14 Phagotrophy in Harmful Algae

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14.1 Introduction

The contributions of phagotrophy to bloom formation and toxicity of harmful algae have not received much attention, although phagotrophy is common among toxic and/or red-tide dinoflagellates and haptophytes (Figs. 14.1 and 14.2). Ingestion of prey can dramatically increase the growth rate of some harmful algae (Li et al. 1999; Jeong et al. 2004, 2005a, 2005b). Predation on competitors or potential grazers may contribute to the ability of some HAB species to form dense, mono-specific blooms (Legrand et al. 1998; Granéli and Johansson 2003b). In some species, grazing may be related to toxicity (Tillmann 2003; Skovgaard and Hansen 2003).

Some toxic dinoflagellates are strict heterotrophs (*Protoperidinium crassipes*) or heterotrophs with a limited capacity for mixotrophy (*Pfiesteria piscicida*, *P. shumwayae*) (Jeong and Latz 1994; Burkholder et al. 2001; Glasgow et al. 2001). Most harmful dinoflagellates are plastidic, bloom-forming species that traditionally have been regarded as photoautotrophs, but evidence is accumulating that many can ingest other cells. Some are harmful because they contain toxins and others because they form high-biomass blooms that disrupt food webs. There is evidence for phagotrophy in many toxic and/or red-tide planktonic dinoflagellates including *Akashiwo sanguinea* (=*Gymnodinium sanguineum*) (Bockstahler et al. 1993; Jeong et al. 2005a), *Alexandrium ostenfeldii* and *A. tamarense* (Jacobson and Anderson 1996; Jeong et al. 2005a), *Ceratium furca* (Smalley et al. 2003), *Cochlodinium polykrikoides* (Jeong et al. 2004), *Dinophysis acuminata*, *D. norvegica* (Jacobson and Andersen 1994; Gisselson et al. 2002), *Gonyaulax polygramma* (Jeong et al. 2005b), *Gymnodinium catenatum*, *G. impudicum*, (Jeong et al. 2005a), *Heterocapsa triquetra* (Legrand et al. 1998; Jeong et al. 2005a), *Karlodinium micrum* (=*Gyrodinium galatheanum*) (Li et al. 2000), *Lingulodinium polyedra* (Jeong et al. 2005a), *Prorocentrum donghaiense*, *P. triestinum*, *P. micans* and *P. minimum* (Jeong et al. 2005a), *Protoceratium reticulatum* (Jacobson and Anderson 1996) and *Scrippsiella trochoidea* (Jeong et al. 2005a). There is also evidence for

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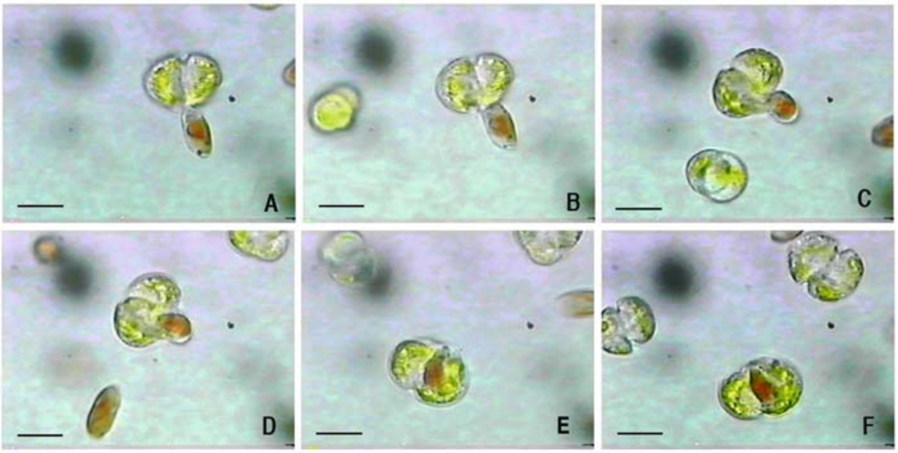

Fig. 14.1. Sequence showing a cell of *Karlodinium micrum* feeding on a cryptophyte alga

Fig. 14.2. Three *Prymnesium parvum* cells catching and preying on a cell of the larger species *Heterocapsa triquetra. Scale bars* 10 µm

phagotrophy in the toxic benthic dinoflagellates *Gambierdiscus toxicus*, *Ostreopsis lenticularis*, *O. ovata*, *O. siamensis*, and *Prorocentrum arenarium* and *P. belizeanum* (Faust 1998) (Table 14.1).

Among the toxic haptophytes, phagotrophy is known in *Chrysochromulina leadbeateri*, *C. polylepis and Prymnesium parvum* (including *P. parvum* f. *patelliferum*) (Johnsen et al. 1999; Jones et al. 1993; Tillmann 1998, 2003) (Table 14.2). In addition to *Chrysochromulina leadbeateri* and *C. polylepis*, whose toxic potential seems to be well established, three other species of *Chrysochromulina* (*C. brevifilum*, *C. kappa*, *C. strobilus*) were found to be toxic to the bryozoan *Electra pilosa* when given as the only food source (Jebram 1980). All these, at least potentially toxic species, have been shown to be phagotrophic as well (Parke et al. 1955, 1959; Jones et al. 1993). Other families

Table 14.1. Evidence for phagotrophy in harmful dinoflagellate species

Species	Evidence for Phagotrophy[a]	References
Alexandrium ostenfeldii	Obs. of food vacuoles with electron microscopy	Jacobsen and Anderson 1996
Alexandrium tamarense	Uptake of radio-labeled bacteria; Obs. of bacteria and flagellates inside cell; Observations of food vacuoles containing algal cells	Nygaard and Tobiesen 1993; Sorokin et al. 1996; Jeong et al. 2005
Cochlodinium polykrikoides	Obs. of feeding and measurement of ingestion of small cryptophytes and other small phytoflagellates	Jeong et al. 2004
Dinophysis acuminata	Obs. of food vacuoles with light and electron microscopy	Jacobsen and Andersen 1994
Dinophysis norvegica	Obs. of food vacuoles with light and electron microscopy	Jacobsen and Andersen 1994; Gisselson et al. 2002
Gambierdiscus toxicus	Obs. of food vacuoles with light microscopy	Faust 1998
Gymnodinium catenatum	Observations of food vacuoles containing algal cells	Jeong et al. 2005
Karlodinium micrum (syn.=*Gyrodinium galatheanum*, *Gymnodinium galatheanum*)	Obs. of feeding on cryptophytes and feeding and growth experiments	Li et al. 1999
Lingulodinium polyedra[b]	Obs. of feeding and of food vacuoles containing algal cells, feeding and growth experiments	Jeong et al. 2005
Ostreopsis lenticularis, O. ovata, O. siamensis	Obs. of food vacuoles with light microscopy	Faust 1998
Pfiesteria piscicida. P. shumwayae	Primarily heterotrophic; obs. of feeding on cryptophytes, other protists and fish tissues; grazing and growth experiments	Burkholder et al. 2001, Lin et al. 2004
Prorocentrum arenarium, *P. belizeanum,* *P. hoffmannianum*	Obs. of food vacuoles with light microscopy	Faust 1998
Prorocentrum minimum (syn.=*P. cordatum*)	Obs. of food vacuoles with ingested cryptophyte material; feeding experiments; obs. of food vacuoles containing algal cells	Stoecker et al. 1997, Jeong et al. 2005
Protoceratium reticulatum (syn.=*Peridinium reticulatum, Gonyaulax grindleyi)*	Obs. of food vacuoles	Jacobson and Anderson 1996
Protoperidinium crassipes	Heterotroph; preys on other dinoflagellates	Jeong and Latz (1994)

[a] Obs. = observation(s)

[b] Not on IOC Taxonomic Reference List of Toxic Algae (Moestrup 2004) but toxic (Steidinger and Tangen 1997)

Table 14.2. Evidence for phagotrophy in harmful haptophyte species

Species	Evidence for phagotrophy	Reference
Chrysochromulina leadbeateri	Ingestion of FLA	Johnsen et al. 1999; Legrand pers. com
Chrysochromulina polylepis	Ingestion of bacteria, small particles and small protists	Manton and Parke 1962; Jones et al. 1993; Nygaard and Tobiesen 1993
Prymnesium parvum f. *parvum* f. *patelliferum*	Feeding measurement of bacteria, observation and measurements of ingestion of various protists	Nygaard and Tobiesen 1993; Tillmann 1998; Legrand et al. 2001; Skovgaard et al. 2003

containing harmful eukaryotic phytoplankton are the diatoms, raphidophytes, and pelagophytes. The ability to ingest other cells is probably lacking in vegetative cells of diatoms due to their valve structure. Nygaard and Tobiesen (1993) measured uptake of radio-labeled bacteria by the toxic raphidophyte, *Heterosigma akashiwo*, but this is the only report of phagotrophy in this family. Phagotrophy has not been reported in the pelagophytes responsible for brown tides. The prokaryotic cyanobacteria also cause harmful blooms, but are not phagotrophic.

Feeding may go undetected in many species because it is sporadic and because the presence of plastids can make food vacuoles difficult to observe. Most, but not all, mixotrophic flagellates can be grown in the absence of prey, and thus their capacity to ingest other cells is often overlooked. More harmful algal species will probably be added to the list of phagotrophs.

14.2 Phagotrophy and its Advantages

Ingestion of prey supports the growth of harmful heterotrophic dinoflagellates, including *Protoperidinium crassipes* (Jeong and Latz 1994) and *Pfiesteria* spp. (Burkholder et al. 2001; Glasgow et al. 2001). *P. crassipes* feeds on other dinoflagellates, including toxic *Lingulodinium polyedra* (Jeong and Latz 1994). Although *Pfiesteria* spp. can retain cryptophyte plastids for short periods, they are mostly heterotrophic and use a peduncle to feed on prey ranging in size from bacteria to fish tissues (Burkholder et al. 2001). The maintenance cost for such a feeding apparatus is calculated to be low compared to the costs for maintaining photosynthetic apparatus (Raven 1997), which may explain the relatively high growth rates of small heterotrophic harmful algae such as *Pfiesteria* compared to their more autotrophic relatives.

The advantages of phagotrophy for photosynthetic algae are diverse (Stoecker 1998, 1999). Most dinoflagellates and haptophytes can grow strictly autotrophically, but some species of dinoflagellates (for example, *Karlodinium micrum, Cochlodinium polykrikoides, Gonyaulax polygramma, Lingulodinium polyedra*) grow much faster with prey than strictly autotrophically (Li et al. 1999; Jeong et al. 2004, 2005a, 2005b). Phagotrophy can make an important contribution to C, N and P budgets in these species. In contrast, although some haptophytes ingest prey when light and inorganic nutrients are sufficient (Skovgaard et al. 2003), growth rates with and without prey are usually similar (Larsen et al. 1993; Pintner and Provasoli 1968). An exception to this generalization is that the simultaneous addition of small diatoms and bacteria can enhance the growth of *Prymnesium parvum* even in nutrient-replete media (Martin-Cereceda et al. 2003).

Some phagotrophic dinoflagellates only feed (or feed at higher rates) when they are P or N limited, but not when they are C or light limited (Li et al. 1999, 2000; Smalley et al. 2003). In the bloom-forming dinoflagellate *Ceratium furca*, internal nutrient ratios (C:P and N:P) regulate feeding, which is induced when cellular ratios deviate from optimum due to N or P limitation (Smalley et al. 2003). In many haptophytes, phagotrophy is also stimulated by nutrient limitation. Both *Prymnesium parvum* and *Chrysochromulina polylepis* have been shown to ingest more bacteria under phosphate deficiency than nutrient-replete conditions (Nygaard and Tobiesen 1993; Legrand et al. 2001). However, ingestion of algal prey (*Rhodomonas baltica*) by *P. parvum* was equally high when the haptophyte was grown under nutrient-replete or N- or P-limiting conditions (Skovgaard et al. 2003).

In mixotrophic dinoflagellates, feeding does not appear to be a response to light limitation and most, but not all, mixotrophic dinoflagellates will not survive or feed in prolonged darkness (reviewed in Stoecker 1999). For example, feeding by *Karlodinium micrum* decreases at low irradiance and is highest at irradiances optimal for autotrophic growth (Li et al. 2000). In contrast, in some haptophytes ingestion is inversely proportional to light intensity, indicating that mixotrophy can be stimulated by both low nutrient and low light conditions (Jones et al. 1995). However, *Chrysochromulina* and *Prymnesium parvum* are not able to survive or grow in the dark, even when bacteria are added as prey (Pintner and Provasoli 1968; Jochem 1999). In contrast, ingestion of fluorescent-labeled bacteria (FLB) by *C. polylepis* has been shown to be higher under high light conditions and with the addition of humic substances, and these differences were explained by greater quantities of bacteria being found in these treatments (Granéli and Carlsson 1998). This indicates that in the presence of abundant bacterial prey, *C. polylepis* ingests prey independent of the light regime.

It is also possible that some harmful algae acquire organic growth factors from ingestion of prey. The photosynthetic dinoflagellate *Gyrodinium resplendens* (not known to be toxic) feeds on other dinoflagellates and can only be cultivated when provided with prey (Skovgaard 2000). Investigators have not been able to successfully cultivate toxic *Dinophysis* spp. (Nishitani et al. 2003). Food vacuoles containing ciliates and other protists have been observed (Jacobson and Andersen 1994; Gisselson et al. 2002) and it is possible that toxic *Dinophysis* spp., although they are photosynthetic, are obligate phagotrophs requiring specific prey. For toxic haptophytes there is no evidence of obligate phagotrophy; *Prymnesium* and toxic *Chrysochromulina* species have been successfully grown in axenic culture (Edvardsen and Paasche 1998).

In addition to the physiological advantages of prey ingestion, phagotrophy can also be an ecological strategy for eliminating or reducing predators and competitors. The dinoflagellate *Pfiesteria piscicida*, when actively toxic, can kill and often consume many of its protistan grazers (Burkholder and Glasgow 1995; Stoecker et al. 2002). Many of the non-thecate mixotrophic dinoflagellates consume cryptophytes and other phytoflagellates, their potential competitors for light and nutrients (Li et al. 1999; Jeong et al. 2005a, 2005b). For example, the estimated grazing impact of dense *Cochlodinium polykrikoides* blooms on cryptophyte populations is high, with the dinoflagellate populations having the potential to remove the entire cryptophyte standing stock within a day (Jeong et al. 2004).

Toxic haptophytes cause negative effects on a range of other planktonic organisms. Field observations during the *Chrysochromulina polylepis* bloom in 1988 in Scandinavian waters led to the hypothesis that *C. polylepis* toxins severely affect other protists (Nielsen et al. 1990) and subsequent laboratory experiments confirmed both allelopathy of *C. polylepis* (Schmidt and Hansen 2001) as well as negative effects on protistan grazers (John et al. 2002). Unfortunately, in these studies on *C. polylepis,* phagotrophy was not addressed. Like *C. polylepis*, *Prymnesium parvum* is known to severely affect other plankton organisms, as has been shown using algal cultures (Granéli and Johansson 2003b), heterotrophic protists (Granéli and Johansson 2003a; Rosetta and McManus 2003; Tillmann 2003) and natural communities (Fistarol et al. 2003).

14.3 Relationship of Phagotrophy to Toxicity

It is interesting that many toxic algae are phagotrophic or closely related to known phagotrophs. Is there a relationship between phagotrophy and toxicity? In the case of the heterotrophic *Protoperidinium crassipes*, it is possible that the toxin or its precursor is derived from prey. *P. crassipes* feeds on other dinoflagellates including toxic red-tide species (Jeong and Latz 1994). However, most mixotrophic toxic algae can be grown strictly autotrophically and retain their toxicity, thus it is unlikely that prey are a source of toxin for these species.

It is also possible that some toxins are involved in prey capture. Dinoflagellates have been observed to "trap" or "paralyze" motile prey before they are ingested (reviewed in Hansen and Calado 1999). Mechanical contact between the dinoflagellate and the prey appears to usually be necessary for the prey to be subdued. It is possible that trichocysts involved in prey capture contain toxins as well as "sticky" material. Interactions between *Pfiesteria piscicida* zoospores and their predators are interesting. Many ciliate species readily consume non-toxic zoospores and grow well, but many types of ciliates die if they are fed toxic zoospores (Stoecker et al. 2002). In some cases, the zoospores then consume the ciliates (Burkholder and Glasgow 1995).

Among the haptophytes, there is good evidence that toxins are involved in prey capture and defense against predation. The feeding frequency of *Prymnesium parvum* on motile prey is positively correlated with toxicity (Skovgaard and Hansen 2003). Non-motile prey is ingested at high rates irrespective of toxin concentration. Moreover, the addition of filtrate of a toxic *Prymnesium* culture to a dilute (and low toxic) *P. parvum* culture with an initial low feeding frequency also results in an increase of feeding frequency on motile prey. Toxicity has also been shown to be a key factor in determining the interaction of *P. parvum* with protistan grazers (Granéli and Johansson 2003b; Tillmann 2003). Whereas low toxicity *P. parvum* is a suitable prey for the heterotrophic dinoflagellate *Oxyrrhis marina*, the dinoflagellate is rapidly killed by *P. parvum* at high toxicity levels. Moreover, under these conditions the former predator (*O. marina*) is ingested by *P. parvum*, thus reversing the normal direction of grazing interactions (Tillmann 2003).

In contrast to *Prymnesium* with its short and stiff haptonema, species of *Chrysochromulina* have a longer and mostly flexible haptonema that may be involved in the feeding process by capturing and transporting prey to the cytostome positioned in the posterior end of the cell (Kawachi et al. 1991; Kawachi and Inouye 1995). In addition, in some species of *Chrysochromulina*, spine scales may have a functional role in food capture (Kawachi and Inouye 1995). The potential role of *Chrysochromulina* toxins in phagotrophy, however, is unknown. Both *Chrysochromulina* and *Prymnesium* species have organelles that can quickly discharge mucus, but the chemical composition of the mucus is not known (Green et al. 1982; Estep and MacIntyre 1989). It is tempting to speculate that muciferous bodies may be involved in phagotrophy as discharge was observed when certain other protist species were added to cultures of the phagotrophic *Chrysochromulina ericina* (Parke et al. 1956). It is not known if toxicity is related to mucus discharge in some species.

It seems likely that phagotrophy and the need to "trap" or "paralyze" prey is related to the evolution of toxicity in at least some toxic phytoplankton. Production of toxin by *Pfiesteria* spp. and immobilization of fish may be an extreme example of this phenomenon (Hansen and Calado 1999), but it may also occur with more subtlety and routinely during predation on protistan prey. A possibly related observation is that toxicity of some, but not all, dinoflagellates and haptophytes increases when they are nutrient limited (see Chap. 18 Granéli and Flynn, this book). In many mixotrophic dinoflagellates and haptophytes, nutrient limitation stimulates feeding (Li et al. 2000; Smalley et al. 2003; Legrand et al. 2001). A connection between toxicity and feeding might explain the link between toxicity and nutrient limitation. However, in some cases, toxicity and feeding are not linked; for example, *Karlodinium micrum* grown as an autotroph in the absence of prey or as a mixotroph with prey do not differ in toxicity (Deeds et al. 2002).

14.4 Significance of Phagotrophy

The recognition that many toxic phytoplankton are phagotrophic challenges traditional approaches to investigating the physiological ecology and community ecology of harmful algal blooms. Most of our estimates of the maximum growth rate of harmful algae are based on laboratory studies using monocultures. Phagotrophy can more than double the growth rates of some harmful algae. For many taxa we have probably underestimated their potential growth rates in nature. Phagotrophy is also important to consider in regard to inorganic nutrient acquisition—phagotrophs can acquire elements from prey under conditions that would appear limiting based on uptake kinetics for dissolved N, P and Fe. Some toxic algae may be obligate phagotrophs, and perhaps by providing suitable prey we may be able to cultivate them, and thus be able to investigate toxin production and other aspects of their physiological ecology.

It is also important to take phagotrophy into account in order to understand toxicity and its variability. Toxicity often declines in culture. If toxins are involved in prey capture or defense against predators, then it is likely that growth in monoculture should select against toxicity. In some cases, it is possible that toxic algae acquire their toxins (or the precursors) from prey and this needs further investigation, particularly for heterotrophic species.

The phagotrophic tendencies of dinoflagellates and haptophytes also may partially explain some of the puzzling aspects of their bloom dynamics and population ecology. Many different types of phytoplankton grow rapidly in response to a combination of light and nutrients, but most do not form monospecific blooms. The ability of some phagotrophic mixotrophs to eat their competitors must contribute to their ability to monopolize resources. The dynamics of some harmful algal blooms are unusual in that high cell densities tend to persist after nutrients are exhausted. Phagotrophic mixotrophs may survive because they are able to eat to obtain limiting elements.

Phagotrophy is not an isolated aspect of the physiological ecology of phytoplankton; in many taxa it may have coevolved with other capabilities such as the ability to use dissolved organic material and allelopathic tendencies.

Several authors, perhaps beginning with Estep and MacIntyre (1989) have suggested that some algal toxins may immobilize, make "leaky" or kill other types of cells in the plankton as part of a nutritional strategy. Allelochemicals may reduce competition or predation, but they can also make resources available. Phagotrophy is one of the elements in the interconnected bag of tricks that lets certain species of phytoplankton dominate resources in the plankton and form toxic or high biomass harmful blooms.

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