21 Pathogens of Harmful Microalgae

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21.1 Introduction

Pathogens are any organisms that cause disease to other living organisms. Parasitism is an interspecific interaction where one species (the parasite) spends the whole or part of its life on or inside cells and tissues of another living organism (the host), from where it derives most of its food. Parasites that cause disease to their hosts are, by definition, pathogens. Although infection of metazoans by other metazoans and protists are the more frequently studied, there are interactions where both host and parasite are single-celled organisms. Here we describe such interactions involving microalgae as hosts. The aim of this chapter is to review the current status of research on pathogens of harmful microalgae and present future perspectives within the field. Pathogens with the ability to impair and kill microalgae include viruses, bacteria, fungi and a number of protists (see reviews by Elbrächter and Schnepf 1998; Brussaard 2004; Park et al. 2004; Mayali and Azam 2004; Ibelings et al. 2004). Valuable information exists from non-harmful microalgal hosts, and these studies will be referred to throughout the text. Nevertheless, emphasis is given to cases where hosts are recognizable harmful microalgae.

21.2 Viruses

Viruses and virus-like particles (VLPs) have been found in more than 50 species of eukaryotic microalgae, and several of them have been isolated in laboratory cultures (Brussaard 2004; Nagasaki et al. 2005). These viruses are diverse both in size and genome type, and some of them infect harmful algal bloom (HAB)-causing species (Table 21.1).

Studies of viral impact on harmful microalgal blooms in coastal waters include host species such as *Heterosigma akashiwo*, *Heterocapsa circular-*

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Ecology of Harmful Algae

Table 21.1. Viruses infectious to marine eukaryotic microalgae (adapted from Brussaard 2004; Nagasaki et al. 2005)

Virus	Host microalga	Virus size (nm)	Virus genome
BtV	*Aureococcus anophagefferens* (Ochrophyta)*	140	dsDNA
CbV	*Chrysochromulina brevifilum* (Haptophyta)	145–170	dsDNA
CeV	*Chrysochromulina ericina* (Haptophyta)	160	dsDNA, 510 kbp
CsNIV	*Chaetoceros salsugineum* (Ochrophyta)	38	(ss+ds)DNA, 6.0 kb
EhV	*Emiliania huxleyi* (Haptophyta)*	170–200	dsDNA, 410–415 kbp
HaNIV	*Heterosigma akashiwo* (Ochrophyta)*	30	No report
HaV	*Heterosigma akashiwo* (Ochrophyta)*	202	dsDNA, 294 kbp
HaRNAV	*Heterosigma akashiwo* (Ochrophyta)*	25	ssRNA, 9.1 kb
HcRNAV	*Heterocapsa circularisquama* (Dinophyta)*	30	ssRNA, 4.4 kb
HcV	*Heterocapsa circularisquama* (Dinophyta)*	197	dsDNA, 356 kb
MpRNA	*Micromonas pussila* (Chlorophyta)	50–60	dsRNA, 24.6 kb
MpV	*Micromonas pussila* (Chlorophyta)	115	dsDNA, 200 kb
PoV	*Pyramimonas orientalis* (Chlorophyta)	180–220	dsDNA, 560 kb
PpV	*Phaeocystis pouchetii* (Haptophyta)*	130–160	dsDNA
PgV	*Phaeocystis globosa* (Haptophyta)*	No report	dsDNA

* Bloom-forming microalgae

isquama, *Phaeocystis pouchetii*, *Emiliania huxleyi*, *Aureococcus anophagefferens* and *Micromonas pusilla* (Nagasaki et al. 1994, 2004; Jacobsen et al. 1996; Gastrich et al. 1998; Zingone et al. 1999, cited in Brussaard 2004 and Nagasaki et al. 2005). Viral infections of *H. akashiwo* and *H. circularisquama* have received special attention due to their negative impacts on aquaculture and aquatic environments.

VLP-containing cells were found at the very final stage of *Heterosigma akashiwo* blooms (Nagasaki et al. 1994). Algicidal agents were also detected in the size fraction smaller than 0.2 μm in the same area and at the same stage of *H. akashiwo* bloom (Imai et al. 1998). These facts imply that virus-induced mortality is an important factor in termination of red tides. Moreover, a sudden collapse of a *H. akashiwo* bloom coinciding with an increase in HaV (*H. akashiwo* virus) was observed in a coastal sea (Tarutani et al. 2000). However, the fate of HaV's produced during the bloom and the origins of viruses that initiate infections are unclear.

The dynamics of the bivalve-killing dinoflagellate *Heterocapsa circularisquama* and its virus (HcRNAV) were studied in Ago Bay, Japan (Nagasaki et al. 2004). The abundance of infectious HcRNAV was high from the bloom peak and throughout the post-bloom period, falling to undetectable levels few weeks later. The proportion of VLP-harboring *H. circularisquama* cells reached 88 %, indicating the significance of viral mortality for termination of the red tides. An increase in viral abundance in sediments was noticed during the bloom period, where sediments stayed infective for at least three months, highlighting the importance of sediments as a reservoir for viruses.

21.2.1 Host Specificity

Viruses infecting microalgae are usually host specific. Tomaru et al. (2004a) investigated the virus sensitivity of *Heterosigma akashiwo* and the host specificity of HaV by using 90 *H. akashiwo* clones and 65 virus clones isolated from the same bloom in the Seto Inland Sea. These authors demonstrated the coexistence of different types of HaV during the bloom, and concluded that viral infections affected both biomass and clonal composition of *H. akashiwo* populations. In the case of *Heterocapsa circularisquama* and its virus HcRNAV, Tomaru et al. (2004b) showed that infection could be strain-specific rather than species-specific. Consequently, a single virus clone cannot exterminate a specific algal species that is composed of different ecotypes. Such strain-specificity can be a drawback for the use of viruses to exterminate harmful algal blooms.

21.3 Algicidal Bacteria

During the last two decades, many algicidal bacteria have been identified and isolated from marine coastal areas and have received considerable attention as terminators of HABs (Doucette et al. 1998; Mayali and Azam 2004). Analyses of small subunit ribosomal DNA has shown that the most common algicidal bacteria are gram-negatives that belong to the gamma-Proteobacteria line (mainly the genera *Alteromonas* and *Pseudoalteromonas*) or the phylum Bacteroides (mainly the genera *Cytophaga* and *Saprospira*). New members of the alpha-Proteobacteria line with algicidal effects have been isolated from a seaweed bed in the Seto Inland Sea, Japan (Imai et al. 2006). Gram-positive algicidal bacteria belonging to the phylum Firmicutes have been reported from Australian waters (Skerratt et al. 2002).

21.3.1 Modes of Algicidal Activity and Specificity

Gliding bacteria such as the genera *Cytophaga* and *Saprospira* are usually direct-attack types, requiring physical contact with the hosts to elicit the algicidal effect, whereas members of the gamma-Proteobacteria and Firmicutes release algicidal compounds into the water (Imai et al. 1993, 1995; Skerratt et al. 2002). Direct-attack type bacteria tend to display a wide range of target microalgae. An interesting role of dissolved organic matter was reported in *Alteromonas* E401, which kills the harmful dinoflagellate *Karenia mikimotoi* (Yoshinaga et al. 1995). A high molecular weight (>10 kD), heat-labile compound showing algicidal activity was produced by the bacterium in response to excreted organic matter (EOM) from *K. mikimotoi*. The algicidal activity was restricted to *K. mikimotoi* and *Gymnodinium catenatum*, with no effects on other dinoflagellates, raphidophytes or diatoms. If this is the case, species-specific algicidal activity against blooming algal species might be induced by the EOM from each microalgal species.

Ectoenzymes, particularly ectoproteases, are suspected to be the algicidal compounds released by certain bacteria. Mitsutani et al. (2001) found that cell extracts from a stationary culture of *Pseudoalteromonas* A25 showed both algicidal and high protease activities.

Gram-negative algicidal bacteria appear to use the AI-2 mechanism (quorum sensing) at mid- to late-stage of log-growth phase (Skerratt et al. 2002). The AI-2 mechanism, rather than acetylated homoserinelactones (AHL), is believed to be involved in inter-species bacteria communication. There is a metabolic benefit for these mechanisms to be activated individually or as bacteria requires, rather than simultaneously and continuously.

The swarming capacity of certain bacteria toward target algal cells is thought to be an advantageous strategy for algicidal strains. Imai et al. (1995) observed the swarming of the bacterium *Alteromonas* S to the valve face of the diatom *Ditylum brightwellii* in early stage of algicidal attack. Skerratt et al. (2002) also reported the swarming of algicidal bacteria to the target microalgae. Swarming might be the result of a signal that targets the cells to the prey. Whether algicidal activity is related to swarming and quorum sensing remains an interesting subject.

21.3.2 Ecology of Algicidal Bacteria and Harmful Microalgae

In northern Hiroshima Bay, the Seto Inland Sea, the dynamics of *Heterosigma akashiwo*-killer bacteria was closely related with that of *H. akashiwo* populations (Imai et al. 1998; Yoshinaga et al. 1998). Gamma-Proteobacteria represented 70–80 % of algicidal bacteria isolated during the termination of red tides (Yoshinaga et al. 1998).

At a station in Harima-Nada, also in the Seto Inland Sea area, the cell density of algicidal *Cytophaga* sp. J18/M01 (originally isolated from the same station in Harima-Nada) increased just after the peak of a small bloom of *Chattonella* spp. (Imai et al. 2001). This bacterium has a wide range of targets, which is reflected in a close relationship between its abundance and the change in total microalgal biomass.

Bacteria heavily colonize macroaggregates, being important for biochemical processes as “hot spots” (Simon et al. 2002). Notably, *Cytophaga* and gamma-Proteobacteria are among the dominant bacteria attached to macroaggregates or marine snow (Doucette et al. 1998). Swarming was observed in the algicidal process by *Alteromonas* sp. and *Cytophaga* sp. (Imai et al. 1995; Skerratt et al. 2002). When a small number of algicidal bacteria cells aggregate around a single microalgal cell or on a macroaggregate, such microscale patchiness can create algicidal hot spots in the sea, and may play an important role in the dynamics of algicidal bacteria and microalgae (Doucette et al. 1998; Imai et al. 1998; Mayali and Azam 2004).

21.3.3 Seaweed Beds as Prevention of HABs

A hitherto-unexplored aspect on the ecology of algicidal bacteria is the huge number of such microorganisms attached onto the surface of seaweeds such as *Ulva* sp. (Chlorophyta) and *Gelidium* sp. (Rhodophyta) (Imai et al. 2002). Maximum numbers of about 10^5~10^6 bacteria g seaweed wet weight^{-1} were detected for bacteria targeting *Karenia mikimotoi, Fibrocapsa japonica* (Ochrophyta), and *Heterosigma akashiwo*. Algicidal bacteria belonged to alpha- and gamma-Proteobacteria and the phylum Bacteroides and were also abundant in the water around seaweed beds.

Based on these studies, a new prevention strategy for red tides in aquaculture area is proposed. Co-culturing of *Gelidium* sp. or *Ulva* sp. and finfish is proposed to be effective in cage cultures (Imai et al. 2002). Many algicidal bacteria will be continuously released from the surface of seaweeds to the surrounding water, contributing to prevent HABs. This strategy may be effective in enclosed and small-scale inlets. Artificial restoration of seaweed beds over large coastal areas should work in a similar way to prevent HAB events.

21.4 Parasitic Fungi

Fungi commonly involved in parasitic associations with microalgae are uniflagellated Chytridiomycetes, usually called chytrids (Ibelings et al. 2004). To a lesser extent, biflagellated forms belonging to the Oomycetes and other types of fungi have also been observed (Mountfort et al. 1996; Elbrächter and Schnepf 1998). Parasite dispersal is via free-swimming, flagellate zoospores. Chytrid zoospores penetrate their hosts' cells using their flagella, and then form an intracellular rhizoid through which the zoospore outside the host is nourished. The zoospore becomes a sporangium that matures and produces new zoospores (Van Donk 1989).

Freshwater diatoms and their chytrid parasites are probably the best-studied planktonic host-parasite systems (Ibelings et al. 2004). Fungal infection causes high mortality of freshwater diatom populations, influencing succession of phytoplankton assemblages (Van Donk 1989). Fungal pathogens of marine microalgae include uni- and biflagellated forms infecting diatoms (Wetsteyn and Peperzak 1991; Elbrächter and Schnepf 1998) and dinoflagellates (Mountfort et al. 1996). Whether the dynamics of marine microalgal assemblages are influenced by pathogenic fungi to the same extent as freshwater assemblages is not yet known.

There is a substantial lack of information about the incidence of parasitic fungi on harmful microalgal species, most likely reflecting low interest by the scientific community rather than the absence of such a phenomenon in nature. Canter (1972) noted that a few freshwater cyanobacteria, including the toxin-producing genera *Microcystis* and *Anabaena*, were susceptible to fungal parasites, but apparently no further studies were done. In the marine environment, diatoms of the genus *Coscinodiscus*, which occasionally form deleterious blooms, are hosts for *Lagenisma coscinodisci* (Schnepf et al. 1978). *Verticillium lecanii*, a fungus isolated from marine waters releases algicidal substances that kill dinoflagellates (Montfort et al. 1996).

21.4.1 Host Specificity

Fungal parasites usually show a narrow host range. The chytrid *Zygorhizidium planktonicum* was reported to infect only two diatom genera, *Asterionella* and *Synedra* (Canter et al. 1992). Further studies demonstrated the co-existence of species-specific variants of *Z. planktonicum* (Doggett and Porter 1995). *Verticillium lecanii* kills the red tide-forming dinoflagellates *Karenia mikimotoi* (formerly *Gymnodinium mikimotoi*) and *Akashiwo sanguinea* (formerly *G. sanguineum*), but does not harm *Heterocapsa triquetra* and three species of *Alexandrium* (Montfort et al. 1996).

21.5 Parasitic Protists

Protists have long been described as parasites of planktonic microalgae (see review by Elbrächter and Schnepf 1998). Included are various zooflagellates, amoebae, and euglenas that infect mostly diatoms (Schweikert and Schnepf 1997; Tillmann et al. 1999; Elbrächter and Schnepf 1998). Dinoflagellates are also known to parasitize planktonic microalgae in marine waters (Park et al. 2004). For example, *Dubosquella melo* infects the red tide-forming dinoflagellate *Noctiluca scintillans* (Cachon 1964), and species of *Paulsenella* have been observed infecting diatoms (Drebes and Schnepf 1988). However, the genus *Amoebophrya* is noticeably the most widespread parasitic dinoflagellate of marine microalgae, infecting several free-living dinoflagellates (Park et al. 2004). In addition, two newly described perkinsozoan flagellates, *Parvilucifera infectans* and *Cryptophagus subtilis*, have been reported to infect marine dinoflagellates and cryptophytes, respectively (Norén et al. 1999; Brugerolle 2002). Together, *Amoebophrya* spp. and *P. infectans* infect over 50 marine dinoflagellates, among them several harmful species (Park et al. 2004). These two parasites have received considerable attention due to their worldwide occurrence and, at times, high virulence against harmful dinoflagellates.

Members of the genus *Amoebophrya* infecting several dinoflagellates were initially described as one species, *Amoebophrya ceratii*, but are now regarded as a cluster of closely related strains or species (Coats et al. 1996; Gunderson et al. 2002; Salomon et al. 2003; Coats and Park 2002). Dispersal is by small (8–10 μm long), free-swimming, biflagellate zoospores (called dinospores) (Cachon and Cachon 1987), which penetrate the host becoming a trophont (Fig. 21.1). The parasite leaves the host as a vermiform stage that differentiates into new dinospores. Prevalence of up to 80 % was reported during epidemic outbreaks of *Amoebophrya* sp. infecting *Akashiwo sanguinea* (Coats et al. 1996). In such cases, *Amoebophrya*-induced mortality might offset in situ growth rates of host dinoflagellates, being relevant to bloom termination.

Infection by *Parvilucifera infectans* is mediated by free-living, 2–4 μm long, biflagellate zoospores that enter the host and develop into thick-walled, round bodies called sporangia (Delgado 1999; Norén et al. 1999) (Fig. 21.2). When mature, zoospores inside the sporangium become active and escape to the water, completing the cycle. A single sporangium can harbor as many as 200 zoospores (Erard-Le Denn et al. 2000). *P. infectans* can cause high mortality when inoculated in cultures of compatible dinoflagellate hosts.

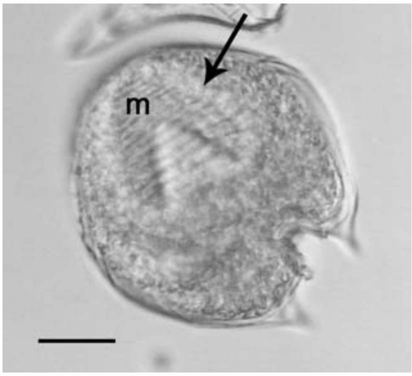

Fig. 21.1. *Protoperidinium* sp. from the Southern Atlantic (Brazilian coast of Arraial do Cabo, Rio de Janeiro state) infected with a trophont of the parasitic dinoflagellate *Amoebophrya* sp. Note the "beehive" aspect of the trophont (*arrow*) and the mastigocoel (*m*), typical of this kind of parasite. Specimen fixed with paraformaldehyde and ethanol. Bright field, 40×. *Scale* 20 μm

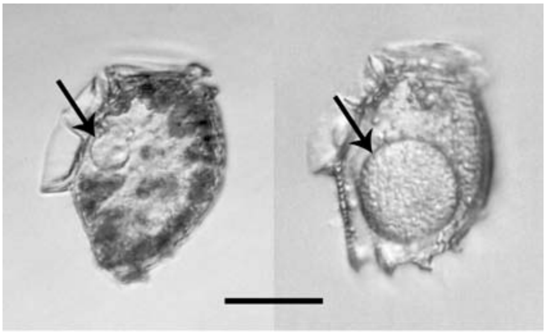

Fig. 21.2. Two cells of *Dinophysis norvegica* from the Baltic Sea infected with *Parvilucifera*. Sporangia (*arrows*) at early (*left cell*) and advanced (*right cell*) developmental stages are shown. Live specimens. Bright field with DIC, 40X. *Scale* 20 µm

21.5.1 Host Specificity

Host specificity for parasitic protists of microalgae is variable. Cross-infection experiments with six species of *Pirsonia* and more than 20 species of diatoms revealed parasites with both narrow and wide host ranges (Kühn et al. 1996). Various strains of *Amoebophrya* have been maintained in culture with their original hosts for successive generations, but attempts to artificially establish uninterrupted infection on dinoflagellate hosts other than the ones from which they were isolated have been unsuccessful, indicating high host specificity for the group (Coats et al. 1996; Park et al. 2004). Notable exceptions are two *Amoebophrya* strains recently isolated from *Alexandrium* spp., which are infectious to several other thecate dinoflagellates (Sengco et al. 2003). *Parvilucifera infectans* appears to be one of the less selective parasitic protists infecting microalgae. Although infection seems to be restricted to dinoflagellates, mostly thecate forms, zoospores originating from a given host are normally infectious to a large array of other dinoflagellates in culture (Delgado 1999; Norén et al. 1999; Erard-Le Denn 2000).

21.5.2 Host Avoidance of Parasitic Infection

Little is known about defense mechanisms elicited by microalgae to escape their parasites. Few insights come from studies of dinoflagellate hosts. Coats and Park (2002) observed that a fraction of cells in cultures of *Karlodinium micrum* inoculated with *Amoebophrya* sp. were resistant to infection. Inducible defense against parasite infection was reported in the PSP-causative dinoflagellate *Alexandrium ostenfeldii*, which responded to water-borne signals from *Parvilucifera infectans* by shifting from motile to resting stages (Toth et al. 2004). Moreover, behavioral features also seem to protect microalgal populations from heavy parasitism. *Amoebophrya* infection in *Akashiwo sanguinea* populations leads to a physical separation between diel-verticalmigrating, non-infected cells and metabolically impaired, infected cells. This in turn helps to prevent parasite epidemics in healthy populations (Coats and Bockstahler 1994).

21.6 Conclusions and Future Perspectives

The influence of pathogens as controlling mechanism for microalgal populations is still a relatively neglected subject (if compared to nutrient limitation and grazing). Infections by freshwater fungi and marine protists are the most conspicuous exceptions to this pattern. This generalized lack of studies might be, at least in part, due to methodological difficulties to recognize the parasites on and inside microalgal cells.

High host specificity and virulence of certain pathogens highlights their potential in controlling host populations, and lends credibility to previous suggestions of their use as mitigation to harmful blooms (Taylor 1968). Uncertainties about host specificity, pathogen stability, and fate within the aquatic food web, and possible negative impacts to other members of the aquatic biota are issues that still must be examined. The use of pathogens as mitigation for harmful algal blooms is thoroughly discussed in Chap. 25.

Bloom termination by viruses and algicidal bacteria releases huge amounts of organic matter that must enter the aquatic food web mainly via the microbial food web component (Kamiyama et al. 2000). If not recycled, this organic matter will most likely contribute to the deterioration of aquatic environments through anoxia. On the other hand, attack of harmful microalgae by parasites like chytrids and protists reorganizes much of the algal biomass into smaller packages – in the form of parasite zoospores – readily available to grazers (Johansson and Coats 2002). Blooming microalgae released from grazing due to toxin production or size refuge weakens matter and energy fluxes to higher trophic levels. Parasitism might re-establish these fluxes via alternative, temporary routes mediated by zoospores (Park et al. 2004).

Finally, it is widely accepted that release from natural enemies favors the success of plants and animals introduced into new territories (Torchin et al. 2003). Whether or not a release from pathogens influences the success of harmful microalgae introduced in coastal areas (e.g., via cargo-vessel ballast water) is still an open question.

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