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# Parasites and Phytoplankton, with Special Emphasis on Dinoflagellate Infections[1]

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ABSTRACT. Planktonic members of most algal groups are known to harbor intracellular symbionts, including viruses, bacteria, fungi, and protozoa. Among the dinoflagellates, viral and bacterial associations were recognized a quarter century ago, yet their impact on host populations remains largely unresolved. By contrast, fungal and protozoan infections of dinoflagellates are well documented and generally viewed as playing major roles in host population dynamics. Our understanding of fungal parasites is largely based on studies for freshwater diatoms and dinoflagellates, although fungal infections are known for some marine phytoplankton. In freshwater systems, fungal chytrids have been linked to mass mortalities of host organisms, suppression or retardation of phytoplankton blooms, and selective effects on species composition leading to successional changes in plankton communities. Parasitic dinoflagellates of the genus *Amoebophrya* and the newly described Perkinsozoa, *Parvilucifera infectans*, are widely distributed in coastal waters of the world where they commonly infect photosynthetic and heterotrophic dinoflagellates. Recent work indicates that these parasites can have significant impacts on host physiology, behavior, and bloom dynamics. Thus, parasitism needs to be carefully considered in developing concepts about plankton dynamics and the flow of material in marine food webs.

**Key Words.** Biological control, dinoflagellate, harmful algal bloom, parasite, parasitism, phytoplankton, protist.

A wide variety of organisms including prokaryotes and eukaryotes act as parasites of phytoplankton (Elbrächter and Schnepf 1998). While prokaryotic pathogens (viruses and bacteria) are well known for smaller phytoplankton species (e.g. chrysophytes, prymnesiophytes, prasinophytes, raphidophytes, and cyanobacteria), they appear to be much less prevalent in dinoflagellates and diatoms (Brussaard 2004; Elbrächter and Schnepf 1998; Proctor 1997). By contrast, eukaryotic parasites (e.g. fungi, perkinsozoa, amoebae, dinoflagellates, euglenoids, kinetoplastids, and other heterotrophic flagellates) are best known from diatom and dinoflagellate hosts, but can also infect various phytoplankton taxa including cyanobacteria, chrysophytes, cryptophytes, chlorophytes and prymnesiophytes (Brugerolle 2002; Elbrächter and Schnepf 1998; Holfeld 1998). Much of the work done on eukaryotic infections of phytoplankton has been descriptive in nature, providing little insight on the biogeography of the parasites or on their roles as top-down controls in food webs. Two notable exceptions, however, are fungal infections of freshwater microalgae and parasitism of marine dinoflagellates by certain protists.

## FUNGAL PARASITES OF PHYTOPLANKTON

Chytridiomycete and Oomycete parasites of freshwater microalgae have received considerable attention since the early work of Canter and Lund over a half-century ago (Canter and Lund 1948, 1951, 1953), with studies describing the occurrence of fungi as parasites of planktonic algae dating to the early 1900s (for review, see van Donk 1989; van Donk and Bruning 1995). Fungal infections of phytoplankton (diatoms, dinoflagellates, desmids, green algae, chrysophytes, and cyanobacteria) have now been documented for lakes and reservoirs of Europe, North and South America, and Asia and are believed to play important roles in the population dynamics of host species (Bailey-Watts and Lund 1973; Boltovskoy 1984; Canter 1972; Canter and Lund 1969; Heaney et al. 1988; Koob 1966; Kudoh and Takahashi 1990, 1992; Pongratz 1966; Reynolds 1973; Sen 1988a,b; Sommer, Wedemeyer and Lowsky 1984; van Donk and Ringelberg 1983; Youngman, Johnson, and Farley 1976).

Infection of planktonic diatoms by fungi has been implicated in mass mortalities of host organisms, suppression or retardation of phytoplankton blooms, shifts in size distribution of host populations, and selective effects on species composition leading to successional changes in plankton communities (Canter and Lund 1951; Heaney et al. 1988; Kudoh and Takahashi 1990; Reynolds 1973; Sommer, Wedemeyer, and Lowsky 1984; van Donk and Ringelberg 1983; Youngman, Johnson, and Farley 1976). For example, Canter and Lund (1951) showed that chytrid parasites can delay the timing and reduce maximum abundance of algal in Esthwaite Water, England, with highly infected populations of *Asterionella formosa* being replaced by *Fragilaria crotonensis* and *Tabellaria fenestrata*. Similarly, Kudoh and Takahashi (1990) showed that fungal infection can control population size of *Asterionella formosa* in a shallow eutrophic lake of Japan. Similar reports for other groups of planktonic microalgae are rather scarce, but there is some evidence that fungal parasites can regulate freshwater dinoflagellate populations. For example, Sommer, Wedemeyer and Lowsky (1984) linked fungal parasitism to changes in population density of *Ceratium hirundinella* in Lake Constance, while Canter and Heaney (1984) and Heaney et al. (1988) have shown that the biflagellate fungus *Aphanomycopsis cryptica* can facilitate the reduction of *Ceratium* populations in the English Lake District.

Most fungal parasites of microalgae have a narrow host range, infecting one or a few closely related algal species, and some are specific to particular host strains (Canter and Jaworski 1978, 1982; Doggett and Porter 1995; Holfeld 1998). Fungal infections are known to occur throughout the year, with different host species being exploited over the seasons (Holfeld 1998). In some instances, the same host species is attacked by different parasites at different times of the year.

Parasite prevalence in individual phytoplankton species appears to be strongly influenced by host abundance. Under low host densities, fungal zoospores must travel relatively further to reach new hosts, with low infection prevalence reflecting low encounter probabilities (Reynolds 1984). The persistence of fungal infections appears to require a minimum threshold density of host cells, with values for parasite species ranging from 0.2 to 50 host cells $ml^{-1}$ (Holfeld 1998). There is also a tendency for parasites of large host species to be sustained at lower host abundances, a relationship that may reflect increased encounter probability stemming from higher output of parasite

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infective stages as host size increases. As host density increases, so does encounter rate, with epidemics more likely to occur once an upper threshold in host density is exceeded (Bruning 1991b, c). Not surprisingly, a sequence of increasing host abundance, followed by rapid rise in parasite prevalence and then bloom decline has been documented on many occasions (e.g. Canter and Lund 1948; Holfeld 1998; Kudoh and Takahashi 1990; Reynolds 1973; van Donk and Ringelberg 1983; Youngman, Johnson, and Farley 1976).

Fungal epidemics are the result of both host and parasite growth rate and may be favored in environmental settings that depress algal growth, or enhance fungal growth. It has thus been suggested that hosts growing in unfavorable conditions may be more susceptible to fungal parasites than ''healthy'' hosts (Reynolds 1984). Many field studies, however, have shown that severe fungal epidemics can appear even when growth conditions are favorable for the host population (Canter and Lund 1948, 1969; Holfeld 1998; Masters 1971; Sen 1987, 1988a,b; van Donk and Ringelberg 1983; Youngman, Johnson, and Farley 1976).

Environmental conditions including light, temperature, and nutrient concentrations influence growth parameters of fungal parasite (e.g. development time of the sporangia, production of new zoospores, infectivity of the zoospores, and infective lifetime of zoospores; van Donk and Bruning 1995) and may be important factors in governing the timing and relative importance of these parasites as top-down controls (Abeliovich and Dikbuck 1977; Blinn and Button 1973; Bruning 1991d; Canter and Jaworski 1981; van Donk and Ringelberg 1983). For example, light limitation in *Asterionella formosa* substantially decreases production of zoospores by the chytrid *Rhizophydium planktonicum*, while also decreasing susceptibility of the host to infection (Bruning 1991a). Under very low light intensity, *Asterionella formosa* apparently becomes totally resistant to parasitism, but is still able to grow slowly. At high light levels, growth of the host exceeds that of the parasite. Using a model that encompassed light effects on host-parasite growth parameters, Bruning (1991b) predicted that epidemics of *R. planktonicum* in *A. formosa* populations would be facilitated by moderate light limitation, with threshold host densities for development of epidemics being $\sim$ 100 cells ml$^{-1}$. Similarly, phosphorous (P) limitation decreases zoospore production and generation time of *R. planktonicum*, while having strong negative impacts on growth of *A. formosa* (Bruning and Ringelberg 1987). Under severe P limitation, growth of the parasite exceeds that of the host, with threshold host densities for development of epidemics being $\sim$ 40 cells ml$^{-1}$ (Bruning 1991c). Thus, light and phosphorous limitation are likely to work synergistically to promote fungal epidemics, at least at high diatom densities (e.g. as P concentrations decrease and self-shading increases in response to bloom formation). Despite intensive study on the importance of physico-chemical factors in regulating fungal parasitism, the effects of biotic factors, such as grazing by freshwater microzooplankton on fungal epidemics, have not been carefully addressed.

In the marine environment, fungal and labyrinthulomycete parasites of macroalgae have received considerable attention (e.g. Küpper and Müller 1999; Müller, Küpper, and Küpper 1999; Raghukumar 2002; Uppalapati and Fujita 2000), but few studies have addressed such infections in planktonic microalgae. Thus far, two genera of uniflagellate fungi (*Olpidium* and *Rhizophydium*) and three genera of biflagellate fungi (*Lagenisma*, *Ectrogella*, and *Phagomyxa*) are known for a few species of marine phytoplankton, all of which are diatoms (Elbrächter and Schnepf 1998). Whether or not fungal parasites of marine phytoplankton exert controls on host populations similar to those of their freshwater counterparts has yet to be explored.

## DINOFLAGELLATE PARASITISM

**Dinoflagellates as hosts.** Dinoflagellates can serve as hosts, parasites, and even hyperparasites (i.e. parasites that infect other parasites). As hosts, dinoflagellates harbor viruses, bacteria, fungi, and other protists. Viruses or virus-like particles (VLPs) are known for only a few dinoflagellates, most of which are athecate species. For example, VLPs have been reported for the freshwater dinoflagellate *Gymnodinium uberrimum* (Sicko-Goad and Walker 1979) and the marine species *Gyrodinium resplendens* (Franca 1976) and *Blastodinium* sp., a parasite of copepods (Soyer 1978). Soyer (1978), however, argued that the VLPs observed in *Gyrodinium resplendent* by Franca (1976) might not actually be viruses. Unambiguous viral infections have recently been documented for two dinoflagellate species. One of these, an athecate zooxanthella from the temperate sea anemone *Anemonia viridis*, is infected by a latent virus that is induced to become lytic by elevated temperature (Wilson et al. 2001). By contrast, *Heterocapsa circularisquama*, a thecate shellfish-killing dinoflagellate, is host to a lytic virus that has a latent period of about two days (Nagasaki et al. 2003; Tarutani et al. 2001).

Bacteria are known to inhabit the cytoplasm and/or nucleus of many dinoflagellate species, including *Gonyaulax spinifera*, *Alexandrium tamarense* (= *Gonyaulax tamarensis*), *Scrippsiella trochoidea*, *Cochlodinium heterolobatum*, *Gyrodinium instriatum*, *Akashiwo sanguinea* (= *Gymnodinium splendens*), *Glenodinium foliaceum*, *Prorocentrum minimum*, and *P. scutellum*. Such relationships are generally believed to be either commensal or mutualistic (Silva 1978, 1990; Silva and Franca 1985; Doucette et al. 1998); however, Kirchner et al. (1999) recently reported that intracellular bacteria of *Noctiluca scintillans* have a negative effect on host growth rate, suggesting a parasitic relationship. Nonetheless, it seems that viruses and bacteria rarely act as pathogens of dinoflagellates.

By contrast, numerous dinoflagellate species are susceptible to eukaryotic parasites (Elbrächter and Schnepf 1998). As discussed above, fungal parasites are only known for a few freshwater dinoflagellates, including *Ceratium hirundinella*, *C. furcoides*, *Peridinium willei* and *P. aciculiferum* (Boltovskoy 1984; Canter and Heaney 1984; Heaney et al. 1988; Holfeld 1998; Sommer, Wedemeyer, and Lowsky 1984). Foremost among protistan parasites of marine dinoflagellates are the perkinsozoan flagellate *Parvilucifera infectans* (Norén, Moestrup, and Rehnstam-Holm 1999) and parasitic dinoflagellates belonging to the genus *Amoebophrya* (Coats 1999). Together these parasites are known to infect about 50 species of marine dinoflagellates (Table 1).

To date, *Parvilucifera infectans* has been reported from 17 species representing 10 genera of dinoflagellates collected from nature, a few of which are toxic and/or harmful species (Table 1). In the lab, *P. infectans* has been transmitted to another nine species of dinoflagellates, but attempts to infect other algal groups have not proven successful (Delgado 1999, Erard-Le Denn, Chrétiennot-Dinet, and Probert 2000). Thus, while *P. infectans* appears to specialize on dinoflagellates, it has a broad host range, with the majority ($\sim$ 80%) of known hosts being thecate taxa. *Parvilucifera infectans* shows a widespread global distribution (Norén et al. 2000; Fig. 1), with infections having been reported from the North Sea (Swedish and Norwegian west coasts), European waters (Atlantic coast and the Mediterranean Sea), the Indian Ocean, eastern North America (Narragansett Bay), and Australia (Tasmania). This parasite was recently recorded in Asian waters, when infections were found in

Table **1**. Occurence of *Parvilucifera infectans* and *Ameobophrya* ssp. in marine dinoflagellates: species infected in nature (■); species infected in laboratory tests (□); nuclear infections (●); cytoplasmic infections (○).

| | *Parvilucifera infectans* (ref[a]) | | *Amoebophrya* spp. (ref[a]) | |
|---|---|---|---|---|
| Athecate Host Species | | | | |
| *Akashiwo sanguinea* | □ | (23) | ■□● | (6, 8, 21) |
| *Cochlodinium polykrikoides* | ■ | (pers. observ.) | ■ | (pers. observ.) |
| *Gymnodinium catenatum* | □ | (23) | | |
| *Gymondinium chlorophorum* (or *Lepidodinium viride* ?) | ■ | (23) | | |
| *Gymnodinium instriatum* | | | ■□○ | (7) |
| *Gymnodinium mikimotoi* | □ | (11) | | |
| *Gyrodinium aureolum* | | | ■ | (15) |
| *Gyrodinium uncatenum* | | | ■○ | (8) |
| *Karlodinium micrum* | | | ■□●○ | (7) |
| *Oxyrrhis marina* | | | ■ | (5) |
| *Phaeopolykrikos* sp. | | | ■ | (21) |
| *Polykrikos kofoidi* | | | ■ | (pers. observ.) |
| Thecate Host Speices | | | | |
| *Alexandrium affine* | □ | (9) | ■□○ | (pers. observ.) |
| *Alexandrium andersonii* | □ | (23) | | |
| *Alexandrium catenella* | ■□ | (9, 23) | ■● | (21, 27) |
| *Alexandrium fundyense* | □ | (11, 22) | | |
| *Alexandrium minutum* | ■□ | (9, 11, 23) | | |
| *Alexandrium ostenfeldii* | □ | (21, 23) | | |
| *Alexandrium tamarense* | □ | (11, 22) | ■□○ | (15, 25) |
| *Ceratium furca* | ■ | (23) | ■○ | (10, 13) |
| *Ceratium fusus* | | | ■● | (3, 10, 17, 18, 21) |
| *Ceratium longipes* | | | ■●○ | (10) |
| *Ceratium macroceros* | | | ■ | (13) |
| *Ceratium tripos* | ■ | (23) | ■● | (2, 3, 10, 17, 18) |
| *Dinophysis acuminata* | ■□ | (1, 22) | | |
| *Dinophysis acuta* | ■□ | (1, 22) | | |
| *Dinophysis dens* | □ | (22) | | |
| *Dinophysis norvegica* | ■□ | (22) | ■●○(?) | (12, 14, 24) |
| *Diplopsalis lenticula* | | | ■ | (19) |
| *Diplopsalis* sp. | ■ | (22) | | |
| *Goniodoma* sp. | | | ■● | (4) |
| *Gonyaulax spinifera* | | | ■■● | (pers. observ.) |
| *Heterocapsa triquetra* | ■ | (22) | ■ | (15) |
| *Kryptoperidinium foliaceum* | | | ■ | (5, 15) |
| *Oblea rotunda* | | | ■ | (15) |
| *Oxytoxum* sp. | | | ■ | (21) |
| *Plectodinium nucleovolatum* | | | ■ | (4, 5) |
| *Preperidinium meunieri* | | | ■ | (15) |
| *Prorocentrum gracile* | | | ■ | (15) |
| *Prorocentrum micans* | ■ | (22) | ■○ | (4) |
| *Prorocentrum minimum* | | | ■□● | (16, 20) |
| *Protoperidinium bipes* | ■ | (9) | | |
| *Protoperidinium brochii* | ■ | (22) | | |
| *Protoperidinium curvipes* | | | ■ | (26) |
| *Protoperidinium divergens* | ■ | (22) | | |
| *Protoperidinium depressum* | | (22) | ■ | (4, 21) |
| *Protoperidinium minutum* | | | ■ | (15) |
| *Protoperidinium pellucidum* | ■ | (22) | ■ | (15) |
| *Scrippsiella trochoidea* | ■□ | (11) | ■● | (8, 21, 27) |

[a] References: (1) Berland, Maestrini and Grzebyk 1995; (2) Borgert 1898; (2) Bütschli 1887; (4) Cachon 1964; (5) Chatton and Biecheler 1935; (6) Coats and Bockstahler 1994; (7) Coats and Park 2002; (8) Coats et al. 1996; (9) Delgado 1999; (10) Elbrächter 1973; (11) Erard-Le Denn, Chrétiennot-Dinet and Probert 2000; (12) Fritz and Nass 1992; (13) Gárate Lizárraga and Siqueiros-Beltrones 2003; (14) Gisselson et al. 2002; (15) Jacobson 1987; (16) Kim, Park and Yih 2002 (17 and 18) Koeppen 1894, 1903; (19) Lebour 1925; (20) Maranda 2001; (21) Nishitani, Erickson, and Chew 1985; (22 & 23) Norén, Moestrup and Rehnstam-Holm 1999; Norén et al. 2000; (24) Salomon, Janson and Granéll 2003; (25) Sengco et al. 2003; (26) Shin 1999; (27) Taylor 1968.

*Cochlodinium polykrikoides*, an important harmful red-tide species along the southern coast of Korea (Fig. 2; pers. observ.).

*Amoebophrya* species have been reported from about 40 different free-living dinoflagellates representing more than 20 genera, three-quarters of which are thecate species (Table 1). These parasites are broadly distributed in the northern hemisphere (Fig. 8), with numerous accounts from the North Atlantic, the North Pacific, and the Mediterranean Sea (Cachon 1964; Coats and Bockstahler 1994; Coats et al. 1996; Elbrächter 1973; Fritz and Nass 1992; Gisselson et al. 2002; Jacobson, 1987; Kofoid and Swezy 1921; Lebour 1917, 1925; Maranda 2001; Nishitani, Erickson, and Chew 1985; Salomon, Janson, and Granéli 2003; Taylor 1968). Ongoing work has also shown *Amoebophrya* spp. to occur in a variety of dinoflagellate hosts (Fig. 3–7) from

Fig **1.** Global distribution of *Parvilucifera infectans*. Filled circles note locations where infections have been observed in photosynthetic and/or heterotrophic dinoflagellates.

coastal waters of Korea (Kim, Park, and Yih 2002; pers. observ.), and infections have also been noted in a *Gymnodinium* species from Hobart, Australia (DWC, unpubl. data).

**Dinoflagellates as parasites.** Research on parasitic dinoflagellates has a very long history, dating to the early work of Pouchet (1885). A large body of information on the taxonomy, morphology, development, and life history of parasitic dinoflagellates has been generated over the years and addressed in several review articles (Cachon 1964; Cachon and Cachon 1987; Coats 1999; Elbrächter and Schnepf 1998). The importance of parasitic dinoflagellates in the ecology of host organisms has received far less attention, with much of what we know on that topic limited to a few commercially important host species (Shields 1994) and some planktonic protists (Coats and Heisler 1989; Coats et al. 1994, 1996).

Of the roughly 2,000 species of modern dinoflagellates, approximately 130 parasitic species have been formally described and another 10–20 remain unnamed (Coats 1999). These 150 or so parasitic dinoflagellates fall into 35 genera of which, five (*Myxodinium*, *Paulsenella*, *Duboscquella*, *Coccidinium*, and *Amoebophrya*) contain species that utilize planktonic microalgae as hosts. *Myxodinium pipens* is an ectoparasite of the chlorophyte *Halosphaera* sp. (Cachon, Cachon, and Bouquaheux 1969), while *Paulsenella* includes three species that parasitize diatoms exclusively (Drebes and Schnepf 1982, 1988; Elbrächter and Schnepf 1998). Among the eight species of *Duboscquella*, only *D. melo* is known to infect dinoflagellates, and it is believe to be specific to the noxious bloom-forming heterotroph *Noctiluca scintillans* (Cachon, 1964). Species of *Coccidinium* are endoparasites of dinoflagellates including *Coolia monotis*, but are poorly characterized, having gone unstudied since the early observations of Chatton and Biecheler (1934, 1936). By contrast, species of *Amoebophrya* are well known and infect a variety of planktonic marine organisms including ciliates, radiolarians, chaetognaths, siphonophores, and other dinoflagellates (Cachon 1964; Cachon and Cachon 1987).

Seven species of *Amoebophrya* are recognized so far, with three of these known to infect dinoflagellate hosts. *Amoebophrya leptodisci* is specific to the heterotrophic dinoflagellate *Pratjetella medusoides*, while *A. grassi* is a hyperparasite of *Oodinium poucheti* and *O. acanthometrae*, the latter species being parasitic dinoflagellates that infect appendicularia and acantheria, respectively (Cachon and Cachon 1987). *Amoebophyra ceratii* is a parasite of free-living photosynthetic and heterotrophic dinoflagellates and has long been thought to lack host specificity (Cachon 1964; Cachon and Cachon 1987; Fritz and Nass 1992). Recent work, however, has questioned that view, as discussed below.

Cachon (1964) noted that *Amoebophrya* infections developed in the nucleus of thecate hosts, except *Prorocentrum micans*, but occurred intracytoplasmically in athecate species. Subsequent studies, however, have demonstrated nuclear infections in some athecate species (e.g. *Akashiwo sanguinea* and *Karlodinium micrum*; Coats and Park 2002) and cytoplasmic infections in some thecate hosts (e.g. *Alexandrium affine*, *Ceratium furca*, *C. longipes*, and *Scrippsiella* sp.; Coats and Bockstahler 1994; Coats et al. 1996; MGP., pers. observ.). While *Amoebophrya* infections can be either intranuclear or intracytoplasmic, they are largely specific to a particular region of the cell in a given host species. *Amoebophrya* spp. that infect *Karlodinium micrum* and *Ceratium longipes* are clear exceptions to this general pattern of site specificity, as infections occur in both the nucleus and cytoplasm, sometimes simultaneously in the same host cell (Coats and Park 2002; Elbrächter 1973; Elbrächter and Schnepf 1998).

While several reports indicate that *A. ceratii* has a broad host range (e.g. Cachon 1964, Nishitani, Erickson, and Chew 1985), most *Amoebophrya* strains established in culture have shown a high degree of host specificity. For example, Coats et al. (1996) were unsuccessful in transmitting *Amoebophrya* from *Akashiwo sanguinea* to *Ceratium furca*, *Gyrodinium uncatenum*, and *Scrippsiella trochoidea* when incubated in single or mixed host assemblages. More recently, Coats and Park (2002) showed that *Amoebophrya* strains from *Akashiwo sanguinea*, *Gymnodinium instriatum*, and *Karlodinium micrum* exhibited marked differences in parasite generation time, dinospore survival, and infectivity, with none of the strains able to successfully cross-infect the alternate host species. These observations, when coupled with molecular studies showing considerable diversity in ssRNA sequence across parasite strains (Gunderson et al. 2002; Janson et al. 2000), suggest that *A. ceratii* represents a species complex composed of several host-specific parasites. Recently, however, two strains of *Amoebophrya* isolated from *Alexandrium* species have shown a broad host range, with infections successfully established in other thecate, but not athecate, dinoflagellates (Sengco et al. 2003; MGP, pers. observ.). Future work to resolve speciation in these parasites needs to define morphological traits useful in sorting species of *Amoebophrya*, contrast variation in ssRNA sequence of *Amoebophrya* strains within and across host taxa, further explore host-specificity, or

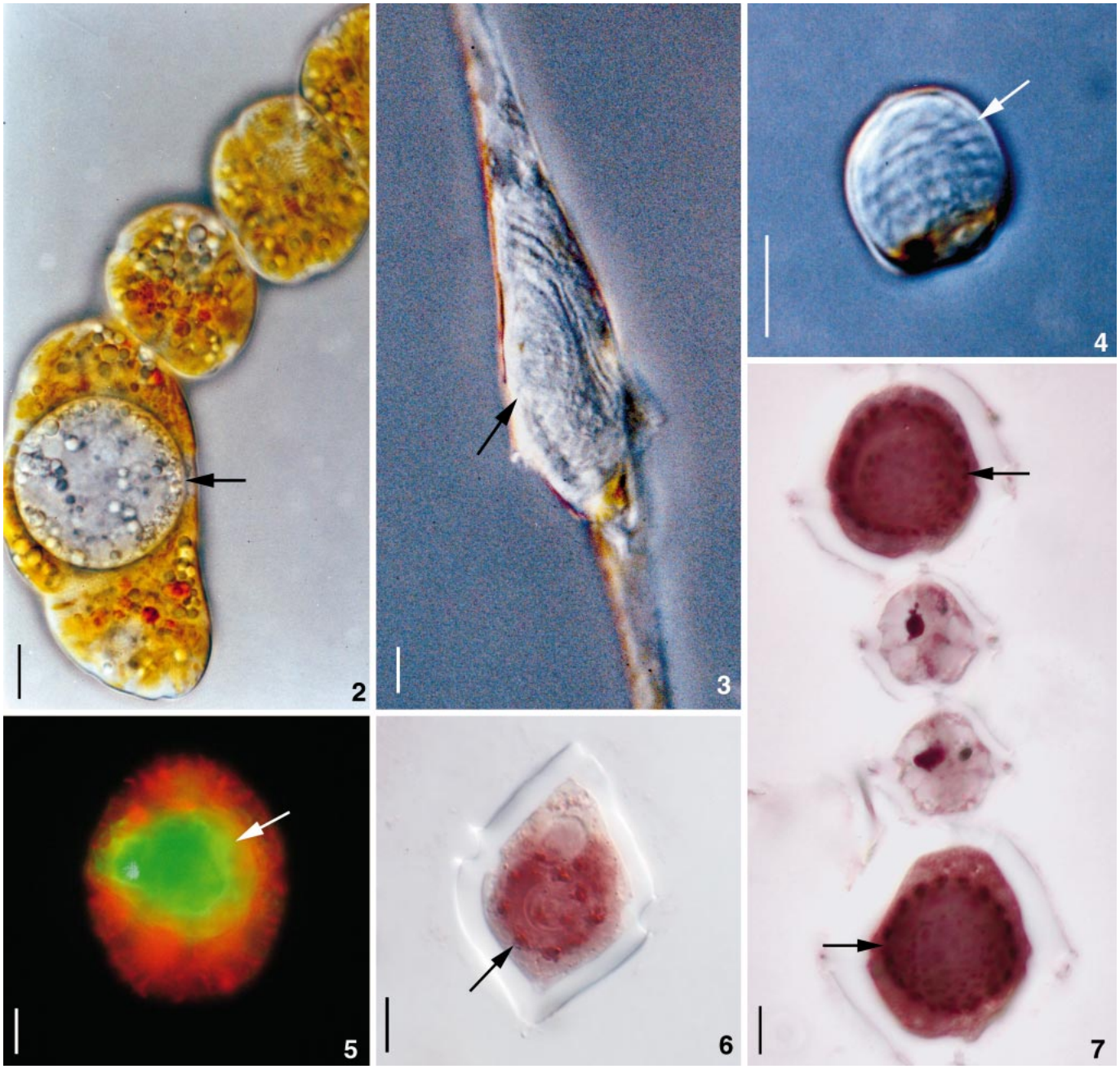


Fig. **2–7.** Representative dinoflagellates infected by eukaryotic parasites; scale bars = 10 μm. Fig. **2.** *Parvilucifera infectans* in *Cochlodinium polykrikoides* from the southern coast of Korea. Arrow marks the developing parasite in the enlarged posterior cell of this chain forming dinoflagellate; DIC imaging. Fig. **3, 4.** *Amoebophrya* sp. in *Ceratium fusus* and *Prorocentrum minimum* from Korean coastal waters. Arrows indicate mature beehive stages of the parasites; DIC optics. Fig. **5.** Mid-infection of *Amoebophrya* sp. ex *Akashiwo sanguinea* from Chesapeake Bay. Arrow points to the green autofluorescing parasite surrounded by red chlorophyll α fluorescence of the host. Fig. **6, 7.** Protargol silver-impregnation of *Amoebophrya* ex *Heterocapsa triquetra* and *Alexandrium affine* from Korea. Arrows mark argentophilic parasite nuclei of mid- to late-stage infections. Note that the anterior and posterior infected cells of *A. affine* are considerably larger that the two central, uninfected cells; stained specimens viewed with DIC optics to reveal host thecae.

lack thereof, for additional parasite strains, examine the biogeography of species/strains, and relate species/strain differences to host phylogeny.

**Methods for detecting infections.** Several methods have been used to detect and/or quantify parasitism of planktonic dinoflagellates, the simplest being direct microscopic examination of living or preserved specimens to visualize relatively mature infections. For example, late-stage infections of *Amoebophrya* in *Alexandrium affine* (Fig. 7) and *A. catenella* produce abnormally large, ''giant cells'' within the long-chains of host cells (Taylor 1968; MGP, pers. observ.). These infections can be easily distinguished when examining fixed or unfixed specimens using brightfield optics. Many other dinoflagellate species infected by *Amoebophrya* fail to develop ''giant cells'' and

Fig. **8.** Global distribution of *Amoebophrya* spp. in free-living dinoflagellates. Filled circles indicate sites where infections have been noted in photosynthetic and/or heterotrophic host species.

thus must be examined more carefully using phase contrast, or preferably differential interference contrast (DIC), to detect the late ''beehive'' stage of the parasite (Fig. 3 and 4). Early and mid-stage infections, however, are usually difficult to distinguish using these techniques. DIC is also valuable in recognizing hosts parasitized by *Parvilucifera infectans*, as the ''waisted'' warts covering the wall of mature sporangia are clearly visible (Norén 2002). A more reliable method to detect immature *Amoebophrya* infections is epifluorescence microscopy (Coats and Bockstahler 1994). When excited with blue light (450–490 nm), *Amoebophrya* emits a green autofluorescence (Fig. 5) that can be detected throughout the life cycle of some strains (e.g. *Amoebophrya* from *Akashiwo sanguinea*, *Gymnodinium instriatum*, and *Karlodinium micrum*). While this approach is useful for detecting and isolating infected hosts for high resolution microscopy or cultivation, its use for quantifying parasite prevalence can be problematic as fluorescence is typically weak in early infections and fades rapidly following fixation. Furthermore, some strains of *Amoebophrya* do not express green autofluorescence until very late in the infection cycle, e.g. *Alexandrium affine* (MGP, pers. observ.), *Ceratium tripos*, and *C. furca* (DWC, pers. observ.). Cytological staining techniques (e.g. acetocarmine, Feulgen reaction, Protargol silver-impregnation, Fig. 6 and 7) are useful in assessing parasite development, site of infection, and prevalence (Coats and Bockstahler 1994; Nishitani, Erickson, and Chew 1985; Wakeman and Nishitani 1981), although these methods are more tedious and time-consuming. Nuclear fluorochromes [e.g. acridine orange, bizbenzimide (Hoechst 33258), SYTOX and DAPI] have also been used to reveal *Amoebophrya* infections and offer a more rapid means for estimating parasite prevalence (Fritz and Nass 1992; Gisselson et al. 2002; Salomon, Janson, and Granéli 2003). Perhaps the most reliable approach to detect and quantify parasitic infections is through the use of fluorescent in situ hybridization (FISH) probes, as recently developed for *Amoebophrya* sp. infecting *Akashiwo sanguinea* in Chesapeake Bay (Gunderson, Goss, and Coats 2001). When applied to host-parasite cultures, the FISH probe specific for *Amoebophrya* was more sensitive in detecting very early infections than the labor-intensive Protargol-impregnation technique.

**Impact of parasitism on marine dinoflagellate populations.** Cachon (1964) reported that *Amoebophrya ceratii* occurred sporadically in a number of Mediterranean host species, but noted that highest infection levels usually coincided with the decline of blooms. Heavy infections (30–40% in *Alexandrium catenella*; 80% in *Ceratium fusus*) were also observed along the western coast of North America, where parasitism by *A. ceratii* was linked to rapid declines in host populations and implicated as an important factor in preventing bloom formation (Nishitani, Erickson, and Chew 1985; Taylor 1968). By contrast, Fritz and Nass (1992) found that $\leq$ 2% of *Dinophysis norvegica* collected from coastal waters of Nova Scotia were infected by *A. ceratii* and argued that parasitism had little effect on host populations. Unfortunately, these early studies were unable to accurately assess the impact of parasitism on host species, due to incomplete estimates of parasite prevalence and/or the lack of information about parasite generation time.

Estimates for parasite development time (i.e. from initial infection to death of the host) first became available about a decade ago with the cultivation of *Amoebophrya* sp. ex *Akashiwo sanguinea* (Coats and Bockstahler 1994). Since then, several other strains have been cultured and shown to have generation times of 2–4 d (Coats and Park 2002; Park et al. 2002b; Sengco et al. 2003). Using data for parasite prevalence in field samples and parasite development time from culture, Coats and Bockstahler (1994) calculated that parasite-induced mortality removed an average of $<$ 2% of *A. sanguinea* populations per day in the main stem of Chesapeake Bay, far less than needed to facilitate the rapid decline of host populations. Similarly low values (0.5–2%) have been recently derived for *Dinophysis norvegica* populations of the Baltic Sea (Gisselson et al. 2002). In the Chesapeake Bay, however, pockets of infected hosts (20–40% parasite prevalence) were concentrated near the pycnocline, several meters below very lightly infected surface blooms of *A. sanguinea* (Coats and Bockstahler 1994). The authors argued that differences in behavior of infected and uninfected cells effectively uncoupled the transmission of parasites to new hosts in the strongly stratified main-Bay, but suggested that such behavior might not limit parasitism in shallow or well-mixed systems. Subsequently, Coats et al. (1996) examined parasitism of host species in a shallow, mixed subestuary of Chesapeake Bay where *Amoebophrya* epidemics (up to 80% prevalence) coincided with the decline of dinoflagellate blooms. In that system, parasitism by *Amoebophrya* was capable of cropping up to 54% of the dominant bloom-forming species, *Gyrodinium uncatenum*, daily.

*Parvilucifera infectans* has also been suggested to have a significant impact on dinoflagellate populations (Norén, Moestrup, and Rehnstam-Holm 1999), although estimates of host mortality rate due to this parasite are not currently available. Nonetheless, Gisselson et al. (2002) found that $\sim$ 20% of the *Dinophysis norvegica* present in a declining North Sea bloom

were infected by *P. infectans* and suggested that parasitism was an important loss factor contributing to bloom dissipation.

**Factors regulating parasitism.** Early studies of *Amoebophrya* spp. provided little information about factors that regulate parasite prevalence, but generally implied that high rates of parasitism were often correlated to elevated host abundance (Cachon 1964; Coats et al. 1996; Nishitani et al. 1984; Taylor 1968). By contrast, Nishitani, Erickson, and Chew (1985) argued that high densities of *Alexandrium catenella* were not a prerequisite for high infection prevalence and suggested that low nutrient concentrations (especially phosphorous) may contribute to epidemic outbreaks of *Amoebophrya ceratii*. Recent culture work has shown that success of *Amoebophrya* sp. ex *Akashiwo sanguinea* is enhanced in nutrient-replete media, suggesting that the parasite was well adapted to exploit dinoflagellate populations in nutrient-enriched environments (Yih and Coats 2000). As noted above for fungal parasites, however, nutrient depletion may impact host growth more than parasite success and thus lead to the formation of *Amoebophrya* epidemics. Other abiotic factors including water temperature, light intensity, and salinity may also be important and need to be addressed in the future. Biotic factors, such as microzooplankton grazing on the dispersal, infective zoospores (= dinospores) of *Amoebophrya* (Johansson and Coats 2002; Maranda 2001), can also play important roles in regulating the spread of infections and need further study.

**Influence of parasites on host biology and behavior.** Members of the *Amoebophrya ceratii* complex are lethal parasites that render their hosts reproductively incompetent (Coats and Bockstahler 1994; Elbrächter 1973; Park et al. 2002b), yet little is known about the cellular processes underlying these complex parasite-host interactions. Recently, Park et al. (2002b) showed that host photophysiology was altered following infection by *Amoebophrya*, but the magnitude and timing of changes varied with dinoflagellate species. Shortly after being infected, photosynthesis of *Akashiwo sanguinea* decreased sharply and lost diel periodicity, whereas parasitized *Gymnodinium instriatum* maintain high photosynthetic performance ($\sim$ 80% of uninfected cells) until very late in the infection cycle and continued to show a diel pattern in photosynthesis, albeit less pronounced than that of uninfected cells. Furthermore, *Amoebophrya* had significant impacts on photophysiological properties of host cells, with chlorophyll *a*-specific light absorption coefficients for infected cells enhanced by as much as 22% to 59% relative to uninfected cells, while maximum quantum yield in photosynthesis was reduced by a factor of about 2, particularly in late infection stages. Observed differences in the responses of these dinoflagellates to parasitism was apparently governed by the location of infection (i.e. nuclear in *A. sanguinea* and cytoplasmic in *G. instriatum*).

Laboratory studies have also shown that *Amoebophrya* infections can alter host behavior. For example, swimming velocity of *Akashiwo sanguinea* decreased following infection, with cells containing nearly mature parasites having a swimming speed 37% less than that of uninfected cells (Park et al. 2002a). Host cells also exhibited strong negative phototaxis in the later part of the infection cycle and failed to display diel vertical migration typical of uninfected populations. These behavioral changes may explain the vertical separation of heavily infected and lightly infected populations of *A. sanguinea* in the main stem of Chesapeake Bay and account for the overall low infection levels observed by Coats and Bockstahler (1994). While seemingly disadvantageous to the parasite, behavioral changes leading to reduced infection prevalence may prevent highly virulent algal pathogens like *Amoebophrya* from exterminating host populations and thus provide a mechanism for both the host and the parasite to survive.

Another modification in host behavior that clearly represents a survival strategy has been reported for *Alexandrium ostenfeldii* parasitized by *Parvilucifera infectans* (Toth et al. 2001). The presence of the parasite induces some *A. ostenfeldii* cells to form temporary cysts. The cysts are resistant to the parasite's infective zoospores, but are short-lived and cells are presumably sensitive to infection following germination. Also, cyst formation imposes a metabolic cost on the host which may give a competitive advantage to non-host species, eventually leading to phytoplankton succession.

**Implications for food web processes.** Despite the widespread distribution and potential of eukaryotic parasites to impact microalgal populations, their influence on the structure and function of planktonic food webs has not been directly addressed. Nonetheless, several lines of evidence indicate that parasites like *Amoebophrya* spp. should play important roles in the flow of material within marine food webs, at least in systems where blooms are susceptible to infection. The occurrence of algal blooms reflects the uncoupling of top-down controls in time or space that may result from inhibition of grazing due to production of toxins (Fiedler 1982; Hansen, Cembella and Moestrup 1992; Huntley et al. 1986; Teegarden, Campbell, and Durbin 2001; Tillmann and Uwe 2002), or exploitation of a size-refuge (i.e. to big to be eaten; Granéli et al. 1993). Algal biomass locked in the form of dinoflagellate blooms may be dispersed by winds, currents, and tidal circulation, or may be deposited to subsurface waters and the benthos as algal cells senesce, form cysts, and sink (Falkowski, Hopkins, and Walsh 1980; Steidinger and Vargo 1988; Tester and Steidinger 1997). Alternatively, the spread of parasites through the host population may transform ungrazed algal biomass into resources that can be recycled within the planktonic community. For *Amoebophrya* infections of dinoflagellates, these recycled resources may be in the form of nanoflagellates (i.e. parasite zoospores), host remains, and dissolved organic substances lost from leaky host cells.

As noted earlier, *Amoebophrya* zoospores are readily eaten by microzooplankton, with loss rates due to grazing capable of depressing parasite prevalence (Johansson and Coats 2002; Maranda 2001). Thus, algal species that exert negative influences on zooplankton may bloom as grazing pressure declines, but then become more susceptible to parasitism as grazing on *Amoebophrya* infective stages decreases. Without controls on the spread of infections, *Amoebophrya* may quickly produce epidemics that promote the crash of blooms within days (Coats et al. 1996). As host densities decline, an excess of zoospores (i.e. those not finding new hosts) is produced and available to grazing by existing microzooplankton. The duration of that trophic link, however, would likely be short, as *Amoebophrya* zoospores only survive for hours to days in the absence of host cells (Coats and Park 2002).

The intracellular growth phase of *Amoebophrya* culminates in the releases of a dispersal vermiform stage and a considerable amount of cell debris from the dead host. Some of the host remains can be taken into a vacuole formed by the vermiform and may be digested before formation of zoospores (Cachon 1964). Most host debris, however, is left behind and is subject to bacterial decomposition. The fraction of the host cell used by *Amoebophrya*, relative to that remaining as debris, has only been estimated for infections of *Akashiwo sanguinea* (Yih and Coats 2000). Calculations for parasite gross growth efficiency in that dinoflagellate indicates that 50–70% of host biomass is lost directly to the water as cell debris.

That *Amoebophrya* infections result in the formation of ''gi-

ant cells'' in some dinoflagellates, but not in others, indicates disparity in the ability of different parasite species or strains to utilize host materials. The production of infected cells that are much larger than uninfected individuals indicates that the parasite not only incorporates existing host biomass, but also utilizes carbon fixed by the host following infection. *Amoebophrya* species that fail to generate ''giant cells'' may shut down host photosynthesis early in the infection cycle, as observed for *Akashiwo sanguinea*, or may not incorporate newly fixed carbon as appears to be the case for *Gymnodinium instriatum* (Park et al. 2002b). For host-parasite systems that do not shut down photosynthesis, yet don't form ''giant cells,'' host photosynthate may be lost to the aqueous environment as dissolved organic matter (DOM). Thus, parasitism of phytoplankton may represent an important mechanism for DOM production, paralleling classically recognized processes like phytoplankton exudation (Fogg 1983; Lancelot 1979; Williams 1990), release by protist and zooplankton (Chase and Price 1997; Ferrier-Pagès, Karner, and Rassoulzadegan 1998; Lampert 1978; Nagata 2000; Nagata and Kirchman 1992; Pelegrí et al. 1998; Strom et al. 1997), and production through viral infection (Bratbak et al. 1990; Fuhrman 1992; Gobler et al. 1997; Shibata et al. 1997; Weinbauer and Peduzzi 1995).

Future studies addressing the importance of phytoplankton parasitism need to consider the fate of parasite ''by-products'' and their impacts on microbial processes. Equally important from the stand point of toxic algal blooms is the fate of toxins following infection of the host.

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## LITERATURE CITED

Abeliovich, A. & Dikbuck, S. 1977. Factors affecting infection of *Scenedesmus obliquus* by a *Chytridium* sp. in sewage oxidation ponds. *Appl. Environ. Microbiol.,* **6**:832–836.

Bailey-Watts, A. E. & Lund, J. W. G. 1973. Observations on a diatom bloom in Loch Leven, Scotland. *Biol. J. Linn. Soc.,* **5**:235–253.

Berland, B. R., Maestrini, S. Y. & Grzebyk, D. 1995. Observations on possible life cycle stages of the dinoflagellates *Dinophysis* cf. *acuminate, Dinophysis acuta* and *Dinophysis pavillardi*. *Aquat. Microb. Ecol.,* **9**:183–189.

Blinn, D. W. & Button, K. S. 1973. The effect of temperature on parasitism of *Pandorina* sp. by *Dargeatdia mammillata* B. Schröder in an Arizona mountain lake. *J. Phycol.,* **9**:323–326.

Boltovskoy, A. 1984. Ralacion huesped-parasito entre el quiste de *Peridinium willei* y el oomicete *Aphanomycopsis peridiniella* n. sp. *Limnobios,* **2**:635–645.

Borgert, A. 1898. Beiträge zur Kenntnis in *Sticholonche zanclea* und Acanthometridenarten vorkommenden Parasiten (Spiralköper Fol, *Amoebophrya* Köppen). *Z. Wiss. Zool.* Abstract A, **63**:141–186.

Bratbak, G., Heldal, M., Norland, S. & Thingstad, T. F. 1990. Viruses as partners in spring bloom microbial trophodynamics. *Appl. Environ. Microbiol.,* **56**:1400–1405.

Brugerolle, G. 2002. *Cryptophagus subtilis*: a new parasite of cryptophytes affiliated with the Perkinsozoa lineage. *Europ. J. Protistol.,* **37**:379–390.

Bruning, K. 1991a. Infection of the diatom *Asterionella* by a chytrid. I. Effects of light on reproduction and infectivity of the parasite. *J. Plankton Res.,* **13**:103–117.

Bruning, K. 1991b. Infection of the diatom *Asterionella* by a chytrid. I. Effects of light on survival and epidemic development of the parasite. *J. Plankton Res.,* **13**:119–129.

Bruning, K. 1991c. Effects of phosphorus limitation on the epidemiology of a chytrid phytoplankton parasite. *Freshwater Biol.,* **25**:409–417.

Bruning, K. 1991d. Effect of temperature and light on the population dynamics of the *Asterionella-Rhizophydium* association. *J. Plankton Res.,* **13**:707–719.

Bruning, K. & Ringelberg, J. 1987. The influence of phosphorus limitation of the diatom *Asterionella formosa* on the zoospore production of its fungal parasite *Rhizophydium planktonicum*. *Hydrobiol. Bulletin,* **21**:49–54.

Brussaard, C. P. D. 2004. Viral control of phytoplankton populations—a review. *J. Eukaryot. Microbiol.,* **51**:125–138.

Bütschli, O. 1883–1887. Protozoa. Abtheilung II. Mastigophora. *In*: Bronn, H. G. (ed.), Klassen und Ordungen des Thier-Reichs. C. F. Winter, Leipzig. **1**:617–1097.

Cachon, J. 1964. Contribution à l'étude des péridiniens parasites. Cytologie, cycles évolutifs. *Ann. Sci. Nat. Zool.,* **6**:1–158.

Cachon, J. & Cachon, M. 1987. Parasitic dinoflagellates. *In*: Taylor, F. J. R. (ed.), The Biology of Dinoflagellates. Blackwell Sci. Publ., Oxford. p. 571–610.

Cachon, J., Cachon, M. & Bouquaheux, F. 1969. *Myxodinium pipiens* gen. nov., sp. nov., péridinien parasite d'*Halosphaera*. *Phycologia,* **8**:157–164.

Canter, H. M. 1972. A guide to the fungi occurring on planktonic blue-green algae. *In*: Desikachary, T. V. (ed.), Proceedings of the Symposium on Taxonomy and Biology of Blue-green Algae. Madras, University of Madras. p. 148–158.

Canter, H. M. & Heaney, S. I. 1984. Observations on zoosporic fungi of *Ceratium* spp. in lakes of the English Lake District: Importance for phytoplankton population dynamics. *New Phytol.,* **97**:601–612.

Canter, H. M. & Jaworski, G. H. M. 1978. The isolation, maintenance, and host-range studies of a chytrid *Rhizophydium planktonicum* Canter emend., parasitic on *Asterionella formosa* Hassall. *Ann. Bot.,* **42**:967–979.

Canter, H. M. & Jaworski, G. H. M. 1981. The effect of light and darkness upon infection of *Asterionella formosa* Hassall by the chytrid *Rhizophydium planktonicum* Canter emend. *Ann. Botany,* **47**:13–30.

Canter, H. M. & Jaworski, G. H. M. 1982. Some observations on the alga *Fragilaria crotonensis* Kitton and its parasitism by two chytridiaceous fungi. *Ann. Bot.,* **49**:429–446.

Canter, H. M. & Lund, J. W. G. 1948. Studies on plankton parasites. I. Fluctuations in the numbers of *Asterionella formosa* Hass. in relation to fungal epidemics. *New Phytol.,* **47**:238–261.

Canter, H. M. & Lund, J. W. G. 1951. Studies on plankton parasites. III. Examples of the interaction between parasitism and other factors determining the growth of diatoms. *Ann. Bot.,* **15**:359–371.

Canter, H. M. & Lund, J. W. G. 1953. Studies on plankton parasites. II. The parasitism of diatoms with special reference to lakes in the English Lake District. *Trans. British Mycol. Soc.,* **36**:13–37.

Canter, H. M. & Lund, J. W. G. 1969. The parasitism on planktonic desmids by fungi. *Österr. Bot. Z.,* **116**:351–377.

Chase, Z. & Price, N. M. 1997. Metabolic consequences of iron deficiency in heterotrophic marine protozoa. *Limnol. Oceanogr.,* **42**:1673–1684.

Chatton, É. & Biecheler, B. 1934. Les Coccidinidae, Dinoflagellés coccodiomorphes parasites de Dinoflagellés, et le phylum des Phytodinozoa. *C. R. Acad. Sci., Paris,* **199**:252–255.

Chatton, É. & Biecheler, B. 1935. Les *Amoebophrya* et les *Hyalosaccus*: leur cycle évolutif. L'ordre nouveau des Coelomastigines dans les Flagellés. *C. R. Acad. Sci., Paris,* **200**:505–507.

Chatton, É. & Biecheler, B. 1936. Documents nouveaux relatifs aux Coccidinides (Dinoflagellés parasites). La sexualité du *Coccidinium mesnili* n. sp. *C. R. Acad. Sci., Paris,* **203**:573–576.

Coats, D. W. 1999. Parasitic life styles of marine dinoflagellates. *J. Eukaryot. Microbiol.,* **46**:402–409.

Coats, D. W. & Bockstahler, K. R. 1994. Occurrence of the parasitic dinoflagellate *Amoebophrya ceratii* in Chesapeake Bay populations of *Gymnodinium sanguineum*. *J. Eukaryot. Microbiol.,* **41**:586–593.

Coats, D. W. & Heisler, J. J. 1989. Spatial and temporal occurrence of

the parasitic dinoflagellate *Duboscquella cachoni* and its tintinnine host, *Eutintinnus pectinis*, in Chesapeake Bay. *Mar. Biol.,* **101**:401–409.

Coats, D. W. & Park, M. G. 2002. Parasitism of photosynthetic dinoflagellates by three strains of *Amoebophrya* (Dinophyta): parasite survival, infectivity, generation time, and host specificity. *J. Phycol.,* **38**: 520–528.

Coats, D. W., Adam, E. J., Gallegos, C. L. & Hedrick, S. 1996. Parasitism of photosynthetic dinoflagellates in a shallow subestuary of Chesapeake Bay, USA. *Aquat. Microb. Ecol.,* **11**:1–9.

Coats, D. W., Bockstahler, K. R., Berg, G. M. & Sniezek, J. H. 1994. Dinoflagellate infections of *Favella panamensis* from two North American estuaries. *Mar. Biol.,* **119**:105–113.

Delgado, M. 1999. A new ''diablillo parasite'' in the toxic dinoflagellate *Alexandrium catenella* as a possibility to control harmful algal blooms. *Harmful Algae News,* **19**:1–3.

Doggett, M. S. & Porter, D. 1995. Further evidence for host-specificity variants in *Zygorhizidium planktonicum*. *Mycologia,* **87**:161–171.

Doucette, G. J., Kodama, M., Franca, S. & Gallacher, S. 1998. Bacterial interactions with harmful algal bloom species: bloom ecology, toxigenesis, and cytology. *In*: Anderson, D. M., Cembella, A. D. & Hallegraeff, G. M. (ed.), Physiological Ecology of Harmful Algal Blooms. NATO ASI Series G: Ecological Sciences, Vol. 41. Springer-Verlag, Heidelberg. p. 619–47.

Drebes, G. & Schnepf, E. 1982. Phagotrophy and development of *Paulsenella* cf. *chaetoceratis* (Dinophyta), an ectoparasite of the diatom *Streptotheca thamesis*. *Helgoländer Meeresunters.,* **35**:501–515.

Drebes, G. & Schnepf, E. 1988. *Paulsenella* Chatton (Dinophyta), ectoparasite of marine diatoms: development and taxonomy. *Helgoländer Meeresunters.,* **42**:563–581.

Elbrächter, M., 1973. Population dynamics of *Ceratium* in coastal waters of the Kiel Bay. *Oikos* (Suppl.), **15**:43–48.

Elbrächter, M. & Schnepf, E. 1998. Parasites of harmful algae. *In*: Anderson, D. M., Cembella, A. D. & Hallegraeff, G. M. (ed.), Physiological Ecology of Harmful Algal Blooms. NATO ASI Series G: Ecological Sciences, Vol. 41. Springer-Verlag, Heidelberg. p. 351–369.

Erard-Le Denn, E., Chrétiennot-Dinet, J.-M. & Probert, I. 2000. First report of parasitism on the toxic dinoflagellates *Alexandrium minutum* Halim. *Estuar. Coast. Shelf Sci.,* **50**:109–113.

Falkowski, P. G., Hopkins, T. S. & Walsh, J. J. 1980. An analysis of factors affecting oxygen depletion in the New York Bight. *J. Mar. Res.* **38**:479–506.

Ferrier-Pagès, C., Karner, M. & Rassoulzadegan, F. 1998. Release of dissolved amino acids by flagellates and ciliates grazing on bacteria. *Oceanol. Acta,* **21**:485–494.

Fiedler, P. C. 1982. Zooplankton avoidance and reduced grazing responses to *Gymnodinium splendens* (Dinophyceae). *Limnol. Oceanogr.,* **27**:961–965.

Fogg, G. E., 1983. The ecological significance of extracellular products of phytoplankton photosynthesis. *Bot. Mar.,* **26**:3–14.

Franca, S. 1976. On the presence of virus-like particles in the dinoflagellate *Gyrodinium resplendens* (Hulburt). *Protistologica,* **12**:425–430.

Fritz, L. & Nass, M. 1992. Development of the endoparasitic dinoflagellate *Amoebophrya ceratii* within host dinoflagellate species. *J. Phycol.,* **28**:312–320.

Fuhrman, J., 1992. Bacterioplankton roles in cycling of organic matter: the microbial food web. *In*: Falkowski, P. G. & Woodhead, D. (ed.), Primary Productivity and Biogeochemical Cycles in the Sea. Plenum Press, New York. p. 361–383.

Gárate Lizárraga, I. & Siqueiros-Beltrones, D. A. 2003. Infections of *Ceratium furca* by the parasitic dinoflagellate *Amoebophrya ceratii* (Amoebophryidae) in the Mexican Pacific. *Acta Bot. Mex.,* **65**:1–9.

Gisselson, L. Å., Carlsson, P., Granéli, E. & Pallon, J. 2002. *Dinophysis* blooms in the deep euphotic zone of the Baltic Sea: do they grow in the dark? *Harmful Algae,* **1**:401–418.

Gobler, C. J., Hutchins, D. A., Fisher N. S., Cosper E. M. & Sanudo-Wilhelmy, S. A. 1997. Release and bioavailability of C, N, P, Se, and Fe following viral lysis of a marine chrysophyte. *Limnol. Oceanogr.,* **42**:1492–1504.

Granéli, E., Olsson, P., Carlsson, P., Granéli, W. & Nylander, C. 1993. Weak 'top-down' control of dinoflagellate growth in the coastal Skagerrak. *J. Plank. Res.,* **15**:213–237.

Gunderson, J. H., Goss, S. H. & Coats, D. W. 2001. FISH probes for the detection of the parasitic dinoflagellate *Amoebophrya* sp. infecting the dinoflagellate *Akashiwo sanguinea* in Chesapeake Bay. *J. Eukaryot. Microbiol.,* **48**:670–675.

Gunderson, J. H., John, S. A., Boman, W. C., II & Coats, D. W. 2002. Multiple strains of the parasitic dinoflagellate *Amoebophrya* exist in Chesapeake Bay. *J. Eukaryot. Microbiol.,* **49**:469–474.

Hansen, P. J., Cembella, A. D. & Moestrup, Ø. 1992. The marine dinoflagellate *Alexandrium ostenfeldii*: paralytic shellfish toxin concentration, composition, and toxicity to a tintinnid ciliate. *J. Plankton Res.,* **28**:597–603.

Heaney, S. I., Lund, J. W. G., Canter, H. M. & Gray, K. 1988. Population dynamics of *Ceratium* spp. in three English lakes, 1945–1985. *Hydrobiology,* **161**:133–148.

Holfeld, H. 1998. Fungal infections of the phytoplankton: seasonality, minimal host density, and specificity in a mesotrophic lake. *New Phytol.,* **138**:507–517.

Huntley, M., Sykes, P., Marin, V. & Rohan, S. 1986. Chemically-mediated rejection of dinoflagellate prey by copepods *Calanus pacificus* and *Paracalanus parvus*: mechanism, occurrence, and significance. *Mar. Ecol. Prog. Ser.,* **28**:105–120.

Jacobson, D. M. 1987. The ecology and feeding biology of thecate heterotrophic dinoflagellates. Dissertation. Woods Hole Oceanographic Institution-Massachusetts Institute of Technology Joint Program. 210 pp. Available on microfilms from University of Michigan Accession Number 101132.

Janson, S. L., Gisselson, P.S., Salomon, P. S. & Granéli, E. 2000. Evidence for multiple species within the endoparasitic dinoflagellate *Amoebophrya ceratii* as based on 18S rRNA gene-sequence analysis. *Parasitol. Res.,* **86**:929–933.

Johansson, M. & Coats, D. W. 2002. Ciliate grazing on the parasite *Amoebophrya* sp. decreases infection of the red-tide dinoflagellate *Akashiwo sanguinea*. *Aquat. Microb. Ecol.,* **28**:69–78.

Kim, Y. G., Park, M. G. & Yih, W. H. 2002. Host-parasite system in a red tide dinoflagellate *Prorocentrum minimum*: (1) Life cycle stages of the parasitic dinoflagellate *Amoebophrya* sp. The Sea, *J. Korean Soc. Oceanogr.,* **7**:221–225.

Kirchner, M., Sahling, G., Schütt, C., Döpke, H & Uhlig, G. 1999. Intracellular bacteria in the red tide-forming heterotrophic dinoflagellate *Noctiluca scintillans*. *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.,* **54**:297–310.

Koob, D. D. 1966. Parasitism of *Asterionella formosa* Hass. by a chytrid in two lakes of the Rawah Wild Area of Colorado. *J. Phycol.,* **2**:41–45.

Koeppen, N. 1894. *Amoebophrya stycholonchae* nov. gen. et sp. ''corps spiral'' de Fol. *Zool. Anz.,* **17**:417–424.

Koeppen, N. 1903. *Hyalosaccus ceratii* nov. gen., nov. sp., parasit Dinoflagellat'. *Zapiski Kiev. Obshch.,* **16**:89–135.

Kofoid, C. A. & Swezy, O. 1921. The Free-Living Unarmored Dinoflagellata. Memoirs of the University of California. Vol 5. Univ. California Press, Berkeley.

Kudoh, S. & Takahashi, M. 1990. Fungal control of population changes of the planktonic diatom *Asterionella formosa* in a shallow eutrophic lake. *J. Phycol.,* **26**:239–244.

Kudoh, S. & Takahashi, M. 1992. An experimental test of host population-size control by fungal parasitism in the planktonic diatom *Asterionella formosa* using mesocosms in a natural lake. *Arch. Hydrobiol.,* **124**:293–307.

Küpper, F. C. & Müller, D. G. 1999. Massive occurrence of the heterokont and fungal parasites *Anisolpidium*, *Eurychasma*, and *Chytridium* in *Pylaiella littoralis* (Ectocarpales, Phaeophyceae). *Nov. Hedw.,* **69**:381–389.

Lampert, W. 1978. Release of dissolved organic carbon by grazing zooplankton. *Limnol. Oceanogr.,* **23**:831–834.

Lancelot, C. 1979. Gross excretion rates on natural marine phytoplankton and heterotrophic uptake of excreted products in the southern North Sea, as determined by short-term kinetics. *Mar. Ecol. Prog. Ser.,* **1**:179–186.

Lebour, M. V. 1917. The Peridiniales of Plymouth Sound from the region beyond the breakwater. *J. Mar. Biol. Assoc. U. K.,* **11**:183–200.

Lebour, M. V. 1925. The Dinoflagellates of Northern Seas. The Mayflower Press, William Brendon & Son, Ltd., Plymouth.

Maranda, L. 2001. Infection of *Prorocentrum minimum* (Dinophyceae) by the parasite *Amoebophrya* sp. (Dinoflagellea). *J. Phycol.,* **37**:245–248.

Masters, M. J. 1971. The ecology of *Chytridium deltanum* and other fungus parasites on *Oocystis* spp. *Canadian J. Bot.,* **49**:75–87.

Müller, D. G., Küpper, F. C. & Küpper, H. 1999. Infection experiments reveal broad host range of *Eurychasma dicksoni* (Oomycota) and *Chytridium polysiphoniae* (Chytridiomycota), two eukaryotic parasites in marine brown algae (Phaeophyceae). *Phycol. Res.,* **47**:217–223.

Nagasaki, K., Tomaru, Y., Tarutani, K., Katanozaka, N., Yamanaka, S., Tanabe, H. & Yamaguchi, M. 2003. Growth characteristics and interspecies host specificity of a large virus infecting the dinoflagellate *Heterocapsa circulaisquama*. *Applied Environ. Microb.,* **69**:2580–2586.

Nagata, T. & Kirchman, D. L. 1992. Release of dissolved organic matter by heterotrophic protozoa: implications for microbial food webs. *Arch. Hydrobiol. Beih. Ergebn. Limnol.,* **35**:99–109.

Nagata, T. 2000. Production mechanisms of dissolved organic matter. *In*: Kirchman, D. L. (ed.), Microbial Ecology of the Oceans. Wiley-Liss, Inc., New York. p. 121–152.

Nishitani, L., Erickson, G. & Chew, K. K. 1985. Role of the parasitic dinoflagellate *Amoebophrya ceratii* in control of *Gonyaulax catenella* populations. *In*: Anderson, D. M., White, A. W. & Baden, D. G. (ed.), Toxic Dinoflagellates. Elsevier Sci. Publ. Co., Inc., New York. p. 225–230.

Nishitani, L., Hood, R., Wakeman, J. & Chew, K. K. 1984. Potential importance of an endoparasite of *Gonyaulax* in paralytic shellfish poisoning outbreaks. *In*: Ragelis, E. P. (ed.), Seafood Toxins. *ACS Symposium Ser.,* **262**:139–149.

Norén, F. 2002. Factors regulating planktonic dinoflagellate populations, with special emphasis on the parasitic dinoflagellate *Parvilucifera infectans*. Dissertation. Department of Marine Ecology, Göteborg University, Sweden. 83 p. ISBN 91-89677-00-5.

Norén, F., Moestrup, Ø. & Rehnstam-Holm, A.-S. 1999. *Parvilucifera infectans* Norén et Moestrup gen. et sp. nov. (Perkinsozoa phylum nov.): a parasitic flagellate capable of killing toxic microalgae. *Europ. J. Protistol.,* **35**:233–254.

Norén, F., Moestrup, Ø., Rehnstam-Holm, A.-S. & Larsen, J. 2000. Worldwide occurrence and host specificity of *Parvilucifera infectans*: a parasitic flagellate capable of killing toxic dinoflagellates. *In*: Hallegraeff, G. M., Blackburn, S. I., Bolch, C. J. & Lewis, R. J. (ed.), Harmful Algal Blooms 2000. Intergovernmental Oceanographic Commission of UNESCO 2001. p. 481–483.

Park, M. G., Cooney, S. K., Kim, J. S. & Coats, D. W. 2002a. Effects of parasitism on diel vertical migration, phototaxis/geotaxis, and swimming speed of the bloom-forming dinoflagellate *Akashiwo sanguinea*. *Aquat. Microb. Ecol.,* **29**:11–18.

Park, M. G., Cooney, S. K., Yih, W. H. & Coats, D. W. 2002b. Effects of two strains of the parasitic dinoflagellate *Amoebophrya* on growth, photosynthesis, light absorption, and quantum yield of bloom-forming dinoflagellates. *Mar. Ecol. Prog. Ser.,* **227**:281–292.

Pelegrí, S. P., Christaki, U., Dolan, J. & Rassoulzadegan, F. 1998. Particulate and dissolved organic carbon production by the heterotrophic nanoflagellate *Pteridomonas danica*, Patterson and Fenchel 1985, fed *Escherichia coli*. *Microb. Ecol.,* **37**:276–284.

Pongratz, E. 1966. De quelques champignons parasites d'organismes planctoniques du Léman. *Schweizer Zeitung Hydrologie Rev. Suisse d'Hydrologie,* **28**:104–132.

Pouchet, G., 1885. Nouvelle contribution à l'histoire des *Péridiniens marins*. *J. Anat. Physiol.,* Paris, **21**:28–88.

Proctor, L. M. 1997. Advances in the study of marine viruses. *Microsc. Res. Tech.,* **37**:136–161.

Raghukumar, S. 2002. Ecology of the marine protists, the Labyrinthulomycetes (Thraustochytrids and Labyrinthulids). *Europ. J. Protistol.,* **38**:127–145.

Reynolds, C. S. 1973. The seasonal periodicity of planktonic diatoms in a shallow eutrophic lake. *Freshwater Biol.,* **3**:89–110.

Reynolds, C. S. 1984. The Ecology of Freshwater Phytoplankton. Cambridge Studies in Ecology. Cambridge Univ. Press, Cambridge.

Salomon, P. S., Janson, S. & Granéli, E. 2003. Parasitism of *Dinophysis norvegica* by *Amoebophrya* sp. in the Baltic Sea. *Aquat. Microb. Ecol.,* **33**:163–172.

Sen, B. 1987. Fungal parasitism of planktonic algae in Shearwater. I. Occurrence of *Zygorhizidium affluens* Canter on *Asterionella formosa* Hass. in relation to the seasonal periodicity of the alga. *Archiv Hydrobiol.* (Suppl.), **76**:101–127.

Sen, B. 1988a. Fungal parasitism of planktonic algae in Shearwater. IV. Parasitic occurrence of a new chytrid species of the blue-green alga *Microcystis aerigunosa* Kuetz. emend. Elenkin. *Archiv Hydrobiol.* (Suppl.), **79**:177–184.

Sen, B. 1988b. Fungal parasitism of planktonic algae in Shearwater. V. Fungal parasites of the green algae. *Archiv Hydrobiol.* (Suppl.), **79**: 185–205.

Sengco, M. R., Coats, D. W., Popendorf, K. J., Erdner, D. L., Gribble, K. E. & Anderson, D. M. 2003. Biological and phylogenetic characterization of *Amoebophrya* sp. ex *Alexandrium tamarense*. Abstract. Second Symposium on Harmful Marine Algae in the U.S. p. 57.

Shibata, A., Kogure, K., Koike, I. & Ohwada, K. 1997. Formation of submicron colloidal particles from marine bacteria by viral infection. *Mar. Ecol. Prog. Ser.,* **155**:303–307.

Shields, J. D. 1994. The parasitic dinoflagellates of marine crustaceans. *Ann. Rev. Fish Dis.,* **4**:241–271.

Shin, E.-Y. 1999. A taxonomical study on the thecate dinoflagellates of Korean coastal waters. Dissertation. Department of Oceanography, Seoul National University, Korea. 240 p.

Sicko-Goad, L. & Walker, G. 1979. Viroplasm and large virus-like particles in the dinoflagellate *Gymnodinium uberrium*. *Protoplasma,* **99**:203–210.

Silva, E. S. 1978. Endonuclear bacteria in two species of dinoflagellates. *Protistologica,* **14**:113–119.

Silva, E. S. 1990. Intracellular bacteria: the origin of dinoflagellate toxicity. *JEPTO,* **10**:124–128.

Silva, E. S. & Franca, S. 1985. The association dinoflagellate-bacteria: their ultrastructural relationship in two species of dinoflagellates. *Protistologica,* **21**:429–446.

Sommer, U., Wedemeyer, C. & Lowsky, B. 1984. Comparison of potential growth rates of *Ceratium hirundinella* with observed population density changes. *Hydrobiologia,* **109**:159–164.

Soyer, M. O. 1978. Particules de type viral et filaments trichocystoides chez les Dinoflagelles. *Protistologica,* **14**:53–58.

Steidinger, K. A. & Vargo, G. A. 1988. Marine dinoflagellate blooms: dynamics and impacts. *In*: Lembi, C. A. & Wunland, J. R. (ed.), Algae and Human Affairs. Cambridge Univ. Press, Cambridge. p. 373–401.

Strom, S. L., Benner, R., Ziegler, S. & Dagg, M. J. 1997. Planktonic grazers are a potentially important source of marine dissolved organic carbon. *Limnol. Oceanogr.,* **42**:1364–1374.

Tarutani, K., Nagasaki, K., Itakura, S. & Yamaguchi, M. 2001. Isolation of a virus infecting the novel shellfish-killing dinoflagellate *Heterocapsa circularisquama*. *Aquat. Microb. Ecol.,* **23**:103–111.

Taylor, F. J. R. 1968. Parasitism of the toxin-producing dinoflagellate *Gonyaulax catenella* by the endoparasitic dinoflagellate *Amoebophrya ceratii*. *J. Fish. Res. Bd. Canada,* **25**:2241–2245.

Teegarden, G. J., Campbell, R. G. & Durbin, E. G. 2001. Zooplankton feeding behavior and particle selection in natural plankton assemblages containing toxic *Alexandrium* spp. *Mar. Ecol. Prog. Ser.,* **218**: 213–226.

Tester, P. A. & Steidinger, K. A. 1997. *Gymnodinium breve* red tide blooms: initiation, transport, and consequences of surface circulation. *Limnol. Oceanogr.,* **42**:1023–1038.

Tillmann, U. & Uwe, J. 2002. Toxic effects of *Alexandrium* spp. on heterotrophic dinoflagellates: an allelochemical defense mechanism independent of PSP-toxin content. *Mar. Ecol. Prog. Ser.,* **230**:47–58.

Toth, G., Norén, F., Selander, E. & Pavia, H. 2001. Parasite-induced morphological defense in a dinoflagellate through water-borne chemical cues. Abstract 189. *Phycologia,* **40**(Suppl.):59.

Uppalapati, S. R. & Fujita, Y. 2000. Carbohydrate regulation of attachment, encystment, and appressorium formation by *Pythium porphyae* (Oomycota) zoospores on *Porphyra yezoensis* (Rhodophyta). *J. Phycol.,* **36**:359–366.

van Donk, E. 1989. The role of fungal parasites in phytoplankton suc-

cession. *In*: Sommer, U. (ed.), Plankton Ecology. Springer-Verlag, Berlin. p. 171–194.
van Donk, E. & Bruning, K. 1995. Effects of fungal parasites on planktonic algae and the role of environmental factors in the fungus-alga relationship. *In*: Wiessner, W., Schnepf, E. & Starr, R. (ed.), Algae, Environment and Human Affairs. Biopress Ltd., Bristol. p. 223–234.
van Donk, E. & Ringelberg, J. 1983. The effect of fungal parasitism on the succession of diatoms in Lake Maarsseveen (The Netherlands). *Freshwater Biol.,* **13**:241–251.
Wakeman, J. S. & Nishitani, L. 1981. Growth and decline of *Gonyaulax catenella* bloom associated with parasitism. *J. Shellfish Res.,* **2**:122.
Weinbauer, M. G. & Peduzzi, P. 1995. Effect of virus-rich high molecular weight concentrates of seawater on the dynamics of dissolved amino acids and carbohydrates. *Mar. Ecol. Prog. Ser.,* **127**:245–253.
Williams, P. J. leB. 1990. The importance of losses during microbial growth: commentary on the physiology, measurement, and ecology of the release of dissolved organic material. *Mar. Microb. Food Webs,* **4**:175–206.
Wilson, W. H., Francis, I., Ryan, K. & Davy, S. K. 2001. Temperature induction of viruses in symbiotic dinoflagellates. *Aquat. Microb. Ecol.,* **25**:99–102.
Yih, W. & Coats, D. W. 2000. Infection of *Gymnodinium sanguineum* by the dinoflagellate *Amoebophrya* sp.: Effect of nutrient environment on parasite generation time, reproduction, and infectivity. *J. Eukaryot. Microbiol.,* **47**:504–510.
Youngman, R. E., Johnson, D. & Farley, M. R. 1976. Factors influencing phytoplankton growth and succession in Farmoor Reservoir. *Freshwater Biol.,* **6**:253–263.

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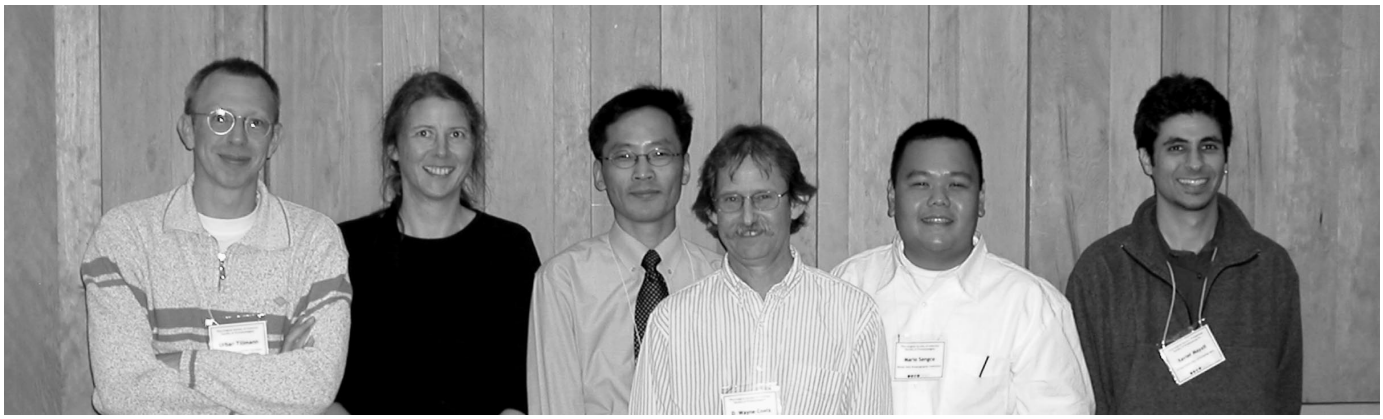

Participants in the symposium on ″Controls of Planktonic Microalgae″. From left to right: Urban Tillmann, Corina Brussaard, Myung Gil Park, Wayne Coats (convener), Mario Sengco, and Xavier Mayali.