. Subtidal zonation has also been described. The cause ofzonation here has been attributed to at least two possible factors: the change in the composition of available lightand the change in light intensity with increased depth.Because of the materials dissolved in seawater, red light isgenerally absorbed within the first few metres from the surface; blue light penetrates deepest. Since the differentgroups of algae have different pigments and thus utilizedifferent portions of the visible spectrum optimally, onetheory explained the alleged deep occurrence of red algae by their ability to make use of blue light, and the apparentabsence of green algae at such depths by their inability toutilize this part of the spectrum as efficiently. The secondtheory attributed the presence of algae at deeper depths totheir ability to simply absorb light, i.e. some algae weereargued to function better or worse as a ‘black body’. Morerecent experiments have supported the latter theory (Ramus, 1983). That light absorption capacity controlsdepth of occurrence was given further credence by moredetailed studies of deep water collections; there is a muchless clear pattern of zonation by pigment group than hadbeen 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 inthis respect have been mentioned above, e.g. desiccation, temperature and salinity. Higher temperatures (27]308C) can result in higher rates of respiration and a breakdown ofphotosynthetic mechanisms. Specifics depend of course onthe individual species. Both increased and decreased salinity (relative to the normal range the species encounters, usually 25]36%) also results in increased rates ofrespiration. Thus, the combination of higher temperaturesand lower salinity can be particularly stressful to marine algae. Another physical factor is the effect of wave impacton seaweed distribution. The relationship between the dragand acceleration forces generated by moving water, and aseaweed’s morphology, physical strength and the force ofattachment, has been shown to affect thallus shape, surface area and abundance. Some seaweeds cope with the impactof increased water movement by reducing surface area,and increasing elasticity; for example, a species with wide blades, Mazaellasplendens (a red seaweed), wasreplaced 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 theabundance and distribution of intertidal seaweeds also actin 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, intropical seas, also herbivorous fish. Sea urchin foodpreference studies have shown an avoidance of some algae,and a preference for others. Avoidance is usually attributedto 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 *phlorotanninsin* brown algae and other complex organic compounds in *Halimeda*) which are strong deterrents toherbivores (Paul and van Alstyne, 1988). Some of these algae are recognized by fish as unpalatable; this benefitsadjacent palatable species of algae which are also avoidedby grazing fish;

an example of a positive interaction. Extensive studies of *Halimeda* have shown that this specieshas 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 compoundsdo form in response to herbivory (van Alstyne,1988), but similar studies using other algae have not foundthis to be the case (Steinberg, 1994).As already indicated, different physical factors differ inecological 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 theintertidal 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, waveaction is important, as it is in the intertidal zone.