Algal cyst dormancy: a temporal escape from herbivory

Karin Rengefors^{1*}, Irene Karlsson¹ and Lars-Anders Hansson²

¹Department of Limnology, Uppsala University, Norbyvägen 20, S-752 36 Uppsala, Sweden

²Institute of Ecology/Limnology, Ecology Building, S-223 62 Lund, Sweden

Many phytoplankton species form resting cysts and remain dormant for part of the year. The subsequent excystment is regulated by the external environment and internal maturation processes. Here we assessed the excystment of the dinoflagellates *Ceratium hirundinella* and *Peridinium aciculiferum* in relation to herbivores and temperature in laboratory and field studies. *C. hirundinella*, which has a grazer-resistant morphology, forms summer blooms, whereas *P. aciculiferum*, which is vulnerable to grazers, grows underneath the ice during winter. In our study, herbivore abundance, and thereby grazing pressure, was low during periods when water temperatures were low, and the abundance of *P. aciculiferum* was high. In the laboratory experiment, excystment of *C. hirundinella* occurred at high temperatures irrespective of whether zooplankton exudate was added or not, whereas at intermediate temperatures, excystment was lower if zooplankton exudate was added. Germination of *P. aciculiferum* cysts was lower in the presence of exudate from a zooplankton culture than in controls at all temperatures. Our studies suggest that dinoflagellates use the presence of zooplankton in addition to temperature as a cue to determine when to excyst. Consequently, not only abiotic factors, but also the composition of the food web, may determine succession and composition of phytoplankton communities.

Keywords: dinoflagellates; cysts; dormancy; germination; predator-avoidance strategy; herbivory

1. INTRODUCTION

A common feature among many planktonic organisms is the presence of a long-lived benthic resting stage. The resting stage has been attributed a number of adaptive functions, but traditionally it has been regarded as a strategy for survival during periods of adverse environmental conditions. Resting stages are also important for dispersal in time and space, as seed banks, and for genetic recombination when produced through sexual reproduction. Lately, it has been proposed that dormant propagules may have a substantial effect on evolutionary dynamics within a population and may provide a means of supporting biodiversity (Lampert 1995; Hairston *et al.* 1996a,b) (McQuoid & Hobson 1995, 1996; Rengefors *et al.* 1996; Rengefors & Anderson 1998).

The species composition of phytoplankton communities is affected by the sizes of individual populations, which in turn are determined by a number of biotic and abiotic factors. One of the main regulating forces is grazing (Sternner 1989). In order to reduce losses due to grazing, phytoplankton have developed a number of different adaptations such as large size, unpalatable shape, indigestibility (Reynolds 1984) and toxicity (Henning *et al.* 1991). An alternative adaptation may be to avoid growth as plankton during times of high grazing pressure by forming cysts and resting on the sediment surface, analogous to diapause-forming copepods. Among animals such as copepods, diapause formation may have evolved

as a means of predator avoidance (Hairston 1987; Slusarczyk 1995; Pijanowska & Stolpe 1996). As a parallel, flagellated phytoplankton may avoid recruitment from sediment to water in the presence of zooplankton, suggesting that formation of resting cysts may be a predator-avoidance adaptation not only among animals, but also among plants (Hansson 1996a,b).

A group of phytoplankton that are prone to predation and that form large and distinct resting stages are the dinoflagellates. Marine dinoflagellate cysts and life histories have been studied in great detail (Anderson & Wall 1978; Dale 1983; Burkholder & Glasgow 1995), whereas there are only a handful of studies performed in freshwater environments (Huber & Nipkow 1922, 1923; Heaney *et al.* 1983; Pollinger *et al.* 1993; Chapman & Pfister 1995). Studies of dinoflagellates in Lake Erken, Sweden, have shown that cyst germination plays an important role in the timing of seasonal planktonic succession (Rengefors & Anderson 1998). The dinoflagellate flora in the lake is divided into two main categories, those growing in the water during summer and overwintering as cysts, and those growing underneath the ice during winter and oversummering as cysts (Rengefors 1998). The two dominant dinoflagellate species in Lake Erken are *Ceratium hirundinella* (O. F. Müller) Dujardin and *Peridinium aciculiferum* (Lemmermann). Detailed studies of their cysts have shown that cyst age, temperature, and an endogenous biological clock are factors involved in the timing of germination (Rengefors & Anderson 1998). At a certain time-interval of the year, and when cysts are mature, temperature determines

*Author for correspondence (karin.rengefors@limno.uu.se).

whether the cysts germinate (Rengefors & Anderson 1998). These results led us to pose the question of whether temperature is the ultimate factor that regulates the optimal timing of germination. Could temperature, for instance, be overridden by some biotic factor such as the presence of predators? Recently, dinoflagellate cysts were shown to germinate in the presence of chemical cues by fish (Burkholder & Glasgow 1995), which suggests that cysts may be able to detect the presence of grazers.

Here, we use field observations and a laboratory experiment to test whether a biotic factor (the risk of being grazed), when controlling for temperature, is used by dinoflagellates as a cue for germination of mature cysts. The two species tested, *C. hirundinella* and *P. aciculiferum*, differ in their sensitivity to herbivory. *C. hirundinella* is considered resistant to grazing owing to its large size (200–300 µm) and extended spines (Heaney & Butterwick 1985; Pollinger 1988), although there is some evidence that it is grazed by large rotifers such as *Asplanchna* spp. (Entz 1927). *P. aciculiferum*, on the other hand, which is much smaller (35–50 µm) and has no spines, is considerably more sensitive to grazing than *C. hirundinella*, especially by grazers such as *Eudiaptomus* spp. (Bern 1990). If dinoflagellate cysts are able to detect and respond to the presence of grazers, we hypothesize that *P. aciculiferum*, being more susceptible to grazers, should have a more pronounced reduction in germination in response to herbivores than *C. hirundinella*.

2. METHODS

(a) Study site

The field studies were performed in the moderately eutrophic Lake Erken (total phosphorus *ca.* 25 µg l⁻¹, and total nitrogen *ca.* 700 µg l⁻¹) (Pettersson 1985), in the south-eastern part of Sweden (59°25'N, 18°15'E). Lake Erken is usually ice-covered for about 18 weeks a year (January–April) and has a theoretical water residence time of seven years (Håkansson 1978). The lake area is 24 km², the mean depth 9 m, and the maximum depth 21 m (Håkansson 1978).

(b) Field study

Plankton samples were taken weekly from September 1995 to September 1996 using vertically and horizontally integrated composite samples. Water was taken at 2 m depth intervals with a 2 m tube sampler and was pooled in a bucket. From each layer, a water sample was taken in proportion to the volume of the respective layer in the lake. These samples were taken from three locations in the lake positioned within the 14 m depth contour (which represents the major area of accumulation sediments providing cyst 'seed banks' (Weyhenmeyer 1996; Rengefors 1997)) and were combined. One litre of water was subsampled and preserved with Lugol's solution for phytoplankton counts. Single phytoplankton counts were made for each sampling occasion, counting the whole bottom area of a 25 ml counting chamber in an inverted microscope (×100 magnification). The remainder of the water (23 l) was concentrated through a 40 µm net for zooplankton counts. The whole sample was counted under an inverted microscope (×100 magnification) after preservation in Lugol's solution. Algal and zooplankton abundances were log-transformed before analyses. As representatives for potential grazers we used total abundance

of the dominant zooplankters, which always constituted more than 90% of the biomass. These included *Eudiaptomus* sp., cyclopoid copepods, *Daphnia* spp., *Bosmina* sp., *Chydorus* sp. and *Asplanchna* sp.

Temperature was measured weekly at 12 m depth in the central part of the lake.

Cysts of *C. hirundinella* (hereafter referred to as *Ceratium*) were collected in the water with a 40 µm plankton net on 28 August 1995. Cysts were stored in cryovials submerged in lake sediment in plastic jars which were tightly sealed and stored in the dark at 4 °C. Cysts of *P. aciculiferum* (hereafter referred to as *Peridinium*) were collected with a 20 µm net in April 1996 and were stored at 4 °C as described above (for more details, see Rengefors (1998)). Cysts were stored for long enough to reach maturity (4.5 months for *Ceratium* and 2.5 months for *Peridinium*) in order to be able to germinate during the experiment (Rengefors 1997).

(c) Laboratory study

For the laboratory experiment, two treatments, one with and one without zooplankton (control) in lake water, were prepared. Live zooplankton were collected in September 1996 with a 200 µm plankton net. The zooplankton were kept in the laboratory in filtered Lake Erken water. Every other day, the zooplankton were fed with 50 ml of a *Rhodomonas* sp. culture in 3 × L16 medium with Wright's solution. The zooplankton culture, from which exudates were collected for the laboratory experiment, mirrored the community composition in Lake Erken well, and was dominated by cyclopoid copepods, *Eudiaptomus* sp., *Chydorus* sp., *Bosmina* sp. and *Daphnia* spp. The concentration of copepods was about ten times larger in the experiment than in the field (530 versus 55 individuals per litre). As a control, filtered (12 µm) Lake Erken water was stored in the dark at 4 °C. To avoid the potential effect of nutrients from the *Rhodomonas* additions to the zooplankton treatment, phosphate was added to both treatments. Phosphate was added to a final concentration of 3 mg of P l⁻¹, according to concentrations in DM-medium (Beakes *et al.* 1988). Previous excystment experiments with *Ceratium* show that nutrients have no effect of ecological significance on germination rates (Rengefors 1997; Rengefors & Anderson 1998).

To test the hypothesis that the presence of herbivores as well as temperature affects the excystment of dinoflagellates, the laboratory study was performed as a 2 × 3 factorial experiment with and without zooplankton exudates at 3 °C, 8 °C and 20 °C. The experiment was conducted in 200 mm × 24 mm Pyrex test tubes with a diameter of 25 mm, with five replicates of each treatment.

The experiment was started by filling ten test tubes with 15 ml of pre-chilled water at each of the three temperatures. Half (five) of the test tubes at each temperature were filled with zooplankton water from which zooplankton had been removed (with a 20 µm filter), and the other half with control water (see above). The tubes were then left to acclimatize again for 4 h. Thereafter, 367 ± 25 (mean ± 1 s.d.) cysts of *Ceratium* and 104 ± 10 (mean ± 1 s.d.) cysts of *Peridinium* were added in a random order to each of the tubes. Eight tubes were immediately preserved with Lugol's solution for initial counts. Tubes were incubated at a light intensity of 8 ± 4 µmol m⁻² s⁻¹ at a 12:12 h light:dark cycle. This light–dark cycle reflects natural conditions when cysts germinate in the lake. Excystment of *Ceratium* is known to be unaffected by the photoperiod (K. Rengefors, unpublished data). Each test tube was connected to a system of continuous aeration to avoid anoxic conditions; a spinal needle, attached to

Figure 1. Plankton abundance (log(individuals l^{-1})) and temperature (at 12 m depth) in Lake Erken from September 1995 until September 1996. Zooplankton (cladocerans, cyclopoid copepods, *Eudiaptomus* sp. and *Asplanchna* sp.) (filled triangles), *Peridinium aciculiferum* (filled circles) and *Ceratium hirundinella* (empty circles). Temperature ($^{\circ}C$) is represented by the grey-shaded area.

thin plastic tubing connected to an aquarium pump, was inserted into each test tube.

Each day, the top 10 ml of water were removed from the test tubes and replaced with filtered and pre-chilled (2–3 h) zooplankton and control water, respectively. The experiment was allowed to run for 17 d to allow for maximum excystment to occur (Rengefors & Anderson 1998). At the end of the experiment, the overlying water was carefully removed, while the cyst suspension was transferred to glass scintillation vials and preserved with Lugol's solution. Cysts were counted in 25 ml sedimentation chambers in an inverted microscope ($\times 100$ magnification). The overlying water was checked for the presence of vegetative cells and cysts as an extra precaution.

3. RESULTS

(a) The field study

The two algal species, *Ceratium hirundinella* and *Peridinium aciculiferum*, showed a clear temporal separation in occurrence in the water column in Lake Erken (figure 1). Vegetative *Peridinium* cells were most abundant during winter and were found as cysts during summer. *Ceratium*, in contrast, was absent from the water column during winter and reached maximum densities when temperature was high (figure 1). The abundance of large grazers was low during the winter months (January–March) but started to increase in April with increased water temperature. Maximum abundances were found in August, and then decreased from September–December.

There was a clear inverse relationship between abundance of *Peridinium aciculiferum* and grazer abundance, and also a tendency for a negative relationship with temperature. Statistical analysis was considered redundant because the patterns were quite clear. There was a positive relationship between *Ceratium* and grazer abundance, as both are favoured by higher temperatures. The positive relation remained even if the grazer community was divided into potential *Ceratium* grazers, such as *Eudiaptomus* or *Asplanchna*. (Entz 1927; Bern 1990, 1994).

(b) Laboratory experiment

There was little or no excystment of *Ceratium* in both control and zooplankton treatments at $3^{\circ}C$ (figure 2a).

The number of non-germinated cysts counted in the zooplankton treatment did not differ significantly from initial values (367 ± 25) at the 5% level. At $8^{\circ}C$, there was a significant difference between the two treatments (ANOVA, $p=0.0001$). In the control, 92% of the cysts had germinated by the end of the experiment, compared with only 36% in the zooplankton treatment. In contrast, at $20^{\circ}C$, germination did not differ between treatments (90% in both cases).

Germination of *Peridinium* cysts was absent or low at $8^{\circ}C$ and $20^{\circ}C$ in the controls as well as in the zooplankton treatments (figure 2b). In neither treatment was the number of non-germinated cysts significantly different (5% level) from the original cyst number. Nevertheless, there was a tendency towards higher excystment in the controls than in the zooplankton treatments (one-way ANOVA, $p=0.04$). Moreover, there was a significant difference in excystment between the two treatments at $3^{\circ}C$ (ANOVA, $p=0.0001$). Whereas 90% of the cysts in the control germinated, only 45% of those in the zooplankton treatment germinated.

4. DISCUSSION

The temporal separation between *Peridinium aciculiferum* and *Ceratium hirundinella* has led us to classify them as a 'winter species' and as a 'summer species', respectively, based on the data of Nauwerck (1963) and Rengefors (1998). A possible explanation of the observed pattern is that *Peridinium* is simply physiologically adapted for maximum growth at low temperatures, and that *Ceratium* is not. In fact, in the laboratory *Peridinium* does not grow above $10^{\circ}C$ (K. Rengefors, personal observations), whereas *Ceratium* does not grow below $7^{\circ}C$ (Huber & Nipkow 1923) as it is a large cell with a low surface-to-volume ratio (Reynolds 1984). However, an additional possibility is that the vulnerable *Peridinium* avoids grazing if it excysts from the sediment when grazer abundance is low, i.e. during winter. The field data strengthen the suggestion that excystment occurs mainly when grazer abundance is low. Earlier plankton data from Lake Erken also show that abundance of *Eudiaptomus* sp. and *Asplanchna* sp. are very low during winter, and reach high

Figure 2. Cyst germination experiment at three different temperatures, 3 °C, 8 °C and 20 °C, and two treatments, with (Z) or without (C) addition of zooplankton exudate. (a) Bars illustrate portion of excysted *Ceratium hirundinella* cysts. (b) Bars illustrate portion of excysted *Peridinium aciculiferum* cysts. Error bars denote one standard deviation.

concentrations only in July and September, respectively (Nauwerck 1963).

The results from the laboratory experiment with *Peridinium* cysts support the observations from the field data. As expected from the studies of Rengefors & Anderson (1998), *Peridinium* showed no or very little germination at high temperatures (above 7 °C). However, grazer exudates seemed to influence germination at all temperatures, illustrated by the tendency of lower excystment in treatments with zooplankton exudates irrespective of temperature (figure 2b). Incubation time (time from start of incubation until germination) at this temperature (and time of the year) is a maximum of 17 days (Rengefors & Anderson 1998), suggesting that some cysts in the zooplankton treatment may either have been completely inhibited by zooplankton filtrate, or were delayed in their excystment. An alternative to zooplankton-mediated delay in excystment is that a

portion of the cysts was completely inhibited from germination. Cysts resting in the sediments may be seen as a temporal and spatial gene pool (Coleman 1983). It is therefore possible that some cysts are inhibited by predation while others are not, just as some copepods have phenotypic differences for timing of diapause (Hairston *et al.* 1996b). Whether or not a phenotypic variation exists for inhibition of germination of dinoflagellate cysts, however, needs further study.

In contrast to *Peridinium*, the germination of *Ceratium* cysts was not expected to be regulated by grazer abundance. Our field data are consistent with that expectation, and showed a positive relationship between grazer abundance and *Ceratium* in the water column of Lake Erken. The laboratory experiment only partly supported the field observations. At high temperatures (20 °C), *Ceratium* excystment was similar irrespective of whether grazer exudate was present or not (figure 2a), which was also true at 3 °C, although little or no excystment occurred at this temperature. At 8 °C, however, germination of cysts treated with zooplankton filtrate was moderated by zooplankton filtrate. A possible interpretation is that only at intermediate temperatures, when temperatures are not optimal for growth, may the presence of grazers be important for the recruitment of *Ceratium* to the water column, whereas at high temperatures, germination occurs regardless of the presence of grazers.

The partial response of *Ceratium* cysts to zooplankton exudates is consistent with the species' life cycle and its lack of sensitivity to predation. Owing to its extended horns, *Ceratium* acquires a body length of up to 300 µm in Lake Erken, which makes it an unlikely prey for most zooplanktivorous grazers. Germination of *Ceratium* cysts occurs in May when the water temperature rises above 6–7 °C (Rengefors & Anderson 1998). During the same time period a sharp increase in zooplankton abundance was observed. Despite the presence of potential grazers, *C. hirundinella* germinated and the population increased during this period (figure 1). Most probably, the losses due to grazing are not very important for the Lake Erken population of *Ceratium*. Consequently, *Ceratium* retains a summer-bloom strategy, which is the likely explanation why zooplankton exudate did not prevent germination of its cysts at temperatures optimal for growth.

Hairston (1987) proposed that predation may also affect dormancy in organisms other than diapausing copepods. Based on our laboratory and field studies, we suggest such a predator-avoidance strategy in *Peridinium*, and to some extent in *Ceratium*, as an explanation for the moderation of cyst germination in the presence of potential grazers. Our results indicate that the presence of potential grazers may restrain the germination rate of dinoflagellates. This conclusion parallels earlier studies, which showed that recruitment of *Peridinium wisconsinense* and *P. pusillum* was considerably lower in lakes with high grazer abundance (Hansson 1996a,b).

A chemical cue, indicating the presence of zooplankton, was enough to restrain or delay germination of both *Ceratium* and *Peridinium* cysts in our experiment. Chemical cues from fish have been suggested to induce the excystment of the dinoflagellate *Pfiesteria piscicida* (Burkholder & Glasgow 1995). In addition, there is evidence from other work that algae are sensitive to kairomones from grazers,

which promote morphological or behavioural changes (Hessen & van Donk 1993; Lampert *et al.* 1994). Because the filtrate added in our experiment was taken from an actively feeding zooplankton community, the chemical cue may be either a metabolite resulting from the feeding activity of the zooplankton, or a substance released from crustacean tissue (Hansson 1996b). However, our study was not designed to assess which substance is active in carrying information from herbivores to algae, only that it occurs in filtered water from a zooplankton culture. As indicated by both the laboratory and field study, temperature regulates the cyst germination in *Peridinium* and *Ceratium*, but that this factor may be overridden by a chemical cue released from herbivores. This means that not only abiotic factors such as temperature, but also the composition of the food web, may affect the succession pattern of algae in lakes. Hence, a plausible scenario may be that during a year when zooplankton abundance is low, for example owing to recruitment of a strong year class of planktivorous fish, a high germination rate of dinoflagellate cysts may be expected, and, consequently, a high abundance of these algae in the phytoplankton community.

In conclusion, our study suggests that resting-stage formation as a predator-avoidance strategy may be present not only in zooplankton (Hairston 1987), but in phytoplankton as well; that is, behavioural consumer-avoidance strategies are not exclusive to animals, but seem to occur among algae. Moreover, our study shows that not one but several environmental cues may be used by organisms as simple as algae to determine the timing for vegetative growth. Knowledge of which environmental cues are involved in breaking dormancy in algae, as well as in zooplankton, may be an important tool in understanding and predicting the often puzzling succession patterns of organisms in natural ecosystems.

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