



Marked changes in diatom and dinoflagellate biomass, composition and seasonality in the Belgian Part of the North Sea between the 1970s and 2000s

Anja Nohe^a, Annelies Goffin^b, Lennert Tyberghein^b, Ruth Lagring^c, Karien De Cauwer^c, Wim Vyverman^a, Koen Sabbe^{a,*}

^a Ghent University, Department of Biology, Laboratory of Protistology & Aquatic Ecology, Krijgslaan 281 (S8), 9000 Ghent, Belgium

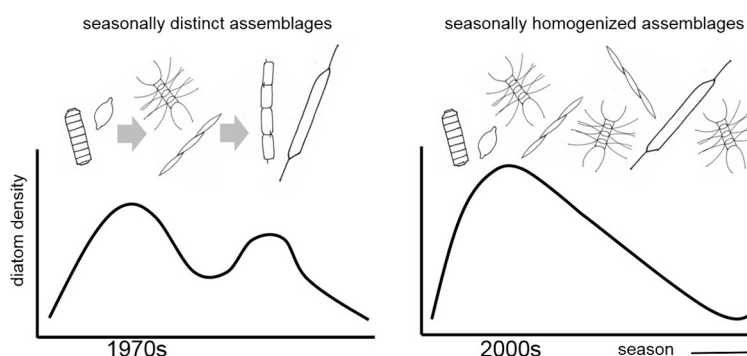
^b Flanders Marine Institute, Wandelaarkaai 7, 8400 Ostend, Belgium

^c Operational Directorate Natural Environment, Royal Belgian Institute of Natural Sciences, Vautierstraat 29, 1000 Brussels, Belgium

HIGHLIGHTS

- Total abundance and biovolume of diatoms and dinoflagellates increased from 1970s to 2000s.
- Diatom bloom pattern changed from a bimodal annual cycle to a unimodal, more extended spring–summer growing season.
- Diatom assemblage composition changed from seasonally distinct to seasonally more homogenized assemblages.
- Potentially harmful algal species significantly increased.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:

Received 6 May 2019

Received in revised form 20 December 2019

Accepted 22 December 2019

Available online 21 January 2020

Editor: Henner Hollert

Keywords:

Phytoplankton

Diatoms

Dinoflagellates

Belgian part of the North Sea

Long-term changes

ABSTRACT

In the last decades, the North Sea has undergone intense environmental changes which have led to regime shifts that affected all trophic levels. Since the 1970s, both increases and decreases in phytoplankton biomass and production have been reported from different parts of the North Sea. Such conflicting observations may be partly caused by methodological differences, but also reflect regional differences related to bathymetry, hydrodynamics, climate, riverine and Atlantic influence. The Belgian part of the North Sea (BPNS) is a hydrodynamically and bathymetrically complex area under strong human influence, which has been characterized by eutrophication (up to the 1980s) and de-eutrophication (1990s onwards), and pronounced long-term changes in turbidity and water temperature. We used a newly recovered and standardized historic dataset, the Belgian Phytoplankton Database (Nohe et al., 2018), to compare the biomass, composition and seasonality of diatom and dinoflagellate assemblages, two key components of the plankton in the BPNS, between the 1970s and 2000s. Diatoms, especially large-sized taxa, showed an increase from late winter to summer, resulting in a more intense and extended growing season in the 2000s. Dinoflagellates increased year-round but especially in summer. Both diatom and dinoflagellate blooms showed a clear shift towards an earlier bloom start. In addition, while in the 1970s distinct seasonal community types were present, a striking seasonal homogenization in community structure had occurred by the 2000s. Finally, we observed a pronounced increase in the abundance of harmful diatom and dinoflagellate genera. The observed changes are most likely due to an increase in sea surface temperature and water

* Corresponding author.

E-mail address: Koen.Sabbe@UGent.be (K. Sabbe).

transparency, and changes in nutrient loads and ratios. Our study underscores the importance of recovering previously inaccessible historic data as they can offer unprecedented insights into long-term change in marine ecosystems, which are essential for properly evaluating the impact of human activities on these ecosystems.

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1. Introduction

Global change, mainly resulting from human activities, is affecting marine ecosystems worldwide (Doney et al., 2012), with potentially serious repercussions for the vital services they provide to humans. Marine phytoplankton drives the ocean carbon pump and global cycles of nutrients and oxygen, and fuels marine food webs (Edwards and Richardson, 2004). Global change affects phytoplankton in complex and multifaceted ways. Higher temperatures (and CO₂) can stimulate overall phytoplankton growth but also reduce it if enhanced stratification decreases nutrient transport to surface waters (Beardall et al., 2009). In addition, recent studies increasingly show that responses to changes in temperature, CO₂, nutrients and light can strongly differ between phytoplankton groups and even species, resulting in altered community composition (e.g. Bach and Taucher, 2019; Chivers et al., 2017). As a result, predicting future responses of marine phytoplankton to global change remains challenging (Hutchins and Fu, 2017). Long-term data on phytoplankton production and community composition can greatly enhance our understanding of the response of phytoplankton to multiple stressors, and allow testing predictive scenarios.

Global change effects will be especially pronounced in shallow coastal ecosystems, which are highly sensitive to climate warming and most directly exposed to human activities (influx of riverine nutrients, pollutants, sediments, etc.). The Belgian part of the North Sea (BPNS, encompassing the Belgian territorial waters and the Belgian Exclusive Economic zone), located in the southernmost part of the North Sea, is a prime example of a heavily impacted shallow coastal zone. In the last half century, the area has been characterized by a pronounced cycle of eutrophication and de-eutrophication. Increasing riverine nutrient loads since the 1960s caused a rise in the coastal water nutrient state which peaked in the 1980s (Billen et al., 2005). Since then, phosphorus loads have considerably decreased due to the prohibition of polyphosphate in washing detergents. Nitrogen reductions however were less successful, resulting in pronounced shifts in the nitrogen to phosphorus ratios (Passy et al., 2013). In addition, sea surface temperature (SST) has increased by >1 °C since the 1960s (Desmit et al., 2019), while Capuzzo et al. (2015) reported a decrease in water transparency, at least in the more offshore region of the BPNS. The latter is in contrast with other studies, which reported increases in water clarity in the German Bight (Wiltshire et al., 2008) and central and coastal North Sea waters (McQuatters-Gollop et al., 2007), suggesting that within the North Sea regional differences may exist in water transparency. At the same time, climate change has resulted in often taxon-specific changes in the abundance and biogeographical range of planktonic organisms (Chivers et al., 2017; Hinder et al., 2012). Mismatches between plankton range movements can result in spatial reorganization of pelagic food webs, with potentially significant impacts on higher trophic levels (Chivers et al., 2017).

As phytoplankton production, biomass build-up and composition are strongly affected by nutrients, light and temperature, but also by biotic interactions with symbionts, parasites and grazers (Lima-Mendez et al., 2015), it can be expected that significant change in the phytoplankton of the BPNS must have occurred during the last decades. In order to evaluate the impact of human-induced and natural variability in factors that control phytoplankton growth, long-term data series of phytoplankton biomass and composition spanning at least several decades are vital. Several highly valuable long-term datasets are available, such as the important Continuous Plankton Recorder (CPR) series, which has been recording phytoplankton biomass and composition

data in the North Atlantic using a consistent methodological approach since the late 1950s (McQuatters-Gollop et al., 2015). In addition, several important regional phytoplankton monitoring series exist in the southern part of the North Sea, such as the Helgoland Roads time series (since 1962; Wiltshire et al., 2010), the Dutch monitoring program (since the early 1970s; Baretta-Bekker et al., 2009), the Dutch Marsdiep time series (since 1974; Philippart et al., 2010), and the French Observation and Monitoring program for Phytoplankton (since 1992; Lefebvre et al., 2011).

Various studies have reported marked changes in phytoplankton biomass and dynamics in the North Sea during the last decades (Cadée and Hegeman, 2002; Hinder et al., 2012; Raitos et al., 2014). These changes often formed part of more comprehensive changes in the whole marine ecosystem, such as the pronounced regime shift of the late 1980s, which included a significant increase in phytoplankton biomass in many parts of the North Sea (Edwards et al., 2006; Raitos et al., 2014). However, other studies have reported declines in phytoplankton biomass and/or production in the North Sea area (Boyce et al., 2010; Capuzzo et al., 2018). Such discrepancies may be artefactual, related to methodological differences, but can also represent real regional differences in long-term trends. Trend analyses of phytoplankton biomass are usually based on pigment (chlorophyll *a* [Chl *a*]), ocean color or CPR-derived Phytoplankton Colour Index (PCI) data, all of which have shortcomings. Chlorophyll *a* analyses usually do not take into account variability in C:Chl *a*, which can be substantial, e.g. as a result of changes in light regime and nutrient status (Alvarez-Fernandez and Riegman, 2014; Capuzzo et al., 2018). Continuous Plankton Recorder-derived PCI data (Hinder et al., 2012; Leterme et al., 2005; Reid and Edwards, 2001) are incomplete as they are biased towards larger species because of the CPR silk mesh size constraint of 270 µm (Llope et al., 2012). In addition, analyses of long-term trends are often based on data with different spatial scales of aggregation [from sub-regions within the North Sea (Capuzzo et al., 2015) to the whole NE Atlantic (Leterme et al., 2005)]. It has been shown that trends can actually differ between subregions of the North Sea that differ in bathymetry, hydrodynamics, temperature, and freshwater and Atlantic influence (Capuzzo et al., 2018; van Leeuwen et al., 2015). With the exception of the Helgoland Roads and Marsdiep time series, which have been running since the 1960s and 1970s respectively, and the CPR series, long-term datasets on phytoplankton composition are rare. This is problematic, as changes in composition, which can be masked in biomass trends, have the potential to affect the size structure and nutritional quality of the phytoplankton and hence the transfer of organic matter and energy to higher trophic levels (Burson et al., 2016; Edwards and Richardson, 2004; Raitos et al., 2014). In addition, taxonomic information is needed to assess changes in biodiversity (which affect ecosystem functioning; Duffy et al., 2017), long-term dynamics of harmful algal bloom (HAB) species, and ecosystem status (bio-indicator approach), making it essential for marine policy and conservation management (McQuatters-Gollop et al., 2017).

In this study we present a comparison of seasonal trends in biomass and composition of phytoplankton, and more specifically diatom and dinoflagellate communities, in the BPNS in the 1970s and 2000s. This analysis is based on a newly compiled dataset, the Belgian Phytoplankton Database (BPD) (Nohe et al., 2018), which represents a comprehensive, quality controlled and standardized compilation of quantitative phytoplankton cell counts from the BPNS since the late 1960s. Many of these data were previously only available as non-digital, hand-written or printed tables and reports in scattered published and non-

published sources. Our analyses reveal fundamental changes in diatom and dinoflagellate assemblage composition, biomass and seasonal dynamics, which are discussed in the light of environmental differences between the 1970s and 2000s in the BPNS.

2. Material and methods

2.1. Study area

The physical and chemical environment of the BPNS is strongly determined by meteorological forcing, which drives seasonal and inter-annual variability in wind, currents, temperature and precipitation, and hence also suspended particulate matter (SPM) concentrations, underwater light climate, riverine discharge and nutrient dynamics (Ruddick and Lacroix, 2006). The BPNS is permanently mixed due to its shallowness (<40 m), water influx from the Atlantic Ocean and strong tidal currents (De Galan et al., 2004; van Leeuwen et al., 2015). It receives most of its freshwater input from the Scheldt river which results in a marked east-west salinity gradient, from about 31.5 close to the Scheldt mouth to about 34 further offshore, the exact position of which depends on Scheldt discharge and Atlantic water intrusion (De Galan et al., 2004). The nutrient status of the BPNS is determined by this Atlantic influx as well (enriched by nutrients from amongst others the rivers Seine and Somme), in addition to local riverine inputs with high nutrient loads (mainly the Scheldt river, but also the Rhine and Meuse) and atmospheric deposition. As a result, as for salinity, there is a pronounced east-west gradient from high nutrient concentrations near the Scheldt river mouth to lower concentrations offshore (e.g. from >80 to about 10 μM for dissolved inorganic nitrogen (DIN), 1.5–2 to <0.5 μM for phosphate, and >40 to <10 μM for silicate in winter 2003) (Brion et al., 2006). Near the coast SPM concentrations are always very high (from 100 mg L^{-1} up to several thousands of mg L^{-1}) and offshore always low (<5 mg L^{-1}), while in the transition area concentrations are intermediate (5–50 mg L^{-1}) (Belgian State, 2012).

2.2. Datasets

All data were extracted from the BPD, a quality checked and standardized compilation of historical phytoplankton count data (cells L^{-1}) since the late 1960s (Nohe et al., 2018). The data mainly derive from non-digital sources such as books, technical project reports and unpublished Master and PhD theses, but also previously undisclosed digital data stored on laboratory computers. The data, obtained from 94

different sampling stations (Fig. 1), mainly span two periods, 1970 to 1978 and 2003 to 2010 (hereafter referred to as '1970s' and '2000s'), for which the datasets were most complete (Nohe et al., 2018). In total, >800 diatom and >470 dinoflagellate counts were included in our analyses (for details see Tables A.5 and A.10). The data set has good seasonal coverage, but displays considerable interannual variability in sampling frequency (Fig. A.1). All samples were analysed with the Utermöhl method with the use of an inverted microscope (Utermöhl, 1958). Phytoplankton in the BPNS and the southern North Sea is dominated by diatoms, dinoflagellates, and the colonial haptophyte *Phaeocystis* (Rousseau et al., 2008). Because data for *Phaeocystis* were largely lacking for the 1970s, we focused on the diatom and dinoflagellate data alone. In order to ensure optimal taxonomic consistency between the 1970s and the 2000s data sets, we aggregated all count data to the genus level (see also Beliaeff et al., 2001; Vyverman et al., 2007). As many dinoflagellate genera contain photo-, mixo- and heterotrophic species (Gómez, 2012), all dinoflagellate data were kept in the analyses, except for *Noctiluca*. Because of its very large size, this taxon is not well represented in the counts, and was therefore omitted from the analyses. In addition, all data from samples taken below 5 m depth were excluded. Benthic diatoms were in some data sets not identified to genus or species level. For this reason, we aggregated all benthic taxa into a single unit. For some analyses, count data were converted to biovolume data. Based on geometrical shape and size data taken from literature and online sources, diatom and dinoflagellate biovolumes were calculated to the lowest taxonomic level possible (usually species) (Hillebrand et al., 1999; Hoppenrath et al., 2009; Horner, 2002; Throndsen et al., 2007). Following Terseleer (2014), diatoms were combined into three classes, viz. small (<6000 μm^3), intermediate (6000 μm^3 – $4.9 \times 10^4 \mu\text{m}^3$) and large (> $4.9 \times 10^4 \mu\text{m}^3$). Because of data gaps and inconsistencies in the environmental data available for the BPNS (i.e. caused by changes in analytical methods for nutrient analyses), environmental data [dissolved inorganic nitrogen (DIN), dissolved inorganic phosphorus (DIP), dissolved silica (DSi), nutrient ratios, sea surface temperature (SST) and SPM] were obtained from two stations in the Walcheren transect (just to the east of the BPNS) of the Dutch Rijkswaterstaat (RWS) long-term monitoring program (Fig. 1; note that for the 1970s data were only available for 1975–1978). For some graphs and analyses, a distinction was made between coastal and offshore stations (Fig. 1). This distinction is based on water mass distribution and therefore on gradients in salinity, nutrients and turbidity, as well as differences in mixing regimes (Baeyens et al., 1984; Capuzzo et al., 2015; De Galan et al., 2004; van Leeuwen et al.,

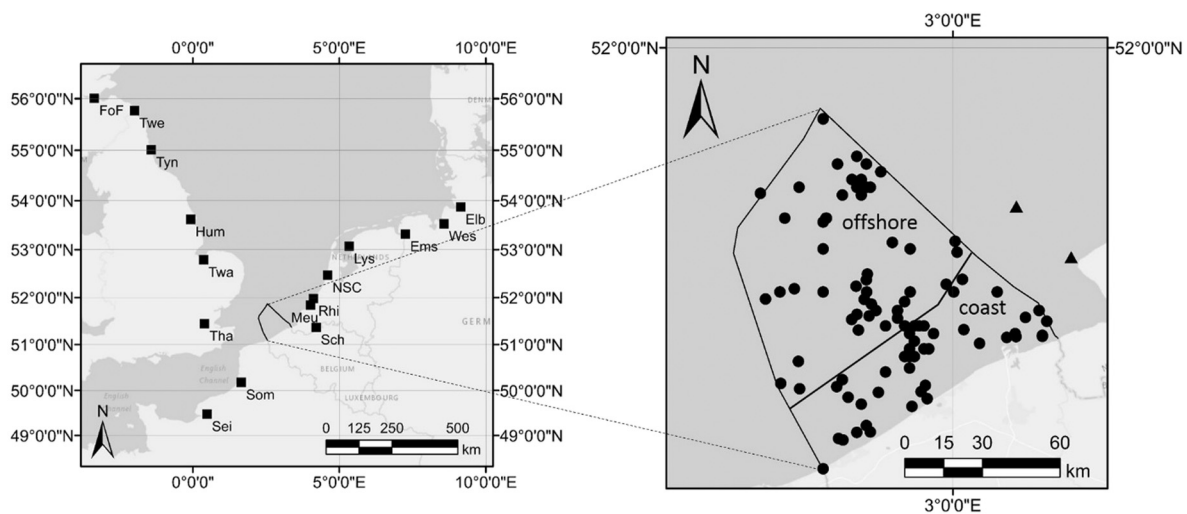


Fig. 1. Map of the North Sea area and the Belgian part of the North Sea (BPNS). The mouths of the main rivers, the sampling locations and the division in a coastal and an offshore area are indicated. The Walcheren stations (RWS monitoring) in the Dutch coastal area are indicated as triangles. Elb = Elbe, FoF = Firth of Forth, Hum = Humber, Lys = Lake IJssel, Meu = Meuse, NSC = North Sea Canal, Rhi = Rhine, Sch = Scheldt, Sei = Seine, Som = Somme, Tha = Thames, Twa = The Wash, Twe = Tweed, Tyn = Tyne and Wes = Weser.

Table 1
Comparison of abundances, biovolumes, dinoflagellate/(diatom + dinoflagellate) ratios and abiotic parameters in the 1970s and 2000s. Mean values, standard deviations (sd) and number of observations (n) are given per study period. p-Values of ANOVA analyses are given. The last column shows the type of transformation applied (if any) to obtain normal distribution. Abiotic and chlorophyll a data derive from the Dutch long-term monitoring program conducted by Rijkswaterstaat (RWS). Values based on all data for a given period are indicated in bold (except for the diatom genera data); values based on seasonal or monthly data are in normal font. Diatom genus data are only shown for the 20 best fitted genera in the PCA analysis (see Fig. 7).

variable	Month/season	1970s			2000s			n _{1970s} /n _{2000s}	mean _{2000s} – mean _{1970s}	p-Value	Transformation (for ANOVA)
		Mean	sd	n	Mean	sd	n				
<i>Abundances (*10³ cells L⁻¹)</i>											
Total diatoms		214	295	712	746	1888	493	1.44	532	<0.001	log ₁₀ (x)
	Winter	151	277	157	891	1441	70	2.24	741	<0.001	log ₁₀ (x)
	Spring	353	393	200	1103	2671	209	0.96	750	<0.001	log ₁₀ (x)
	Summer	186	193	163	337	552	164	0.99	151	0.81	log ₁₀ (x)
	Autumn	145	199	192	392	571	50	3.84	247	<0.01	log ₁₀ (x)
Total dinoflagellates		3	4	450	19	30	196	2.30	16	<0.001	log ₁₀ (x)
	Winter	1	1	69	8	17	34	2.03	6	<0.001	log ₁₀ (x)
	Spring	2	2	122	27	38	73	1.67	26	<0.001	log ₁₀ (x)
	Summer	4	6	119	22	31	49	2.43	18	<0.001	log ₁₀ (x)
	Autumn	3	5	136	8	16	40	3.40	5	0.27	log ₁₀ (x)
<i>Actinoptychus</i>		1.28	3.45	695	5.54	31.26	392	1.77	4	<0.001	log ₁₀ (x + 1)
<i>Asterionellopsis</i>		13.12	52.51	696	132.03	832.57	452	1.54	119	<0.001	log ₁₀ (x + 1)
<i>Cerataulina</i>		1.76	19.14	670	4.04	16.18	376	1.78	2	<0.001	log ₁₀ (x + 1)
<i>Chaetoceros</i>		16.01	114.10	694	57.75	194.06	485	1.43	42	<0.001	log ₁₀ (x + 1)
<i>Cylindrotheca</i>		0.65	12.02	585	15.38	41.76	214	2.73	15	<0.002	log ₁₀ (x + 1)
<i>Cymatosira</i>		0.07	0.63	471	40.21	41.40	109	4.32	40	<0.003	log ₁₀ (x + 1)
<i>Dactyliosolen</i>		4.40	16.43	647	3.05	22.17	371	1.74	–1	<0.004	log ₁₀ (x + 1)
<i>Delphineis</i>		2.72	7.04	651	8.02	5.57	126	5.17	5	<0.005	log ₁₀ (x + 1)
<i>Ditylum</i>		0.11	0.62	561	2.25	6.74	411	1.36	2	<0.006	log ₁₀ (x + 1)
<i>Guinardia</i>		33.51	95.78	695	118.99	299.96	456	1.52	85	<0.001	log ₁₀ (x + 1)
<i>Leptocylindricus</i>		3.98	26.65	676	20.56	85.28	394	1.72	17	<0.001	log ₁₀ (x + 1)
<i>Odontella</i>		1.78	4.41	698	4.67	11.76	435	1.60	3	<0.001	log ₁₀ (x + 1)
<i>Paralia</i>		22.86	36.18	706	78.50	562.63	438	1.61	56	<0.001	log ₁₀ (x + 1)
<i>Pseudo-nitzschia</i>		5.24	21.25	673	66.16	180.05	461	1.46	61	<0.001	log ₁₀ (x + 1)
<i>Rhaphoneis</i>		9.20	16.75	705	12.17	59.60	422	1.67	3	<0.001	log ₁₀ (x + 1)
<i>Rhizosolenia</i>		14.01	46.92	707	83.10	629.64	450	1.57	69	<0.001	log ₁₀ (x + 1)
<i>Skeletonema</i>		5.57	36.67	678	14.64	77.87	421	1.61	9	<0.001	log ₁₀ (x + 1)
<i>Thalassionema</i>		14.76	45.34	690	25.34	108.63	434	1.59	11	0.77	log ₁₀ (x + 1)
<i>Thalassiosira</i>		18.43	39.71	706	115.44	549.75	489	1.44	97	<0.001	log ₁₀ (x + 1)
Benthic diatoms		31.79	77.76	707	7.16	25.49	453	1.56	–25	<0.001	log ₁₀ (x + 1)
<i>Biovolumes (*10⁹ μm³ L⁻¹)</i>											
Total diatoms		3.99	6.24	653	25.44	65.45	455	1.44	21	<0.001	log ₁₀ (x)
	Winter	1.43	1.69	143	17.07	28.46	64	2.23	16	<0.001	log ₁₀ (x)
	Spring	5.89	8.05	177	32.89	67.86	192	0.92	27	<0.001	log ₁₀ (x)
	Summer	7.02	7.49	155	25.89	80.03	153	1.01	19	<0.001	log ₁₀ (x)
	Autumn	1.52	2.22	178	4.48	10.48	46	3.87	3	0.15	log ₁₀ (x)
Total dinoflagellates		0.04	0.09	450	0.52	0.97	194	2.32	0.47	<0.001	log ₁₀ (x)
	Winter	0.03	0.05	69	0.23	0.51	35	1.97	0.20	<0.001	log ₁₀ (x)
	Spring	0.03	0.07	122	0.81	1.35	73	1.67	0.78	<0.001	log ₁₀ (x)
	Summer	0.06	0.12	123	0.50	0.63	49	2.51	0.44	<0.001	log ₁₀ (x)
	Autumn	0.04	0.10	136	0.24	0.52	40	3.40	0.20	<0.001	log ₁₀ (x)
<i>Dinoflagellates/(diatoms + dinoflagellates)</i>											
	Jan	0.0115	0.0110	25	0.0098	0.0098	11	2.27	–0.0017	0.66	log ₁₀ (x + 1)
	Feb	0.0120	0.0134	25	0.0044	0.0030	10	2.50	–0.0076	0.09	log ₁₀ (x + 1)
	Mar	0.0138	0.0089	35	0.0125	0.0156	26	1.35	–0.0012	0.68	log ₁₀ (x + 1)
	Apr	0.0106	0.0242	49	0.0159	0.0164	29	1.69	0.0052	0.28	log ₁₀ (x + 1)
	May	0.0177	0.0238	41	0.0303	0.0400	25	1.64	0.0126	0.11	log ₁₀ (x + 1)
	Jun	0.0255	0.0355	26	0.0225	0.0233	17	1.53	–0.0031	0.78	log ₁₀ (x + 1)
	Jul	0.0146	0.0173	34	0.0493	0.0485	16	2.13	0.0347	<0.001	log ₁₀ (x + 1)
	Aug	0.0297	0.0357	25	0.0824	0.1328	15	1.67	0.0527	0.06	log ₁₀ (x + 1)
	Sep	0.0492	0.0505	53	0.0634	0.0533	14	3.79	0.0141	0.35	log ₁₀ (x + 1)
	Oct	0.0372	0.0490	79	0.0449	0.0473	13	6.08	0.0076	0.58	log ₁₀ (x + 1)
	Nov	0.0178	0.0126	31	0.0097	0.0082	6	5.17	–0.0081	0.14	log ₁₀ (x + 1)
	Dec	0.0108	0.0057	23	0.0091	0.0080	14	1.64	–0.0017	0.45	log ₁₀ (x + 1)
<i>Abiotics</i>											
DIN (μmol L ⁻¹)		23.30	10.10	165	16.78	10.55	186	0.89	–6.53	<0.01	–
	Winter	37.63	11.73	28	31.54	12.55	44	0.64	–6.09	0.04	–
	Spring	26.24	13.40	36	18.03	16.94	46	0.78	–8.21	<0.05	–
	Summer	10.72	6.00	54	3.97	4.59	48	1.13	–6.75	<0.001	–
	Autumn	18.62	9.28	47	13.56	8.12	48	0.98	–5.06	<0.01	–
DIP (μmol L ⁻¹)		2.94	1.80	141	1.12	0.82	540	0.26	–1.82	<0.001	–
	Winter	3.84	1.61	27	1.59	1.29	127	0.21	–2.25	<0.001	–
	Spring	2.26	1.23	32	0.82	0.54	136	0.24	–1.44	<0.001	–
	Summer	1.92	0.58	43	0.84	0.63	144	0.30	–1.08	<0.001	–
	Autumn	3.74	3.78	39	1.23	0.83	133	0.29	–2.51	<0.001	–
DSi (μmol L ⁻¹)		7.65	4.30	158	8.23	5.18	186	0.85	0.57	0.07	–
	Winter	16.18	4.57	28	16.51	5.86	44	0.64	0.33	0.80	–

Table 1 (continued)

variable	Month/season	1970s			2000s			n _{1970s} /n _{2000s}	mean _{2000s} – mean _{1970s}	p-Value	Transformation (for ANOVA)
		Mean	sd	n	Mean	sd	n				
DIN:DIP	Spring	5.98	7.38	34	4.47	6.28	46	0.74	–1.51	0.33	–
	Summer	1.61	1.00	49	2.99	3.24	48	1.02	1.38	<0.05	–
	Autumn	6.84	4.24	47	8.93	5.32	48	0.98	2.09	<0.05	–
		9.05	4.59	139	19.86	21.14	538	0.26	10.81	<0.001	–
	Winter	10.97	4.18	26	34.26	37.44	127	0.20	23.29	<0.01	–
	Spring	13.16	8.14	32	24.65	26.05	134	0.24	11.49	<0.05	–
DSi:DIP	Summer	5.45	3.03	43	5.47	5.97	144	0.30	0.02	0.98	–
	Autumn	6.60	2.99	38	15.04	15.09	133	0.29	8.44	<0.001	–
		2.62	1.68	138	9.25	9.73	542	0.25	6.63	<0.001	–
	Winter	4.90	1.91	26	17.61	17.93	127	0.20	12.71	<0.001	–
	Spring	2.14	2.60	32	5.24	7.53	134	0.24	3.10	<0.05	–
	Summer	0.75	0.64	42	4.28	3.68	144	0.29	3.53	<0.001	–
SST (°C)	Autumn	2.68	1.55	38	9.85	9.78	133	0.29	7.17	<0.001	–
		12.27	5.05	165	12.02	5.33	191	0.86	–0.25	<0.001	–
	Winter	5.09	1.82	28	6.25	2.09	44	0.64	1.16	<0.05	–
	Spring	8.44	2.61	35	9.05	3.25	54	0.65	0.61	0.36	–
SPM (mg L ^{–1})	Summer	16.9	1.96	54	18.20	1.95	48	1.13	1.30	<0.01	–
	Autumn	14.04	2.91	48	14.65	2.94	45	1.07	0.61	0.32	–
		21.39	23.28	164	19.02	23.99	188	0.87	–2.37	0.42	log ₁₀ (x + 1)
	Winter	42.62	34.56	30	28.44	36.65	44	0.68	–14.18	0.04	log ₁₀ (x + 1)
	Spring	23.23	23.43	35	14.94	10.86	48	0.73	–8.29	0.25	log ₁₀ (x + 1)
	Summer	10.89	9.76	52	10.77	13.61	48	1.08	–0.12	0.57	log ₁₀ (x + 1)
Chl a (µg L ^{–1})	Autumn	18.1	14.94	47	22.72	23.95	48	0.98	4.62	0.49	log ₁₀ (x + 1)
		5.91	5.58	163	6.47	9.18	185	0.88	0.56	0.49	–
	Winter	2.07	1.58	30	1.35	0.87	43	0.70	–0.72	<0.05	–
	Spring	7.23	5.91	33	14.79	14.12	48	0.69	7.56	<0.01	–
	Summer	9.09	6.61	51	5.79	4.55	48	1.06	–3.30	<0.01	–
	Autumn	4.05	3.20	49	3.29	2.00	46	1.07	–0.76	0.17	–

2015). The number of coastal vs. offshore samples is very balanced between the two periods. In the 1970s, 34% (244) of the samples were offshore samples, while 66% (474) were coastal. In the 2000s, 30.6% (161) of the samples were from the offshore area and 69.4% (365) from the coastal area.

2.3. Data analyses

Overall changes in abundance and biovolume of diatoms and dinoflagellates, the dinoflagellate/(diatom + dinoflagellate) abundance ratio (Hernández-Fariñas et al., 2014) and environmental data between the 1970s and the 2000s were evaluated using one-way ANOVAs. Prior to analysis, data were tested on normality (visually using qq-plots and the Shapiro-Wilk test of normality) and homogeneity of variances (using the Levene's test), and log₁₀(x)- or log₁₀(x + 1)-transformed if needed (which type of transformation was applied is listed in Table 1 last column). The analyses were done for the two periods as a whole and per season (all data) or month (for the dinoflagellate/(diatom + dinoflagellate) ratio). Analyses for individual diatom genera were only done for the two periods as a whole.

To unravel changes in seasonal trends in the datasets in more detail, the datasets of coastal diatoms and coastal dinoflagellates were analysed with a general additive mixed modelling (GAMM) approach. For this, the *mgcv* package (Wood, 2017) in the open-source software R was used (R Core Team, 2019). Space (sampling location set as random effect) and time (seasonal smoother) were incorporated in the models. By incorporating 'taxonomist' as a random effect, a possible taxonomist dependent identification bias was excluded from the models. The data were log₁₀(x)-transformed prior to analysis and a Gaussian distribution was used in the models. In addition, a log-link function was used to ensure that the fitted values are always positive (Philippart et al., 2010). One cubic regression spline (cc) *f*(JulianDay) was used to model the seasonal trend. This type of smoother ensures that the value of the smoother at the far left point of the gradient is the same as at the far right point which is convenient to model an annual cycle (Zuur et al., 2009). The models were expanded with different residual auto-correlation structures: autoregressive correlation

(*corAR1*), continuous autoregressive correlation (*corCAR1*), compound symmetry structure (*corCompSymm*), exponential correlation (*corExp*), Gaussian (*corGaus*) and linear correlation (*corLin*), rational quadratic (*corRatio*) and spheric spatial correlation (*corSpher*). The best model for each dataset was identified by the lowest Akaike information criterion (AIC), which takes into account the model fit versus the complexity of the model calculation (Zuur et al., 2009).

Changes in community composition and seasonality were visually evaluated using heatmaps (81 taxa) and Principal Components Analysis (PCA), based on log₁₀(x + 1) transformed relative abundance data of genera which reached a total relative abundance of 10% in at least one sample (41 diatom and 6 dinoflagellate taxa). As the length of gradient (measure of turnover in species composition in the data set, cf. Lepš and Šmilauer, 2014) is <4, we opted for this eigenvalue based ordination method with an underlying linear species response model. PCA were carried out using Canoco 5 (<http://www.canoco5.com/>).

Finally, diatom and dinoflagellate seasonality was analysed using fulcrum analysis which allows investigating changes in the phenology of phytoplankton blooms (Kromkamp and Van Engeland, 2010). The relative annual cumulative abundance was calculated for the total diatom and dinoflagellate abundance data. The day of the year on which 50% of the total annual abundance was reached (i.e. the fulcrum), was identified by fitting a binomial *glm* smoother to the data.

3. Results

3.1. Environmental changes in the Walcheren transect between the 1970s and 2000s

In the 1970s, DIN, and more particular DIP values were significantly higher than in the 2000s, especially in summer (Fig. 2, Table 1). In contrast, DSi values showed no significant overall change, except in summer and autumn when DSi values were slightly but significantly higher in the 2000s (Fig. 2, Table 1). As a result, DIN:DIP and DSi:DIP ratios significantly increased from the

1970s to 2000s (except for summer DIN:DIP values which remained similar), reaching average values close to Redfield ratios (16:1 for DIN:DIP and 15:1 for DSi:DIP) in winter and early spring (Table 1). The SST significantly and markedly increased between the two periods in winter and summer, with values being on average 1.16 °C and 1.3 °C higher respectively, but not in spring and autumn (note that the apparent significant overall decrease between the two periods is due to the fact that more winter data were available for the 2000s and more summer data for the 1970s). Winter SPM values were significantly lower during the 2000s, but did not differ during the rest of the year (Fig. 2, Table 1). The Chl a concentration was significantly higher during spring in the 2000s, but lower during winter and especially summer (Table 1).

3.2. Changes in diatom and dinoflagellate cell numbers, biovolume and seasonal trends between the 1970s and 2000s

Both diatom and dinoflagellate cell numbers significantly increased between the 1970s and 2000s (Table 1, Fig. 3), especially in the coastal zone (Fig. A.2). Diatoms mainly increased during winter and spring, but not in summer, while dinoflagellates mainly increased during spring and summer (Table 1, Fig. 3A and D). Similar trends can be seen in diatom and dinoflagellate total biovolume, but here diatom values are significantly higher from winter to summer, and not in autumn, while dinoflagellate total biovolume is significantly higher in all seasons (Table 1, Fig. 3G and J). The trends of 20 important (see below, derived from PCA analysis) diatom genera underscore the general diatom trend: all genera increased in abundance between the two periods, except for *Dactyliosolen* and benthic diatoms which significantly decreased, and *Thalassionema* which did not show any change in its annual mean abundance (Table 1).

For the GAMM models, different auto-correlation structures were tested and the models were assessed through their AIC results (Tables A.1–A.4, A.6–A.9). Tables A.5 and A.10 summarize for each dataset the model configurations and results of the best model fits. In the 1970s, diatom cell numbers typically display two annual peaks, in spring and autumn (Fig. 3A and B), while in the 2000s only one more extensive peak, which starts earlier and is followed by a more pronounced decline in autumn, can be observed (Fig. 3A and C). The total biovolume data underscore this trend, with two (albeit less distinct) peaks (spring, summer) in the 1970s (Fig. 3G and H) which merge and become more pronounced in the 2000s, followed by a marked decrease in autumn (Fig. 3G and I). In both dinoflagellate cell numbers and total biovolume, the spring and autumn blooms merge into one extended and pronounced spring to autumn growing season, with the highest values in the summer months (Fig. 3D and F, J and L). As a result of the strong summer increase in dinoflagellate cell numbers, dinoflagellate/(diatom + dinoflagellate) ratios were higher from spring to autumn in the 2000s, but this increase was only significant for July (Table 1). While total biovolume of all size classes has increased between the 1970s and the 2000s, the contribution to the overall diatom biovolume increase between the two periods is mainly due to an increase in the contribution of genera in the largest size class (i.e. *Guinardia* spp., *Thalassiosira* spp., *Bacteriastrum* spp., *Rhizosolenia* spp., *Lauderia* spp., *Coscinodiscus* spp. and *Cerataulina* spp.), especially in early spring and summer (Figs. 4, A.3), resulting in one extended peak which has a prominent earlier start in late winter. The fulcrum analyses (Fig. 5) confirm this forward shift in the diatom bloom, with the fulcrum being reached three weeks earlier in the 2000s than in the 1970s. This forward shift however was just not significant ($p = 0.06$). For dinoflagellates the forward shift is significant ($p = 0.008$) and more pronounced, with the fulcrum being attained no less than two months earlier.

3.3. Changes in diatom and dinoflagellate composition and seasonal dynamics

In total, 57 diatom and 25 dinoflagellate genera have been observed in the BPNS since the 1970s. Of these, 13 diatom and 11 dinoflagellate genera were only recorded in the 1970s (Fig. 6). Most of these were rare, except for the diatoms *Cyclotella* and *Discostella*, and the dinoflagellates *Glenodinium* and *Peridinium*. Five diatom (*Corethron*, *Detonula*, *Hemiaulus*, *Lithodesmium* and *Brockmanniella*) and dinoflagellate genera (*Diplopsalis*, *Gonyaulax*, *Heterocapsa*, *Katodinium* and *Pyrophacus*) were only observed in the 2000s. Many diatom genera have markedly increased between the 1970s and the 2000s, e.g. *Asterionellopsis*, *Chaetoceros*, *Cylindrotheca*, *Ditylum*, *Guinardia*, *Odontella*, *Pseudo-nitzschia*, *Rhizosolenia*, *Thalassiosira*, *Thalassionema* and *Plagiogrammopsis* (Figs. 6, A.4). Many of these (except *Pseudo-nitzschia*) also have higher winter abundances, display an extended growing season until September (without the July–August gap apparent in the 1970s), and have overall lower values in October and November, all of which corroborates the trends observed in the total diatom abundance and biovolume data (Figs. 3, 4 and 5). The only category that seems to decline between the two periods are benthic diatoms (Fig. 6). Several dinoflagellate genera as well have increased since the 1970s, such as *Alexandrium*, *Gymnodium*, *Gyrodinium*, *Prorocentrum*, *Protoperidinium* and *Scrippsiella*, with especially higher values in late spring and summer, confirming the trends observed in Fig. 3D–F, J–L.

Changes in composition and seasonal dynamics were investigated using PCA (Fig. 7). To avoid the analysis being heavily biased by the general increase in cell numbers between the two periods, we used the relative abundance values of the 47 most important diatom and dinoflagellate genera (cf. Section 2.3). Data from both periods were used in a joint PCA, after which samples belonging to each period were (per season) highlighted with different (light vs. dark) colors to reveal shifts in composition in autumn–winter, spring and summer respectively (Fig. 7A–C). The first two PCA axes (Fig. 7) capture about 38% of the total variation in the dataset. This seems rather low but is comparable to values reported for PCA analyses of ecological data reported in the literature (e.g. 43% in ter Braak, 1994; 36% in Lepš and Šmilauer, 2014). Due to the noisy nature of ecological data sets, even low percentages explained are still quite informative (ter Braak, 1986; ter Braak, 1994).

In both periods, a seasonal succession in composition is present, with a change from an autumn–winter assemblage (1) dominated by diatoms with a benthic to tycho planktonic life style (e.g. benthic diatoms, *Paralia* and *Rhaphoneis*) and smaller, more heavily silicified, planktonic diatom taxa (e.g. *Actinocyclus*, *Thalassionema*, *Thalassiosira*), over an intermediate assemblage (2), mainly characterized by smaller colonial species *Asterionellopsis*, *Chaetoceros* and *Pseudo-nitzschia*, to a summer (June to August) assemblage (3) with mainly larger, often colonial and lightly silicified species such as *Cerataulina*, *Dactyliosolen*, *Guinardia*, *Leptocylindrus* and *Rhizosolenia* (Fig. 7D). Strikingly, while especially assemblage 1 and 3 are distinct in the 1970s, with assemblage 2 being less prevalent, there is a clear shift towards assemblage 2 in almost all seasons in the 2000s, revealing a trend towards seasonal homogenization of the typical succession present in the BPNS in the 2000s. This is confirmed by the seasonal trends in the individual taxa (Figs. A.4, 7): despite significant increases in mean cell numbers between the 1970s and the 2000s in the 20 taxa best fitted in the PCA (except *Thalassionema* and benthic diatoms, Table 1), there is an overall decline in median abundance values (Fig. A.4) and relative abundances (Fig. 7) in some important representatives of assemblage 1 (benthic diatoms, *Paralia*, *Rhaphoneis* and *Thalassionema*) and assemblage 3 (*Cerataulina*, *Dactyliosolen* and *Leptocylindrus*), with other genera of assemblage 1 displaying a shift towards earlier peak abundances (winter–early spring for *Thalassionema* and *Thalassiosira*) and important representatives of assemblage 3 showing a clear decline in late summer and autumn (*Guinardia* and *Rhizosolenia*). In contrast, almost all representatives of

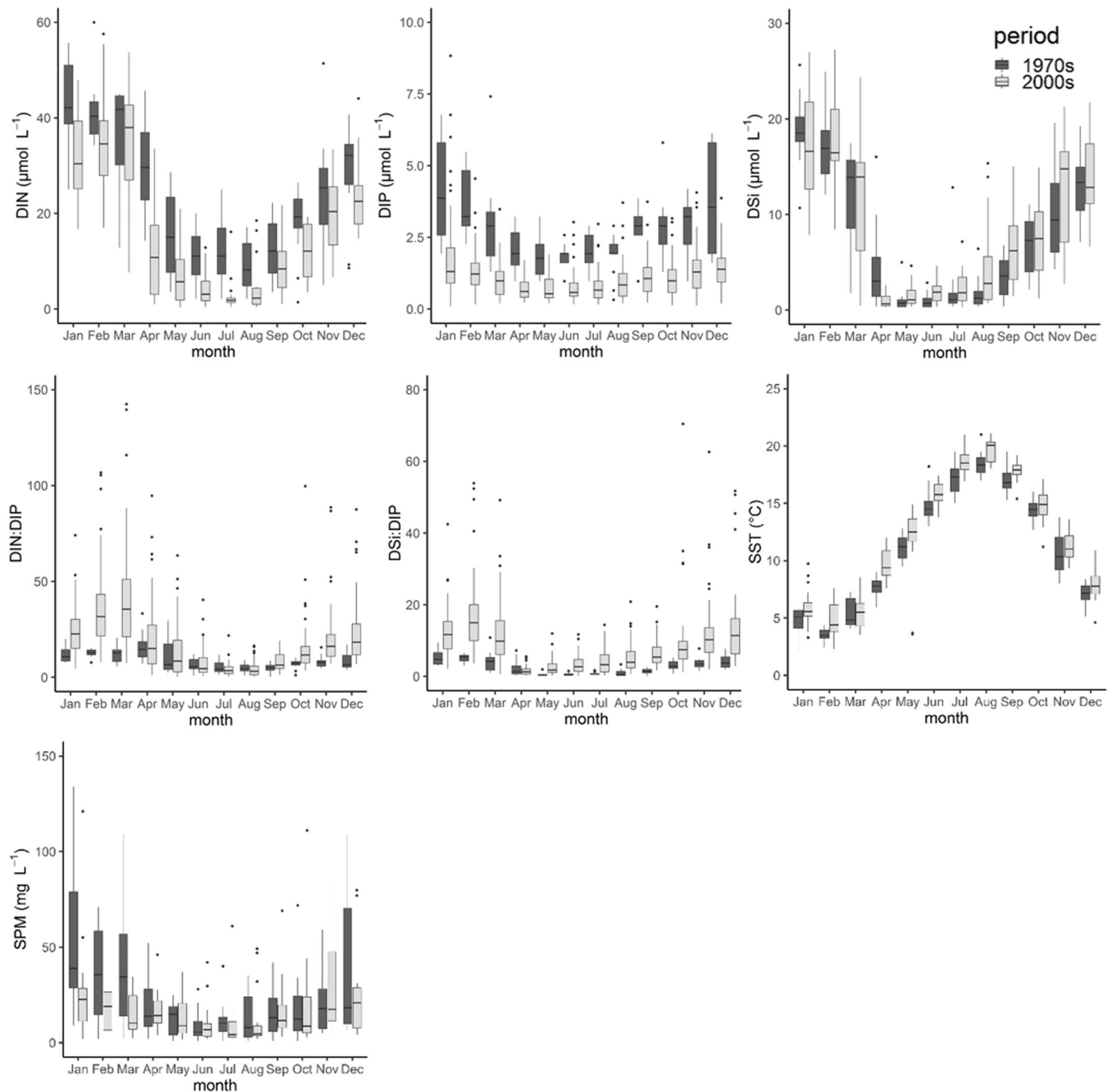


Fig. 2. Seasonality of environmental parameters measured in the Walcheren transect (station Walcheren2 and Walcheren20) (Dutch North Sea coast). Data derived from the long-term monitoring of Rijkswaterstaat (RWS).

assemblage 2 show a pronounced increase in median abundance values (Fig. A.4) and relative abundances (Fig. 7) throughout the year (especially *Chaetoceros*, *Ditylum* and *Pseudo-nitzschia*).

4. Discussion

4.1. Pronounced changes in diatom and dinoflagellate abundance, biovolume and composition in the BPNS between 1970s and 2000s

Using the Belgian Phytoplankton Database (Nohe et al., 2018), a newly compiled, standardized dataset of phytoplankton count data from the shallow and heavily impacted BPNS, we compared biomass, seasonality and structure of diatom and dinoflagellate assemblages

between the 1970s and 2000s. This revealed the following major changes: (1) a pronounced increase in diatom and dinoflagellate total biovolume, with diatoms mainly increasing from winter to summer (but not in autumn), and dinoflagellates in spring and summer; (2) a shift from a bimodal annual diatom bloom pattern (spring and summer-autumn) to a single, more extended growing season which starts 3 weeks earlier (February), ends in mid-summer (July) and is mainly dominated by large diatoms; (3) a similar shift in dinoflagellates from a bimodal annual bloom pattern to a single, extended bloom from May to September; (4) a marked change in diatom assemblage composition, from seasonally distinct assemblages in the 1970s to a seasonally more homogenized assemblage in the 2000s; and (5) a significant increase in potential HABs, such as

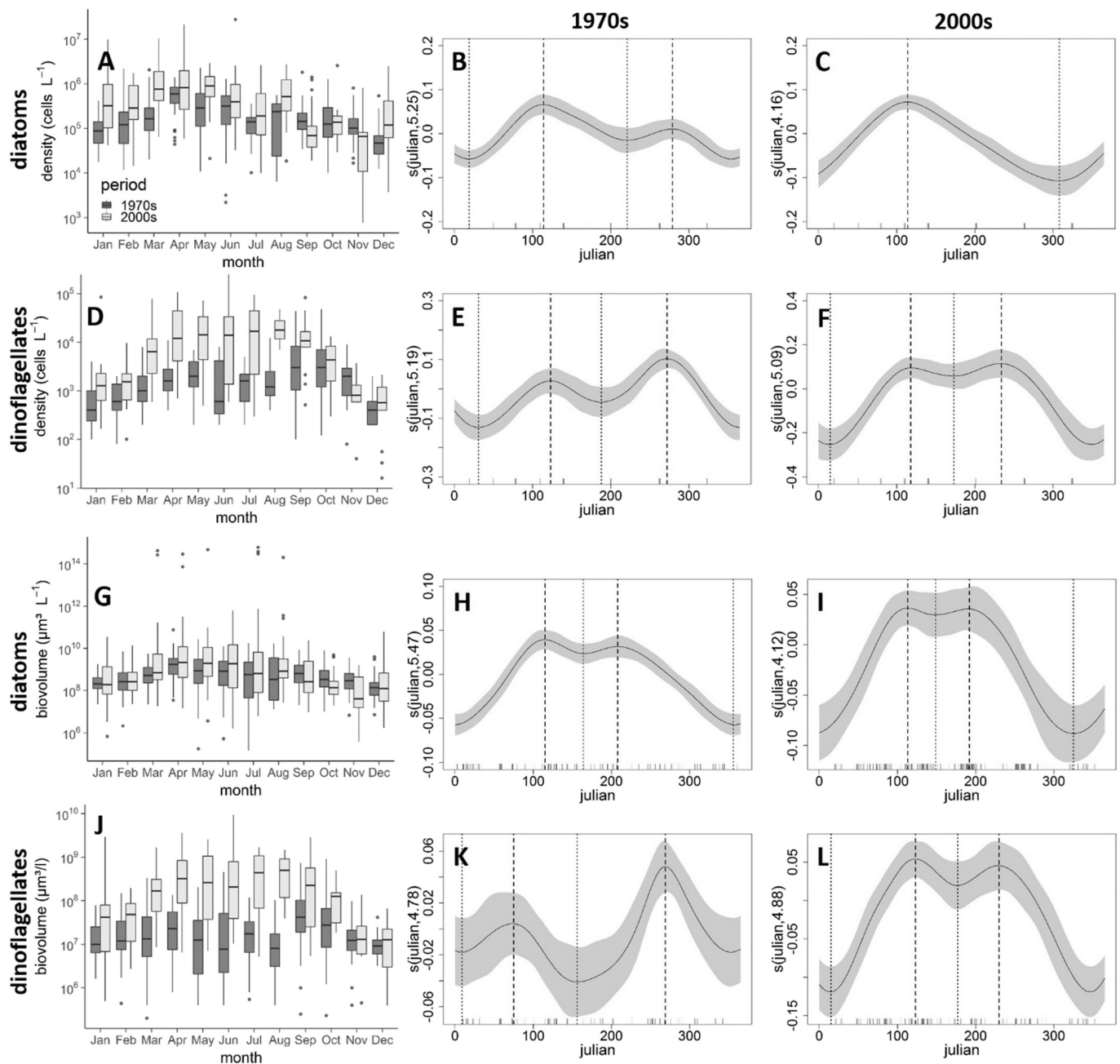


Fig. 3. Seasonal trends of the diatom and dinoflagellate abundances (A–F) and biovolumes (G–L) in the coastal area. The solid line is the smoothing curve fitted by the GAMM model and the grey area represents the 95% confidence bands. A Diatom abundances, B GAMM diatom abundance in the 1970s, C GAMM diatom abundance in the 2000s, D dinoflagellate abundances, E GAMM dinoflagellate abundance in the 1970s, F GAMM dinoflagellate abundances in the 2000s, G diatom biovolumes, H GAMM diatom biovolumes in the 1970s, I GAMM diatom biovolumes in the 2000s, J dinoflagellate biovolumes, K GAMM dinoflagellate biovolumes in the 1970s and L GAMM dinoflagellate biovolumes in the 2000s. The start of the blooms is indicated as dotted lines. The date of the bloom peak is indicated with a dashed line. The numbers between brackets on the y-axes indicate the estimated degrees of freedom. The higher the number, the more non-linear the curve, while numbers close to 1 indicate a linear functional response.

Pseudo-nitzschia and several dinoflagellate genera (e.g. *Prorocentrum* and *Alexandrium*).

4.2. BPNS diatom and dinoflagellate trends in a wider North Sea perspective

Increases in overall phytoplankton biomass from the 1970s to the 1990s/2000s have been reported in various studies from the North Sea (Antoine et al., 2005; Philippart et al., 2000; Raitsos et al., 2014), especially in association with a pronounced regime shift in the late 1980s (Beaugrand et al., 2014; Reid and Edwards, 2001). Since the late 1990s, however, phytoplankton biomass and primary production in many regions of the North Sea appear to have stabilized (Cadée and

Hegeman, 2002; Capuzzo et al., 2015; Prins et al., 2012) or even decreased (Capuzzo et al., 2018; Desmit et al., 2019). Data on diatoms and dinoflagellates alone are rarer and usually more limited to the most recent decades. Several long-term data sets (i.e. including the 1970s) revealed increases in diatom abundance in the wider North Sea area from the 1970s to the 2000s (Beaugrand et al., 2014; Hinder et al., 2012; Wiltshire et al., 2008; Wiltshire et al., 2015). Diatom and dinoflagellate datasets from the southern part of the North Sea usually only date back to the (early) 1990s, but here as well significant increases in both diatoms and dinoflagellates have been observed (Alvarez-Fernandez and Riegman, 2014; Baretta-Bekker et al., 2009; Hernández-Fariñas et al., 2014; Hickel, 1998; Prins et al., 2012). The

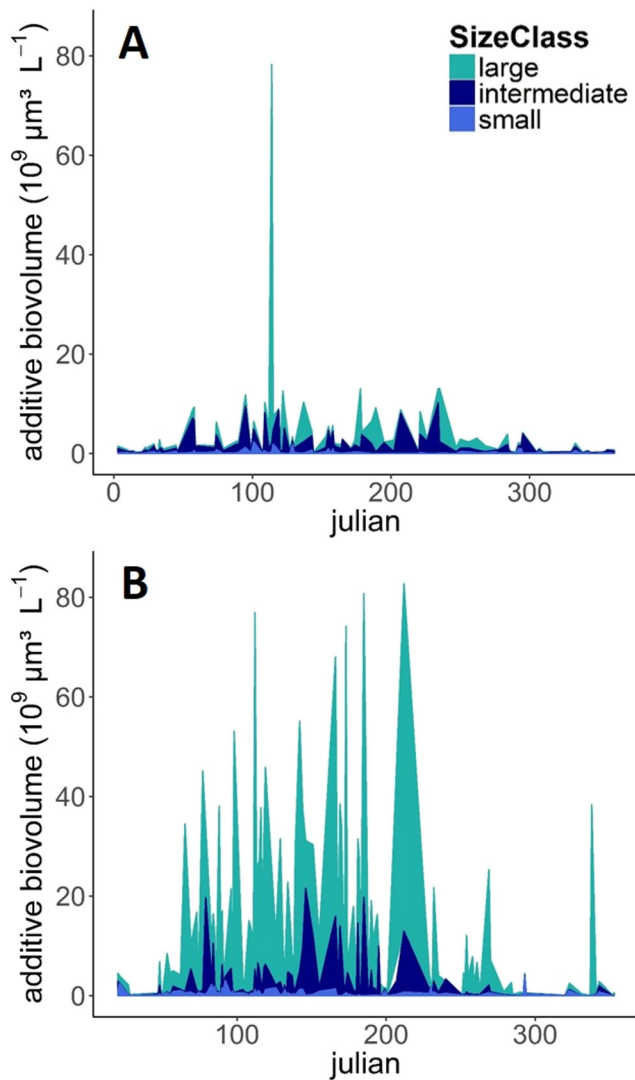


Fig. 4. Annual cycle of small, intermediate and large diatoms in the coastal stations of the BPNS for A 1970s and B 2000s.

shift from a bimodal to a unimodal, earlier and more extended diatom and dinoflagellate seasonal bloom pattern has also been observed in other areas in the southern bight of the North Sea (Alvarez-Fernandez and Riegman, 2014; Baretta-Bekker et al., 2009; Gieskes et al., 2007; Philippart et al., 2010; Raitos et al., 2014; Reid and Edwards, 2001), but not further north (e.g. Helgoland; Wiltshire et al., 2008), although here as well increased winter phytoplankton densities were observed (Capuzzo et al., 2015; Wiltshire et al., 2008).

The typical succession from a late winter–early spring assemblage 1 (dominated by benthic, tychoplanktonic and more heavily silicified planktonic species) over spring assemblage 2 (with mainly smaller colonial taxa) to a late spring–summer assemblage 3 (dominated by large and more lightly silicified diatoms) appears to have been typical of the BPNS until the 1990s (e.g. Rousseau et al., 2002). The remarkable shift from seasonally distinct to seasonally more uniform assemblages in the 2000s, with an increased importance of typical assemblage 2 representatives such as *Chaetoceros* and *Pseudo-nitzschia* in all seasons, has to our knowledge not yet been reported from other parts of the North Sea. Interestingly, Prins et al. (2012) reported a similar increase of *Chaetoceros* (especially *C. socialis*, which is also a dominant species in the BPNS) since the 1990s in the Dutch part of the North Sea, and the shift towards larger diatom taxa in the BPNS (Figs. 4, A.3) agrees with observations in the German Bight (Wiltshire et al., 2010). The increase in HAB taxa in the BPNS has also been reported from other areas in the North Sea (Hernández-Fariñas et al., 2014; Gobler et al., 2017) and agrees with a global increase of HAB blooms and toxic events in the last 25 years (Anderson et al., 2012).

4.3. Environmental effects on changes in diatom and dinoflagellate abundance, biovolume and composition

From the 1970s to the 2000s, the abiotic environment in the BPNS has significantly changed, especially with respect to temperature, nutrients and light, which are, both directly and indirectly, key determinants of phytoplankton production and community structure. In the 2000s, average winter and summer temperatures were higher, winter SPM lower, and DIN and DIP concentrations lower but DSi equal or higher. These changes in nutrient concentrations resulted in increased nutrient ratios more closely approximating Redfield ratios in winter and early spring. Most of the abiotic changes can be directly related to human activities, such as climate warming and (de-)eutrophication (cf. above).

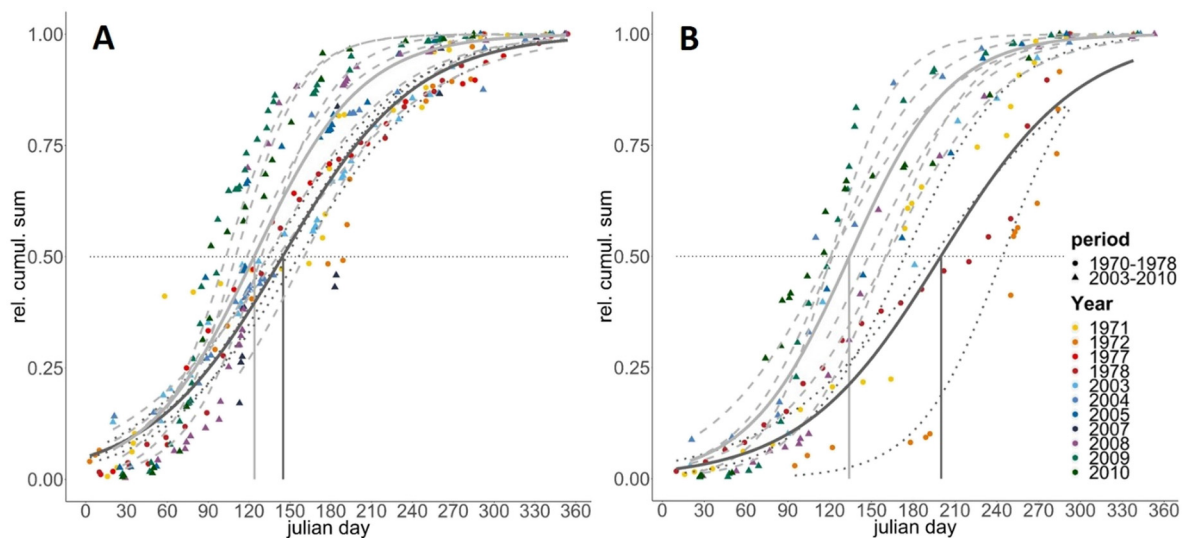


Fig. 5. Fulcrum analysis of the relative cumulative sum of the annual cell abundances. A binomial *glm* smoother function is fitted on each annual data subset. In addition, a 'mean' smoother per period is added (as thick line). Black: 1970s, grey: 2000s. The Julian day on which half of the annual phytoplankton cell abundance (the fulcrum) is reached is indicated. A Diatoms, B dinoflagellates. Years with insufficient seasonal coverage were not included in the analyses.

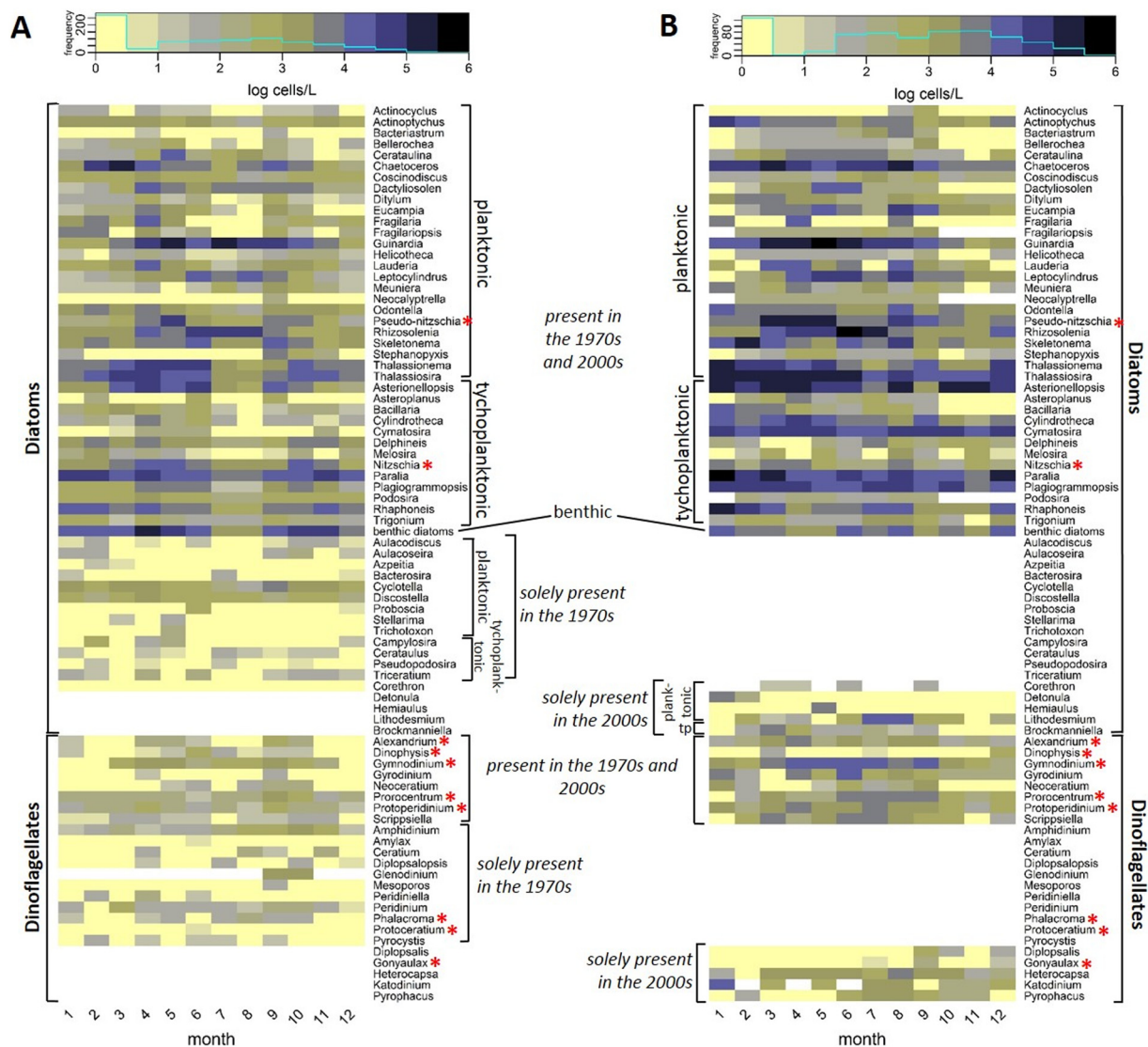


Fig. 6. Heatmaps and histograms of seasonal changes in the logarithmically transformed diatom and dinoflagellate cell counts based on the monthly mean values for A 1970s and B 2000s. Potentially toxic genera are labelled with a red asterisk. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Decreases in DIN and especially DIP have been reported throughout the southern part of the North Sea since the 1970s (Alvarez-Fernandez and Riegman, 2014; Burson et al., 2016; Lefebvre et al., 2011; Prins et al., 2012). In the BPNS, DIN and DIP concentrations in the 2000s generally remained above phytoplankton growth limiting concentrations throughout the year (DIN >4 μM , DIP >0.8 μM ; Table 1; Kromkamp et al., 1995). Likewise, increases in DSI have been observed in the southern part of the North Sea, possible as a result of reduced riverine eutrophication and hence lower DSI uptake by riverine diatom blooms (Alvarez-Fernandez and Riegman, 2014; Prins et al., 2012). While DSI may have been limiting during summer in the 1970s (DSi ~1.6 μM , Table 1), values were generally not limiting in the 2000s (summer DSI >2.5 μM , Table 1). The observed increases in diatoms and dinoflagellates are most likely not caused by changes in nutrient concentrations but rather their altered ratios. The unbalanced reduction in DIN and DIP resulted in a more balanced DIN:DIP ratio which often exceeds the Redfield ratio in the 2000s, especially in winter and spring (Burson et al., 2016; McQuatters-Gollop et al., 2007). In combination with stable and more balanced DSI levels, this may have contributed to the observed increase in diatom biomass since the 1970s. The more balanced DIN:DIP ratios may also explain the earlier and more intense diatom spring bloom in the 2000s (but see below). DSI availability has been

considered as a key factor driving the typical succession between seasonally distinct diatom communities in the BPNS before the 2000s (Rousseau et al., 2008): the first assemblage with more heavily silicified species would be dominant in winter and early spring until DSI becomes depleted, after which more lightly silicified species take over. The shift to larger species (assemblage 2 and especially 3) would mainly be related their lower DSI requirement [but possible also to their (size-related) higher resistance to grazing (Terseleer, 2014)]. As winter and spring DSI concentrations have not significantly changed between the two study periods, it is unlikely that the decline of the typical winter-early spring assemblage is related to DSI availability. Terseleer (2014) also found no link between DSI availability and the magnitude of the first spring bloom, which suggests that other factors than winter nutrient stocks control bloom formation in early spring.

The observed increase in diatom and dinoflagellate biomass coincides with a significant increase in winter and summer SST since the 1970s (Table 1). This increase was most pronounced in the late 1980s (Raitos et al., 2014) and coincided with a stepwise increase in phytoplankton biomass (Raitos et al., 2014; Reid and Edwards, 2001). The tight relationship between SST and phytoplankton biomass is supported by observations of McQuatters-Gollop et al. (2007) and Raitos et al. (2014) who showed that North Sea ocean color anomalies very closely

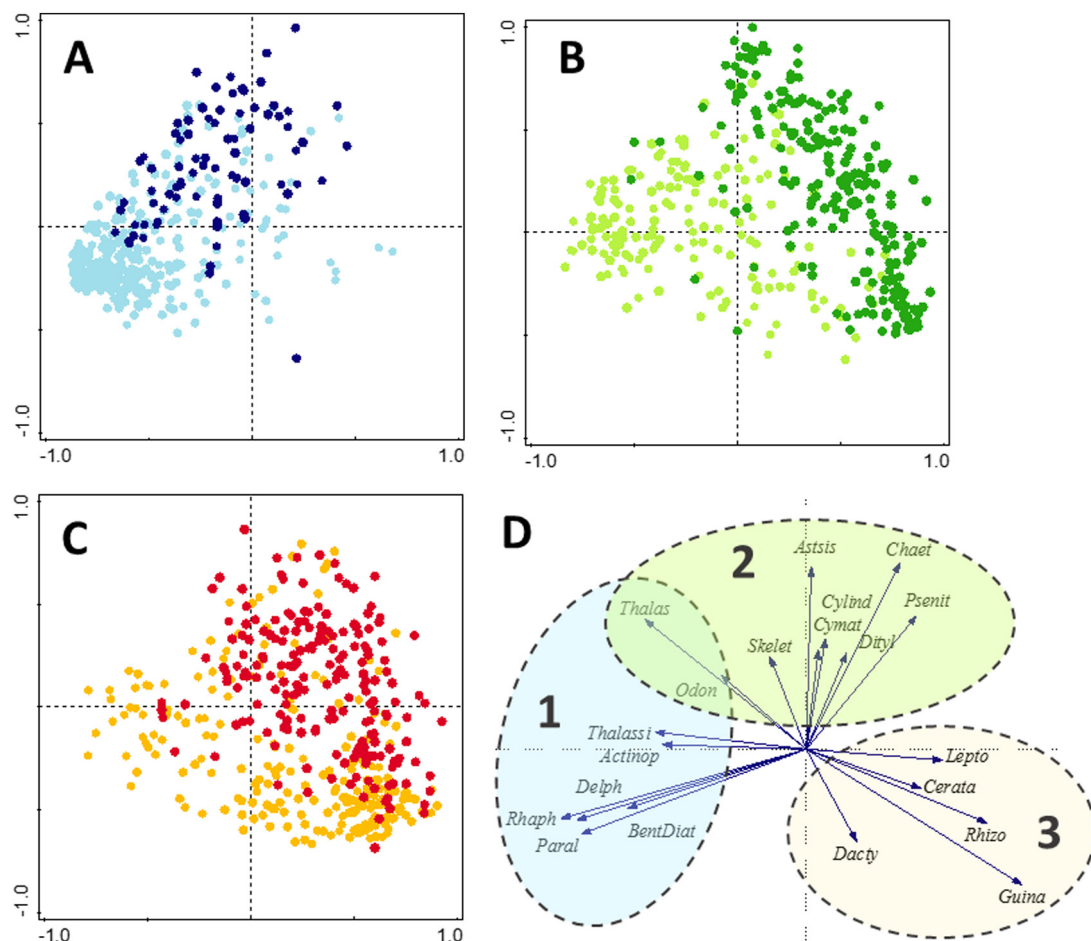


Fig. 7. Principal Component Analysis (PCA) of the logarithmically transformed diatom and dinoflagellate relative abundance data. A Autumn-winter (September–February), B spring (March–May), C summer (June–August), D genera. Ellipses indicate the three typical successive assemblages in the BPNS. Light blue, light green and orange represent the 1970s (A–C). Dark blue, dark green and red represent the 2000s (A–C). Only the 20 best fitted genera are shown. Fig. A.5 shows all fitted genera. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

track SST changes in the North Sea since the 1950s. The exact mechanism(s) underlying the impact of SST on phytoplankton biomass remain as yet unclear. Increased SST can enhance species-specific growth rates (Montagnes and Franklin, 2001), but indirect effects such as increased stratification and changes in top-down control related to latitudinal shifts in grazers (Chivers et al., 2017) can also be important. Given the fact that BPNS waters are well-mixed throughout the year, an effect of enhanced stratification seems unlikely. A long-term decline in calanoid copepods in the German Bight (Boersma et al., 2015) has been linked with a simultaneous increase in phytoplankton (Wiltshire et al., 2015). A similar decline in small copepods was also reported for the North Sea by Capuzzo et al. (2018). Copepods are also important grazers on phytoplankton in the BPNS (Daro et al., 2006), but to our knowledge no information is as yet available on long-term zooplankton trends in the BPNS. The observed changes in diatom and dinoflagellate assemblage composition can also be directly or indirectly related to SST. *Chaetoceros* spp. have been associated with higher SST but also increased light availability (Wiltshire et al., 2015) and higher nutrient availability (Prins et al., 2012). This is consistent with the general increase of this genus throughout the growing season in the 2000s. Wiltshire et al. (2015) also reported an earlier and extended growing season for *Guinardia delicatula*, and related this to its preference for higher temperatures. Climate warming may also be responsible for the overall increased importance of dinoflagellates in summer in the 2000s, as these are generally associated with warmer and less turbulent conditions (Baretta-Bekker et al., 2009; Prins et al., 2012). The capacity of many dinoflagellates for mixotrophic growth, and more specifically

their ability to access alternative P sources, may also contribute to explaining their dominance during summer when nutrient levels are at their lowest (Burson et al., 2016). Competition with dinoflagellates may as such also be implicated in the earlier decline in diatom cell numbers and biomass in mid-summer and autumn, although competition with other phytoplankton and/or increased zooplankton grazing can also be involved.

Changes in light availability may also be linked with the observed increase in diatom and dinoflagellate biomass and the earlier start of the blooms in the BPNS in the 2000s. Light is a primary control on phytoplankton growth in the North Sea area (Wiltshire et al., 2008), and our data show that winter SPM is significantly lower in the 2000s (Table 1). It is not clear what causes these lower SPM values, but several hypotheses have been put forward: (1) recovery of subtidal benthic algal biofilms, which contribute to stabilizing the surface layer of sediments and thereby reducing resuspension (Capuzzo et al., 2015; Madsen et al., 1993); (2) changes in trawling activities, which have been linked to changes in water clarity by disturbance and resuspension of bottom sediments (Callaway et al., 2007; Capuzzo et al., 2015; Jennings et al., 1999); (3) changes in the weather patterns, which can lead to changes in the hydrodynamics and the disturbance of subtidal sediments (Capuzzo et al., 2015; Fettweis et al., 2012), and (4) changes in the strength of coastal erosion and riverine sediment transport to the BPNS (Capuzzo et al., 2015; Fettweis et al., 2012). Increased water transparency in late winter and early spring, in combination with higher SST and more balanced nutrient ratios (albeit lower total DIN and DIP concentrations) (Table 1), may explain the earlier start and higher intensity

of the diatom spring bloom in the 2000s. Rousseau et al. (2002) pointed out that the onset of the spring bloom in the BPNS is dependent on a specific light threshold. Lohmann and Wiltshire (2012) showed that atmospheric circulation patterns in winter, which increased the inflow of warmer and especially more transparent water off Helgoland, favored earlier blooms. Likewise, McQuatters-Gollop et al. (2007) and Raitos et al. (2014) identified light and SST, but not nutrient concentrations, as the most important controls on spring bloom initiation in the North Sea area. In contrast, an increase in water clarity was observed in the German Bight, but this did not lead to changes in phytoplankton spring bloom dynamics (Wiltshire et al., 2008), suggesting that SST may be a more dominant factor.

The increased importance of large diatoms in the BPNS is surprising, as higher SST and lower nutrient concentrations are expected to select for smaller-sized taxa (Beardall et al., 2009; Burson et al., 2016; Terseleer, 2014). A similar increase of large diatoms in the German Bight was related to their higher resistance to copepod grazing (Wiltshire et al., 2010). Interestingly, it has been proposed that large species may also particularly benefit from elevated CO₂ concentrations as due to their lower surface-to-volume ratios they are more restricted in carbon acquisition than smaller species (Bach and Taucher, 2019).

4.4. Potential implications of the observed changes in diatom and dinoflagellate biomass, composition and seasonality for marine ecosystem services

Coastal ecosystems such as the BPNS deliver multiple highly valuable ecosystem services, from nutrient cycling to primary and secondary productivity which supports economically important fisheries and aquaculture activities (Doney et al., 2012). The changes observed in diatoms and dinoflagellates in the BPNS can have important repercussions for these services. We observed a pronounced increase in HAB taxa, the reasons for which are as yet unclear, and are probably multifactorial. HABs have been linked with increased eutrophication (Anderson et al., 2012), but this would not explain why HAB genera increased in the southern North Sea during a period of de-eutrophication. Increased SST seems to be a more likely factor, especially for dinoflagellates which perform better under warmer conditions. Indeed, Gobler et al. (2017) showed that ocean warming increased the temporal and spatial availability of thermally suitable habitat for the dinoflagellate genus *Alexandrium* in the North Sea. It is clear that the increase in HAB taxa in the North Sea area is a worrying trend from a socio-economic point of view which needs to be carefully monitored in the future. Changes in phytoplankton distributions and seasonality in general may also lead to trophic mismatches and altered carbon transfer through the food web (Edwards and Richardson, 2004; Philippart et al., 2010; Schlüter et al., 2012; Townsend et al., 1994; Wiltshire and Manly, 2004). Primary consumer species, especially in late summer and autumn, rely on phytoplankton carbon production (Philippart et al., 2010), and our study shows that phytoplankton biomass is especially lower in these seasons in the 2000s. Given the central role of phytoplankton in marine food webs, the observed changes may thus have far-reaching environmental and socio-economic consequences.

4.5. Importance of recovering historic data sets for understanding the effects of global change in marine ecosystems

Contemporary marine ecosystems are affected by numerous global change phenomena, from climate warming to ocean acidification and changes in nutrient status related to eutrophication or de-eutrophication. Understanding and ultimately predicting how the interplay between these factors affects the structure and functioning of marine ecosystems require a long-term perspective. In the present study we show how the recovery and disclosure of previously inaccessible, non-digital data can shed new light on how marine diatom and dinoflagellate communities have changed in a heavily impacted coastal area, the BPNS. The rescued data not only provide further evidence for

significant changes in diatom and dinoflagellate biomass and seasonality, which corroborate trends observed in other parts of the North Sea area, but also reveal a previously undetected aspect of phytoplankton change in the BPNS, with diatom assemblages becoming more homogenized throughout the growing season. Historic data thus provide a unique and invaluable window into the structure and dynamics of marine ecosystems under past environmental and anthropogenic conditions, and further efforts to uncover and disclose 'lost' historic data sets should therefore be strongly encouraged.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Rijkswaterstaat (RWS) and all laboratories involved in the monitoring programs of Dutch waters for making their long-term datasets available. We also want to thank the four anonymous reviewers for their helpful comments and efforts towards improving our manuscript.

This study was part of the 4DEMON project financed by BELSPO (BR/121/A3/4DEMON) and was supported by the LifeWatch data archeology project. We also acknowledge financial support from Ghent University (BOF-GOA 01G01911).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2019.136316>.

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