

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), *Emiliania huxleyi* and *Prymnesium* (parvum?) (Haptophyta), *Pseudonitzschia australis* (Bacillariophyceae), and *Aureococcus anophagefferens* (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 *Emiliania 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 diarrhoeic 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 *Emiliania 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 sometime as functional organelles. Thus, this normally non photosynthetic 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.

Amphidinium, Cochlodinium, Gyrodinium

Members of *Gyrodinium* are heterotrophic with a large displacement of the girdle. The rDNA-ITS regions from species of this genus form a monophyletic cluster (Shao et al. 2004), and 28S rDNA sequences confirm this (Hansen and Daugbjerg 2004). Similarly, the single sequence available from *Cochlodinium*, for the toxic species *C. polykrikoides*, suggests that it forms a distinct genus, with high bootstrap support (Shao et al. 2004). The genus *Amphidinium* comprises naked benthic species. In a recent study, 12 *Amphidinium* species were subject to phylogenetic analyses based on 28S rDNA sequences. This analysis revealed that *Amphidinium* species with minute left-deflected epicones were monophyletic, including the type species *A. operculatum* (Jørgensen et al. 2004). The epicone shape and size was the only morphological character that united the *Amphidinium sensu stricto* species. The morphology of the plastids and pyrenoids were not useful characters. In this analysis, *A. operculatum* appears on a long branch, suggesting that it is distantly related to the other species. The distinct nature of *A. operculatum* was confirmed by Murray et al. (2004) who further showed insignificant variation

between strains: *A. carterae* and *A. massartii*, on the other hand, showed a high variation between strains.

Cyanobacteria (Blue-Green Algae)

Anabaena*, *Aphanizomenon*, *Nodularia

Large populations of species of *Anabaena* and *Aphanizomenon* are found in both fresh and brackish waters, including the Baltic Sea. Several species of *Anabaena* seem to be present in the Baltic Sea, with *A. lemmermannii* typically found in the open sea, and *A. inequalis* in near-shore areas where the influence of land-derived nutrients is more marked. The sequences from the regulatory *hetR* gene from these two species have been compared (Janson and Graneli 2002): one isolate of *A. lemmermannii* was distinct from two isolates of *A. inequalis*. Even though the two isolates of *A. inequalis* were morphologically indistinguishable, they diverged at the *hetR* locus. As part of the same study *Aphanizomenon* spp. were analyzed: on the basis of morphological characters, they were divided into the variants *Aph. flos-aquae* var *flos-aquae* and var *klebahnii*. These two variants were separated by 2.5 % difference in sequence at *hetR*, and the Baltic Sea *Aphanizomenon* sp. was 0.2 % different from *Aph. flos-aquae* var *klebahnii*. The morphological characters used to separate the variants were cell sizes and shape of the colony. The Baltic Sea *Aphanizomenon* sp. would fall under

Aph. flos-aquae var *klebahnii* using these criteria. These data demonstrate that diversity within the genera *Anabaena* and *Aphanizomenon* could be underestimated if only morphological characters are used. The hidden diversity suggested by *hetR* sequences is supported by a study of *Aphanizomenon flos-aquae* var *klebahnii* isolates from a Finnish lake, where several different rDNA-ITS types were identified (Laamanen et al.

2002). In this study, the rDNA-ITS diversity was somewhat lower in the Baltic

Sea *Aphanizomenon* samples than in the lake, but there was no detectable difference in morphology: this is consistent with the study of Barker et al. (2000a) who found no sequence variation at the *cpcBA*-IGS locus in samples of *Aphanizomenon* collected directly from the water column in the Baltic Sea. *Nodularia* is a genus of heterocyst-forming cyanobacteria, some members of which can form extensive blooms, particularly in brackish waters.

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Baltic Sea is one area where such blooms occur. Three morphologically defined species have been described: *N. baltica*, *N. litorea*, and *N. spumigena*. Several studies suggest that all toxic strains belong to the same cluster or species, the bloom-forming planktonic *N. spumigena*, as shown by 16S rDNA data and

sequence variation in several protein-coding genes and non-coding spacer regions (Barker et al. 1999; Bolch et al. 1999; Lehtimäki et al. 2000; Moffitt et al. 2001; Janson and Graneli 2002). Most studies point to zero, or a very low, variation within the 16S rRNA gene, with the exception of Moffitt et al. (2001) where significant variation was detected within the 16S rRNA gene, even though strains found to be polymorphic at this locus were indistinct at the more variable *cpcBA*-IGS (see Bolch et al. 1999). The *cpcBA*-IGS, rDNAITS and *gvpA*-IGS were analyzed in 13 strains of *N. litorea*/*N. spumigena* from the Baltic Sea (Barker et al. 1999) where it was reported that phenotypic groupings based on cell sizes were incongruent with the grouping of genotypes, calling into question the validity of *N. litorea*. A subsequent population genetic analysis of a large number of Baltic Sea *Nodularia* filaments supports the occurrence of a single planktonic species, *N. spumigena* (Barker et al. 2000b; Hayes et al. 2002)

Microcystis

Microcystis is a genus of unicellular colony-forming cyanobacteria where the taxonomy is still in a state of considerable flux and confusion. The *Microcystis aeruginosa* species complex dominates in many freshwater systems in both temperate and tropical regions. The life cycle of this species includes both pelagic and benthic

stages in temperate regions, with the pelagic stage predominating in the summer. As would be expected for such a globally important toxic organism, *Microcystis* has been subject to several studies seeking to reconcile its molecular and morphological taxonomy. The shape of the colony has been used extensively to classify *Microcystis* species in many taxonomic treatments. However, it now appears that this may be a poor character to define species, and, as a consequence of this, five species of *Microcystis* previously distinguished by their colony shape have been merged into *M. aeruginosa* (Otsuka et al. 2001). Another factor is the spatial distribution of cells in the water, in that a region or depth can be specifically occupied by genetically distinct strains as seen for marine unicellular cyanobacteria (Rocap et al. 2002). In a study of a French lake using rDNA-ITS sequences, it was shown that there was no distinct spatial clustering of populations (Humbert et al.

2005). The production of the toxin microcystin is an example of where the use of genetic analysis has not always been helpful in accurately predicting the distribution of a specific phenotypic character. Some studies show that strains that produce microcystin differ in rDNA-ITS sequence from non-toxic strains (Janse et al. 2004). This is in contrast to earlier findings using the *cpcBA*-IGS as

a high-resolution marker (Tillett et al. 2001). In practice, it is only the presence of the toxin-associated genes, e.g., *mcyAB* that is likely to provide an unambiguous indication of toxic potential.

General Ecology

The greatest diversity and abundance of harmful dinoflagellates occurs in estuaries and coastal marine waters, coinciding with higher nutrient supplies from land sources and/or upwelling (Taylor and Pollinger 1987; Graham and Wilcox 2000). These organisms tend to be large in comparison to other phytoplankton, averaging about 45 μm on the major cell axis (estimated from Hallegraeff 2002), although some can be as small as $\sim 5\text{--}7 \mu\text{m}$. Their size and higher cellular surface-to-volume ratios generally result in lower affinities for dissolved nutrients than smaller taxa, and may have selected for mixotrophy in photosynthetic species (Smayda 1997). Nevertheless, many species are capable of rapid growth. Review of the experimental literature revealed that contrary to previous generalizations, only 15 % of larger free-living harmful species had growth rates $>1.0 \text{ day}^{-1}$; the fastest reported, *Prorocentrum minimum*, was 3.54 day^{-1} (Smayda 1997). As a survival mechanism, some species rapidly form temporary cysts in response to sudden adverse conditions, as well as other types of cysts with resistant coverings as part of their sexual and asexual life

histories (see synopsis in Parrow and Burkholder 2003). The larger size of many species (and in some cases, production of toxins and other bioactive substances) may deter various predators. Nevertheless, grazers are a major influence on the ecology of harmful dinoflagellates (Chaps. 20, 22, and 27, this book).