

## ALLELOPATHIC EFFECTS OF CYANOBACTERIAL FILTRATES ON BALTIC DIATOM

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**Abstract.** Allelopathy may be one of the factors affecting the formation of massive and harmful algal blooms in aquatic environments. Recent studies indicate that blooms of cyanobacteria in the Baltic Sea has grown significantly in last decades, so it is important to determine the allelopathic interactions between the dominant species of cyanobacteria and microalgae. In this work we investigated the influence of allelopathic compounds on the growth of *Skletonema marinoi* by addition of cell-free filtrate of the Baltic cyanobacterium *Nodularia spumigena* cultures grown under different temperature (15-25°C). Additionally the effects of filtrates of both an exponential and a stationary growing culture of *N. spumigena* were tested on diatom. These studies indicate that high temperature affected the donor species by increasing its production of allelochemicals. The highest drop of growth of analyzed diatom were observed after the addition of cell-free filtrate obtained from *N. spumigena* grown at 25°C and constituted 70% of their control. *N. spumigena* was only allelopathic in exponential growth phase, whereas the cyanobacteria filtrate from stationary phase have any effect on *S. marinoi*. These findings suggest that *N. spumigena* may reveal allelopathic activity and that the production of allelopathic substances is influenced by the temperature and growth phase of cyanobacteria.

**Keywords:** allelopathy, Baltic Sea, blooms, cyanobacteria

### Introduction

The term "allelopathy" as first defined by Molisch (1937), who indicated that these are positive or negative biochemical interactions between all types of plants. Rice (1979) included into these definition interaction between micro-organisms and Inderjit & Dakshini (1994) indicated that allelopathic activity is also present in the aquatic environment, especially between cyanobacteria and microalgae. Allelopathic interaction is widespread, can occur in all aquatic ecosystems and among all groups of aquatic primary producers (Gross 2003). The production of allelopathic compounds by phytoplankton were identified in several groups of phytoplankton such as Cyanobacteria, Dinophyta, Raphidophyta and Prymnesiophyta. There are also few reports about the possibility of producing such compounds by green algae and diatoms (Subba Rao & Smith 1995; Chiang *et al.* 2004). In addition, it is believed that allelopathy may be one of the factors affecting the structure of phytoplankton (Legrand *et al.* 2003) and the formation of massive blooms of cyanobacteria and algae in many freshwater, brackish and marine water bodies (Smayda 1997; Weissbach *et al.* 2010).

The mass occurrence of cyanobacteria may have different implications for the surrounding ecosystem. Cyanobacterial blooms can cause mortality of fish and other aquatic animals, and reduce water quality (Stal *et al.* 2003). The ability of cyanobacteria to the impact on other aquatic organisms such as viruses, bacteria, fungi, phytoplankton, zooplankton and fish has been demonstrated in various laboratory studies (Landsberg 2002; Legrand *et al.* 2003). Blooms of cyanobacteria in the Baltic Sea are generally noted in the nineteenth century, but in recent years, their appearance has significantly increased (Kahru *et al.* 1994; Stal *et al.* 2003). Blooms of cyanobacteria in the Baltic Sea consists of two groups - picocyanobacteria from the genus *Synechococcus* and larger filamentous cyanobacteria like *Nodularia spumigena*, what is one of the most important species of cyanobacteria forming harmful blooms in the Baltic Sea (Kahru *et al.* 1994). Moreover picoplanktonic cyanobacteria may constitute up to 80% of the total biomass of cyanobacteria and 50% of the total primary production in cyanobacteria blooms (Stal *et al.* 2003; Jasser 2006).

The production and release of allelopathic compounds is an intriguing conception, in which substances are secreted by the interacting species. Various species of

cyanobacteria are known to produce intra- and extra-cellular metabolites with diverse biological activities, such as antialgal (Kaya *et al.* 2002), antibacterial (Isnansetyo *et al.* 2003), antifungal (Kundim *et al.* 2003) and antiviral activity (Shih *et al.* 2003; Noaman *et al.* 2004). Relatively little is known about the inhibitory effect of secondary metabolites of cyanobacteria on coexisting organisms (Sivonen & Jones 1999). The occurrence of allelopathic effects are common in cyanobacteria and algae, but the specific mode of action of several secreted compounds is still unknown. In many cases it is difficult to demonstrate direct evidence of allelopathic interactions in natural phytoplankton communities. It is therefore important to characterize the allelopathic effects in controlled experiments to investigate the nature of the substances released and their mode of action on target organisms.

The main aim of this work was to estimate the allelopathic effect of cyanobacterium *N. spumigena* on diatom *S. marinoi*. *S. marinoi* was chosen for this study because it constitutes very important component of the spring diatom blooms in the Baltic Sea. In this study, the influence of allelopathic compounds on the growth of analyzed species was investigated by addition of cell-free filtrate of *N. spumigena* cultures grown under varied temperature conditions and different growth phase of cyanobacteria. Provision of information on allelopathic interactions may contribute to a better understanding of the occurrence of massive blooms of cyanobacteria in many aquatic ecosystems, including the Baltic Sea.

## Materials and methods

### *Algal material and culture conditions*

The experiments were conducted on filamentous cyanobacterium *Nodularia spumigena* (BA-15) and diatom *Skeletonema marinoi* (BA-98). The strains were isolated from the coastal zone of the Gulf of Gdańsk (southern Baltic Sea) and are maintained as unialgal cultures in the Culture Collection of Baltic Algae (<http://ccba.ug.edu.pl>) at the Institute of Oceanography, University of Gdańsk, Poland (Latała 2003; Latała *et al.* 2006). Tests on the “batch cultures” were carried out in 100 ml glass Erlenmeyer flasks containing sterilized F/2 medium (Guillard 1975). The media were prepared from Baltic water with a salinity of about 8 psu, which was filtered through glass fiber filters (Whatman GF/C). The cyanobacterium strain was incubated under a 16:8 h light:dark cycle at three temperature (15, 20 and 25°C) and PAR irradiances of 10  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ . The cultures were acclimated to every temperature condition and then cyanobacterial cultures were used as a source of inoculum for the establishment of the allelopathy experiments. We also compared the allelopathic effects of *N. spumigena* cultures in exponential and stationary growth phases. *N. spumigena* culture was kept in the incubation chamber until it reached the exponential or stationary growth phase, as monitored by culture density measurements. The effects of cell-free filtrates of both the stationary and an exponentially growing culture were tested on *S. marinoi* using

the same procedure as above. Tested diatom grown in constant conditions of 20°C, 10  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  and 8 psu.

### *Experiment setup*

Allelopathic interactions was determined by using the method proposed by Śliwińska *et al.* (2011). Allelopathic interaction was studied by adding the cell-free filtrate obtained from cyanobacterial culture to tested diatom. The filtrate was filtered through Whatman GF/C filters. Next the cell-free filtrate ( $V = 5 \text{ ml}$ ) was added to 50 ml Erlenmeyer flasks containing tested algae ( $V = 50 \text{ ml}$ ). In all experiments, the ratio of cyanobacteria to target species in the Erlenmeyer flasks was adjusted to 1:1 based on the chlorophyll *a* contents of the cultures thus the proportion of cyanobacteria in relation to target algae was equal to 80:80  $\mu\text{g chl } a \text{ l}^{-1}$ . Control samples were prepared by adding mineral medium F/2 with a volume equal to the added cell-free filtrate obtained from cultures of cyanobacteria. After 1, 3 and 7 days of exposure the culture density of the target species was determined. Culture density was determined by the number of cells and optical density (OD). The number of cells was measured microscopically using Bürker chamber and OD was measured spectrophotometrically at 750 nm with a Multiskan GO Thermo Scientific UV-VIS spectrophotometer. The results of cell number and OD cultures were used to determine the linear correlation between the measured parameters. Determined relationships were then used to estimate the number of cells in the cultures tested only on the measurements of the OD. Tests were conducted in triplicate and all analyzed diatom were obtained from early exponential growth phase.

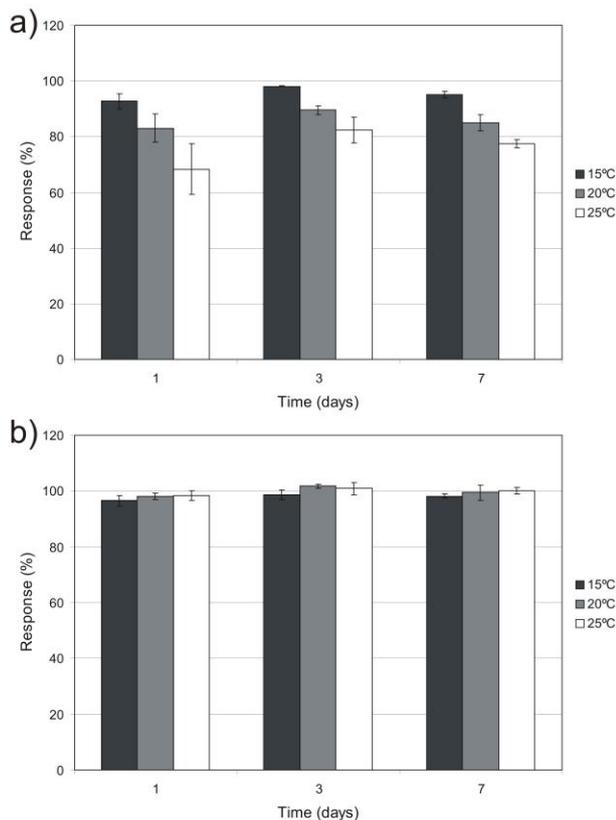
### *Statistical analyses*

Analysis of variance (ANOVA) was used to test for differences in the all analyzed parameters between the target algae cultures treated with cyanobacterial cell-free filtrates and the control, over the experimental period. A post hoc test (Tukey's HSD) was used to show which treatments significantly differed from the control and from each other. All tests are in a significance level of  $P = 0.05$ , and data are reported as means  $\pm$  SD. The statistical analyses were performed using the SSP Statistica® 10.

## Results

The results showed that Baltic cyanobacterium *N. spumigena* significantly decreased the number of cells of diatom *S. marinoi* compared to their control (Fig. 1). Addition of cell-free filtrate from *N. spumigena* cultures grown under different temperature inhibited the growth of analyzed species in various range. In this work we show, that high temperature affected the donor species by increasing its production of allelochemicals and the highest drop of growth was observed after the addition of cell-free filtrate obtained from *N. spumigena* grown at 25°C.

In the experiment the minimum cells response of *S. marinoi* cultures constituted 70% of their control. We also found (Fig. 1) that growth phase of cyanobacterium has a impact of their allelopathic interaction on *S. marinoi*. *N. spumigena* has only allelopathic potential in exponential growth phase, whereas the culture filtrate from stationary phase has any allelopathic effect on *S. marinoi*.



**Fig 1.** Effects of filtrates from a) exponential and b) stationary growth phase of culture *N. spumigena* grown at 15, 20 and 25°C on *S. marinoi* expressed as the response (%) of cells density in the treated algal cultures in relation to the control (n = 3, mean±SD).

## Discussion

Production of harmful substances is common, but not identical for all species forming massive blooms and are no clear reasons for the synthesis of these compounds (Legrand *et al.* 2003, Gross 2003). It is possible that their function enables deterrence of predators and inhibition of co-occurring species of phytoplankton (Turner *et al.* 1997; Liu *et al.* 2010). In addition, it is suggested that in the Baltic Sea cyanobacterial allelopathy may cause their dominance after the maximum concentration of cells is formed by environmental factors (Granéli & Johansson 2003a, b; Suikkanen *et al.* 2004, 2005). The use of biological tests is the first step in identifying which group of allelopathic compounds is responsible for causing harmful effects in the aquatic environment (Fistarol *et al.* 2004a, b).

In the relatively few studies have documented the impact of allelopathic effects of cyanobacteria. In this work, the influence of allelochemicals on the growth of *S. marinoi* was investigated by addition of cell-free filtrate of Baltic nitrogen-fixing cyanobacteria *N. spumigena* cultures grown under varied temperature and different growth phase of cyanobacteria. These studies indicate that high temperature and only exponential growth phase affected the tested cyanobacteria by increasing its production of allelopathic compounds. In this work we show, that the highest drop of growth was observed after the addition of cell-free filtrate obtained from *N. spumigena* grown at 25°C and the minimum cells response of *S. marinoi* cultures constituted 70% of their control. The Keating (1977, 1978) also showed a decrease the diatom cells after the addition of the filtrate from the waters of the lake, which cyanobacteria was the dominated species and after addition cell-free filtrate of cyanobacterial monocultures. Similar results were noted by Lafforgue *et al.* (1995), who proved that the low biomass of *Fragilaria crotonensis* in the Aydat lake in 1984 was probably the result of growth inhibition by extracellular metabolites excreted in the growing population of *Anabaena* sp. Moreover, Lam and Silvester (1979) showed allelopathic interaction between the *Anabaena oscillarioides* or *Microcystis aeruginosa* and *Chlorella* sp. In their study *A. oscillarioides* and *M. aeruginosa* significantly inhibited the growth of *Chlorella* sp., while *M. aeruginosa* also negatively affected on the growth of *A. oscillarioides*.

Many studies have shown that cyanobacteria may release allelopathic substances into the medium (Oufdou *et al.* 1998; Østensvik *et al.* 1998). Cyanobacterial peptides, hepatotoxins and microcystin cause the allelopathic effect of higher plants (MacKintosh *et al.* 1990; Pflugmacher 2002) and phytoplankton (Kearns & Hunter 2001, Singh *et al.* 2001). Cyanobacterial allelopathy appear to be especially common for freshwater species (Gross 2003), but recent studies have shown that there is evidence for inhibition of cryptomonads and diatoms also by brackish cyanobacteria (Suikkanen *et al.* 2004). The study of these authors have shown that two blue-green algae *Aphanizomenon flos-aquae* and *Nodularia spumigena*, which are common species during summer blooms in the Baltic Sea, causing decrease the number of cells *Rhodomonas* sp. and *Thalassiosira weissflogii*, which grow as a monoculture. Also in natural phytoplankton communities from the Baltic Sea, cyanobacterial cell-free filtrate caused a decrease the number of cryptomonas and an increase the number of cells of other cyanobacteria, green algae, dinoflagellata and nannoflagellata (Suikkanen *et al.* 2005).

Only several authors showed that the production of allelopathic compounds may be caused by temperature. Ame *et al.* (2003) noted that production of higher amounts microcystin by cyanobacteria was caused by temperature higher than 23°C. In temperature 20°C the cyanobacterium *Cylindrospermopsis raciborskii* also showed the highest production of cylindrosperopsin (Griffiths & Saker 2003). Moreover nodularin production by cyanobacteria was low in temperatures about 7-16°C (Lehtimaki *et al.* 1997). These findings indicate that cya-

nobacteria *N. spumigena* reveal allelopathic substances and their production may depend of temperature, which was also consistent with the results obtained in this work. Vance (1965) noted, that in order to affect the competitors of the producer, allelochemicals should be excreted already during exponential growth and not only during cell lysis. Moreover, Suikkanen *et al.* (2004) showed that the filtrate from the exponential growth phase *N. spumigena* had a distinct negative allelopathic effect on both *T. weissflogii* and *Rhodomonas* sp., whereas the stationary culture filtrate did not affect the target species. These results are also consistent with the results obtained in this work. Suikkanen *et al.* (2004) also reported that the allelopathic activity was observed only in cultures where nodularin concentration was low. Therefore it is suggested that it is unlikely that the observed effect of nodularin induced allelopathic activity and other compounds must be responsible for the observed effects (Suikkanen *et al.* 2006).

Allelopathy may play an important role in the succession of species, the formation of massive blooms and even the appearance of invasive species. Some species of phytoplankton are known to produce and release secondary metabolites that can interact with coexisting organisms. There are not many reports about the causes and consequences of allelopathic effects of cyanobacteria in the Baltic Sea. It is therefore important to conduct more detailed studies of this phenomenon. Provide new information on the allelopathy of cyanobacteria and microalgae may be important in understanding the phenomenon of the emergence of massive blooms of algae in many aquatic ecosystems, including the Baltic Sea.

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### Abstrakt

Allelopatia może być kluczowym czynnikiem wpływającym na tworzenie się masowych zakwitów sinic w wielu wodnych ekosystemach. Badania pokazują, że zakwity sinic w Morzu Bałtyckim w ostatnich dekadach znacznie się nasiliły, dlatego tak ważne jest określenie stopnia oddziaływania allelopatycznego dominujących w tym akwenu gatunków fitoplanktonu. W przeprowadzonych badaniach określono wpływ związków allelopatycznych produkowanych przez bałtycką sinicę *Nodularia spumigena* hodowaną w różnych temperaturach (15-25°C) na wzrost okrzemki *Skeletonema marinoi*. Dodatkowo w niniejszej pracy porównano wpływ przesączu komórkowego uzyskanego z hodowli sinic będących w fazie logarytmicznego i stacjonarnego wzrostu. Badania wykazały, że temperatura modyfikuje allelopatyczne oddziaływania i na przykład najwyższy spadek wzrostu zaobserwowano u *S. marinoi* po dodaniu przesączu uzyskanego z kultur *N. spumigena* hodowanych w 25°C. Wynosił on 70% w stosunku do kontroli. Ponadto w pracy stwierdzono, że *N. spumigena* wykazywała oddziaływanie allelopatyczne na badaną okrzemkę jedynie wtedy, gdy dodawany przesącz komórkowy pochodził z fazy logarytmicznego wzrostu. Wyniki uzyskane w niniejszej pracy sugerują, że bałtyckie sinice mogą wykazywać oddziaływanie allelopatyczne w stosunku do okrzemek a produkcja związków allelopatycznych może być zależna od temperatury oraz fazy wzrostu, w której znajdują się organizmy donorowe.

**Słowa kluczowe:** allelopatia, sinice, Morze Bałtyckie, zakwity