

Basin-specific changes in filamentous cyanobacteria community composition across four decades in the Baltic Sea

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ARTICLE INFO

Keywords:

Filamentous cyanobacteria
Climate change
Salinity
Temperature
Long-term monitoring

ABSTRACT

Almost every summer, dense blooms of filamentous cyanobacteria are formed in the Baltic Sea. These blooms may cause problems for tourism and ecosystem services, where surface accumulations and beach fouling are commonly occurring. Future changes in environmental drivers, including climate change and other anthropogenic disturbances, may further enhance these problems. By compiling monitoring data from countries adjacent to the Baltic Sea, we present spatial and temporal genus-specific distribution of diazotrophic filamentous cyanobacteria (Nostocales) during four decades (1979–2017). While the summer surface salinity decreased with a half up to one unit, the surface temperature in July–August increased with 2–3 °C in most sub-basins of the Baltic Sea, during the time period. The biovolumes of the toxic *Nodularia spumigena* did not change in any of the sub-basins during the period. On the other hand, the biovolume of the non-toxic *Aphanizomenon* sp. and the potentially toxic *Dolichospermum* spp. increased in the northern parts of the Baltic Sea, along with the decreased salinity and elevated temperatures, but *Aphanizomenon* sp. decreased in the southern parts despite decreased salinity and increased temperatures. These contradictory changes in biovolume of *Aphanizomenon* sp. between the northern and southern parts of the Baltic Sea may be due to basin-specific effects of the changed environmental conditions, or can be related to local adaptation by sub-populations of the genera. Overall, this comprehensive dataset presents insights to genus-specific bloom dynamics by potentially harmful diazotrophic filamentous cyanobacteria in the Baltic Sea.

1. Introduction

Filamentous cyanobacteria play a key role in aquatic nutrient cycling, and therefore, the effect of the ongoing climate change on their future presence is increasingly addressed (Burford et al., 2019). However, cyanobacteria blooms may also be harmful, either by producing toxins (Moestrup et al., 2009) and/or by accumulating in the surface potentially resulting in beach fouling and closures of beaches. High biomasses are also problematic when they sink and their degradation can cause hypoxia in the deep water. The Baltic Sea, one of the largest brackish-water bodies in the world, has a long history of multi-stressors and long-term data series, and hence, can be used to study consequences of e.g. eutrophication, for mitigation purposes (Reusch et al., 2018). Lindström (1855) observed a bloom of what probably was

cyanobacteria in the Baltic Sea already in the summer of 1854, and filamentous cyanobacteria have increased in abundance along with nutrients introduced to coastal environments during the recent century (Finni et al., 2001). Nowadays, dense blooms of filamentous cyanobacteria are formed almost every summer in the Baltic Sea (Kahru and Elmgren, 2014; Wasmund et al., 2018). Harmful algal events caused by the cyanobacteria are reported to the IOC-UNESCO Harmful Algae Event Database (HAEDAT, <http://haedat.iode.org>), and will be compiled in a report for the North Atlantic, including the Baltic Sea (Bresnan et al., in prep.).

The blooms are dominated by three taxa, *Nodularia spumigena* (Mertens ex Bornet and Flahault 1886), *Aphanizomenon* sp. (A. Morren ex É. Bornet and C. Flahault 1888), and *Dolichospermum* spp. ([Ralfs ex Bornet and Flahault] P. Wacklin, L. Hoffmann and J. Komárek, 2009)

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<https://doi.org/10.1016/j.hal.2019.101685>

Received 22 May 2019; Received in revised form 23 September 2019; Accepted 29 September 2019

Available online 11 October 2019

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(Klawonn et al., 2016). These three taxa were recently demonstrated to sum up to the total surface pelagic nitrogen fixation in the Baltic Sea (Klawonn et al., 2016). The non-toxic *Aphanizomenon* sp. generally dominates in the northern parts of the Baltic Sea, e.g. Gulf of Bothnia, probably due to its low salinity preferences (Lehtimäki et al., 1997; Rakko and Seppälä, 2014), similar to the potentially toxic *Dolichospermum* spp. (Brutemark et al., 2015; Teikari et al., 2019). Toxic strains of *Dolichospermum* spp. have been found in the Gulf of Finland (Halinen et al., 2008; Fewer et al., 2009) and in the Gulf of Gdańsk (Kobos and Mazur-Marzec, 2017). The toxic *N. spumigena* is more abundant in the southern parts of the Baltic Proper (Wasmund et al., 2018), where the toxin nodularin has been found in thousands of years old sediment cores (Ceglowska et al., 2018).

Scenario modeling suggests an expected increased precipitation and elevated temperatures over the next 100 years in the Baltic Sea (HELCOM, 2013). This would result in a reduced salinity of ca. 3 units and temperature increases of ca. 2–5 °C until year 2100 (Meehl et al., 2007). Increased temperatures are predicted to increase the abundance of cyanobacteria (Fu et al., 2007; Paerl and Huisman, 2008; Davis et al., 2009; Karlberg and Wulff, 2013), while a decreased salinity might shift the phytoplankton community composition towards more freshwater genera (Wulff et al., 2018). However, the filamentous cyanobacteria did not manage to outcompete the existing spring bloom community under elevated temperatures in an experimental study (Olofsson et al., 2019). Previous monitoring studies of the Central and Northern Baltic Sea indicate an increased surface water temperature during summer, as well as basin-specific decreases in salinity since 1979, along with an increase in cyanobacteria abundance (Suikkanen et al., 2007, 2013; Kuosa et al., 2017). Increased sea surface temperatures were also detected in a satellite study, where number of days with > 17 °C almost doubled from 1982 to 2014 (Kahru et al., 2016). A decreased salinity has also been reported for the southern parts of the Baltic Proper, along with a decrease in the toxic *N. spumigena* (Wasmund et al., 2011). Synergistically with temperature and salinity changes, increased nutrient availability, from e.g. riverine runoff and internal feedback from sediments, has probably enhanced cyanobacteria blooms further north in the Baltic Sea (Jaanus et al., 2011; Kahru and Elmgren, 2014; Andersson et al., 2015). Additional genus-specific studies are needed, focusing on the entire Baltic Sea, from the Bothnian Sea to the Arkona basin, to fully understand the bloom dynamics of the main bloom forming genera of diazotrophic filamentous cyanobacteria.

By compiling four decades of monitoring data from seven countries adjacent to the Baltic Sea, this study aims to (A), demonstrate genus-specific community composition of the dominating filamentous cyanobacteria for six sub-basins and its temporal trends, and (B) relate this to surface water salinity and temperature changes in the different areas. Hence, the aim is to provide early indications of climate-driven changes in filamentous cyanobacteria bloom dynamics.

2. Methods

2.1. Study area

The Baltic Sea is a brackish semi-enclosed sea area divided into several sub-basins with different characteristics regarding salinities and nutrient loads. This study includes monitoring data during 1979–2017 from stations spread across the Baltic Sea areas where strong cyanobacteria blooms regularly occur (Fig. 1). Due to its narrow connection to the ocean in the southwest and large freshwater input mainly in the north and east, a salinity gradient establishes reaching from a mean surface salinity of about 12 in the southwest to about 3 in the north and east. In order to examine basin specific changes in salinity and community composition, the gradient was split accordingly: the Bothnian Sea with 4.5–6.5 in salinity, the Gulf of Finland with 4.5–5.5 in salinity, the Northern Baltic Proper with 6.0–7.0 in salinity, the Central Baltic Sea with 6.5–7.5 in salinity, the Southern Baltic Proper with 7.0–8.0 in

salinity, and the Arkona Basin with 7.5–8.5 in salinity.

2.2. Monitoring data

Monitoring data of biovolume ($\text{mm}^3 \text{L}^{-1}$) were compiled for the years 1979–2017 from the Finnish (part of HELCOM COMBINE monitoring program [HELCOM, 2017]; data available at: https://www.syke.fi/en-US/Open_information) and Polish (from 2006 part of the HELCOM COMBINE monitoring program), as well as the German, Estonian, Lithuanian, and Danish datasets (all available at the ICES HELCOM database: <https://ices.dk/marine-data/dataset-collections/Pages/HELCOM.aspx>), with variation between datasets, see Table 1. The compiled dataset was used in order to determine the spatial and temporal distribution of the three dominating diazotrophic filamentous cyanobacteria *Nodularia spumigena*, *Aphanizomenon* sp. and *Dolichospermum* spp. as well as the total biovolume of the three filamentous cyanobacteria taxa referred to as Nostocales. The cyanobacteria biovolumes were calculated based on filament sizes (Olenina et al., 2006). The HELCOM Phytoplankton Expert Group (PEG) provides yearly updates of a list with biovolumes of fixed size-classes used for the calculation of phytoplankton biomass in routine monitoring of Baltic Sea phytoplankton (http://ices.dk/marine-data/Documents/ENV/PEG_BVOL.zip).

The surface (0–10 m) salinities and temperatures (°C) during summer (July and August) were extracted from the Swedish (Swedish National Oceanographic Data Centre at the Swedish Hydrological and Meteorological Institute, data available at: <https://sharkweb.smhi.se>), as well as the previously mentioned datasets (Table 1). The summer mean (July and August) and total biovolume of the three filamentous cyanobacteria, as well as salinity and temperature (°C), were calculated and used for annual trend and linear regression tests within each sub-basin (see Statistical analyses).

2.3. Statistical analyses

For the annual trends in biovolume of filamentous cyanobacteria, an initial visual examination of the data using the non-linear GAM model within the package ‘Tidyverse’ in R was applied (Wickham, 2017). The visual examination determined mainly linear relationships in biovolume over time, and therefore, linear model regressions using the package ‘Tidyverse’ in R were used. These trend analyses were used to test for significant basin- and taxon-specific changes over time, as well as changes in salinities and temperatures for each sub-basin over the time period. Cyanobacterial biovolumes in combination with either salinities or temperatures were also examined using linear model regression for each taxon and basin, in order to find significant relationships. All data used in the regression models were tested for normal distribution by Shapiro-Wilk tests using the ‘stats’ package in R (R Core team, 2016). Square root transformation was performed in case of non-normal distribution. In addition, Permutational Multivariate Analysis of variance (PerMANOVA) was used to test for covariation of salinity and temperature, as well as their interactions, with changes in cyanobacteria biovolume using the *adonis* function in the package ‘vegan’ in R (Anderson, 2001; Oksanen et al., 2019). Significance level of trends and relation to environmental parameters were set as $p < 0.05$.

3. Results

3.1. Biovolumes of filamentous cyanobacteria based on monitoring data

The highest non-transformed mean biovolume of filamentous cyanobacteria during summer (July and August) was observed in the Central Baltic Proper, whereas the overall highest value was found in the Southern Baltic Proper (Table 2). Bothnian Sea had both the lowest mean value of total biovolume and the lowest maximum value. The

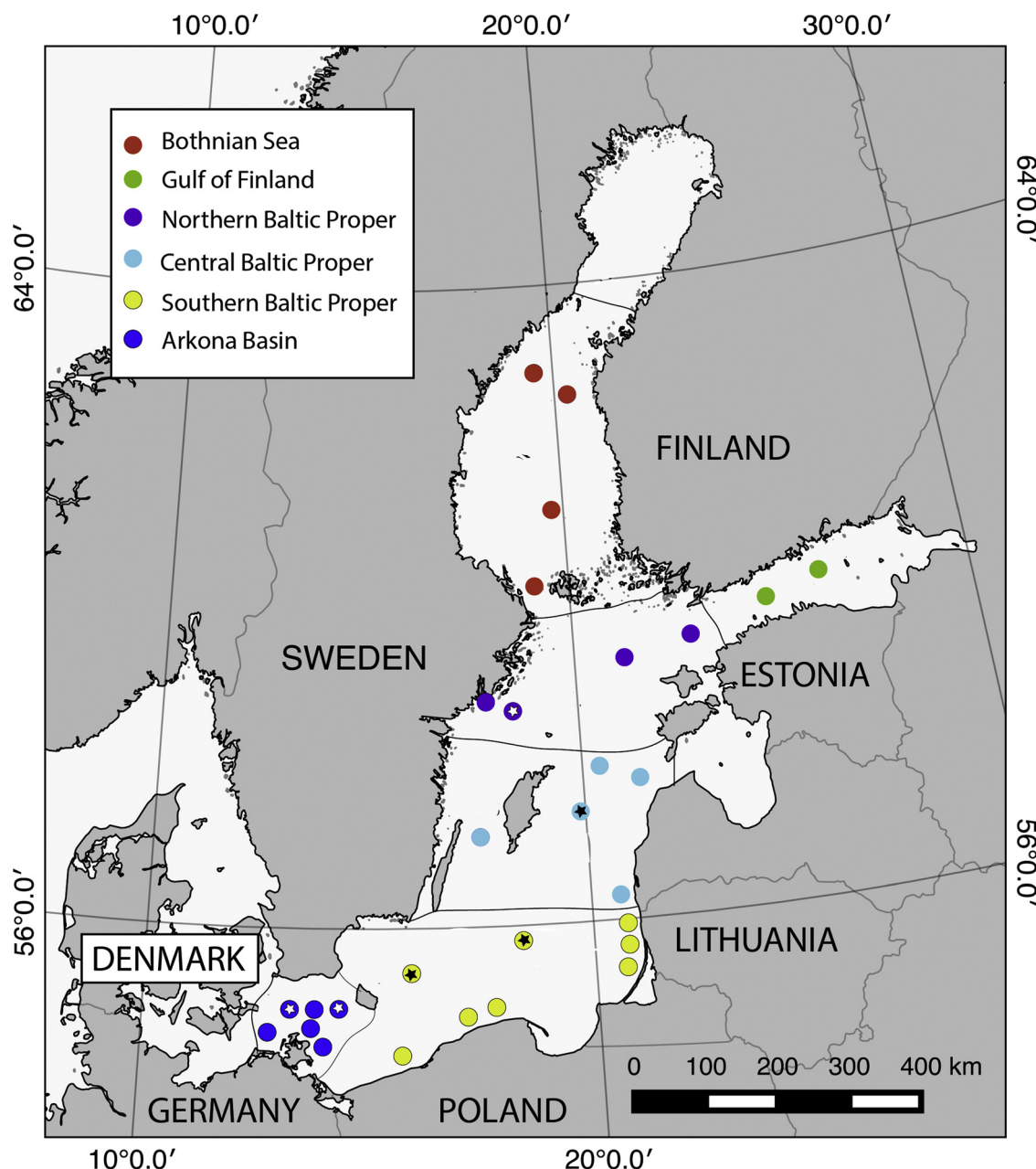


Fig. 1. Map showing the sampling stations in the Baltic Sea for the data used. The data emanates from long term monitoring programs in Sweden, Finland, Denmark, Estonia, Lithuania, Germany, and Poland. Stars indicate frequently sampled stations by at least two countries and colors denote the sub-basins. For details see Table 1.

highest mean value of *Aphanizomenon* sp. was observed in the Gulf of Finland while the lowest was observed in the Bothnian Sea, but it was close to the mean value of the Southern Baltic Proper. The highest mean value of *Dolichospermum* spp. was observed in the Northern Baltic Proper, while the lowest mean value was observed in the Bothnian Sea. The highest mean value of *Nodularia spumigena* was observed in the Central Baltic Proper, while the lowest was observed in the Bothnian Sea. Overall there was a large variation between years and samplings, as demonstrated by the high standard deviation (Table 2).

The biovolume of *Aphanizomenon* sp. increased significantly between 1979 and 2017 in the Bothnian Sea and the Gulf of Finland (linear regression, $p < 0.05$, Fig. 2, Table 3). In contrast, the biovolume of *Aphanizomenon* sp. decreased in the Southern Baltic proper and the Arkona Basin and did not change in the remaining basins. The biovolume of *Dolichospermum* spp. increased in the Bothnian Sea and the Central Baltic Proper, while it did not change significantly in the

other regions (Fig. 2, Table 3). The biovolume of *N. spumigena* did not change in any of the sub-basins (Fig. 2, Table 3). The same patterns as for *Aphanizomenon* sp. were observed for the total biovolume of Nostocales (Fig. 2, Table 3).

Although an increase in biovolume of *Aphanizomenon* sp. in the northern parts of the Baltic Sea was observed, the proportion of the genus of the rest of the community of diazotrophic cyanobacteria did not change (Fig. 3, Table 3). On the other hand, the decrease in biovolume of *Aphanizomenon* sp. in the southern basins resulted in a decrease in its relative proportion of the total Nostocales community in the Central Baltic proper (linear regression, $p = 0.016$) and the Southern Baltic Proper (linear regression, $p = 0.013$). The relative proportion of *N. spumigena* to the total Nostocales did not change during the period (Fig. 3, Table 3). The proportion of *Dolichospermum* spp. of the total Nostocales community increased significantly in the Central and Southern Baltic Proper (linear regression, $p < 0.001$ and 0.028 ,

Table 1
Monitoring stations. List of monitoring stations and parameters used in the present study: sub-basins, station names, countries sampling at the station, coordinates of latitude and longitude, sampling years, and number of samples per summer (July and August).

Sub-basin	Station	Country	Latitude	Longitude	Parameters	Sampling years	Samples per summer
Bothnian Sea	US5B	Finland	62.58	19.98	Phytoplankton, Salinity + Temperature	1979-2015	1-2
	SR5	Finland	61.09	19.58	Phytoplankton, Salinity + Temperature	1979-2015	1-2
	F64	Finland	60.20	19.15	Phytoplankton, Salinity + Temperature	1979-2015	1-2
	C3	Sweden	62.39	18.57	Salinity + Temperature	1979-2017	1-2
Gulf of Finland	LL3A	Finland	60.07	26.35	Phytoplankton, Salinity + Temperature	1979-2015	1-2
	LL7	Finland	59.85	24.83	Phytoplankton, Salinity + Temperature	1979-2015	1-2
	LL12	Finland	59.48	22.90	Phytoplankton, Salinity + Temperature	1979-2015	1-2
	LL17	Finland	59.03	21.08	Phytoplankton, Salinity + Temperature	1979-2015	1-2
Northern Baltic Proper	LL23, BY31	Finland, Sweden	58.58	18.23	Phytoplankton, Salinity + Temperature	1979-2017	2-6
	B1	Sweden	58.80	17.62	Salinity + Temperature	1979-2017	1-5
	BY15, BMP J1, TF0271	Finland, Sweden, Estonia, Germany, Lithuania	57.32	20.05	Phytoplankton, Salinity + Temperature	1979-2017	2-6
	BY38	Finland	57.12	17.67	Phytoplankton, Salinity + Temperature	1979-2015	1-2
Central Baltic Proper	BMP J2	Lithuania	55.92	20.33	Phytoplankton, Salinity + Temperature	1996-1998	1
	J56	Lithuania	56.92	20.34	Phytoplankton, Salinity + Temperature	2009, 2012, 2013, 2015	1
	SL3, 32, 34a	Estonia	57.97- 58.07	20.53- 21.98	Phytoplankton, Salinity + Temperature	2011-2015	1-2
	BMP K2, BY5, TF0213	Finland, Sweden, Poland, Denmark, Germany	55.25	15.98	Phytoplankton, Salinity + Temperature	1979-2017	2-5
	BMP K1, TF0259	Finland, Poland, Germany, Lithuania	55.55	18.40	Phytoplankton, Salinity + Temperature	1979-1984, 1986-1988, 2016	1-2
	BMP K56	Poland	54.26	15.53	Phytoplankton, Salinity + Temperature	2006, 2008-2015	1
	BMP K12	Poland	54.63	16.80	Phytoplankton, Salinity + Temperature	2006, 2008-2015	1
Arkona Basin	BMP K51	Poland	54.83	17.35	Phytoplankton, Salinity + Temperature	2006, 2008-2015	1
	K32, K41, K18	Lithuania	55.31-55.77	21.89- 21.08	Phytoplankton, Salinity + Temperature	2008-2015	1-2
	BMP K4, BY2, TF0109	Finland, Lithuania, Germany	55.00	14.08	Phytoplankton, Salinity + Temperature	1979-2017	2-5
	BMP K7, TF0069	Denmark, Germany, Lithuania	55.00	13.30	Phytoplankton, Salinity + Temperature	1979-1997, 2001, 2006, 2009	1-2
	BMP K5, TF0113	Germany	54.93	13.50	Phytoplankton, Salinity + Temperature	1981, 1983, 1984, 1987, 1990, 1991, 1993-2016	1-2
	TF011, OMO11	Germany	54.54	13.77	Phytoplankton, Salinity + Temperature	1998, 2010, 2011, 2013-2015	1-3
	BMP K8, TF0030	Germany	54.72	12.78	Phytoplankton, Salinity + Temperature	1990, 1991, 1993-2016	1-3
	OMO9, TFO9	Germany	54.62	13.03	Phytoplankton, Salinity + Temperature	1998, 2010, 2011, 2013-2015	1-2

Table 2

Biovolume of filamentous cyanobacteria. Mean summer concentration of cyanobacterial biovolume ($\text{mm}^3 \text{L}^{-1}$), standard deviation (SD), standard error (SE), number of samplings (n), and maximum value in the Baltic Sea sub-basins during 1979–2016.

Basin	Species	Mean	SD	SE	n	Max
Bothnian Sea	<i>Aphanizomenon</i> sp.	0.079	0.080	0.008	84	0.316
	<i>Dolichospermum</i> spp.	0.001	0.002	0.002	84	0.018
	<i>Nodularia spumigena</i>	0.017	0.034	0.004	84	0.198
	Total Nostocales	0.098	0.081	0.023	84	0.326
Gulf of Finland	<i>Aphanizomenon</i> sp.	0.143	0.150	0.019	62	1.054
	<i>Dolichospermum</i> spp.	0.014	0.025	0.003	62	0.127
	<i>Nodularia spumigena</i>	0.045	0.132	0.017	62	0.876
	Total Nostocales	0.203	0.218	0.028	62	1.070
Northern BP	<i>Aphanizomenon</i> sp.	0.106	0.089	0.010	81	0.392
	<i>Dolichospermum</i> spp.	0.013	0.063	0.007	81	0.562
	<i>Nodularia spumigena</i>	0.036	0.085	0.009	81	0.718
	Total Nostocales	0.155	0.164	0.018	81	1.095
Central BP	<i>Aphanizomenon</i> sp.	0.127	0.188	0.016	133	1.248
	<i>Dolichospermum</i> spp.	0.006	0.011	0.001	133	0.065
	<i>Nodularia spumigena</i>	0.107	0.260	0.023	133	2.149
	Total Nostocales	0.241	0.352	0.031	133	2.223
Southern BP	<i>Aphanizomenon</i> sp.	0.081	0.175	0.012	206	1.642
	<i>Dolichospermum</i> spp.	0.006	0.025	0.002	206	0.279
	<i>Nodularia spumigena</i>	0.080	0.266	0.019	206	2.940
	Total Nostocales	0.168	0.366	0.026	206	3.707
Arkona Basin	<i>Aphanizomenon</i> sp.	0.116	0.153	0.010	216	0.874
	<i>Dolichospermum</i> spp.	0.012	0.033	0.002	216	0.273
	<i>Nodularia spumigena</i>	0.081	0.262	0.018	216	2.837
	Total Nostocales	0.209	0.350	0.023	216	3.213

respectively; Fig. 3, Table 3). This was related to an increase in its biovolume in the Central Baltic proper while the other genera did not change, and a decrease in biovolume of *Aphanizomenon* sp. in the Southern Baltic proper, while the biovolume of *Dolichospermum* spp. did not change during the period.

3.2. Environmental parameters and cyanobacteria biovolume

The summer surface salinity significantly decreased in all sub-basins of the Baltic Sea except for the Gulf of Finland and the Arkona Basin (Fig. 4, Table 3). Although the salinity of the Gulf of Finland did not change, the values were among the lowest of all sub-basins. The largest

decrease in salinity was observed in the Bothnian Sea, with a decrease of almost one unit. The total biovolume of Nostocales as well as the biovolume of *Aphanizomenon* spp. had a significant negative regression with salinity in the Bothnian Sea (linear regression, $p = 0.013$ and $p = 0.042$, respectively. Fig. 5, Table 3). This was supported by the PerMANOVA test (Table 4), where changes in the total biovolume of Nostocales (pseudo-F = 3.90, $p = 0.003$) as well as in *Aphanizomenon* sp. (pseudo-F = 7.90, $p = 0.004$) covaried with salinity changes in the Bothnian Sea. Changes in biovolume of *Aphanizomenon* sp. were related to changes in salinity in both the Northern Baltic Proper (PerMANOVA, pseudo-F = 3.46, $p = 0.031$) and the Southern Baltic Proper (PerMANOVA, pseudo-F = 4.45, $p = 0.012$). However, no significant regressions were observed in either of the basins between salinity and biovolume of *Aphanizomenon* sp. (Table 3). Salinity changes were also related to changes in total Nostocales biovolume in the Arkona Basin (PerMANOVA, pseudo-F = 3.90, $p = 0.021$), but with no significant regressions (Table 3). The biovolume of *Dolichospermum* spp. had a positive regression with salinity in the Southern Baltic Proper (linear regression, $p = 0.045$; Fig. 5, Table 3), but with no significant covariance of the variables in the PerMANOVA test (Table 4).

The surface temperature as average during July and August increased significantly in the Gulf of Finland, Northern Baltic Proper, the Central Baltic Proper, and the Arkona Basin since the 1980s (Fig. 6, Table 3). Here, the average summer temperature increased with up to 2–3 °C, but with large variation between basins and years. The total Nostocales biovolume and temperature did not have any significant regression in any of the sub-basins (Fig. 7, Table 3). The biovolume of *Aphanizomenon* sp. had a negative regression with temperature in the Arkona Basin (linear regression, $p = 0.040$), as well as in the Southern Baltic Proper (linear regression, $p = 0.042$). The biovolume of *Dolichospermum* spp. had a significant positive regression with temperature in the Bothnian Sea (linear regression, $p = 0.005$), but a negative one in the Arkona Basin (linear regression, $p = 0.010$). This relationship was supported by the PerMANOVA test where temperature and biovolume of *Dolichospermum* spp. covaried in the Arkona basin (pseudo-F = 2.92, $p = 0.048$, Table 4). The biovolume of *N. spumigena* did not have a significant regression with either temperature or salinity (Table 3). There was no interaction effect of temperature and salinity on changes in biovolume observed in the PerMANOVA test (Table 4).

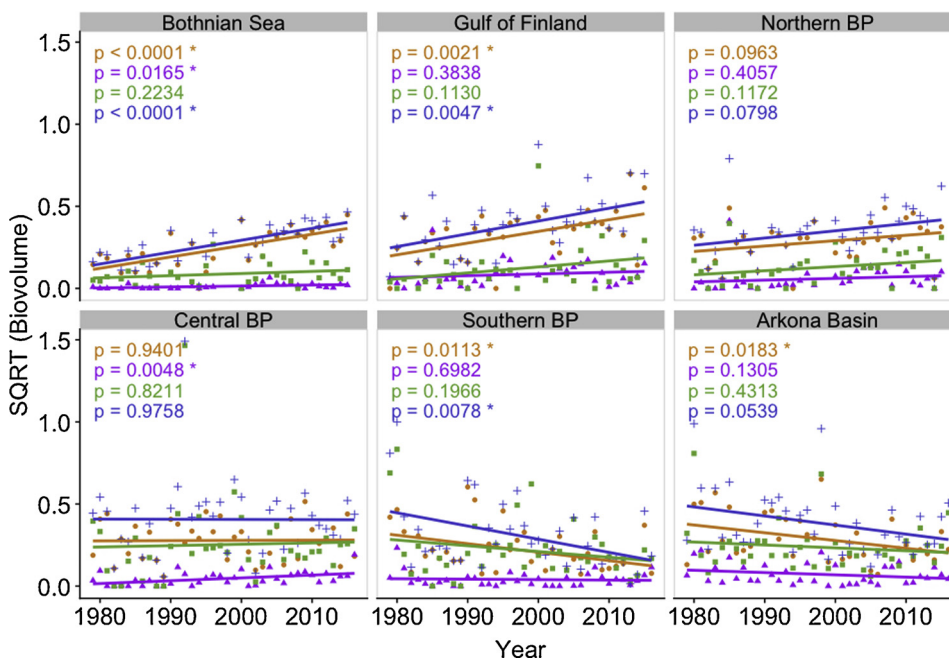


Fig. 2. Biovolume ($\text{mm}^3 \text{L}^{-1}$) of *Aphanizomenon* sp. (orange), *Dolichospermum* spp. (purple), *Nodularia spumigena* (green), and total Nostocales (blue) for the period 1979–2017 (details are given in Table 1) as seasonal means during July and August. Square root transformation of biovolume was performed to achieve normal distribution. Linear model regression lines are included as well as p-values.

Table 3

Results of the linear regressions. Statistical parameters of the linear regression between filamentous cyanobacteria (biovolume), their relative proportion, salinity as well as temperature, and time. In addition, linear regression for each of the three genera and salinity and temperature. The data are from the period 1979–2017 representing surface water in July and August. The cyanobacteria biovolume data were square root transformed to achieve normal distribution.

Basin	Variable	n	Intercept	Slope	R ²	p-value
Bothnian Sea	<i>Aphanizomenon</i> sp.	31	−13.6	0.007	0.48	< 0.0001*
	<i>Dolichospermum</i> spp.	31	−1.2	0.001	0.18	0.0165*
	<i>Nodularia spumigena</i>	31	−2.5	0.001	0.05	0.2234
	Total Nostocales	31	−14.2	0.007	0.52	< 0.0001*
	Salinity	32	46.2	−0.021	0.65	< 0.0001*
	Temperature	32	−59.6	0.038	0.07	0.1364
	Prop. <i>Aphanizomenon</i> sp.	31	−4.2	0.002	0.02	0.4398
	<i>Aphanizomenon</i> sp. vs. Temperature	30	−0.01	0.017	0.06	0.1958
	<i>Aphanizomenon</i> sp. vs. Salinity	30	1.04	−0.149	0.14	0.0418*
	Prop. <i>Dolichospermum</i> spp.	31	−1.8	0.001	0.10	0.0917
	<i>Dolichospermum</i> spp. vs. Temperature	30	−0.07	0.006	0.25	0.0050*
	<i>Dolichospermum</i> sp. vs. Salinity	30	0.12	−0.020	0.09	0.1172
	Prop. <i>Nodularia spumigena</i>	31	7.0	−0.003	0.04	0.2970
	<i>Nodularia spumigena</i> vs. Temperature	30	−0.01	0.007	0.03	0.4046
	<i>Nodularia spumigena</i> vs. Salinity	30	0.40	−0.055	0.04	0.2820
	Nostocales vs. Temperature	30	−0.01	0.019	0.08	0.1413
	Nostocales vs. Salinity	30	1.23	−0.179	0.20	0.0130*
Gulf of Finland	<i>Aphanizomenon</i> sp.	34	−13.9	0.007	0.26	0.0021*
	<i>Dolichospermum</i> spp.	34	−2.0	0.001	0.02	0.3838
	<i>Nodularia spumigena</i>	34	−7.1	0.004	0.08	0.1130
	Total Nostocales	34	−15.2	0.008	0.22	0.0047*
	Salinity	32	17.6	−0.006	0.03	0.3510
	Temperature	32	−167	0.093	0.28	0.0021*
	Prop. <i>Aphanizomenon</i> sp.	34	−0.3	0.000	0.00	0.9057
	<i>Aphanizomenon</i> sp. vs. Temperature	32	0.28	0.004	0.00	0.7931
	<i>Aphanizomenon</i> sp. vs. Salinity	32	−0.17	0.105	0.07	0.1339
	Prop. <i>Dolichospermum</i> spp.	34	3.9	−0.002	0.02	0.4007
	<i>Dolichospermum</i> spp. vs. Temperature	32	0.08	0.001	0.00	0.9079
	<i>Dolichospermum</i> sp. vs. Salinity	32	−0.06	0.031	0.03	0.3465
	Prop. <i>Nodularia spumigena</i>	34	−2.6	0.001	0.01	0.5605
	<i>Nodularia spumigena</i> vs. Temperature	32	0.28	−0.008	0.01	0.6016
	<i>Nodularia spumigena</i> vs. Salinity	32	0.05	0.020	0.00	0.7760
	Nostocales vs. Temperature	32	0.46	−0.002	0.00	0.8886
	Nostocales vs. Salinity	32	−0.09	0.101	0.05	0.2141
Northern BP	<i>Aphanizomenon</i> sp.	33	−6.3	0.003	0.09	0.0963
	<i>Dolichospermum</i> spp.	33	−2.1	0.001	0.02	0.4057
	<i>Nodularia spumigena</i>	33	−4.9	0.003	0.08	0.1172
	Total Nostocales	33	−8.5	0.004	0.10	0.0798
	Salinity	36	34.5	−0.014	0.38	< 0.0001*
	Temperature	36	−86.7	0.051	0.14	0.0219*
	Prop. <i>Aphanizomenon</i> sp.	33	7.6	−0.003	0.03	0.3257
	<i>Aphanizomenon</i> sp. vs. Temperature	32	0.13	0.010	0.02	0.5108
	<i>Aphanizomenon</i> sp. vs. Salinity	32	1.03	−0.118	0.07	0.1586
	Prop. <i>Dolichospermum</i> spp.	33	−4.6	0.002	0.10	0.0754
	<i>Dolichospermum</i> spp. vs. Temperature	32	0.08	−0.000	0.00	0.9793
	<i>Dolichospermum</i> sp. vs. Salinity	32	0.537	−0.075	0.04	0.2593
	Prop. <i>Nodularia spumigena</i>	33	−2.0	0.001	0.01	0.6948
	<i>Nodularia spumigena</i> vs. Temperature	32	0.03	0.007	0.01	0.6014
	<i>Nodularia spumigena</i> vs. Salinity	32	0.81	−0.106	0.07	0.1554
	Nostocales vs. Temperature	32	0.22	0.001	0.01	0.6688
	Nostocales vs. Salinity	32	1.41	−0.169	0.08	0.1198
Central BP	<i>Aphanizomenon</i> sp.	38	0.0	0.000	0.00	0.9401
	<i>Dolichospermum</i> spp.	38	−3.4	0.002	0.20	0.0048*
	<i>Nodularia spumigena</i>	38	−1.4	0.001	0.00	0.8211
	Total Nostocales	38	0.6	−0.000	0.00	0.9758
	Salinity	37	39.4	−0.016	0.50	< 0.0001*
	Temperature	37	−68	0.043	0.11	0.0359*
	Prop. <i>Aphanizomenon</i> sp.	38	15.7	−0.008	0.15	0.0156*
	<i>Aphanizomenon</i> sp. vs. Temperature	37	0.44	−0.007	0.01	0.6473
	<i>Aphanizomenon</i> sp. vs. Salinity	37	−0.25	0.081	0.03	0.3386
	Prop. <i>Dolichospermum</i> spp.	38	−6.2	0.003	0.34	0.0001*
	<i>Dolichospermum</i> spp. vs. Temperature	37	−0.01	−0.004	0.31	0.5226
	<i>Dolichospermum</i> sp. vs. Salinity	37	0.35	−0.042	0.05	0.1738
	Prop. <i>Nodularia spumigena</i>	38	−8.5	0.004	0.07	0.1085
	<i>Nodularia spumigena</i> vs. Temperature	37	0.16	0.006	0.00	0.7648
	<i>Nodularia spumigena</i> vs. Salinity	37	0.64	−0.055	0.01	0.5860
	Nostocales vs. Temperature	37	0.43	−0.000	0.00	0.9816
	Nostocales vs. Salinity	37	0.18	0.035	0.00	0.7426
Southern BP	<i>Aphanizomenon</i> sp.	38	10.5	−0.005	0.17	0.0113*
	<i>Dolichospermum</i> spp.	38	0.6	−0.003	0.00	0.6982
	<i>Nodularia spumigena</i>	38	7.2	−0.004	0.05	0.1966
	Total Nostocales	38	16.3	−0.010	0.18	0.0078*

(continued on next page)

Table 3 (continued)

Basin	Variable	n	Intercept	Slope	R ²	p-value
Arkona Basin	Salinity	37	31.8	−0.012	0.32	0.0002*
	Temperature	37	−63	0.040	0.09	0.0626
	Prop. <i>Aphanizomenon</i> sp.	38	15.0	−0.007	0.16	0.0127*
	<i>Aphanizomenon</i> sp. vs. Temperature	38	0.83	−0.033	0.11	0.0412*
	<i>Aphanizomenon</i> sp. vs. Salinity	38	−0.78	0.139	0.05	0.1585
	Prop. <i>Dolichospermum</i> spp.	38	−4.7	0.002	0.13	0.0282*
	<i>Dolichospermum</i> spp. vs. Temperature	38	0.24	−0.010	0.07	0.1164
	<i>Dolichospermum</i> sp. vs. Salinity	38	−0.52	0.078	0.11	0.0449*
	Prop. <i>Nodularia spumigena</i>	38	−9.3	0.005	0.08	0.0834
	<i>Nodularia spumigena</i> vs. Temperature	38	0.21	−0.002	0.00	0.9367
	<i>Nodularia spumigena</i> vs. Salinity	38	−0.76	0.137	0.03	0.3305
	Nostocales vs. Temperature	38	0.934	−0.033	0.05	0.1900
	Nostocales vs. Salinity	38	−1.71	0.279	0.09	0.0627
	<i>Aphanizomenon</i> sp.	38	9.7	−0.005	0.15	0.0183*
	<i>Dolichospermum</i> spp.	38	2.8	−0.001	0.06	0.1305
	<i>Nodularia spumigena</i>	38	3.77	−0.002	0.02	0.4313
	Total Nostocales	38	11.4	−0.006	0.10	0.0539
	Salinity	39	15.9	−0.004	0.02	0.3709
	Temperature	39	−90.3	0.054	0.12	0.0345*
	Prop. <i>Aphanizomenon</i> sp.	38	5.0	−0.002	0.05	0.1738
	<i>Aphanizomenon</i> sp. vs. Temperature	38	0.77	−0.026	0.11	0.0397*
	<i>Aphanizomenon</i> sp. vs. Salinity	38	−0.25	0.072	0.02	0.3513
	Prop. <i>Dolichospermum</i> spp.	38	0.6	−0.000	0.00	0.8263
	<i>Dolichospermum</i> spp. vs. Temperature	38	0.39	−0.017	0.17	0.0095*
	<i>Dolichospermum</i> sp. vs. Salinity	38	−0.28	0.047	0.04	0.2465
	Prop. <i>Nodularia spumigena</i>	38	−4.6	0.003	0.05	0.1896
	<i>Nodularia spumigena</i> vs. Temperature	38	0.58	−0.018	0.03	0.2706
	<i>Nodularia spumigena</i> vs. Salinity	38	−0.53	0.103	0.03	0.2856
	Nostocales vs. Temperature	38	1.03	−0.035	0.09	0.0648
	Nostocales vs. Salinity	38	−0.95	0.176	0.07	0.1134

* denotes a p-value < 0.05.

4. Discussion

By using monitoring data covering four decades, this study demonstrates ongoing changes in the biovolume of diazotrophic filamentous cyanobacteria and their relative proportions, in relation to surface salinity and surface temperature, in the different sub-basins of the Baltic Sea. The genera of filamentous cyanobacteria that have increased during the period are of freshwater origin, i.e. *Aphanizomenon*

sp. and *Dolichospermum* spp. The biovolume of the non-toxic *Aphanizomenon* sp. increased in the Bothnian Sea and the Gulf of Finland, and the potentially toxic *Dolichospermum* spp. increased in the Bothnian Sea and the Central Baltic Proper. Basin-specific increase in biovolume of filamentous cyanobacteria may lead to decreased oxygen concentrations in the deep water (Conley et al., 2009) and enhanced eutrophication via nitrogen fixation (Klawonn et al., 2016; Olofsson et al., in review).

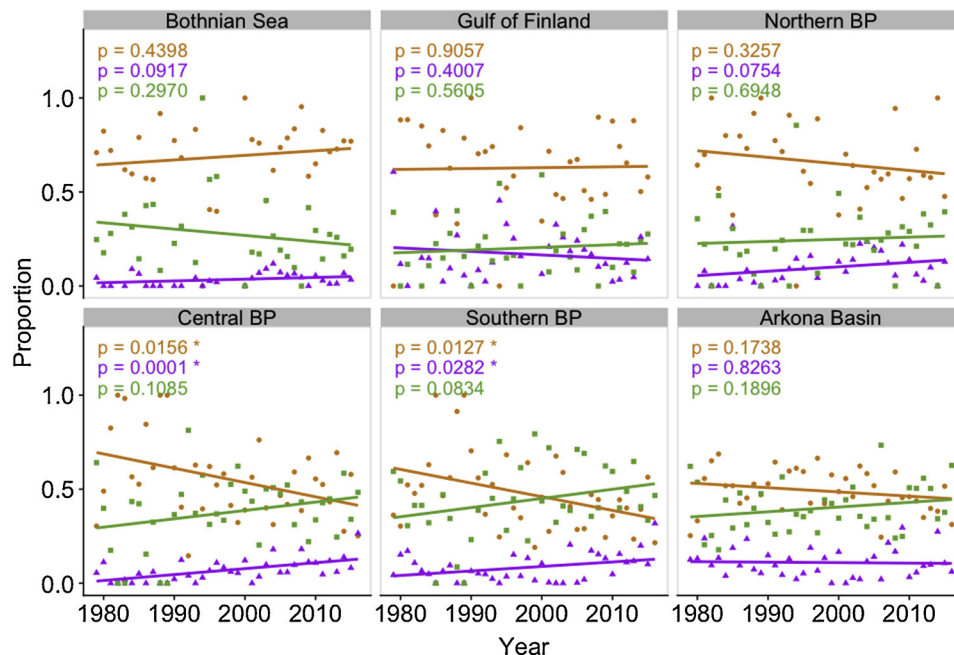


Fig. 3. Relative proportion of *Aphanizomenon* sp. (orange), *Dolichospermum* spp. (purple), *Nodularia spumigena* (green), and total Nostocales (blue) for the period 1979–2017 during July and August. Linear regression model trend lines are included as well as p-values.

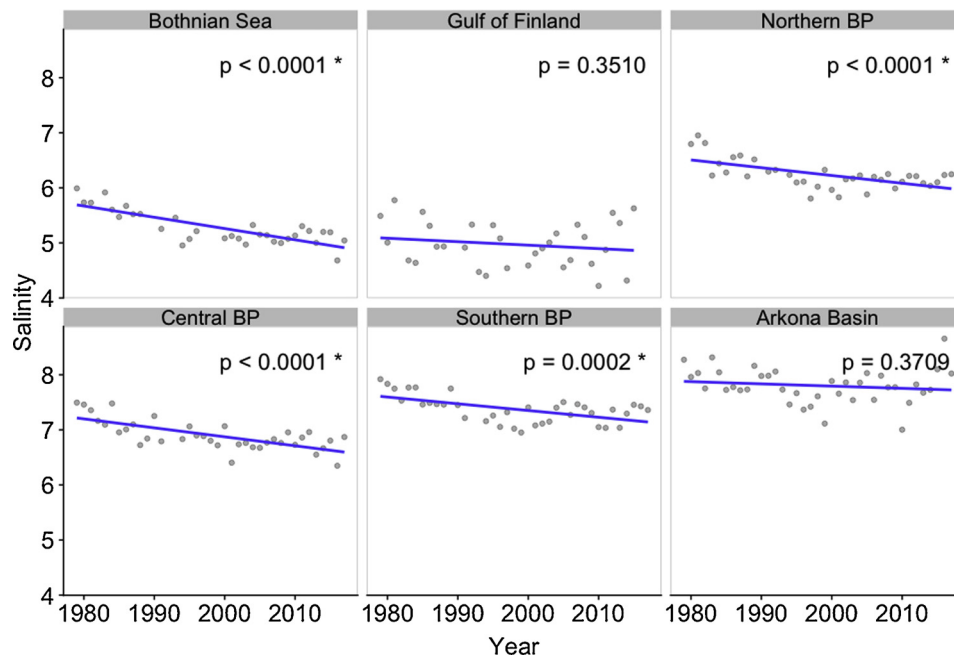


Fig. 4. Surface salinity for the period 1979–2017 as average during July and August. Linear model regression lines are included as well as p-values.

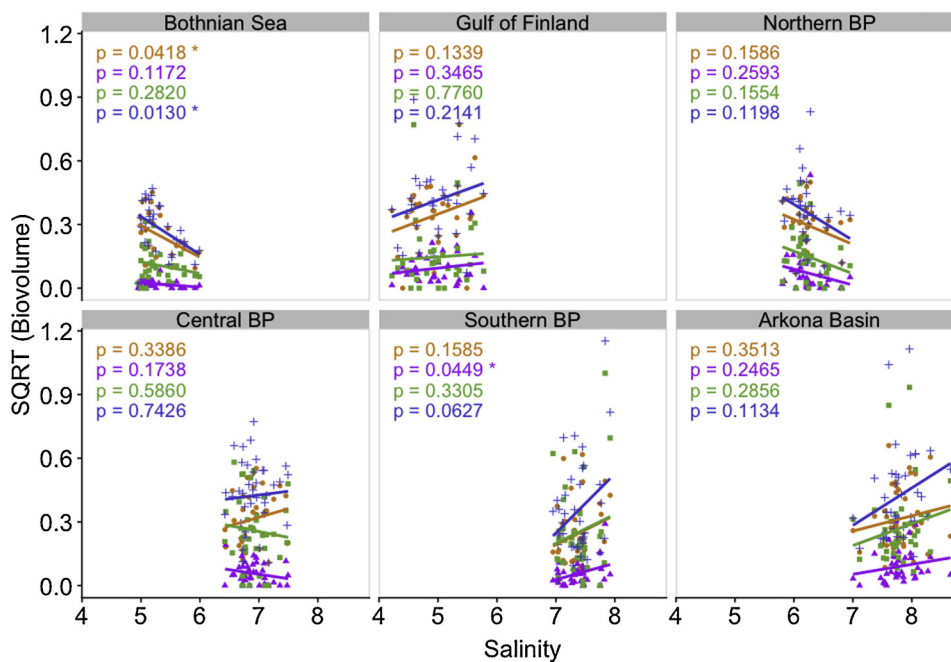


Fig. 5. Linear regression between *Aphanizomenon* sp. (orange), *Dolichospermum* spp. (purple), *Nodularia spumigena* (green), and total Nostocales (blue) (square root transformed), and surface salinity (0–10 m). The data shown is annual means during July and August. Linear regression model trend lines are included as well as p-values.

The observed decrease in surface salinities during summer was supported by previous publications (Suikkanen et al., 2007, 2013; Wasmund et al., 2011; Kuosa et al., 2017). Along with the decrease, Suikkanen et al. (2007; 2013) and Kuosa et al. (2017) demonstrated an increase in total cyanobacteria biomass for the central and northern parts of the Baltic Sea. The present study also demonstrates an increase in total biovolume of filamentous diazotrophic cyanobacteria (mostly comprised by *Aphanizomenon* sp.) in the northern parts of the Baltic Sea, but a decrease in *Aphanizomenon* sp. in the Southern Baltic Proper and in the Arkona Basin, since the 1980s. The decreased salinity in the Bothnian Sea explained the increase in biovolume of *Aphanizomenon* sp. based on covariance in the PerMANOVA test in addition to a significant regression between salinity and biovolume of the taxa during the four decades. Although the filamentous cyanobacteria manage to grow

outside of their preferred salinities, *Aphanizomenon* sp. grows fastest at salinities from 0 up to maximum of 10 (Lehtimäki et al., 1997; Rakko and Seppälä, 2014). In the Bothnian Sea, the salinity decreased with almost one unit during the four decades, supposedly in favor of the growth rate by *Aphanizomenon* sp. *Dolichospermum* spp. strains isolated from the Gulf of Finland were also demonstrated to grow best at the lowest salinity, here of 0 as compared to 3 and 6 (Brutemark et al., 2015; Teikari et al., 2019). This is in concert with Wulff et al. (2018), where the growth of *Dolichospermum* spp. was enhanced by a decreased salinity from 6 to 3. The multifactorial laboratory study by Wulff et al. (2018) suggests that a community shift towards more freshwater adapted genera is more likely than a decrease in total abundance of filamentous cyanobacteria, under decreased salinity conditions. We also show that the relative proportion between the Nostocales genera

Table 4

Results of the PerMANOVA. Statistical parameters of the PerMANOVA test between salinity and temperature in relation to biovolume of *Aphanizomenon* sp., *Nodularia spumigena*, or *Dolichospermum* spp. and total Nostocales.

Group/Genera	Basin	Variable	Pseudo-F	R ²	p-value
<i>Aphanizomenon</i> sp.	Bothnian Sea	Salinity	7.90	0.22	0.0040*
		Temperature	2.12	0.06	0.1288
	Gulf of Finland	Salinity	1.52	0.05	0.2148
		Temperature	1.69	0.06	0.8811
	Northern BP	Salinity	3.46	0.05	0.0310*
		Temperature	1.68	0.02	0.1529
	Central BP	Salinity	0.82	0.02	0.4176
		Temperature	0.44	0.01	0.6613
	Southern BP	Salinity	4.45	0.06	0.0120*
		Temperature	1.76	0.02	0.1718
	Arkona Basin	Salinity	0.55	0.01	0.1139
		Temperature	2.33	0.05	0.1359
<i>Dolichospermum</i> spp.	Bothnian Sea	Salinity	0.96	0.05	0.3766
		Temperature	1.29	0.07	0.2727
	Gulf of Finland	Salinity	1.27	0.04	0.2717
		Temperature	2.58	0.08	0.0629
	Northern BP	Salinity	0.51	0.010	0.7313
		Temperature	0.38	0.01	0.8232
	Central BP	Salinity	0.21	0.01	0.9151
		Temperature	0.60	0.02	0.5894
	Southern BP	Salinity	0.52	0.01	0.7063
		Temperature	0.40	0.01	0.7822
	Arkona Basin	Salinity	1.25	0.03	0.2727
		Temperature	2.92	0.08	0.0480*
<i>Nodularia spumigena</i>	Bothnian Sea	Salinity	2.13	0.08	0.1129
		Temperature	0.64	0.02	0.5794
	Gulf of Finland	Salinity	0.39	0.02	0.7433
		Temperature	0.18	0.01	0.9111
	Northern BP	Salinity	1.42	0.02	0.2647
		Temperature	0.30	0.00	0.8521
	Central BP	Salinity	0.09	0.00	0.9600
		Temperature	0.14	0.00	0.9391
	Southern BP	Salinity	1.32	0.02	0.2388
		Temperature	0.34	0.01	0.8052
	Arkona Basin	Salinity	1.35	0.04	0.5105
		Temperature	0.70	0.01	0.7343
Nostocales	Bothnian Sea	Salinity	9.11	0.24	0.0030*
		Temperature	1.11	0.03	0.3417
	Gulf of Finland	Salinity	1.89	0.06	0.1469
		Temperature	0.98	0.03	0.3846
	Northern BP	Salinity	1.99	0.03	0.1219
		Temperature	0.32	0.00	0.8022
	Central BP	Salinity	0.18	0.01	0.8931
		Temperature	0.59	0.02	0.5844
	Southern BP	Salinity	2.68	0.04	0.0589
		Temperature	0.34	0.00	0.8032
	Arkona Basin	Salinity	3.90	0.09	0.0210*
		Temperature	1.74	0.04	0.1828

* denotes a p-value < 0.05.

has changed over time in the southern sub-basins, where the relative proportion of *Aphanizomenon* sp. decreased in the Central and Southern Baltic Proper, while the proportion of *Dolichospermum* spp. increased in the same sub-basins.

In the present study, *Dolichospermum* spp. had a positive regression with salinity (from 7 to 8) in the Southern Baltic Proper, in contrast with observations of its preferred salinities. A mechanism behind the observed contrasting patterns between basins can be local adaptation, where different populations are adapted to different spatial niches. The population genetics of Baltic Sea filamentous cyanobacteria is known to be highly diverse (Bertos-Fortis et al., 2016), indicating a complexity in the response to changes in environmental factors. Many studies addressing salinity preferences in filamentous cyanobacteria are using only one strain per species, i.e. only isolated from one area (e.g.

Lehtimäki et al., 1997; Rakko and Seppälä, 2014). With this low spatial and genetic variation in the previous studies, it is therefore hard to project how a genus will react to salinity changes in their natural environment. Since the salinity ranges are highly variable within and between the basins, with ranges of ca. 4–6 in the Bothnian Sea and ca. 7–8 the Southern Baltic Proper, the chance of the cyanobacteria to adapt to a salinity niche is high. Although high overlap in salinities between adjacent basins, the fact that contradicting correlations were found for *Aphanizomenon* sp. and *Dolichospermum* spp. in the northern and southern parts, respectively, suggests basin-specific strains of the taxa. Several studies indicate that responses of strains to salinity stress differ, which can partly be related to place of isolation (Laamanen et al., 2002; Lehtimäki et al., 1997; Rakko and Seppälä, 2014).

Along with elevated temperatures, harmful blooms of cyanobacteria are predicted to increase in the future (Paerl and Huisman, 2008). Although the surface temperatures increased with several degrees in four of the six sub-basins during the recent decades, this was never connected to an increase in total biovolume of filamentous cyanobacteria. The total biovolume of Nostocales decreased in the Southern Baltic Proper, where the salinity also decreased, while the temperature was stable. On the other hand, the Nostocales biovolume did not change in Arkona, where the temperature increased but there was no change in the salinity. The potentially toxic *N. spumigena* is the dominating species of filamentous cyanobacteria in the southern parts of the Baltic Sea (Table 2), supposedly due to its relatively high salinity preferences (Lehtimäki et al., 1997; Mazur-Marzec et al., 2005; Rakko and Seppälä, 2014). The biovolume of *N. spumigena* did not change during the four decades, with no significant relation to neither salinity nor temperature. Similar to salinity, there is a difference in temperature preferences among the cyanobacteria genera, where *N. spumigena* generally grows better at higher temperatures as compared to *Aphanizomenon* sp. (Lehtimäki et al., 1997), and high temperature preference has also been demonstrated for *Dolichospermum* spp. (Suikkanen et al., 2010). This can be why *Aphanizomenon* sp. was negatively correlated with temperature in the Southern Baltic Proper and the Arkona Basin, where the temperature range is higher as compared to the Bothnian Sea (ca. 16–18 °C vs. 15–16 °C, respectively). The biovolume of *Dolichospermum* spp. was also negatively correlated with the increasing temperature in the Arkona Basin, but in contrast, positively correlated with temperature in the Bothnian Sea, which could be that the basins harbor different sub-populations adapted to distinct temperature niches. The difference in temperature preferences between the genera causes a niche separation reflected in their seasonality and spatial distribution, where *Aphanizomenon* sp. starts to grow already in May–June as compared to *N. spumigena* and *Dolichospermum* spp. with their peak during July (Suikkanen et al., 2010; Wasmund, 2017).

The present study demonstrates that the relative biovolume of freshwater originating genera is increasing in the northern parts of the Baltic Sea, where *Dolichospermum* spp. were probably enhanced by the elevated temperatures and *Aphanizomenon* sp. by the decreased salinity. Overall, the elevated surface temperatures did not independently affect the total diazotrophic cyanobacterial biovolume and local variation may occur, e.g. blooms of *N. spumigena* have increased in the Gulf of Gdańsk in the recent decade (Mazur-Marzec et al., 2006). The results from the present study demonstrate the complexity of the two factors tested, where both affect the growth of filamentous cyanobacteria in the Baltic Sea. In addition, the changes in species composition can also be affected by additional factors governing their presence, e.g. nutrients, changed physical features such as mixing or stratification, and/or interaction with other planktonic organisms (e.g. Degerholm et al., 2006; Mohlin et al., 2012). Southern Baltic proper had some extremely high values of cyanobacteria biovolume in the beginning of the study period, as also described by Wasmund et al. (2011), which can affect the overall trend for the following years. These high values were about 10 times higher than what regularly occur in the area during summer (Wasmund et al., 2019). The increase in total Nostocales biovolume in

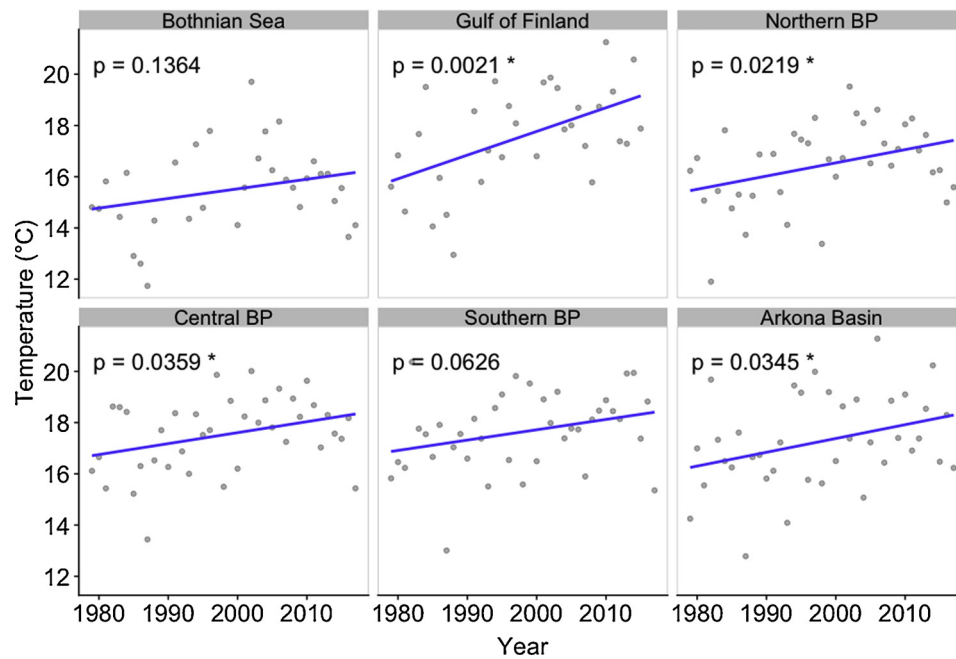


Fig. 6. Surface temperature (°C) for the period 1979–2017 as average during July and August. Linear model regression lines are included as well as p-values.

the northern parts of the Baltic Sea can be a result of a decreased salinity in favor of freshwater genera as previously discussed, but also a result of elevated nutrient loads in combination to increased temperatures (Suikkanen et al., 2007, 2013). Inorganic phosphate availability is known to positively enhance the growth of filamentous cyanobacteria (Olofsson et al., 2016). Suikkanen et al. (2013) found an increase in dissolved inorganic phosphorus in the Gulf of Finland, while not in the Northern Baltic Proper, and an increase in temperature and cyanobacteria in both sub-basins. In the present study, the biovolume of *Aphanizomenon* sp. increased in the Gulf of Finland during the four decades, and even though there was no significant change in surface salinities, the values were among the lowest of the sub-basins examined, and probably already in favor of the growth of *Aphanizomenon* sp.

The surface salinity is projected to decrease in the Baltic Sea due to increased precipitation (HELCOM, 2013). However, the reason for the observed decrease in the present study can be basin-specific, and of different origin. For the Bothnian Sea, it can be related to precipitation, river runoff having a larger effect on the surface salinity as compared to exchange with more saline water through the Belt Sea. The 1980s and late 1990s were wetter than the following decades in the Baltic Sea area, increasing the river runoff, and thus, decreasing the surface salinity (Johansson, 2018). For the Southern Baltic Sea, the decrease in surface salinity could in addition be related to fewer inflows of saline North Sea water during the recent decades, which has also increased the temperatures in the deep water (Naumann et al., 2018). The sea surface temperature increase is probably related to a warmer climate during the recent decades as compared to four decades ago (HELCOM,

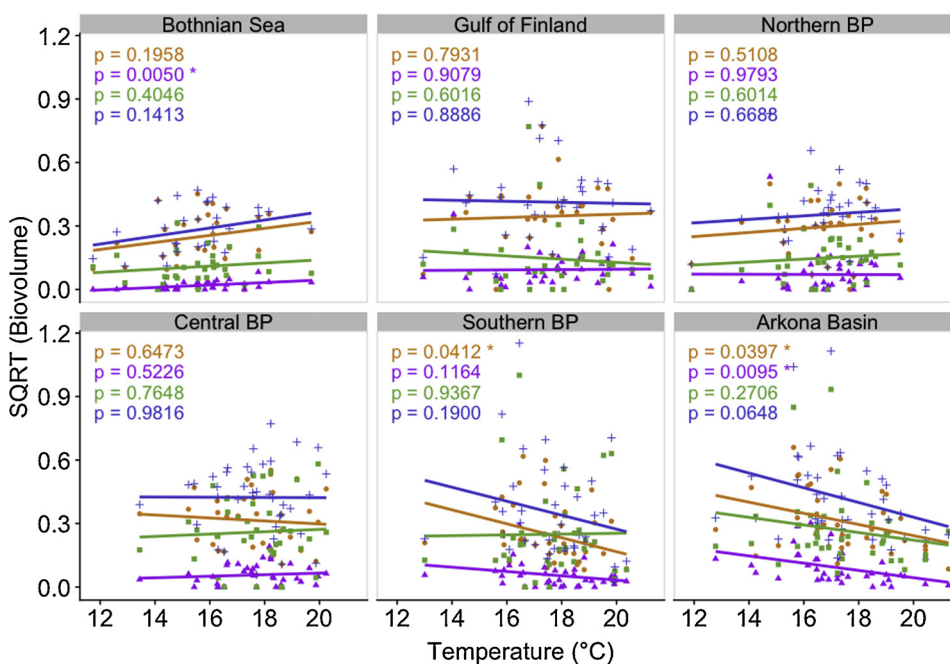


Fig. 7. Linear regression between *Aphanizomenon* sp. (orange), *Dolichospermum* spp. (purple), *Nodularia spumigena* (green), and total Nostocales (blue) (square root transformed), and surface temperature (°C, 0–10 m). The data shown is annual means during July and August. Linear regression model trend lines are included as well as p-values.

2013). It has also been demonstrated that with more cyanobacteria accumulating in the surface layer, the water temperature will increase even further (Johansson, 2015).

5. Conclusion

Long-term studies of genus-specific effects of the ongoing climate change are of highest importance when addressing the future situation of harmful cyanobacteria (Burford et al., 2019). This study indicates how diazotrophic filamentous cyanobacteria communities can respond to changes in salinities and temperatures, and also how difficult it can be to predict, due to the complexity of the two factors. For example, the temperature increased in most of the sub-basins during the period (1979–2017), but the total biovolume of filamentous diazotrophic cyanobacteria only increased in two out of six basins, and not with an overlapping pattern. It also demonstrates that the different cyanobacterial genera responded differently to changes in the environmental parameters, and the same genera responded differently between basins. Due to its long growth season, and capability to grow at low temperatures, the cumulative biomass of *Aphanizomenon* sp. will probably continue to increase along with the decreasing salinity, especially in the northern parts of the Baltic Sea. With no significant associations between the biovolume of the toxin producer *N. spumigena* and salinity or temperature, its biovolume did not change in any of the sub-basins during the period. This along with the increase in potentially non-toxic genera might result in less toxic blooms, unless toxic freshwater species, e.g. toxic strains of *Dolichospermum* spp. (Teikari et al., 2019) inhabit the Baltic Sea in the future under less saline conditions. If the environment for the cyanobacteria continues to change in the same pace and direction we can, according to the present study, expect more blooms in the northern parts of the Baltic Sea, and supposedly a continuation of the decrease in the southern parts.

Declaration of Competing Interest

None.

Acknowledgements

Thanks to Markus Lindh and Lasse Johansson at SMHI for statistical consulting. This study is a part of the project Estimating Nitrogen fixation in past and future climates of the Baltic Sea funded by the Swedish research council Formas grant nr. 214-2013-1449 and by project CoCLiME which is part of ERA4CS, an ERA-NET initiated by JPI Climate, and funded by EPA (IE), ANR (FR), DLR (DE), UEFISCDI (RO), RCN (NO) and FORMAS (SE), with co-funding by the European Union (Grant 690462). CoCLiME funding from Swedish research council Formas, grant number 2017-1737. We thank the HELCOM Phytoplankton Expert Group (PEG), whose members are the principal originators of the phytoplankton data stored in the database of the International Council for the Exploration of the Sea (ICES), and to colleagues that have spent numerous hours by the microscope.[SS]

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