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The bloom of nitrogen-fixing cyanobacteria in the northern Baltic Proper stimulates summer production

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ABSTRACT

In the northern Baltic Sea Proper, total nitrogen (TN) increases during the summer bloom of filamentous heterocystous cyanobacteria. To follow the fate of the nitrogen they fix, we studied several N fractions during the bloom. We measured cyanobacterial biomass, TN, particulate organic N (PON, two size fractions), dissolved organic N (DON), and PON sedimentation in two areas in 2011. TN increased mainly due to increasing PON, but also to DON. Cyanobacteria contributed about 20% of the PON increase and ~10% of the TN increase. About half the PON changes (increase, then decrease) could be explained by the sum of cyanobacteria, other autotrophs (>2 μm) and zooplankton, indicating that the bloom stimulates primary and secondary production. TN decreased after the bloom mainly due to declining PON > 10 μm, but sedimentation rates did not increase and could explain little of the post-bloom N-loss. There was little settling of undecomposed cyanobacteria.

The seasonal development of *Aphanizomenon* sp. and N pools was similar among stations and areas. For *Nodularia spumigena* between-station variability increased once patchy surface accumulations developed. A brief *Dolichospermum* spp. bloom indicated that sampling frequency may be more important than spatial resolution for capturing dynamics of this bloom.

Regional index terms

Northern Europe
Baltic Sea
Northern Baltic Proper

1. Introduction

Cyanobacteria are photosynthetic prokaryotes found in all aquatic environments. Many are diazotrophic, i.e. able to fix atmospheric dinitrogen, and important providers of new nitrogen (N) to their surroundings (Howarth et al., 1988; Karl et al., 2002). In the Baltic Proper, summer blooms of filamentous heterocystous cyanobacteria, i.e. *Aphanizomenon* sp., *Nodularia spumigena*, and *Dolichospermum* spp. (earlier referred to as *Anabaena* spp.; Wacklin et al., 2009) are accompanied by increased concentrations of total nitrogen (TN) in the upper mixed layer (Larsson et al., 2001; Rolff et al., 2007). The N fixation implied by this increase is several hundred thousand tons of N each year, making it one of the largest sources of N to the Baltic Proper (Larsson et al., 2001; Wasmund et al., 2005), similar to the load from land and atmospheric deposition (Bartnicki et al., 2011; HELCOM, 2011).

The summer TN increase in the Baltic Proper is well documented (Larsson et al., 2001; Rolff et al., 2007), but less is known about its components and fate. Only a minor part of the TN increase is due to an increase in cyanobacterial biomass (Rolff et al., 2007). Hence, other particulate or dissolved N fractions must dominate the bloom-associated TN increase. Firstly, decaying cyanobacteria may contribute to accumulation of both detritus and dissolved N. Moreover, studies have shown that diazotrophic cyanobacteria leak a considerable fraction of recently fixed N as either ammonium (NH_4^+, Ploug et al., 2010; Ploug et al., 2011) or dissolved organic nitrogen (DON, Glibert and Bronk, 1994). As a result of N uptake by the spring bloom, the upper mixed layer of the Baltic Proper is depleted in dissolved inorganic nitrogen (DIN: $NO_2^-/NO_3^- + NH_4^+$) in early summer and any released NH_4^+ will hence be assimilated by N-limited phytoplankton, stimulating primary and potentially also secondary production (Karlson et al., 2015, Adam et al., 2016). Most freshly formed DON is likely to be available to phytoplankton and heterotrophic bacteria (Korth et al., 2012; Hoikkala et al., 2015), and may reach higher trophic levels via the microbial loop (Azam et al., 1983). On the other hand, some refractory DON forms could potentially accumulate during a bloom. An additional pathway for fixed N in the pelagic food web is the direct ingestion of diazotrophic cyanobacteria by zooplankton, but quantitative information on this pathway is limited (Wannicke et al., 2013; Karlson et al., 2015). Hence, fixed N appears to contribute to the build-up of a variety of particulate and dissolved pools during the course of the bloom. Some of this N will eventually be transferred to higher trophic levels or be lost from the upper mixed layer by sedimentation.

Disentangling the different pathways and fates of fixed N is essential to understand the response of Baltic Sea productivity and oxygen

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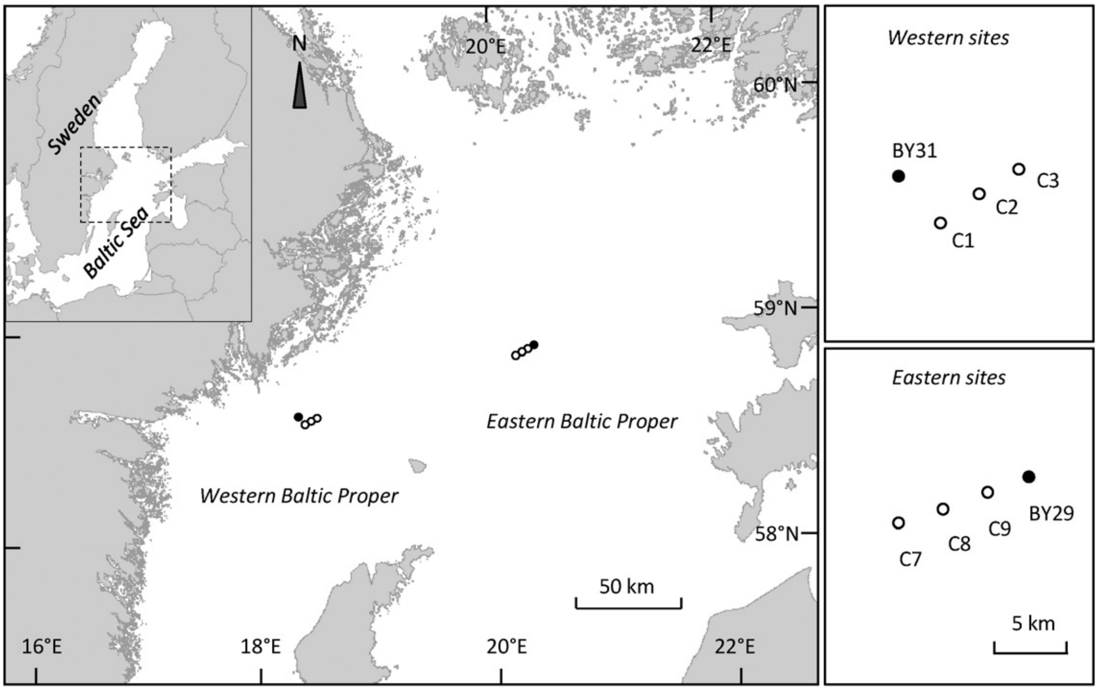

Fig. 1. Map of sampling areas. Filled circles are the Swedish National Marine Monitoring stations BY31 (Western Baltic Proper) and BY29 (Eastern Baltic Proper). Empty circles are this study's additional stations C1–C3 (Western Baltic Proper) and C7–C9 (Eastern Baltic Proper), where sediment traps were deployed during summer 2011.

conditions to changes in cyanobacterial production. Such changes may occur as a result of nutrient load mitigations or climate change (Karlson et al., 2015). We here explore the TN increase and its fate in more detail than has been done in previous studies. Specifically, we are interested in the contribution of different forms of particulate and dissolved N, and if the post-bloom TN decrease can be coupled to increased sedimentation rates. We followed the bloom dynamics of the three main filamentous N-fixing cyanobacterial taxa and the build-up and loss of major N pools during their bloom in two areas in the northern Baltic Proper (Fig. 1). Four stations in each area were sampled for concentrations of cyanobacteria, TN, DIN, DON and two size-fractions of particulate organic nitrogen (PON). For one of the stations (BY31), we used monitoring data on phytoplankton and zooplankton biomass to further characterize the particulate N pool. Sediment traps were deployed at six stations, three in each area, to follow particulate N loss from the upper mixed layer during the bloom. By this approach we aimed to gain insight into potential pathways for fixed N in the Baltic Sea and to estimate the annual nitrogen fixation based on the N increase.

2. Materials and methods

2.1. Sampling strategy and stations

Samples were taken from May to September 2011 (7–9 occasions, Table 1) at four stations in the Landsort Deep area of the north-western Baltic Proper (western area), and at four stations in the north-eastern Gotland basin of the Baltic Proper (eastern area). Stations in each area were about 3.3 km apart. Sampling was made during the cruises of the Swedish National Marine Monitoring Program (SNMMP) with M/S *Fyrbyggaren*. Normally, the SNMMP samples only station BY31 in the western area (biweekly) and station BY29 in the eastern area (monthly), makes no PON and DON measurements, and monitors cyanobacteria and sedimentation only at BY31.

2.2. Water samples

At each station, depth profiles of temperature and salinity were measured with a CTD (Multi Parameter CTD 90M, Sea & Sun. Marine Tech).

Table 1
Sampling program in 2011.

	Landsort deep area of the north-western Baltic Proper (western area)				North-eastern Gotland basin of the Baltic Proper (eastern area)			
Station	BY31	C1	C2	C2	BY29	C7	C8	C9
Position	58°35′ N, 18°14′ E	58°34′ N, 18°17′ E	58°35′ N, 18°19′ E	58°36′ N, 18°23′ E	58°53′ N, 20°19′ E	58°51′ N, 20°09′ E	58°52′ N, 20°12′ E	58°52′ N, 20°15′ E
May 9	x	x	x	x	x			
May 26	x	x	x	x				
June 8	x	x	x	x	x	x	x	x
June 21	x	x	x	x	x	x	x	x
July 6	x	x	x	x	x	x	x	x
July 20	x	x	x	x	x	x	x	x
Aug 3	x	x	x	x	x	x	x	x
Aug17	x	x	x	x	x	x	x	x
Sept 21	x	x	x	x	x	x	x	x