

Niche separation of Baltic Sea cyanobacteria during bloom events by species interactions and autecological preferences

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ABSTRACT

Cyanobacterial blooms regularly occur in the Baltic Sea during the summer months, with filamentous, heterocystous *Nodularia spumigena* and *Dolichospermum* sp. and the coccoid picocyanobacterium *Synechococcus* spp. as important species. Under calm conditions, *N. spumigena* accumulate at the surface, whereas *Dolichospermum* sp. and *Synechococcus* sp. remain at the subsurface, in the upper water layer. This vertical separation allows co-occurring species to compete for the same resources. The factors that determine the vertical distribution within blooms, however, are mostly unknown. The present study examined the growth rates of these three cyanobacterial species in a two-factorial experiment, with temperature (16 and 24 °C) and radiation (38 and 150 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) conditions mimicking those at the water surface and directly below. To determine whether interactions between the three species influenced their growth rates (and therewith also their vertical distribution), paired and multi-species cultures were established. In the single-species cultures, the autecological preferences of the species matched the assumed natural occurrence in bloom events: *N. spumigena* grew best under high and *Dolichospermum* sp. and *Synechococcus* sp. under low light conditions (maximum growth rates at the preferred conditions: $\mu = 0.48 \pm 0.017$, 0.88 ± 0.092 , and 0.67 ± 0.012 , respectively). High temperatures were tolerated by *N. spumigena*, but inhibited the growth of *Dolichospermum* sp. and *Synechococcus* sp. These results suggested that the factors resulting in the vertical separation of species within a bloom are species-specific: *N. spumigena* responded predominantly to irradiance and only slightly to temperature, *Dolichospermum* sp. was intensely affected by temperature and less by irradiance, and *Synechococcus* sp. responded more strongly to irradiance than to temperature. The interactions in paired and multi-species cultures revealed beneficial and detrimental effects, depending on species composition and abiotic conditions. Under the environmental conditions in which the three species occur, however, similar interactions resulted in no or only slight inhibition. Our observations demonstrate how autecological preferences together with the avoidance of negative interactions determine the vertical distribution of cyanobacteria during bloom events in the Baltic Sea.

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1. Introduction

Cyanobacterial blooms are observed worldwide in limnic, brackish, and marine systems. Their formation is favored by the higher temperatures that accompany global warming (Paerl and Huisman, 2009; Wasmund, 1997). Among the numerous undesired consequences of these massive proliferations are the repression of

biological diversity and economic losses associated with the recreational value of the affected waters, due to toxin production, and the subsequent poisoning of fish and filter feeders (Ferrão-Filho and Kozłowski-Suzuki, 2011). However, cyanobacterial blooms also provide ecosystem services, such as the maintenance of homeostasis and nutrient stoichiometry in the global ocean (Deutsch et al., 2007).

Eutrophication in the last several decades has led to an expansion of cyanobacterial blooms (O'Neil et al., 2012; Paerl and Huisman, 2009, 2008). In the Baltic Sea, the first scientific reports of cyanobacterial blooms date back to the 19th century (Finni et al., 2001), but by now they may cover large areas of the Baltic Proper (Kahru and Elmgren, 2014). Compared to other phytoplankton

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groups, cyanobacteria seem to have distinct preferences for certain environmental conditions (Olli and Seppälä, 2001). During the summer months, the higher water temperatures and low N:P ratios (after the diatom spring blooms) promote mass occurrences of cyanobacteria, which are able to fix atmospheric nitrogen (Bianchi et al., 2000; Stal et al., 1999; Wasmund, 1997). These blooms significantly impact the carbon (Ploug et al., 2011), nitrogen, and phosphorus cycles of the Baltic Sea (Stal et al., 1999; Wasmund et al., 2001). For example, total cyanobacterial nitrogen fixation in the Baltic Sea is estimated to be 370,000 t yr⁻¹, which is almost as high as the annual riverine input of 480,000 t and twice as high as the atmospheric load of 196,000 t yr⁻¹ (Wasmund et al., 2001), and may contribute 55% of total nitrogen input (Stolte et al., 2006; Wasmund et al., 2005).

Baltic Sea cyanobacterial blooms consist of filamentous, diazotrophic species, which are accompanied by small coccoid ones, whereby the dominant group may differ between years and bloom stage (Ohlendieck et al., 2000; Walsby et al., 1995). The large, filamentous species *Nodularia spumigena*, *Aphanizomenon* sp., and *Dolichospermum* sp. may produce toxins, whereas Baltic Sea *Aphanizomenon* strains (not included in this study) are considered to be non-toxic. *N. spumigena* produces the hepatotoxin nodularin, and *Dolichospermum* sp. microcystins (Halinen et al., 2007). Coccoid, non-heterocystous picocyanobacteria such as *Synechococcus* spp. roughly measure <1 µm but they may comprise up to 80% of the total cyanobacterial biomass and account for 50% of the total primary production in a cyanobacterial bloom (Stal et al., 2003). Baltic Sea *Synechococcus* spp. are not capable of nitrogen fixation and hence depend on dissolved nitrogen sources (Bauersachs et al., 2009), which may be provided from, amongst others, filamentous species (Ohlendieck et al., 2000).

Different cyanobacterial species differ in their tolerance ranges of abiotic factors, which is manifested in distinct vertical distributions in bloom events (Hajdu et al., 2007; Olli et al., 2015; Olli and Seppälä, 2001; Walsby et al., 1995). In general, *Aphanizomenon* sp. is positioned slightly deeper than other cyanobacterial species, closer to the bottom of the surface layer (Hajdu et al., 2007; Walsby et al., 1995). *N. spumigena*, *Dolichospermum* sp., and *Synechococcus* sp. are confined to the upper water

layer, with *N. spumigena* at the direct surface and *Dolichospermum* sp. at the subsurface (Hajdu et al., 2007). Throughout the upper 30 m of the euphotic zone, *Synechococcus* sp. appears and is most abundant in the upper 15–20 m (Stal et al., 2003), with a relatively even vertical distribution (Hajdu et al., 2007). If conditions are not calm, however, these strict vertical distributions can be disrupted. *N. spumigena* and *Dolichospermum* sp. control their vertical movement by gas vesicles and may thus re-occupy their vertical niche rapidly after wind events (Walsby et al., 1995), whereas *Synechococcus* sp. is subject to only minimal sinking losses due to its small size but does not possess facilities for vertical movement (Stal et al., 1999). The reasons for this vertical distribution of cyanobacteria are widely unknown, but could include autecological preferences for abiotic conditions and interactions between co-occurring phytoplankton species.

The Baltic Sea is a stratified water body with a permanent halocline between 60 and 100 m and an additional thermocline at 5–20 m during summer. During calm periods (and thus blooms emergence), the temperatures and irradiance of even the top layer (i.e., the water layer above the thermocline), gradually decreases with depth (Olli and Seppälä, 2001). This might be largely explained by irradiance but elevated temperatures also decrease the critical depth for cyanobacteria, by altering the stratification of the water column and vertically decreasing the top layer (Stal and Walsby, 2000). While these changing light and temperature regimes should be the most important abiotic factors affecting the vertical distribution of different cyanobacterial species, because nutrient concentrations are stable in the upper water layer during calm weather, co-occurring species also interact with each other with beneficial or detrimental effects. Allelopathic interactions may hamper toxin-sensitive phytoplankton species (Hulot and Huisman, 2004) and change microbial food webs (Weissbach et al., 2011), whereas resource competition may disadvantage inferior species (Interlandi and Kilham, 2001). Co-existing species, however, may also profit from nutrient remineralization and fixation (Ohlendieck et al., 2000; Stal and Walsby, 1998). This study evaluated the importance of different factors that may shape the spatial distribution of cyanobacteria. Specifically, we asked whether autecological preferences of temperature and irradiance reflect the vertical distribution of the different species in the field.

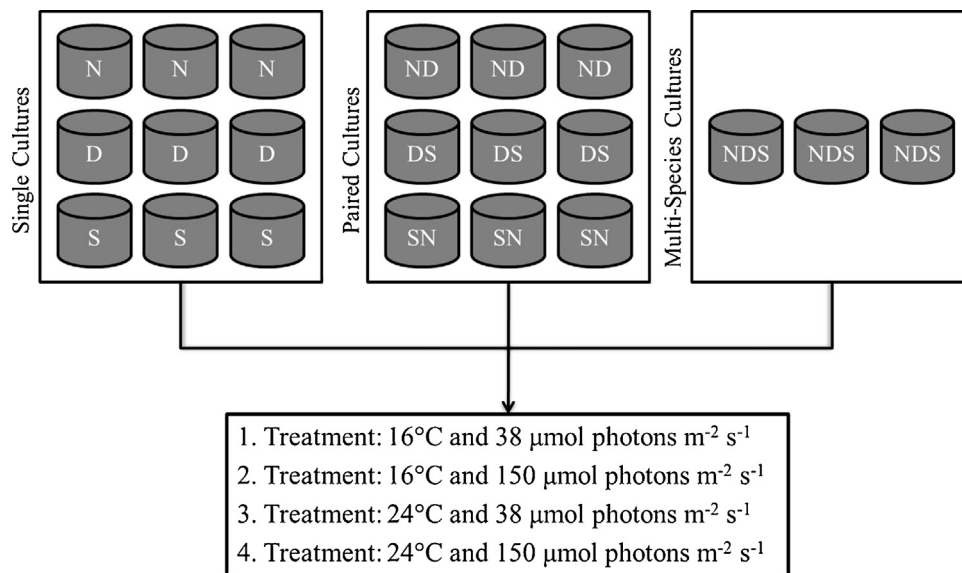


Fig. 1. Experimental set-up: Light and temperature conditions as well as species compositions in the four different treatments. N = *N. spumigena*, D = *Dolichospermum* sp., S = *Synechococcus* sp.

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