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Effects of cyst resuspension on germination and seeding of two bloom-forming dinoflagellates in the Baltic Sea

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ABSTRACT: The implications of cyst resuspension on germination and subsequent seeding of the 2 spring-bloom dinoflagellates *Scrippsiella hangoei* (Schiller) Larsen and *Peridiniella catenata* (Levender) Balech from the Baltic Sea were investigated in a field study and laboratory experiments. Sedimentation of resuspended cysts was monitored by an automated sediment trap in 2 consecutive winters prior to and throughout the germination period off the SW coast of Finland. The effects of increased irradiances and water motion on germination and germling survival were tested by incubating cysts at different light levels and in turbulent water. Cyst fluxes of both species were low during the calm and cold winter of 1998/1999. In 1999/2000, heavy storms caused strong resuspension of *S. hangoei* cysts. Light significantly increased the germination frequency of *S. hangoei* cysts and supported germling survival and cell division. In *P. catenata*, the percentage of excystment was not significantly influenced by light and germination was successfully completed in both darkness and light. Subsequent growth of the species, however, required light, although maximum cell numbers were encountered at an irradiance as low as 10 µmol m^{-2} s^{-1}. Small-scale turbulence reduced the germination frequency of *S. hangoei* but did not affect excystment in *P. catenata.* No negative effects on subsequent growth were detected. The favourable effects of light on germination and germling survival of *S. hangoei* emphasize that resuspension would be advantageous for the bloom initiation of this species. Cyst resuspension seems to be less important in *P. catenata* population dynamics, since germination can be successfully completed in darkness and the amount of cysts transported to the water surface is insignificant even with strong turbulent mixing. It is concluded that cyst resuspension may be advantageous for dinoflagellate bloom initiation, depending on its extent and timing and the specific germination requirements of the respective organism.

KEY WORDS: Cysts · Dinoflagellates · Germination · *Peridiniella* · Resuspension · *Scrippsiella* turbulence

INTRODUCTION

The pelagic appearance of many dinoflagellate species is dependent on benthic resting cysts as the source of seed populations. This is particularly true in temperate regions, where the formation of resting cysts is a common strategy to survive unfavourable conditions, and germinating cysts often provide the inoculum for bloom initiation (Anderson & Wall 1978, Heaney et al. 1983, Rengefors 1998).

Generally, cyst germination has been considered as a biologically driven phenomenon, a change from 1 physiological state to another which, in turn, is regulated by physiological properties of the cyst such as dormancy, temperature adaptations, or oxygen and light requirements (Pfiester & Anderson 1987). Recently, it has been proposed that biological-physical interactions are also involved in this process (Donaghay & Osborn 1997).

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Although dinoflagellate blooms are commonly associated with calm weather and stability of the water column (Margalef 1978), reports of bloom outbreaks following periods of strong vertical mixing (Usup & Azanza 1998) suggest that turbulence might play a role in the initial phase of planktonic population development. Increased turbulent mixing caused by wind, tides, or upwelling often leads to enhanced cyst resuspension (Balch et al. 1983, Villanoy et al. 1996, Kremp & Heiskanen 1999). Nehring (1996) hypothesized that planktonic cysts could seed a new vegetative population more efficiently than benthic cyst populations because the conditions for germination and survival of the germling, such as temperature, light or nutrient availability, may be more favourable in the pelagic environment than down in the sediment. The role of cyst resuspension as a prerequisite for seeding has also been emphasized in models of dinoflagellate population dynamics (Villanoy et al. 1996, Eilertsen & Wyatt 1998). However, because of the high densities and, hence, sinking velocities of the cysts (Anderson et al. 1985), their resuspension and persistance in the upper water column is dependent on sufficiently strong turbulent mixing.

Turbulence is a very complex physical parameter, affecting phytoplankton cells on a wide range of space and time scales. Vertical mixing, representing mesoscale turbulence, has a direct relevance to phytoplankton cell physiology because it determines light penetration and supply of nutrients (Estrada & Berdalet 1998). The entrainment by water motion exposes the phytoplankton cells to varying irradiances and thus affects their photobiological properties (Cullen & MacIntyre 1998). Small-scale turbulence, i.e. shear (Lazier & Mann 1989), directly affects the growth of phytoplankton cells. Dinoflagellates have been shown to be very sensitive to shear (Pollingher & Zehmel 1981, Thomas & Gibson 1990). It is not clear how shear acts on the cysts. However, cyst germination is a complex process involving fundamental physiological changes (Binder & Anderson 1990) and cell division (Pfiester & Anderson 1987) which are particularly vulnerable to turbulence (Berdalet 1992). In order to evaluate the seeding potential of resuspended cysts, it is, thus, important to determine the species-specific response of germination and germling survival to small-scale turbulence and to different irradiance regimes.

Scrippsiella hangoei (Schiller) Larsen and *Peridiniella catenata* (Levander) Balech are 2 important dinoflagellates of the vernal phytoplankton community in the Baltic Sea (Niemi 1975, Larsson et al. 1986, Larsen et al. 1995) which are responsible for a significant fraction of the production in that region. Typically, the 2 species co-exist, but interannual fluctuations in their relative dominance have been reported (Kononen & Niemi 1984, Algaline 2000: www2.fimr.fi/algaline/algaline.htm). Both dinoflagellates produce resting cysts in late spring which start to germinate in early winter after a mandatory dormancy period of 6 mo (Kremp 2000a, Kremp & Anderson 2000). The decrease in *S. hangoei* cysts observed at this time of the year in field populations at the sediment surface, however, is much higher than the *in situ* germination potential of the species would suggest (Kremp 2000b). The beginning of the germination period frequently coincides with stormy weather that has a high potential for causing resuspension (Niemi & Åström 1987, Heiskanen et al. 1998).

Therefore, the objective of this study was to evaluate if cyst resuspension can play a role in the population dynamics of the 2 dinoflagellates *Scrippsiella hangoei* and *Peridiniella catenata* and if the seeding of one or the other species could be favoured by different weather conditions during the winter months through differential resuspension and responses to its effects. Cyst resuspension was quantified in a field study throughout 2 subsequent winters using sedimentation traps. The effects of meso- and small-scale turbulence on germination, including actual excystment, germling survival, and formation of vegetative cells, were studied by irradiance and turbulence experiments in the laboratory.

MATERIALS AND METHODS

Field study. Resuspended resting cysts of *Scrippsiella hangoei* and *Peridiniella catenata* were collected by an automated sediment trap (PPS $^{3}/_{4}$, Technicap/France, height:diameter ratio = 4) deployed at 15 m depth at the 30 m-deep Storfjärden sampling station (59° 51′ N, 23° 13′ E, SE of the Hanko peninsula, Finland, Baltic Sea). The trap was set to collect settling material at intervals of approximately 12 d between December and May 1998/1999 and 1999/2000. Formalin, at a final concentration of 2%, was used as a preservative in the collecting chambers. After retrieval of the trap, the settled material from the subsamples was suspended in a known volume of sea water and the cyst numbers were determined from 2 ml aliquots of this suspension using an inverted microscope (250× magnification). Mean daily cyst fluxes were calculated for each settling period.

Irradiance experiments. The effect of different irradiances on cyst germination and subsequent growth was tested by incubating mature cysts of *Scrippsiella hangoei* and *Peridiniella catenata* under different light conditions. The cysts were obtained from the flocculent surface layer of sediment cores taken with a Limnos gravity corer (Kansanen et al. 1991) at the Storfjärden sampling station in June 1999 shortly after the

termination of the spring bloom. Cysts were stored for 6 mo in the sediment slurry at 2°C and total darkness until their mandatory dormancy interval was completed (Kremp 2000a, Kremp & Anderson 2000). Prior to the experiment, the cyst suspension was sonicated for 5 min in a Branson 2200 sonication bath and sieved through 50 and 20 µm nylon sieves to remove larger particles and detritus and concentrate the cysts of *S. hangoei* and *P. catenata*. One ml of this cyst preparation was then pipetted into polystyrene culture tubes filled with 10 ml modified Erdschreiber medium (Throndsen 1978). The tubes were randomly divided into 6 groups (for the 6 treatments) of 36 vials (4 replicates for 9 sampling occasions). For determining initial cyst abundances, an additional set of 10 vials was immediately fixed with acid Lugol's solution. All steps of the cyst processing were carried out in a dark room with an infrared lamp as the only source of light to avoid possible effects of short-term exposure to low light in the dark control.

The sets of culture tubes were incubated at 6 irradiances: dark control; 0.1, 1, 10 and 100 µmol m^{-2} s^{-1}, (representing mean irradiances measured during the winter months at the sediment surface, 15, 10, 5 and 1 m water depth: M. Lindström, Tvärminne Zoological Station, pers. comm.); and darkness after a short exposure to light. The different irradiance levels were obtained by adjusting the distance of the experimental tubes differently to the light source mounted above. For the low irradiance levels (0.1 and 1 µmol m^{-2} s^{-1}), tubes were placed in plastic boxes covered with shaded acryl plates. Irradiances were measured by a Li-Cor irradiance meter. The tubes for the dark treatment were wrapped in several layers of black plastic and placed in a dark box immediately after the cyst processing. For the short-term illumination treatment, the respective tubes were exposed for 2 h to an irradiance of 100 µmol m^{-2} s^{-1} before they were added to the dark box. The incubation was carried out at 2°C (±1°C). The tubes illuminated at 100 µmol m^{-2} s^{-1}, however, experienced temperature differences of about 4°C due to their short distance from the lamp. Light was set to a 10:14 h L:D cycle, which is equivalent to the average daylength in nature between December and March, when the germination of *Scrippsiella hangoei* and *Peridiniella catenata* takes place in the northern Baltic Sea.

To monitor the time course of germination throughout the 4 wk incubation, 4 replicate samples were removed from each treatment at 3 d intervals and fixed with Lugol's solution. To prevent exposure to light levels higher than those in the experiment, the dark and shaded boxes were carried to a dark room equipped with an infrared light for removal of the tubes for sampling. The concentrations of full and empty cysts and motile cells were determined by examining 2 ml subsamples of each replicate tube in an inverted microscope (250× magnification). The percentage of germinated cysts in the cyst suspension was measured as the increase of empty cysts compared to the initial number for *Scrippsiella hangoei. Peridiniella catenata* does not leave clearly recognizable empty cyst walls behind when excysting, and thus the percentage of germination for this species was calculated from the decrease in full cysts compared to the initial number. In this study, germination was considered as a complex process that includes germling survival and first cell divisions in addition to actual excystment. Therefore, a ratio of emerged motile cells to germinated cysts was calculated as an additional index that characterizes germination beyond the actual excystment. The results were analyzed using a Student's *t*-test.

Water-motion study. As for the irradiance study, cysts of *Scrippsiella hangoei* and *Peridiniella catenata* were obtained from sediment samples stored in the laboratory until the maturation of cysts was completed. Following sonication and sieving, 3 ml subsamples of the cyst suspension were inoculated in 200 ml glass bottles containing 100 ml of modified Erdschreiber medium (Throndsen 1978). A plankton wheel was used to study the small-scale effects of water motion on cyst germination and subsequent growth. The rotation of the wheel generated turbulence in the fluid in horizontally mounted bottles as an effect of the oscillating boundry of bottle wall and fluid (Peters & Redondo 1997). This method does not allow the quantification of the applied turbulence in fluid dynamic terms. However, it was considered sufficient for the purpose of finding out if there is an effect of shear on germination and growth. Four replicate bottles on 7 sampling occasions were fastened to the plankton wheel, and the wheel was rotated at a speed of 2 rpm intermittently on a 12:12 h on:off cycle for 28 d. A light source was put up above the wheel, providing irradiances between 200 µmol m^{-2} s^{-1} at the top and 100 µmol m^{-2} s^{-1}at the bottom of the wheel. A group of 28 bottles was placed on a stable board as a still-water control treatment, for which the irradiance was adjusted to 150 µmol m^{-2} s^{-1}. The experiment was carried out in a temperaturecontrolled room set at 2°C. Fluctuations between 1 and 4°C occurred, depending on the light cycle. The L:D cycle was shifted by 6 h relative to the on/off cycle of the plankton wheel to ensure that the on-phase would extend into the dark phase. To determine the initial cyst concentrations of *S. hangoei* and *P. catenata*, 10 additional bottles were preserved immediately after preparation.

The time course of germination and subsequent formation of the vegetative inoculum was recorded by repeated sampling (every 3rd or 4th day) throughout

the 4 wk of the experiment. For cell counts, 50 ml of the preserved and well-mixed bottle contents were filled into an Utermöhl chamber, and the cells were allowed to settle for 24 h. The chamber was then examined for cysts and cells and the data was analyzed as decribed above.

RESULTS

Resuspension of cysts

During the winter of 1998/1999, cyst fluxes of 10^3 to 10^6 cysts m^{-2} d^{-1} were measured for *Scrippsiella hangoei*, the maximum sedimentation rate of 0.8×10^6 cysts m^{-2} d^{-1} occurring in December 1998 (Fig. 1). *Peridiniella catenata* cysts were found at much lower concentrations in the sediment traps, resulting in cyst fluxes of 10^3 to 10^4 cysts m^{-2} d^{-1}. Generally, the resuspension of cysts was strongest between December and February and this pattern was observed again during the following winter. Then cyst fluxes of *S. hangoei* exceeded the values of the preceding year by more than an order of magnitude. In December 1999, cyst fluxes of approximately 2×10^7 cysts m^{-2} d^{-1} were measured after heavy storms. Despite the marked increase in resuspended *S. hangoei* cysts, the number of *P. catenata* cysts settling to the sediment traps in 1999/2000 was similar to that measured during the preceding winter.

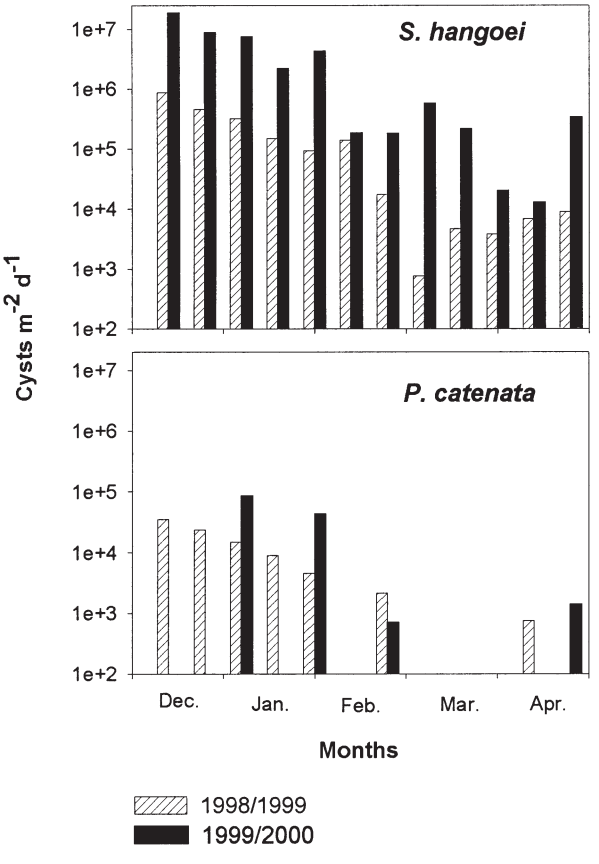

Fig. 1. *Scrippsiella hangoei* and *Peridiniella catenata*. Sedimentation of resuspended resting cysts off the SW coast of Finland, Baltic Sea, at 15 m depth at Storfjärden sampling station

Effects of irradiance on cyst germination

Germination occurred in both species at all irradiance treatments as well as in the dark control (Fig. 2). The germination frequency of *Peridiniella catenata* was nearly 100% after 4 wk incubation, and did not differ significantly among the treatments ($p > 0.05$). However, in complete darkness significant germination ($p < 0.05$) occurred several days later than when cysts had been exposed to light. Germination proceeded rapidly once it had started, until most of the cysts had germinated. Compared to *P. catenata*, the cysts of *Scrippsiella hangoei* germinated at considerably lower frequencies, the observed maximum percentage at 10 µmol m^{-2} s^{-1} illumination comprising only 35% of the incubated cysts. The differential response to the treatments was more pronounced in this species. Significantly more cysts ($p < 0.05$) germinated in the light treatments than in darkness. Short-term exposure to light did not increase the germination frequency.

The ratios of cells to germinated cysts plotted in Fig. 3 show that the successful completion of germination is, in both species, influenced by light. However, the survival and growth of the germling cells differed between the 2 species and at the different irradiances. *Scrippsiella hangoei* cells generally appeared earlier in the experimental tubes than vegetative cells of *Peridiniella catenata*, simultaneously with the first few empty cysts. The cell:germinated cyst ratio tended to increase, but remained for a long period below 1. During the last week of the experiment, cell:germinated cyst ratios increased rapidly at 10 and 100 µmol m^{-2} s^{-1}. Both irradiances led to significantly higher ($p < 0.05$) cell:germinated cyst ratios compared to darkness and low irradiances, and the results show that germination was completed most successfully at the highest applied irradiance. *P. catenata* germlings and vegetative cells developed differently from those of *S. hangoei*. After the onset of germination, cell numbers, except for the 100 µmol m^{-2} s^{-1} treatment, immediately exceeded the number of germinated cysts (cell:germinated cyst ratios >1). However, in darkness and at irradiances below 10 µmol m^{-2} s^{-1}, cell:germinated cyst ratios soon

decreased to 1, remaining low until the end of the experiment. Interestingly, after short-term exposure to light, the initial growth period with cell:germinated cyst ratios >1 lasted several days longer than in the dark and other low-light treatments. In *P. catenata*, the cell:cyst ratio was highest at 10 µmol m^{-2} s^{-1}. At this irradiance the cell:germinated cyst ratio of *P. catenata* was significantly higher ($p < 0.05$) than that of *S. hangoei*.

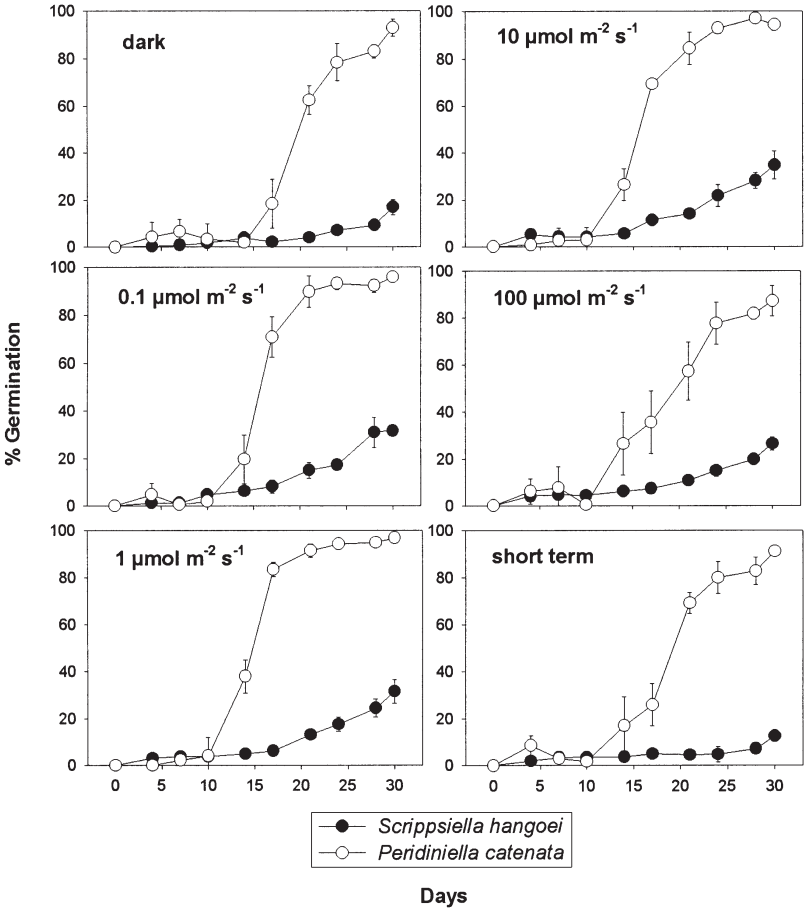

Fig. 2. *Scrippsiella hangoei* and *Peridiniella catenata* cysts. Effect of darkness and increasing irradiances on excystment. Time course and germination success (mean % ± SD, n = 4) of mature cysts incubated at 6 irradiances at 2°C and a 10:14 h L:D cycle

Germination success in turbulent and still water

The effect of water motion on the excystment of *Scrippsiella hangoei* and *Peridiniella catenata* is shown in Fig. 4. Whereas in *S. hangoei* the final excystment percentage was significantly lower ($p < 0.05$) in turbulent water compared to the still-water control treatment, *P. catenata* excystment was not affected by water motion. The differences in both, maximum excystment percentages as well as the time course of germination, were not significant (Student's *t*-test; $p > 0.05$, analysis of covariance; $p > 0.05$) in this species. Excystment generally occurred at a higher frequency in *P. catenata* (approx. 70%) than in *S. hangoei* (15 to 30%).

In *Scrippsiella hangoei*, germling survival and first cell divisions were not affected by water motion (Fig. 5). The ratio of cells:germinated cysts increased in both treatments rapidly above 1. By the end of the experiment, cell numbers had increased 4-fold over germinated cysts both in the turbulent and the still-water treatment. Water motion also affected the successful completion of *Peridiniella catenata* germination positively. After 4 wk of incubation, the cells:germinated cyst ratio in the shaken bottles was significantly higher ($p < 0.05$) than in the still-water control.

DISCUSSION

Cyst resuspension prior to bloom initiation

The *Scrippsiella hangoei* and *Peridiniella catenata* cysts collected in winter by sedimentation traps are considered to consist entirely of resuspended cysts, because encystment and sedimentation of newly formed cysts are restricted in both species to a short period in late spring (Kremp & Heiskanen 1999, Kremp 2000a). During the winter of 1999/2000, more cysts, particularly of *S. hangoei*, were resuspended than during the preceding winter. It can be assumed that these annual differences resulted from the different weather conditions prevailing during the 2 winters (Table 1). In 1998/1999, the winter on the Finnish SW coast was rather calm and cold with a long ice period, whereas the winter of 1999/2000 was characterized by mild and stormy weather, particularly during December and January.

During the first winter, cysts of both species were resuspended in a proportion of approximately 20:1 (*Scrippsiella hangoei* and *Peridiniella catenata*) which is comparable to their proportion at the sediment surface (Kremp unpubl. data). In 1999/2000, however, cysts of *P. catenata* were either not encountered at all in the sediment trap samples or occurred in a much

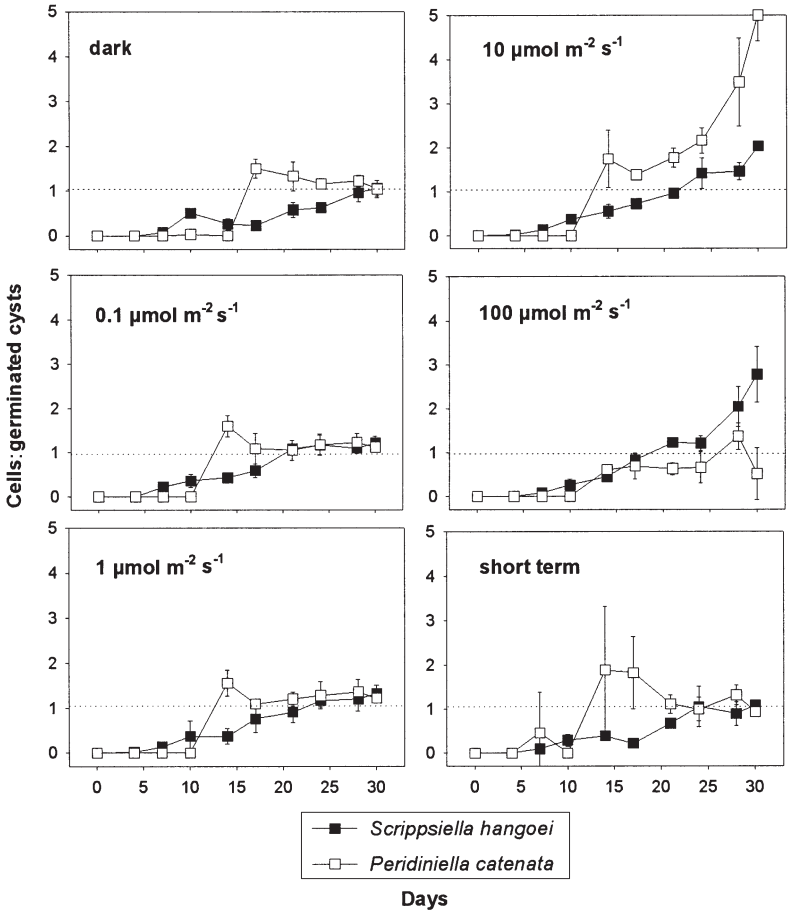

Fig. 3. *Scrippsiella hangoei* and *Peridiniella catenata*. Germling survival after germination expressed as the ratio of cells to germinated cysts in different irradiance regimes at 2°C and a 10:14 h L:D cycle. Error bars represent SDs (n = 4). Dotted line marks the threshold of successful completion of germination, i.e. formation of 1 motile cell per germinated cyst

lower proportion than those of *S. hangoei* (<1:100). It is possible that physical forcing affected the 2 cyst types differentially, as different cyst size and morphology can lead to different settling velocities (Anderson et al. 1985). The small (20 µm), spherical cyst of *S. hangoei* may be more susceptible to mixing than the much larger (25 to 30 µm), discoid cyst of *P. catenata*.

Responses of germination to varying light conditions

Peridiniella catenata excysted as successfully in total darkness as at the different light levels. Although some differences in the timing of germination were observed, nearly all cysts had germinated within approximately 2 wk in all treatments, indicating that light is not controlling excystment in this species. Such rapid germination in complete darkness has only been observed in a very few dinoflagellates with a short dormancy period that maintain a physiological state of competency (Anderson et al. 1987) throughout the resting period. Although *P. catenata* cysts have a long dormancy period, it can be assumed that they remain in an activated state as well, because the cysts contain chlorophyll and maintain red autofluorescence throughout the entire resting period (Kremp 2000a). The possibility that a brief low-light impulse is needed to trigger the excystment of *P. catenata*, as in *Scrippsiella trochoidea* (Binder & Anderson 1986), can be excluded since special precautions had been undertaken to avoid any light 'contamination'. Apparently the release from mandatory dormancy in December/January (Kremp 2000a) is sufficient to initiate germination. Alternatively an endogenous rhythm, as described by Anderson & Keafer (1987), might be responsible for the regulation of the synchronized onset of excystment.

The high ratio of cells:germinated cyst, occurring immediately after the onset of germination in darkness and nearly at all applied irradiance levels, suggests that the resources of the *Peridiniella catenata* cysts were sufficient to ensure not only the survival of the germling but also the first cell divisions. Interestingly, the completion of germination was even more successful initially in the treatment where cysts had briefly been exposed to bright light before dark incubation. The maximum cell:cyst ratio measured at 10 µmol m^{-2} s^{-1} (Fig. 3) indicates that germling survival and subsequent cell division of this species are successful at very low light levels. Apparently the photosynthesis of *P. catenata* cells is most effective at this irradiance. Photoinhibition might occur at higher light levels, which could be an explanation for the low cells:germinated cyst ratios observed at 100 µmol m^{-2} s^{-1}. As suggested for *Amphidinium carterae*, which shows a similar response to light (Samuelsson & Richardson 1982), this might reflect a genotypic adaptation to life in a poor light environment.

In *Scrippsiella hangoei*, germination was clearly favoured by light. This is the common response of most of the dinoflagellate species studied so far (Anderson et al. 1987, Bravo & Anderson 1994, Rengefors & Anderson 1998). In contrast to *Peridiniella catenata*, *S. hangoei* cysts are in a state of deep physiological rest during dormancy (Kremp & Anderson 2000), and thus the trans-

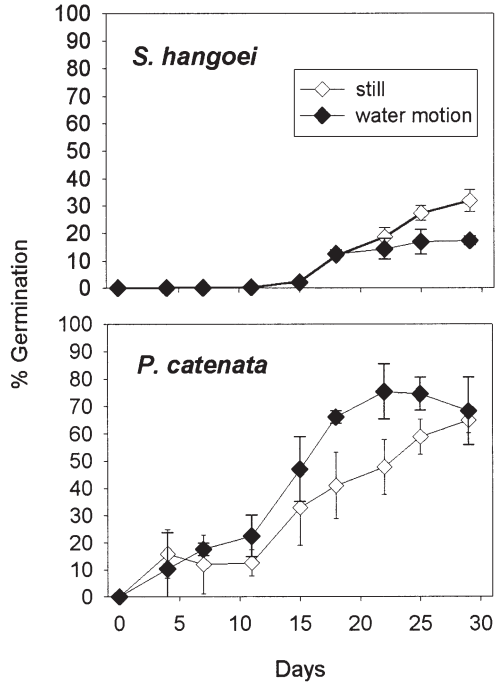

Fig. 4. *Scrippsiella hangoei* and *Peridiniella catenata*. Effect of water motion on excystment. Germination percentage (mean % ± SD, n = 4) in replicate vials mounted on a plankton wheel and rotated at 2 rpm, and in still-water vials at 2°C, 150 µmol m^{-2} s^{-1}, and 12:12 h L:D cycle

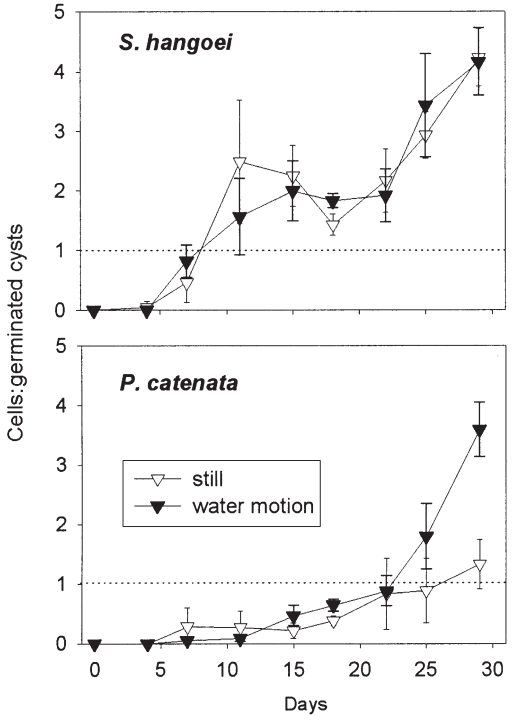

Fig. 5. *Scrippsiella hangoei* and *Peridiniella catenata*. Development in turbulent and still water after excystment (mean ratios of cells:germinated cysts ± SD). Dotted line marks the threshold of successful completion of germination

formation from the dormant to the vegetative state is probably very slow without an external supply of energy, as suggested by Anderson et al. (1987). The germination percentages at the end of the experiments were generally very low for *S. hangoei*. This is not surprising, since the cysts used for the experiments came from sediment samples that presumably also contained old (i.e. nongerminable or dead) cysts (Kremp & Anderson 2000) in addition to the recently matured cysts from the preceding bloom. Furthermore, the germination of *S. hangoei* cysts proceeded more gradually than of *P. catenata*. Apparently the 2 species exhibit very different germination strategies despite their overlapping vegetative phase and the similar timing of their cyst stage.

The results suggest that light is important for the germling survival and subsequent growth of *Scrippsiella hangoei*, as a significant increase in motile cells in relation to germinated cysts was only observed at the highest applied irradiance of 100 µmol m^{-2} s^{-1}. The ratios of cells:germinated cysts remained below 1 for more than 2 wk after the onset of germination, suggesting that germling survival and cell division are not very successful in this species. This confirms field observations (Kremp 2000b) and emphasizes the importance of light for the successful completion of germination in this species.

Germination in turbulent water

This study demonstrates for the first time that water motion affects dinoflagellate cyst germination. The response of germination to the applied turbulence was different in *Scrippsiella hangoei* and *Peridiniella catenata*. Whereas germination of *P. catenata* was not significantly influenced by water motion, orbital shaking had a negative effect on the excystment of *S. hangoei*.

Table 1. Wind (Finnish Meteorological Institute, Helsinki) and ice conditions (Tvärminne Zoological Station, Hanko) in winter during the study periods on the SW coast of Finland

No. of days with mean wind speeds >14 m s^{-1}		
Month	1998/1999	1999/2000
December	4	12
January	4	9
February	4	5
March	2	2
April	0	1
Duration of ice period at Storfjärden sampling station		
	1998/1999	1999/2000
	11 Jan–8 Apr	No ice cover

One reason for the reduced germination might have been that turbulence affected the biosynthetic metabolism of the cyst, a mechanism of cell damage proposed by Berdalet (1992) which would be particularly momentous prior to and during germination, a phase of general physiological activation (Binder & Anderson 1990).

When excystment was achieved, the completion of germination was, in both species, not impaired by turbulence. This is a somewhat unexpected result, as the survival and division of germling cells were expected to be particularly vulnerable to water motion. Inhibition of cell division is 1 of the most commonly reported effects of small-scale turbulence (White 1976, Pollingher & Zemel 1981, Berdalet 1992). Furthermore, flagella damage and modification of swimming behaviour (White 1976) have been demonstrated to be responsible for growth inhibition. In this study, the dinoflagellate cells, however, apparently multiplied rapidly immediately after germination. Presumably, the more favourable light period (12:12 h L:D) which was applied to enhance the response of the organisms to experimental conditions played a role here, since the same effect was observed both in the turbulence- and the still-water control treatment.

It is possible that the applied turbulence was lower than the so-called 'effect threshold' which is defined for dinoflagellates as a dissipation rate of 0.18 $cm^2\ s^{-3}$ (Thomas & Gibson 1990). The problem of using orbital shakers to generate small-scale turbulence is that they do not allow quantification of the turbulent energy dissipation and resulting shear intensity (Peters & Redondo 1997). The device used in the present study presumably generated moderate turbulence at a rotation speed of 2 rpm. Thomas et al. (1995) related the rotation of a comparable plankton wheel at 2 to 4 rpm to rates of strain of 2.2 to 4.4 rad s^{-1}. According to Estrada & Berdalet (1998), these would represent an energy dissipation of 0.08 to 0.18 $cm^2\ s^{-3}$ and thus remain below the threshold. Nevertheless, the applied turbulence would have been realistic with respect to conditions in coastal waters, since such energy dissipation would be equivalent to turbulent mixing at wind speeds of $\gtrsim$20 m s^{-1} (Estrada & Berdalet 1998).

Cyst resuspension and seeding of the vegetative population

Given the indifferent response of *Peridiniella catenata* cyst germination to light and turbulence and the favourable effect of increased irradiance and water motion on the survival and growth of the germinated cells, cyst resuspension should, in general, be beneficial for the seeding of a new vegetative *P. catenata* population. It seems, however, that recruitment directly from the sediment surface would not be disadvantageous for this species. The cysts germinate very successfully in complete darkness, and the new cells can survive the first days after excystment without external energy. Thus, they would be able to swim actively to the photic layer of the water column. The germination of *Scrippsiella hangoei* cysts would be favoured by the elevated light levels when resuspended in upper water layers, but at the same time turbulence would impair the process due to the observed small-scale effects. Nevertheless, it can be assumed that the seeding of an inoculum population would be more successful when cysts are resuspended, since germling survival, which is generally poor in this species particularly in darkness and at low irradiances, is clearly favoured in the euphotic water layer, even under conditions of prolonged mixing. Taking into account that in stormy winters approximately 20 times more *S. hangoei* cysts are resuspended than in calm winters, cyst resuspension would favour the build-up of a large inoculum population of this species, since significantly more cysts can germinate in the euphotic layer. For *P. catenata*, the measured cyst fluxes imply that cysts of this species would always be scarce in the water column irrespective of the weather conditions, and thus resuspension during the germination period would not substantially affect the development of a *P. catenata* inoculum.

To asses the role of cyst resuspension in the seeding and the subsequent vegetative development of *Scrippsiella hangoei* and *Peridiniella catenata*, it is necessary to consider the timing and duration of turbulent mixing and cyst resuspension. For *P. catenata*, for example, temporary cyst resuspension by individual storms in autumn and early winter could be advantageous because the reserves of the cysts could be replenished in the euphotic zone, and these would later support germling growth. This, in turn, would favour germling survival if conditions during germination were to become suddenly unfavourable. *S. hangoei* would, presumably, benefit from prolonged cyst resuspension by moderate water motion throughout December, January and February, the period of major germination (Kremp & Anderson 2000), when germling survival is particularly important in establishing an inoculum population. Furthermore, cyst resuspension can be important when coinciding with ice formation, as planktonic cysts will be incorporated into the ice, where conditions may be even more favourable for germination than in the water column. *S. hangoei* has been shown to germinate in ice (Kremp & Anderson 2000), and it can be assumed that also *P. catenata* is able to excyst at the low temperatures in the brine chanels, since motile cells of this species have been

observed in Baltic sea-ice (Ikävalko & Thomsen 1997). Germination in the brine channels of the sea-ice would have the advantage that the germlings would be directly released to the water layer underneath the ice. Here, stratification may provide optimal growth conditions and favour the formation of 'under-ice' blooms of the 2 species which have been repeatedly observed in the Baltic Sea (Niemi & Åström 1987, Larsen et al. 1995). Likewise, resuspension prior to ice formation would support bloom formation under the ice, since a large inoculum is believed to enhance dinoflagellate bloom formation when conditions are favourable (Nehring 1996, Anderson 1998).

It is intriguing to relate the interannual variation in the abundance and dominance patterns of *Scrippsiella hangoei* and *Peridiniella catenata* to the weather conditions and the intensity of cyst resuspension prior to and during the germination period. In fact, *S. hangoei* seems to be particularly abundant after mild and stormy winters (Kononen & Niemi 1984, Heiskanen & Kononen 1994, Algaline 2000: www2.fimr.fi/algaline/algaline.htm) whereas *P. catenata* blooms have been observed in strong winters with a long ice period (Niemi & Åström 1987, Haecky et al. 1998). It could be hypothesized that prolonged and intense resuspension of *S. hangoei* cysts in mild winters contributes to the build-up of a large inoculum population which may favour rapid bloom formation. The development of the vegetative *P. catenata* population in cold and calm winters, in contrast, may benefit from efficient recruitment under ice, independent of cyst resuspension. However, the period between winter storms when cyst germination takes place and the actual spring bloom can last several months in the northern Baltic Sea, and weather conditions hardly remain stable throughout such long periods of time. Thus, the maintainance of the inoculum population under variable conditions becomes another critical factor that influences the bloom initiation of the vernal dinoflagellates in the Baltic Sea. The details of survival and growth of *S. hangoei* and *P. catenata* during winter, however, are not yet known.

The example of the 2 Baltic spring-bloom dinoflagellates suggests that cyst resuspension may play a role in dinoflagellate bloom initiation. It may enhance bloom initiation and influence the species composition. If, and to what extent, resuspension affects vegetative development depends much on the germination and growth characteristics of the respective species, particularly on their response to light and small-scale turbulence. Furthermore, the timing and magnitude of cyst resuspension and the general germination potential of the cyst pool also determine if a dinoflagellate species can benefit from resuspension during its initial phase of population development.

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