Benthic fauna affects recruitment from sediments of the harmful cyanobacterium *Nodularia spumigena*

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**ABSTRACT**

Physical disturbance and feeding by macrofauna in the sediment can potentially affect bloom initiation of phytoplankton species that have benthic stages in their life cycle. In this experimental study, we investigated how different species of macrozoobenthos can affect the recruitment of *Nodularia spumigena* from the sediment to the water column. *N. spumigena* is a toxic, nitrogen-fixing filamentous cyanobacterium, which forms large summer blooms in the Baltic Sea. Benthic recruitment from resting stages (akinetes) and vegetative cells deposited on the seafloor have long been suspected to initiate the blooms. We found that, depending on species-specific traits, deposit-feeding macrofauna (an amphipod, *Monoporeia affinis*, a bivalve, *Macoma balthica* and an invasive polychaete, *Marenzelleria cf. arctica*) has the potential to either reduce or facilitate recruitment of this cyanobacterium. Shorter filament length in treatments with fauna than in the treatment without indicates feeding on or mechanical destruction of *N. spumigena* by the animals. Our results show the importance of an often overlooked aspect of phytoplankton bloom initiation, the role of macrozoobenthos.

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1. Introduction

Many types of plankton survive unfavorable periods by producing benthic resting stages, which settle to the sediment, from which future pelagic populations are recruited (Reynolds and Walsby, 1975; Ståhl-Delbanco et al., 2003). It is of particular importance to understand the processes involved in the initiation of harmful phytoplankton blooms, which are a common problem in eutrophicated aquatic ecosystems (e.g. Paerl, 1988; Anderson et al., 2002). The abiotic factors known to trigger germination of phytoplankton resting stages include altered temperature (e.g. Huber, 1985; Karlsson-Elfgren et al., 2004), light conditions (e.g. Huber, 1985; van Dok and Hart, 1997; Karlsson-Elfgren et al., 2004), and concentrations of inorganic nutrients (e.g. Huber, 1985; van Dok and Hart, 1997; Ståhl-Delbanco et al., 2003) and oxygen (e.g. Cáceres and Reynolds, 1984; Rengefors and Anderson, 1998) as well as wind-induced resuspension (e.g. Rengefors et al., 2004; Verspagen et al., 2004; Misson and Latour, 2012). Less is known on the effects of biotic factors such as bioturbation (the feeding and physical disturbance by benthic fauna in the sediment) on the recruitment of resting stages. Benthic fauna can however be an important factor structuring populations of pelagic organisms that spend part of their life cycle in the sediment (Hairston et al., 2000; Ståhl-Delbanco and Hansson, 2002).

Bioturbation can be divided into two main categories: particle reworking and burrow ventilation (Kristensen et al., 2012), which can both affect the fate of benthic propagules (e.g. ecosystem engineers; Jones et al., 1994; Kristensen et al., 2012). Particle reworking (i.e. movement of particles) occurs through burrow construction and maintenance, as well as ingestion and defecation. Burrow ventilation (i.e. movement of water) occurs when animals flush their burrows with overlying water for respiratory and feeding purposes. Depending on the mode of bioturbation, deposited propagules can either be buried deeper in the sediment or be resuspended to the water column. Ingestion and gut passage are negative if the propagules are digested and assimilated, but can be beneficial if they are egested intact on the sediment surface, encapsulated in nutrients, so called pelletization. Kremp et al. (2003) found that germination of marine dinoflagellate cysts was enhanced by passage through the gut of deposit-feeding polynactaeas, likely an effect of higher nutrient availability. Burrow ventilation can assist in resuspension, and can also stimulate mineralization of organic matter in the sediment and hence increase nutrient availability. Benthic invertebrates have been found to stimulate recruitment of freshwater cyanobacteria, probably by increasing nutrient availability in the pore water (Ståhl-Delbanco and Hansson, 2002). The effects of fauna on nutrient fluxes are complex and often indirectly
mediated through stimulation of bacterial activity. For example, bioturbation can result either in enhanced phosphate (P) binding to sediment or in temporarily increased sediment P release when bioturbation reaches deeper, reduced sediment layers with dissolved P in the pore water (Hietanen et al., 2007; Norkko et al., 2011). The species-poor sediments of the Baltic Sea have proven ideal for studies of the links between species interactions and ecosystem processes (Karlson et al., 2010, 2011). This species-poor system is also well suited for experiments to test the overall effects of bioturbation on phytoplankton recruitment.

In the Baltic Sea, recurring summer blooms of nitrogen-fixing filamentous cyanobacteria are considered to have increased in recent decades (Poutanen and Nikkilä, 2001). These blooms are often dominated by the hepatotoxic species Nodularia spumigena. The blooms are often detected by pop of Nodularia spumigena, which is considered a potential human health hazard and may have large effects on the Baltic Sea ecosystem (Karljainen et al., 2007). Factors contributing to the initiation of the N. spumigena blooms in the Baltic Sea are not well understood. Unlike Aphanothece, the other dominant bloom-forming cyanobacterium in the Baltic, N. spumigena is not common in the water column all year around. It appears suddenly and generally without a detectable preceding seed population (Wahl and Larsson, 2007).

In the shallow Peel-Harvey estuary and the Gippsland Lakes in Australia, where large blooms of N. spumigena have also occurred, the recruitment and germination of blooms was strongly linked to the germination and deposition of akinetes (cyanobacterial resting cells) in the sediment (Huber, 1984; 1985; Myers et al., 2011). Whether N. spumigena blooms originate in the same way in the Baltic Sea is still largely unresolved. Akinetes have so far been reported only rarely in water and sediment samples from the Baltic Sea and it is likely that the summer population of N. spumigena in the Baltic Sea is formed both from germinating akinetes and small numbers of vegetative filaments overwintering in the sediment or water column (Suikkanen et al., 2010).

N. spumigena blooms often appear first in the offshore regions of the Baltic proper (Niemistö et al., 1989) and its recruitment seems to be higher from field sediment samples taken from the open sea below 35 m depth than from shallow sediments above 10 m. This suggests that deeper sediments, inhabited by deposit-feeders, can provide much of the inoculum for blooms (Suikkanen et al., 2010). Previous studies have shown that cyanobacterial bloom material is deposited on the sediment floor (Bianchi et al., 2000; Voss et al., 2005) and that deposit-feeders can feed on N. spumigena and bury cyanobacterial filaments in the sediment (Karlson et al., 2008; 2010; Nascimento et al., 2008). The macrofaunal community is dominated by three species that differ in their mode of bioturbation (Vittasalo-Fröen et al., 2009; Karlson et al., 2010, 2011). The potential for benthic fauna to affect the recruitment of N. spumigena from the sediment is therefore clear, but no experiments have tested the significance of benthic fauna for the recruitment of N. spumigena in the Baltic Sea.

As a consequence of stratification and eutrophication, the deeper waters of the open Baltic proper, covering up to a third its bottom area, are oxygen-deficient (Conley et al., 2002). In addition, seasonal hypoxia and anoxia in shallow waters of the Baltic have also increased in recent decades, with detrimental effects on the benthic macrofauna (Karlson et al., 2002; Conley et al., 2011). Anoxic bottoms release phosphorus (Conley et al., 2002), the primary limiting nutrient for nitrogen-fixing cyanobacteria (Moisander et al., 2003; Walve and Larsson, 2007). The internal feedback loop, by which sediment release of phosphorus enhances cyanobacterial blooms, has been described as a self-sustaining ‘vicious circle’ (Vahtera et al., 2007). If oxygen-deficient sediment devoid of fauna facilitates recruitment of N. spumigena, this would strengthen the evidence for a link between eutrophication, anoxia and cyanobacterial blooms.

The aims of this study were to test: (i) if N. spumigena can be recruited from settled, aged filaments and akinetes added to intact sediment microcosms, representingoxic and hypoxic sub-thermocline sediment conditions in the Baltic and (ii) if species of benthic macrofauna with different modes of bioturbation will differ in their effects on such recruitment of N. spumigena.

2. Methods

2.1. Culturing N. spumigena and producing akinetes

Nodularia spumigena strain KAC66, isolated from the Baltic Sea and obtained from C. Esplund, Linnaeus University, Sweden, was grown in batch culture for 2 months at 18 °C at 45 μmol m−2 s−1 light:dark cycle with nutrients ([f2 medium, Guillard, 1975] at salinity 6. Once enough biomass was obtained, we induced akinete formation by greatly reducing the nutrient concentration in the culture flask and keeping the culture in darkness for ca. 2 months (first at 18 °C, then at 4 °C) (Huber, 1985; Pandey, 1989; cf. also Myers et al., 2011). The cyanobacterial suspension was then checked for akinetes under an inverted microscope and stored at 4 °C until start of the experiment. The final suspension of filaments was brown-colored and did not float, unlike growing N. spumigena. Of the cells, 37% were classified as akinetes, which appeared red-brownish in phase contrast, often formed chains and were larger and more spherical than vegetative cells (cf. Komárek et al., 1993).

2.2. Collection of sediment and animals

On 9 July 2010, sediment was collected with a 25 cm × 25 cm Olausson box corer, anoxic sediment from 90-m depth close to the Landsort deep (58°43′N, 17°56′E) and oxic sediment from 30-m depth at Hälldamman (58°50′N, 17°32′E). Care was taken to minimize sediment disturbance during sampling. Sediment cores were sub-sampled from the box corer by carefully inserting 30-cm long Plexiglass tubes (46 mm diameter, sediment column depth ca. 15 cm). In all, 35 anoxic cores and 7 oxic cores were collected. Benthic macrofauna for use in the experiment were collected at Hälldamman with a benthic sled. The dominant macrofaunal species in this area, as in most of the northern Baltic proper, are the deposit-feeding amphipod Monoporeia affinis, the facultatively deposit- or suspension-feeding bivalve Macoma balthica and the invasive deposit-feeding polychaete Marenzelleria sp. (arctica (Albertsson and Cederwall, 2008). Animals and sediment cores were stored in darkness with gentle air-bubbling at the Askö laboratory at the approximate in situ temperature of 5 °C. The water column of the anoxic cores was oxygenated by air bubbling to allow survival of added macrofauna (see Section 2.4). There were several reasons for adding animals to anoxic sediment. Firstly, we knew from experience that the sediment from 90 m was azoic. Hence, using it, we could create treatments differing only in the macrofauna species present, without sieving or otherwise changing the chemistry and structure of the sediment. The absence of fauna in the 90 m sediment was confirmed by sieving a few test cores, and by only added animals being found at the end of the experiment. Secondly, by introducing fauna to a previously anoxic sediment we could compare the effects of bioturbation on recruitment from sediment from a single site. Finally, previous experiments had shown that the fauna will survive such treatment (Modig and Olafsson, 2001).

2.3. Water chemistry

Samples of the filtered Baltic water (see below) and of near-bottom water from 7 randomly selected cores from both the anoxic
and oxic sites were collected with a sterile syringe, filtered through 0.2 μm Millipore filters and immediately frozen. Thereafter phosphate, ammonium and nitrate concentrations were analyzed at the accredited laboratory at the Department of Systems Ecology, Stockholm University. Most of the water in all cores were thereafter carefully replaced with filtered Baltic water from below the thermocline (salinity 6, containing 13 μg L⁻¹ PO₄-P, 6 μg L⁻¹ NH₄-N and 102 μg L⁻¹ NO₃⁻+NO₂⁻-N), without disturbing the sediment surface. The phosphate concentration in the water was then adjusted to ca. 150 μg L⁻¹ PO₄-P (a realistic concentration at the depth of 90 m where the anoxic sediment was collected (Swedish marine monitoring program, pers. comm. S. Nyberg, Dept. Systems Ecology), to lower the N:P ratio in the microcosms, as this favors cyanobacterial germination and growth (Ståhl-Delbanché et al., 2003).

2.4. Experimental set-up

On 20 July 2010, after 2 weeks of air bubbling, the anoxic cores had developed an oxidized surface layer a few mm deep (visible through the Plexiglass). We used 28 of these cores to create four different treatments, all of which later received an addition of cyanobacterial filaments and akinetes (see Section 2.5). To three treatments we added 6 individuals of similar size (corresponding to relevant field densities of 3600 individuals m⁻²) of either M. affinis (treatment MA), M. balthica (MB) or Marenzellera cf. arctica (MZ), to the re-oxygenated sediment. The fourth treatment received no animal addition (NF). The bivalves had a shell length of 4–6 mm and a shell-free dry weight of about 2 mg, the same as the amphipods and polychaetes. To confirm this, 10 individuals of each species, were dried at 60 °C and weighed. Since these species differ in their feeding and sediment reworking activities (Vitasalo-Frösen et al., 2009; Karlson et al., 2010, 2011), we wanted to test if recruitment of N. spumigena would differ among sediments with different macrofauna species or without macrofauna.

Two treatments without addition of aged cyanobacterial filaments and akinetes were included in the experiment as controls, to check if any filaments and akinetes were already present in anoxic and oxic sediment (AN and ON, respectively, n = 7).

All cores were kept under in situ sub-thermocline conditions (5 °C and 16:8 L:D cycle of faint green light of 0.5–1 μmol m⁻² s⁻¹, spectral maximum at 500 nm). This light level is sufficient for germination of N. spumigena (Huber, 1985) and the spectral maximum is ideal for cyanobacterial growth in the Baltic Sea (Kratzer, 2000).

2.5. Experimental procedures

The experiment was started 4 August 2010, by adding 4.9 g cm⁻² of the concentrated and homogenized suspension of filaments and akinetes (corresponding to 1.0 × 10¹⁵ cells m⁻²) to the NF, MA, MB and MZ cores using a Pasteur pipette. The amount added corresponds to field measurements of sedimentation from a cyanobacterial bloom at its termination (Tallberg and Heiskanen, 1998). The cores were ordered randomly in the constant-temperature room and air bubbling was stopped to allow filaments and akinetes to settle. After 24 h, the water column height was measured and air bubbling was carefully restarted, to mix the water column without visibly disturbing the sediment surface. To quantify how much of the added material remained suspended, a 25 mL water sample was taken from a few randomly selected cores, preserved with acid Lugol's solution (ca. 1% final concentration) and stored in darkness at 8 °C. N. spumigena has a high survival rate when transferred from culture to natural water (Engström-Öst et al., 2002).

On 11 August and 18 August 2010, a 25 mL water sample was taken from each core and preserved in Lugol prior to filament analyses. The experiment was terminated directly after the 2nd sampling by sieving the sediment through 500 μm mesh. Recovered animals were dried at 60 °C and weighed. The 14-day experiment was long enough for N. spumigena akinetes to germinate (Huber, 1985).

2.6. Filament counts and lengths

N. spumigena filaments were counted in 25 mL samples, after 24 h settling in Utermöhl chambers, using an inverted microscope (Leica Leitz Diavert, at 125 ×). We counted at least 100 counting units (filaments of 100 μm, about 25 cells) or all in the sample, if less, noting condition and length of the filaments. Filament length was measured using an object micrometer attached to the microscope.

2.7. Statistics

Differences in individual biomass of the macrofaunal species were analyzed using ANOVA. Differences in the number of N. spumigena filaments in the water column between treatments and dates (days 11 and 18) were analyzed using repeated measures ANOVA (linear mixed-effects model) with treatment as a fixed effect and date as a random effect, followed by Tukey’s HSD post hoc comparisons. Abundance data were first log-transformed in order to meet ANOVA assumptions of normality and sphericity. Differences between treatments in filament length were analyzed in the same way, but without transformation of data. All analyses used the statistical package R 2.13.1 (R Development Core Team, 2011). Only treatments with added N. spumigena were included in the analyses as the control treatments had negligible amounts of filaments (see Section 3).

3. Results

3.1. Animal survival and biomass

All added animals survived the experiment and no other animals were recovered from the anoxic sediment. There was no significant difference in shell-free dry weight between the treatments: M. affinis (MA): 1.82 ± 0.27 mg, Marenzellera cf. arctica (MZ): 1.98 ± 0.20 mg and M. balthica (MB): 2.07 ± 0.32 mg (mean ± standard deviation), (F₂,₇ = 2.33, p = 0.12). This corresponds to a total dry weight of 12 ± 1 mg per core (or 7 g m⁻²). The natural faunal community in the oxic sediment treatment (ON) was about 50% M. cf. arctica, 30% M. balthica (small individuals) and 20% M. affinis, with a single individual of the predatory priapulid Halicyrtus spinosus in one of the cores and the total number of macrofauna was 4.9 ± 1.9 individuals (mean ± standard deviation) per core, or 2900 individuals m⁻². This corresponds to a total biomass of about 10 mg shell-free dry weight per core or 6 g m⁻².

3.2. Filament counts and lengths

Only negligible quantities of N. spumigena were found in the water column of the treatments with no added cyanobacteria AN (anoxic sediment) and ON (oxic sediment) after 14 d (0.17 ± 0.37 and 0.01 ± 0.02 filament units mL⁻¹, respectively), indicating that few akinetes or vegetative cells of N. spumigena were present in our experimental sediments when collected. For all treatments combined, the N. spumigena filaments had a mean length of 307 ± 273 μm, (n = 2256). In general, the filaments were in good condition, without clear differences in condition among treatments. After 24 h, only 0.40 ± 0.065% (mean and standard deviation) of the added N. spumigena filaments and akinetes remained in
cyanobacteria as food (Karlsen et al., 2010; A.M.L. Karlson, unpublished), but due to nutritional inadequacy the cyanobacteria do not promote faunal growth (Karlsen et al., 2008; Nascimento et al., 2009; Karlson and Motzuraitis, 2011). Hence we expect some of the observed reduction in cyanobacteria in faunal treatments to be due to permanent loss, even though temporary burial of intact filaments may also contribute to the reduction.

The similar size and the well-studied ecology of the animals used allow us to discuss mechanisms behind the observed patterns. M. cf. arctica and M. balthica are facultative suspension- or deposit-feeders (Dauer et al., 1981; Ólafsson, 1986) that can consume cyanobacteria both in the sediment and the water column. M. balthica was observed to filter-feed actively as the cyanobacterial material was added. It is of particular interest that M. cf. arctica might suppress cyanobacterial recruitment. This invasive species has been shown to enhance both utilization of settled spring bloom material (Karlsen et al., 2011) and long-term retention of phosphorus in muddy bottoms (Norkko et al., 2011). The latter authors suggest that M. cf. arctica might facilitate the switch from a seasonally hypoxic (below 2 mg O₂ L⁻¹) to a normoxic system. M. cf. arctica could thus support ecosystem remediation in several ways.

In contrast, the treatment with the motile surface-stirring amphipod M. affinis was significantly more filaments in the water than in the other faunal treatments, with no significant difference from the treatment without fauna. Resuspension of filaments by amphipod bioturbation seems a natural explanation. Similarly, Ståhl-Delbarco and Hansson (2002) found that an active bioturbator (an isopod) had a larger positive effect on the recruitment of freshwater cyanobacteria than a less active one (an arthropod larva). Furthermore, Viitasalo et al. (2007) found that resuspension by M. affinis may enhance the hatching of zooplankton eggs in surface sediment, but that predation on eggs cancels this positive effect at high amphipod densities.

Our study cannot show whether germination from akinetes or ingestion/burial of added filaments caused the observed differences among faunal treatments. Bioturbation encompasses several processes that can affect phytoplankton recruitment. Regardless of the exact mechanism (i.e. particle transportation or ingestion), we found that how benthic animals influence recruitment of cyanobacteria depends on the species involved. Apart from N. spumigena, two other dominant bloom-forming genera of cyanobacteria occur in the Baltic, the hepatotoxic genus Anabaena and a species of Aphanizomenon that is considered non-toxic (Lehtimäki et al., 1997). Anabaena spp. seem to depend strongly on benthic recruitment, while Aphanizomenon sp. is holo-planktonic and thus less likely to be influenced by the benthos (Suikkanen et al., 2010). Changes in the benthic ecosystem could therefore potentially lead to differences in the recruitment of cyanobacteria and affect the ratio between toxic and non-toxic taxa. Two recent studies on the freshwater cyanobacterium Microcystis found that toxin-producing strains had higher recruitment from sediment than non-toxic strains (Schöne et al., 2010) and that recruited cells contained more toxin than benthic ones (Misson et al., 2011). Modeling has suggested that without benthic recruitment Microcystis blooms could be reduced by 50% (Verspagen et al., 2005). Most of this recruitment was attributed to wind-induced resuspension (Verspagen et al., 2004; Misson and Latour, 2012), and the role of bioturbation for recruitment and toxicity of blooms was not studied.

N. spumigena recruitment was as high in the absence of fauna as in the treatment with the active bioturbator M. affinis, but cyanobacterial filaments were longer than in all treatments with fauna. This treatment was oxygenated to ensure similar water chemistry to the faunal treatments, to allow valid comparisons. Results from an unpublished pilot study showed, however, that N.

### 4. Discussion

*N. spumigena* recruited successfully to the water column in our experiment, even though the temperature and light intensity used to mimic deep bottom conditions were far below the optimum for growth of this species. Bioturbation by the deposit-feeders affected recruitment of *N. spumigena* differently. Two species, the bivalve *M. balthica* and the polychaete *Marenzelleria cf. arctica*, greatly reduced the number of *N. spumigena* filaments in the water column during the 2-week experiment, compared to the treatment with no added fauna and the treatment with the amphipod *M. affinis*. Shorter filament lengths in treatments with fauna than in the treatment without suggest feeding or mechanical destruction by the animals. Previous studies have shown that all the animals tested can utilize suspension. The first days the added filaments and akinetes were visible as a thin layer on the sediment surface. Filament lengths differed significantly between treatments ($F_{2,24} = 8.59, p < 0.001$), with filaments in the no fauna treatment (NF) significantly longer than in the other three treatments with added *N. spumigena* (Tukey’s HSD post hoc test, $p < 0.04$, Fig. 1). There were no significant differences between weeks 1 and 2 ($F_{1,24} = 0.007, p = 0.935$). Interestingly, we also found significant differences in the number of *N. spumigena* filaments in the water column among the treatments with added cyanobacteria ($F_{3,24} = 14.48, p < 0.001$). The NF and MA treatments had significantly more *N. spumigena* filaments in the water column than the MZ and MB treatments (Fig. 2) (Tukey’s HSD, $p < 0.02$). We found no significant differences in the amount of *N. spumigena* filaments in the water column between weeks 1 and 2 ($F_{1,24} = 2.04, p = 0.166$), and no significant interaction between treatments and dates ($F_{2,24} = 2.09, p = 0.129$).
spumigena can recruit successfully from fully anoxic sediment. Anoxia has been reported to stimulate germination of cyanobacteria (Cáceres and Reynolds, 1984), hence there are several ways in which anoxic sediments might facilitate recruitment of cyanobacteria (i.e. suppressed bioturbation, high P, low oxygen). Future studies should use full factorial designs to study how abiotic and biotic conditions interact to affect recruitment.

Bloom initiation is complex and the release of phosphorus by anoxic sediments might be a major driver in the Baltic Sea (Vathera et al., 2007). In addition, water temperature, wind direction and nutrient concentrations in the surface water are important determinants of bloom development (Kahrri et al., 2007). Hence, a direct correlation between benthic faunal composition and cyanobacterial bloom intensity is not to be expected. In the northern Baltic Sea cyanobacterial blooms and especially N. spumigena may have increased in recent decades (e.g. Poutanne and Nikkilä, 2001), but the abundance and biomass of M. affinis, which was associated with high cyanobacterial recruitment in our study, have decreased since the 1980s, while the two species we found to suppress cyanobacterial recruitment, M. balthica and M. cf. arctica, have increased (Albertsson and Cederwall, 2008). Issues of faunal density-dependence and scale make extrapolations from our experiment difficult, but the potential role of benthic fauna in bloom initiation has clearly been overlooked. Our study shows that it deserves further attention.

In conclusion, our study indicates that changes in benthic macrofauna may have effects at the ecosystem scale by altering cyanobacterial bloom initiation. Sediments inhabited by facultatively suspension-feeding macrofauna, including the invasive species M. cf. arctica, are likely to suppress cyanobacterial recruitment, while the amphipod M. affinis or the absence of fauna may facilitate it. Our results indicate the importance of an often overlooked benthic–pelagic coupling, the role of macrozoobenthos in phytoplankton bloom initiation.

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References


