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Looking back to the future—micro- and nanoplankton diversity in the Greenland Sea

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Abstract

Anthropogenic perturbations and climate change are severely threatening habitats of the global ocean, especially in the Arctic region, which is affected faster than any other ecosystem. Despite its importance and prevailing threats, knowledge on changes in its micro- and nanoplanktonic diversity is still highly limited. Here, we look back almost two decades (May 1–26, 2002) in order to expand the limited but necessary baseline for comparative field observations. Using light microscopy, a total of 196 species (taxa) were observed in 46 stations across 9 transects in the Greenland Sea. Although the number of observed species per sample ranged from 12 to 68, the diversity as effective species numbers (based on Shannon index) varied from 1.0 to 8.8, leaving about 88% as rare species, which is an important factor for the resilience of an ecosystem. Interestingly, the station with the overall highest species number had among the lowest effective species numbers. During the field survey, both number of rare species and species diversity increased with decreasing latitude. In the southern part of the examined region, we observed indications of an under-ice bloom with a chlorophyll *a* value of 9.9 µg l^{-1} together with a nitrate concentration < 0.1 µM. Further, we recorded non-native species including the Pacific diatom *Neodenticula seminae* and the fish-kill associated diatom *Leptocylindrus minimus*. Our comprehensive dataset of micro- and nanoplanktonic diversity can be used for comparisons with more recent observations and continuous monitoring of this vulnerable environment—to learn from the past when looking towards the future.

Keywords Biodiversity · Climate change · Microalgae · Diatoms · Polar · Phytoplankton

Introduction

Globally, ecosystems undergo dramatic changes due to climate change and anthropogenic perturbations. Since the Arctic ecosystem (here defined as north of 70°) is experiencing climate change at a much higher speed compared with the rest of the globe, it has been designated as one of the most vulnerable (IPCC 2018) and, thus, might exemplify future situations of other environments. The most apparent transformation is the Arctic ice system, becoming seasonal rather than perennial within the next 50 years due to elevated air and surface water temperatures (Wassmann and Reigstad 2011). With less ice, the growth season of phytoplankton may be prolonged (Lebrun et al. 2019; Renaut et al. 2018). Although a rapidly changing environment is expected for the phytoplankton communities in the Arctic region, knowledge on how this will affect their composition and diversity is still very limited.

High diversity among and within species is important in all ecosystems, elevating resilience to environmental change (Hooper et al. 2012). Due to human perturbations at the planetary scale, biodiversity is currently suffering from an increased risk of great losses (Kannan and James 2009; Steffen et al. 2015). On the other hand, a biodiversity *change* can be as devastating, resulting in potential effects on ecosystem services (Dornelas et al. 2014). Thereby studies need

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to include metrics estimating species richness, together with changes in species composition (Hillebrand et al. 2018). Combination of species numbers and diversity metrics enables quantification of the rare biosphere in, for example, a phytoplankton community. The importance of recruitment from the rare biosphere has been demonstrated for bacteria as a response to environmental changes (Sjöstedt et al. 2012) but may also be important for resilience in microplanktonic communities in the Arctic region. A decreased diversity can result in a less resilient ecosystem, i.e., with only few species in each functional group resulting in a community at a high risk upon species loss (Snoeijs-Lejonmalm 2017).

Microplanktonic communities can, for example, be disturbed by the introduction of non-native species, where human activities facilitate the global movement at a higher rate than would occur naturally (Molnar et al. 2008). Although the Arctic region was long considered a low-risk environment due to harsh conditions and limited access, elevated temperatures and ice retreat have now opened up for shipping and tourism, facilitating the introduction of non-native, potentially invasive species (Chan et al. 2019; Melia et al. 2016; Ricciardi et al. 2017). Near-surface transport is expected to increase with elevated temperature and, thus, affect the natural spread of microplankton species (Arrigo and van Dijken 2004; Jones et al. 2003; Poulin et al. 2010), as reported for the North Sea (Nehring 1998). Newly introduced species have the potential to affect local food chains through, for example, production of harmful substances or by altering the nutritional value for grazers.

A recent comprehensive study compiling invasive species events in the Arctic only briefly addressed microalgae (Chan et al. 2019), since knowledge on changes in these communities is limited (Niemi et al. 2011; Assmy et al. 2017) and are often conducted using sequencing techniques (Kilias et al. 2014; Karlusich et al. 2020). Although species lists "on the surface of the sea between Europe and Greenland as well as from the Davis Straight" have been reported as far back as 1873 (Cleve 1873), they were dominated by diatoms due to the ease of preservation compared with flagellates and other phytoplankton. Species lists (published in English) 5–10 years before our study include Gradinger and Baumann (1991), Samtleben et al. (1995), Bauerfeind et al. (1997), Booth and Smith (1997), von Quillfeldt (1997), and Kohly (1998). This list can be expanded to seas and basins on similar latitudes such as the Laptev Sea (Tuschling et al. 2000), the Barents Sea (Ratkova and Wassman 2002; Sergeeva et al. 2018), Baffin Bay (Lafond et al. 2019), and waters around Svalbard (Owrid et al. 2000).

Since both changes in species composition and introductions of non-native species can drastically affect the Arctic ecosystem food web, a species diversity baseline to detect early ecosystem changes is highly needed. Thus, by defining a baseline of species diversity and community composition we may monitor ecosystem changes for management purposes. The present study looks back almost two decades with the aims to (a) assess micro- and nanoplankton species diversity in the Greenland Sea along the ice-covered coastline and (b) to reveal potential northward spread of species across a latitudinal gradient. Hence, this study may work as a template for future monitoring surveys.

Material and methods

Site description

The expedition with the Swedish icebreaker Oden covered the East Greenland Current from north of Fram Strait to south of Denmark Strait as a part of the Arctic Ocean 2002 program (AO-02, see e.g., Nilsson et al. 2008 and Rudels et al. 2005 for further details on the physicochemical parameters along the transects). More specifically, the expedition followed the east side of Greenland (82° 14' N to 64° 46' N) and was conducted between April and June in 2002. The Fram Strait north of Svalbard and Greenland was covered with sea ice at the time of sampling (indicated in Fig. 1). The micro- and nanoplankton sampling was conducted between the 1st and 26th of May along 9 transects with a total of 46 sampling stations (Fig. 1 and Table 1). All sampling transects started from the sea and continued towards the ice-covered coastline of east Greenland.

CTD data for salinity and temperature were obtained using a CTD SBE 911 + instrument (see Rudels et al. 2005). Salinity ranged between 32 and 35 across stations and was similar between surface (~ 2 m) and deep waters (10–50 m), suggesting a well-mixed upper water mass. The lowest salinities were observed close to the ice edge (Table 1). Air temperature during the expedition ranged from – 30° C in the north (83° N) to 0° C between Greenland and Iceland (65° N). Water temperatures showed larger variation between stations, as compared with between surface and deep waters (– 1.82 to 0.22 °C, stations 10–76, and – 1.72 to 6.61 °C in stations 80–95, Table 1). Higher temperatures were observed furthest away from the ice and towards the south, coinciding with stations sampled later in the season.

Sea water sampling, inorganic nutrients, and light intensity

Prior to each water sampling, fluorescence was measured to estimate the depth of the deep chlorophyll *a* maximum (DCM), using a handheld "mini CTD" of ADM model, equipped with a fluorometer. Seawater samples were collected from the SeaBird Carousel rosette sampler equipped with 12 L Niskin bottles, or from Go-Flo sampling bottles. Generally, seawater was sampled from the surface (1–3 m

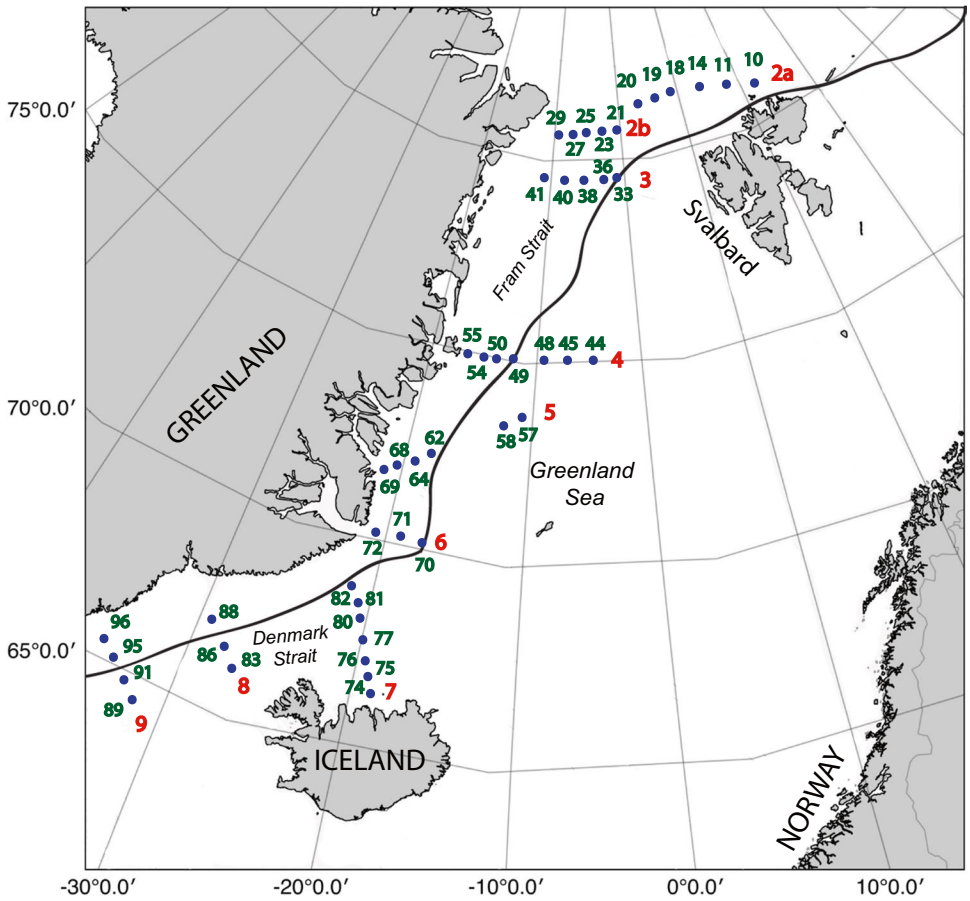

Fig. 1 Expedition map with stations as blue dots, transect numbers in red, and station numbers in green. All transects started from the ocean heading towards the east coast of Greenland. The black line indicates the ice edge in May 2002 (ice map retrieved from the Danish Meteorological Institute)

depth depending on weather conditions) hereafter called "surface" and from DCM (10–50 m), hereafter referred to as "deep" sampling. If there was no distinct DCM due to a well-mixed water column or low chlorophyll *a* (Chl *a*) values, seawater was sampled from 20-m depth (sampling depths for each station and parameter can be found in Table S1). Inorganic nutrient concentrations (nitrate, nitrite, phosphate, and silicate) were extracted from the expedition database. In short, inorganic nutrients were analyzed on an auto-analyzer according to the WOCE protocol (Gordon et al. 1993). Light intensity (PAR 400–700 nm) in air was occasionally measured using a light meter (International Light 1400 A) equipped with a PAR sensor (IL SEL033).

Micro- and nanoplankton community composition and diversity

From each depth (Table S1), 2 L of seawater was gently filtered onto each of two 2-µm Nucleopore polycarbonate filters (1 L each), one put in acidic and one in basic Lugol's solution for later qualitative and quantitative analyses using the Utermöhl technique (Utermöhl 1958). All cells from each of the filters were rinsed into a concentrated sample that was left to settle for counting (transects, views) in the sedimentation chamber. Large, less abundant cells were counted in low magnification and small, abundant cells in higher magnification, in order to include as many cells as possible. Fewer transects were counted for the common organisms and the whole bottom area of the chamber (equal to 1-L concentrated sample) for the less abundant ones. On-board documentation (photographs and video recording) and initial quantitative and qualitative analyses on non-preserved samples were performed using light microscopy (Zeiss inverted Axiovert 135, magnification 100x, 400x, and 1000x). Differential illumination contrast was used to permit a more detailed structural analysis of cells. Preserved samples were analyzed in more detail in the laboratory to confirm the on-board estimates. Organisms > 2 µm were identified at the lowest possible taxonomic level and from here on referred to as "species" although sometimes only higher taxonomic levels were identified. The complete list of identified species (taxa) was included in all analyses performed. Flagellates and miscellaneous organisms (size range 3–10 µm) were classified as autotrophs when chloroplasts were observed. The *main* taxonomic sources were Medlin and Priddle (1990), Tomas (1997 and references therein), Witkowski et al. (2000), and current and earlier versions of AlgaeBase (https://www.algaebase.org/). Species names and

Table 1 Station details including transect, station number, sampling date (YYMMDD), surface/deep water temperature (°C) and salinity, station depth (m), PAR (µmol photons m^{-2} s^{-1}) in air at measuring time (UTC), ice presence, and coordinates, nd = no data

Transect	Station	Date	Temperature	Salinity	Station depth	PAR	Ice presence	Coordinates
2a	**10**	02–05-01	− 1.58/ − 1.55	34.38/34.38	198	400 (10:00)	Ice-covered	81.00 N, 18.22 E
	11	02–05-01	− 1.57/ − 1.46	34.26/34.28	388	nd	Ice-covered	81.13 N, 18.11 E
	14	02–05-02	− 1.82/ − 1.81	34.36/34.36	2781	500 (14:00)	Ice-covered	81.38 N, 16.06 E
	18	02–05-03	− 1.82/ − 1.82	34.33/34.33	1462	370 (12:30)	Ice-covered	82.15 N, 06.55 E
	19	02–05-03	− 1.83/ − 1.83	34.33/34.33	2131	nd	Ice-covered	82.23 N, 05.58 E
	20	02–05-04	− 1.86/ − 1.86	34.29/34.29	2593	450 (12:30)	Thin ice	82.21 N, 03.06 E
2b	**21**	02–05-06	− 1.85/ − 1.85	34.39/34.39	nd	435 (14:45)	Thick ice	81.30 N, 00.02 W
	23	02–05-07	− 1.83/ − 1.83	33.97/34.00	3850	470 (11:15)	Thick ice	81.26 N, 04.09 W
	25	02–05-09	− 1.71/ − 1.71	32.00/32.01	2179	460 (12:30)	Thin ice	81.22 N, 07.16 W
	27	02–05-09	− 1.72/ − 1.72	31.95/31.95	1066	nd	Ice-covered	81.26 N, 08.37 W
	29	02–05-09	− 1.70/ − 1.72	32.00/32.01	324	nd	Ice-covered	81.27 N, 08.97 W
3	**33**	02–05-12	− 1.74/ − 1.74	34.14/34.14	2621	660 (12:50)	Ice-covered	79.18 N, 00.03 W
	36	02–05-13	− 1.65/ − 1.67	32.66/32.72	1998	720 (13:05)	Thin ice/open water	79.10 N, 03.58 W
	38	02–05-13	− 1.74/ − 1.75	32.4832.48	1143	nd	Ice-covered	79.00 N, 05.25 W
	40	02–05-14	− 1.77/ − 1.76	32.60/32.60	188	670 (12:20)	Thick ice	79.01 N, 08.06 W
	41	02–05-14	− 1.75/ − 1.75	32.52/32.52	266	nd	Ice-covered	78.97 N, 09.95 W
4	**44**	02–05-16	− 0.52/ − 0.59	34.85/34.85	3715	505 (12:15)	Open water	75.00 N, 01.93 W
	45	02–05-16	− 0.42/ − 0.41	34.86/34.86	3639	nd	Open water	74.99 N, 04.01 W
	48	02–05-17	0.22/0.10	34.81/34.84	3355	920 (12:30)	Open water	75.00 N, 09.30 W
	49	02–05-17	0.49/0.65	34.76/34.83	3006	nd	Ice-edge	75.00 N, 10.73 W
	50	02–05-17	− 0.16/0.25	34.53/34.72	2508	nd	Ice-covered	74.99 N, 11.28 W
	54	02–05-18	− 1.82/ − 1.82	34.30/34.30	485	950 (12:50)	Mostly covered	74.96 N, 12.89 W
	55	02–05-18	− 1.74/ − 1.73	33.52/33.67	157	nd	Ice with holes	75.00 N, 14.30 W
5	**57**	02–05-19	− 0.11/ − 0.15	34.67/34.67	2994	303 (15:40)	Open water	73.50 N, 10.00 W
	58	02–05-19	0.37/0.33	34.72/34.72	2796	nd	Open water	73.25 N, 12.00 W
	62	02–05-20	− 1.77/ − 1.79	34.12/34.16	1000	750 (09:00)	Ice with holes	72.55 N, 16.83 W
	64	02–05-20	− 1.75/ − 1.75	33.85/33.89	259	nd	Ice-covered	72.38 N, 18.20 W
	68	02–05-21	− 1.73/ − 1.71	32.68/32.71	397	nd	Ice-covered	72.00 N, 21.02 W
	69	02–05-21	− 1.72/ − 1.77	32.64/32.73	589	nd	Ice with leads	71.95 N, 21.38 W
6	**70**	02–05-24	− 1.82/ − 1.82	33.74/22.74	272	360 (09:00)	Drifting ice	70.00 N, 20.24 W
	71	02–05-24	− 1.83/ − 1.83	33.76/33.76	395	nd	Thick ice	70.00 N, 20.83 W
	72	02–05-25	− 1.79/ − 1.79	32.84/32.84	527	906 (13:00)	Ice-covered	70.00 N, 21.51 W
7	**74**	02–05-26	− 1.78/ − 1.78	32.85/32.86	456	850 (12:30)	Ice covered	69.61 N, 21.83 W
	75	02–05-26	− 1.81/ − 1.81	33.52/33.53	407	nd	Thick ice, few holes	69.35 N, 21.49 W
	76	02–05-26	− 1.73/ − 1.81	33.77/33.84	534	nd	Ice edge	69.09 N, 21.24 W
	77	02–05-26	− 1.63/ − 1.63	34.17/34.20	981	nd	Open water	69.01 N, 21.23 W
	80	02–05-27	1.26/1.23	34.67/34.67	772	270 (12:45)	Open water	67.77 N, 20.52 W
	81	02–05-27	3.53/3.57	34.84/34.84	248	nd	Open water	67.20 N, 20.34 W
	82	02–05-27	2.84/2.77	34.70/34.70	387	nd	Open water	66.84 N, 20.00 W
8	**83**	02–05-28	5.67/5.67	35.07/35.07	170	287 (13:35)	Open water	66.26 N, 25.56 W
	86	02–05-28	− 1.26/ − 1.27	34.10/34.10	537	nd	Open water	66.76 N, 26.78 W
	88	02–05-28	− 1.80/ − 1.82	33.38/33.56	288	nd	Drifting ice, small holes	67.30 N, 28.14 W
9	**89**	02–05-29	6.61/6.60	35.08/35.08	2264	142 (12:15)	Open water	64.77 N, 31.73 W
	91	02–05-29	6.31/6.32	35.06/35.06	1522	nd	Open water	65.19 N, 32.65 W
	95	02–05-30	− 1.72/ − 1.71	32.94/32.95	230	740 (12:45)	Thick ice, few holes	65.77 N, 34.30 W
	96	02–05-30	− 1.79/ − 1.80	33.02/33.02	274	nd	Thick ice	65.88 N, 34.73 W

authorities were updated in February 2021, using AlgaeBase and WoRMS (http://www.marinespecies.org/index.php).

Biodiversity was calculated and presented in three ways (complete list in Table S2). Firstly, species number (species per sample) was provided for each station and depth where micro- and nanoplankton samples were collected. Secondly, "effective species number" was calculated for each sample by taking the exponential of Shannon entropy, i.e., effective species number = exp (Shannon index), based on Jost (2006) and Jost et al. (2010). The effective species number is an advantageous metric in field samplings by enabling comparison between samplings in terms of species diversity as it weights the number of species to its relative abundance, and in comparison to Shannon entropy, it obeys the doubling principle (Jost et al. 2010; Leinster and Cobbold 2012; Olofsson et al. 2020). Thirdly, the difference between effective species numbers and observed species in a given sample provides the number of rare species, i.e., the number of species only present in low abundance.

Chlorophyll *a* concentration

For Chl *a* analysis, 250–3000 ml of seawater from surface and deep samples (for depths see Table 2) were filtered onto GF/F filters, immediately frozen in liquid nitrogen (–196 °C) and stored in –80 °C. Filtration took place in dim light at + 4 °C to minimize the influence of light and temperature. For extraction, 1.5 ml of 100% MeOH was added, and the extraction and HPLC-analysis continued according to Wright and Jeffrey (1997) using an absorbance diode-array detector (Spectraphysics UV6000LP). The HPLC system was calibrated with pigment standards from DHI Lab, Denmark. Chl *a* is expressed as μg l^{-1}.

Statistical analyses and data handling

Biodiversity calculations and non-metric multi-dimensional scaling (NMDS) plots were conducted using the package "vegan" in R (Oksanen et al. 2018; R Core Team 2018). All data were processed and plotted using the package "Tidyverse" in R (Wickham 2017). Pearson correlations were performed between species diversity metrics (species number in a sample, effective species number, rare species, and percent rare species) and latitude and cell abundance for the surface samples using Microsoft Excel 2020. NMDS plots were produced using the "metaMDS" function in R, which is optimized for community ecology data. We applied the function for species groups across surface stations and the "envfit" function to correlate it to environmental factors. The same procedure was also applied for diversity metrics across the surface stations and environmental factors. Significant correlations were set to $p < 0.05$.

Results

Station characteristics

One hundred ninety-six different species/taxa (where of 73 were identified to species level) were observed during the expedition and demonstrate the diverse Arctic micro- and nanoplankton communities (Table S2). The number of species observed increased with the number of collected samples when traveling from north to south, with a polygonal curve fit ($R^2 = 0.994$, $n = 56$; Fig. S1). However, there were some discontinuities of the curve related to distance but also reflecting the patchiness of the micro- and nanoplankton communities. This means that the total number of species continuously increased as entering new plankton communities, but at a decreasing rate. Communities consisted of cryptophytes, chrysophytes, diatoms, dinoflagellates, haptophytes, prasinophytes, raphidophytes, ciliates, (additional) autotrophic flagellates, heterotrophic flagellates, euglenophytes, choanoflagellates, and miscellaneous plankton of size range 3–10 μm (dominated by very small flagellates) (Fig. 2; Tables 3 and 4). The relative abundance of groups from the different samples indicated a large variation in community composition between stations (Fig. 3). The NMDS analysis on phytoplankton groups and environmental factors in surface samples demonstrated no significant associations (Fig. 4a).

Inorganic nutrient concentrations were > 0.3 μM at all stations except two stations with high Chl *a* concentrations (> 9 μg l^{-1}; Table 2). Similar nutrient concentrations at surface, and deep samples suggested a well-mixed upper water mass, a pattern mostly reflected also in the species distribution and Chl *a* concentrations (Fig. 2 and Table S3).

Micro- and nanoplankton diversity

The total number of observed species in each sample varied between 12 and 68, and the biodiversity expressed as effective species numbers ranged between 1.0 and 8.8 (Fig. 5 and Table 2), with no correlation between the two variables (Pearson, $r = -0.12$, $n = 56$). The difference between effective species numbers and observed species indicates that 88 ± 8% of the species belonged to the rare fraction, i.e., a large number of species were present in a very low abundance (Fig. 5). The number of observed species was positively correlated to the number of rare species (Pearson, $r = 0.99$, $n = 56$), and number of observed species was also positively correlated to the percent rare species in a sample (Pearson,

Table 2 Chl *a* concentration at surface/DCM with sampling depths and inorganic nutrients (nitrate, phosphate, silicate, and nitrite) from surface/deep samples and sampling depths

St	Chl *a* ($\mu g\ l^{-1}$)	Chl *a* depth (m)	Nitrate (μM)	Phosphate (μM)	Silicate (μM)	Nitrite (μM)	Nutrients depth (m)
10	1.02/0.80	2/20	9.91/9.95	0.67/0.67	3.88/3.92	0.01/0.01	10.0/20.4
11	1.09/0.89	10/20	9.86/9.81	0.65/0.65	3.75/3.66	0.02/0.02	2.0/20.2
14	0.12/0.11	2/20	9.00/8.98	0.63/0.63	3.58/3.44	0.00/0.00	2.5/19.7
18	0.11/0.07	2.5/20	8.33/8.35	0.58/0.59	2.73/2.69	0.00/0.00	8.9/19.3
19	0.12/0.11	2/20	8.24/8.30	0.58/0.58	3.78/3.32	0.00/0.00	2.4/19.6
20	0.10/0.16	2/20	8.87/8.82	0.61/0.61	3.04/3.02	0.01/0.01	4.0/20.7
21	0.13/0.13	2/20	9.99/9.99	0.67/0.67	3.62/3.64	0.01/0.01	4.3/19.7
23	0.10/0.12	2/20	5.82/5.85	0.52/0.53	4.54/4.82	0.00/0.00	2.1/19.9
25	0.09/0.08	2/20	2.63/2.66	0.75/0.74	6.20/6.35	0.00/0.00	3.4/20.1
27	0.08/0.08	2/20	2.86/2.91	0.81/0.82	6.50/6.46	0.00/0.00	2.2/19.9
29	0.05/0.08	2/20	2.73/2.82	0.77/0.77	6.32/6.41	0.00/0.00	4.5/20.1
33	1.43/1.23	2/30	6.18/6.35	0.49/0.50	3.84/3.92	0.02/0.02	9.4/20.2
36	0.12/0.13	2/20	4.40/4.50	0.71/0.70	7.45/7.62	0.01/0.01	10.4/21.2
38	0.11/0.15	2/15	3.63/3.75	0.70/0.70	6.52/6.75	0.01/0.01	9.8/20.5
40	0.19/0.12	2/20	3.89/3.88	0.72/0.71	6.87/6.92	0.01/0.01	10.2/20.3
41	0.12/0.11	2/20	3.24/3.26	0.68/0.68	5.75/5.75	0.00/0.00	9.7/20.5
44	1.36/0.88	2/20	10.06/10.25	0.69/0.72	4.27/4.29	0.04/0.03	14.5/30.5
45	0.97/0.83	2/30	10.80/10.77	0.78/0.78	5.95/5.65	0.03/0.03	14.1/28.9
48	0.48/0.63	6/50	10.48/10.78	0.74/0.77	5.42/6.03	0.03/0.02	12.2/30.8
49	0.36/0.71	2/40	10.78/11.01	0.75/0.77	5.33/5.45	0.03/0.02	11.4/29.5
50	0.28/0.33	2/35	10.12/10.32	0.72/0.74	5.46/5.46	0.04/0.04	9.3/30.3
54	0.48/0.44	2/20	9.19/9.20	0.66/0.66	5.04/4.88	0.02/0.02	8.6/20.3
55	0.41/0.20	2/20	6.03/6.38	0.60/0.60	5.83/5.79	0.01/0.01	10.1/19.7
57	6.92/6.70	2/20	7.12/7.15	0.52/0.53	1.92/2.03	0.05/0.05	9.9/20.9
58	10.39/8.69	2/16	3.38/3.78	0.28/0.32	0.14/0.13	0.06/0.06	10.3/20.9
62	6.44/6.19	2/10	6.62/8.59	0.48/0.62	3.10/4.66	0.06/0.04	15.0/29.2
64	0.23/0.21	2/20	7.26/7.34	0.61/0.61	5.19/5.16	0.06/0.06	19.2/30.2
68	0.22/0.29	2/20	3.12/3.32	0.57/0.58	3.87/4.04	0.03/0.03	20.1/40.0
69	0.31/0.37	2/20	2.97/2.83	0.56/0.56	3.78/3.77	0.04/0.05	10.2/30.8
70	0.14/0.26	2/20	6.64/6.70	0.61/0.61	4.93/4.81	0.04/0.04	10.1/19.3
71	0.27/0.28	2/20	6.87/6.72	0.62/0.63	4.55/4.62	0.05/0.05	10.1/19.8
72	0.16/0.18	2/20	3.63/3.63	0.56/0.57	4.53/4.50	0.03/0.03	9.5/19.6
74	0.15/0.14	2/20	3.76/3.76	0.58/0.57	4.35/4.46	0.03/0.03	10.7/20.6
75	0.15/0.16	2/20	5.95/6.00	0.60/0.61	4.77/4.78	0.03/0.03	10.1/19.8
76	0.15/0.23	2/20	6.86/7.14	0.62/0.63	4.75/4.77	0.05/0.05	11.7/19.5
77	0.45/0.40	2/25	8.26/8.44	0.67/0.67	4.72/4.61	0.07/0.08	10.2/20.0
80	5.65/3.30	2/18	6.18/6.31	0.52/0.53	3.40/3.45	0.10/0.10	11.2/22.1
81	2.48/3.98	2/20	7.16/7.47	0.60/0.62	4.63/4.75	0.11/0.12	9.1/20.3
82	3.69/4.68	2/20	2.09/2.29	0.33/0.33	2.44/2.47	0.07/0.07	10.2/19.2
83	0.57/0.58	2/20	13.15/13.17	0.90/0.90	6.60/6.63	0.19/0.19	10.1/19.9
86	3.87/4.46	4/15	4.77/4.92	0.47/0.49	3.40/3.49	0.08/0.07	11.7/22.2
88	0.13/0.22	2/20	5.18/5.75	0.62/0.62	4.69/4.79	0.05/0.05	7.4/19.8
89	0.60/0.57	2/20	13.03/13.04	0.94/0.93	6.35/6.50	0.24/0.24	14.4/30.8
91	0.65	2/20	14.80/14.94	0.96/0.96	6.79/6.76	0.27/0.27	10.6/28.7
95	9.87/6.30	2/20	0.09/0.07	0.26/0.26	3.08/3.08	0.02/0.02	9.9/20.6
96	0.33/0.35	2/10	4.09/4.04	0.57/0.58	3.98/3.97	0.04/0.04	10.0/19.9

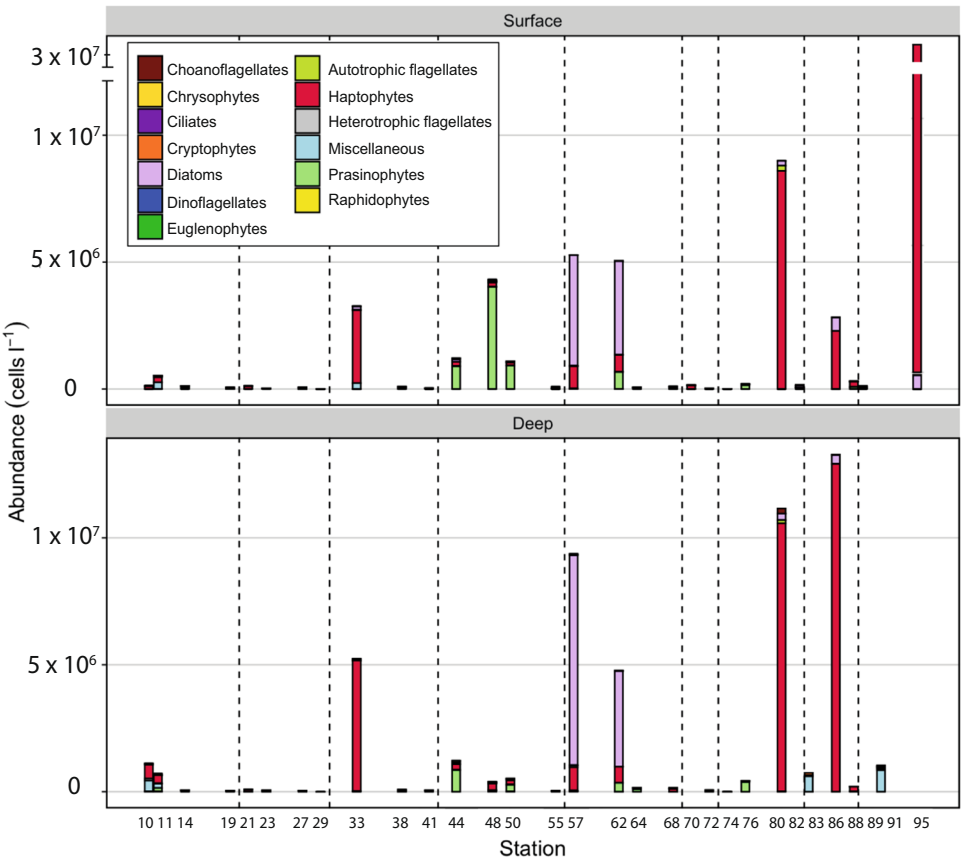

Fig. 2 The abundance of micro- and nanoplankton groups (cells l^{-1}) at the different stations from the surface and deep sampling. Vertical dashed lines indicate transects 2a, 2b, 3, 4, 5, 6, 7, 8, and 9 (see Table 1 for details)

$r = 0.63$, $n = 56$). The total abundance and number of species found in a sample was also positively correlated (Pearson, $r = 0.63$, $n = 56$), as well as abundance and number of rare species (Pearson, $r = 0.66$, $n = 56$). There was a weak negative correlation between effective species number and total abundance in a sample (Pearson, $r = -0.40$, $n = 56$) and a negative correlation between effective species number and percent rare species (Pearson, $r = -0.72$, $n = 56$). The number of rare species was correlated with percent rare in sample (Pearson, r = 0.71, n = 56) but only weakly negative with effective species number (Pearson, $r = -0.24$, $n = 56$).

The percent rare species in a sample was associated to a combination of latitude, ice coverage, phosphate, and silicate, while abundance was partly associated with Chl *a*, and species number and rare species were associated with each other but with no environmental factors, and effective species numbers were not related to any environmental variables (NMDS analysis; Fig. 4b). The latitude vector pointed to the opposite direction as Chl *a* in the NMDS plot, and latitude was negatively correlated both to species number (Pearson, $r = -0.71$, $n = 56$) and to rare species (Pearson, $r = -0.72$, $n = 56$), while only weakly to percent ($r = -0.54$, $n = 56$) and abundance ($r = -0.35$, $n = 56$), suggesting higher Chl *a* and species numbers were observed further south. Ice presence was negatively correlated with both species number ($r = -0.57$, $n = 56$) and rare species ($r = -0.57$, $n = 56$), suggesting less species under the ice as compared with open water.

Micro- and nanoplankton abundance

At 11 stations, cell numbers were $> 1 \times 10^6$ cells l^{-1} (Fig. 2, and Table S2) but were dominated by different species. For example, the most abundant species on station 33 was the haptophyte *Phaeocystis* sp., with up to 2.9×10^6 cells l^{-1} at the surface and 5.1×10^6 cells l^{-1} in the deep sampling, both as single cells and in colonies. Further, the most abundant species on stations 44 (both depths), 48 (surface), and 50 (both depths) were the small (1–3 µm) prasinophyte *Micromonas* sp., with cell numbers up to 4.0×10^6 cells l^{-1}. Station 57 and 62 were dominated by diatoms, where *Chaetoceros socialis* was the most abundant diatom at station 57 with 4.0×10^6 cells l^{-1} (surface) and 8.0×10^6 cells l^{-1} (deep). Again, the most abundant species on stations 80, 86, and 95 at both sampling depths were *Phaeocystis* sp., with 29.0×10^6 cells l^{-1} at station 95 (surface). Station 95 had the lowest nitrate concentration

Table 3 Micro- and nanoplankton groups provided in cells l^{-1} from the surface samplings and "ns" means that this particular station was not sampled

St. nr	Diatoms	Dinoflagellates	Chrysophytes	Cryptophytes	Haptophytes	Prasinophytes	Raphidophytes	Flagellates	Choanoflagellates	Heterotrophic flagellates	Ciliates	Misc. (3–10 µm)	Euglenophytes
10	26,703	104	1		100,001	2601	1	1		1	402		
11	27,608	9501	1	3	201,002	2	3400	26,001		2	1301	259,001	
14	203	4408		1	69,000	2	1	1			204	42,002	
19	5401	1303			21,000	26,600	5300				204	5300	
21	5802	6102		10,000	94,000	1	1				403	10,000	
23	3	3007	100	900	11,000	11,000	1				1103		
27	103	9707	1		38,300	5300	900	11,900			600		
29	205	5			1	2		1			201		
33	119,506	18,512		16,001	2,874,001	3	1	3			7303	233,001	
38	13,805	6	1	1	53,000	26,001		2			303	1	
41	1008	2606		1	32,000	1	1	1			200		
44	81,102	1706	703	53,000	171,000	885,000					4709	16,000	
48	3202	22,009	37,100	37,001	152,301	4,018,603		26,000			3301	16,001	
50	102	7206	100	42,001	101,001	920,502		2			3501	16,000	1
55	63,307	208		1	21,001	2		1301			602	1	
57	4,350,202	15,305		3	862,301	2	2000	21,002			2705	1	
62	3,678,408	13,506	1	2	658,001	662,001	5200	2	16,000		6507	16,001	
64	408	2707	100	2	21,000	37,002					3205	2	1
68	12,809	20,811	1	1	52,000	17,301		1			900		1
70	17,707	5313		1	132,000	3000		1			401		
72	6210	318			21,001	2			1		902		
74	3510	5312		1	2	3	1	2			905	1	
76	3806	8312	1	2	37,000	148,002					2205	1	
80	180,405	4309		3	8,594,001		1	206,000			4708	2	
82	71,806	3613			1		1	4	35,500		6910	52,000	
83	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	
86	518,201	4011	100		2,282,001	1	3500	1	16,400		3704		
88	6908	5109		1702	205,001	82,600		1	16,000		2507		
89	50,502	2014	1	2	22,002	1		2	32,000		5504	16,001	
91	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	
95	530,710	4510	200	69,001	28,618,001	1	1	2	901		6109	200	

Table 4 Micro- and nanoplankton groups given in cells l^{-1} from the deep samplings and "ns" means that this particular station was not sampled

St. nr	Diatoms	Dinoflagellates	Chrysophytes	Cryptophytes	Haptophytes	Prasinophytes	Raphidophytes	Flagellates	Choanoflagellates	Heterotrophic flagellates	Ciliates	Misc. (3–10 um)	Euglenophytes
10	16,601	12,304	2	1	540,004	4800	13,000	21,000		85,003	604	419,001	
11	63,001	605	2	2	312,001	127,000	16,000	2		21,001	601	169,000	
14	5	205		1	58,000					1	103	2	
19	2	2804		1700	26,300		1	5300			201		
21	202	3504		5300	79,000	1300	1700				503		
23	2	2702		5300	42,000	5300	900	5300			103		
27	402	6		1	37,000		1	1			101		
29	603	104		2	2	2		2			402		
33	67,201	605		2	5,139,000	1	1	1			710	26,000	
38	29,907	1707	1	3	47,000	3	1	2	1		301	1	
41	1705	103		2	53,000	1			1		301		
44	64,401	5510	1401	69,000	216,500	848,002					3307	16,000	
48	38,506	8508	402		250,001	1	42,000	21,000		26,001	2104	2	
50	16,201	40,312	100	16,001	158,000	249,001	14,000				1903	21,000	
55	25,405	8		1	32,000			4			304	2	1
57	8,264,803	11,107	21,200	32,001	909,801	3	20,000	74,001			5306	32,001	
62	3,757,209	11,707	21	16,001	633,000	344,002	2600	2			5604		
64	609	710	1	1	52,000	96,602	1				3003	1	
68	11,509	12,109		18,600	106,000	1701		1			403		
70	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	
72	8509	8908		2600	48,000	2	1				802	1	
74	1610	11	100	2	1	4	1	1			704		
76	2003	7908	1	1	42,002	376,001	1	1			2205	1	1
80	255,904	2713	1	1	10,553,000	2	1	127,001	201,300		2509	16,001	
82	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	
83	508	2013	1	89,001	8503	3	1	37,002	1		1307	603,001	
86	346,410	512	100	1	12,909,000	1	1	1	21,700		3806		
88	3508	4010	1	1	178,000	16,003	1	1	1		1104	1	
89	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	
91	10,103	35,112		32,001	53,001	2	1	29,500	26,000		5307	847,001	
95	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	

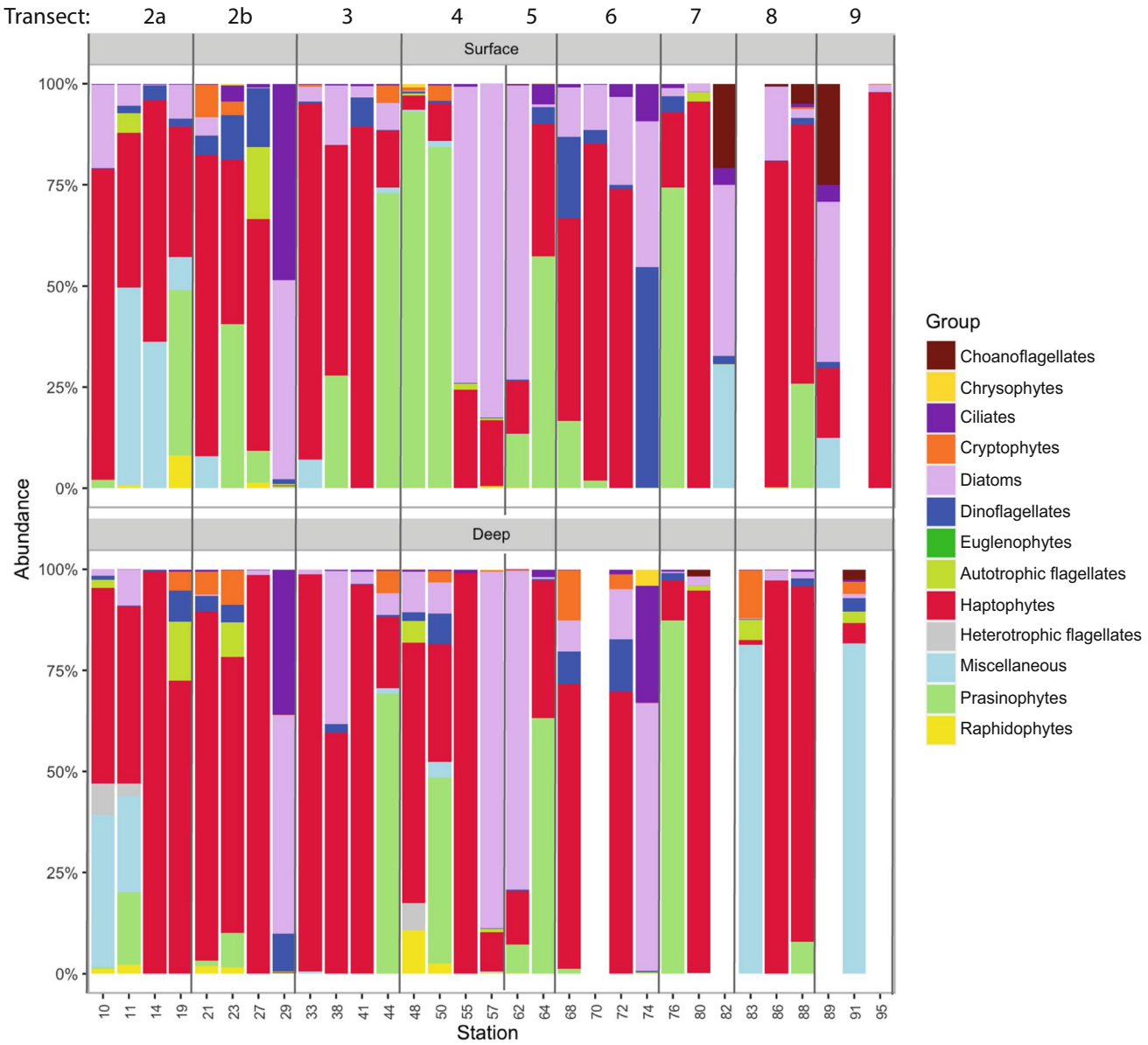

Fig. 3 The relative abundance of micro- and nanoplankton groups in the different stations from surface (upper panel) and deep (lower panel) water samplings

(< 0.1 µM; Table 1) but was replete in silicate (not used by, e.g., *Phaeocystis* sp.).

Diatom distribution

Diatoms were found at all sampled stations (Tables 3 and 4). Particularly two centric genera were frequently observed in large numbers: *Chaetoceros* spp. and *Thalassiosira* spp. (Table S2), and pennate diatom genera such as *Pseudo-nitzschia* sp. and *Fragilariopsis* spp. were frequently observed with the highest abundance at station 95 surface (3.9×10^5 cells l^{-1}) and station 57 deep (1.9×10^5 cells l^{-1}), respectively. The nearby station 58 (not sampled for plankton) had the lowest silicate concentration (0.14 µM, Table 1) and Chl *a* concentration of 10.4 µg l^{-1} (Table 2). Resting spores of *Chaetoceros socialis*, *Fragilariopsis oceanica*, and several species of *Thalassiosira* were observed mainly at stations 80–95, with up to 8×10^4 spores l^{-1}. Resting spores of *F. oceanica* and *Thalassiosira* spp. were also found at stations 33, 57, and 62, with no overall pattern in relation to ice coverage or temperatures.

Dinoflagellate distribution

Generally, dinoflagellates were observed in much lower abundances as compared with diatoms, prasinophytes,

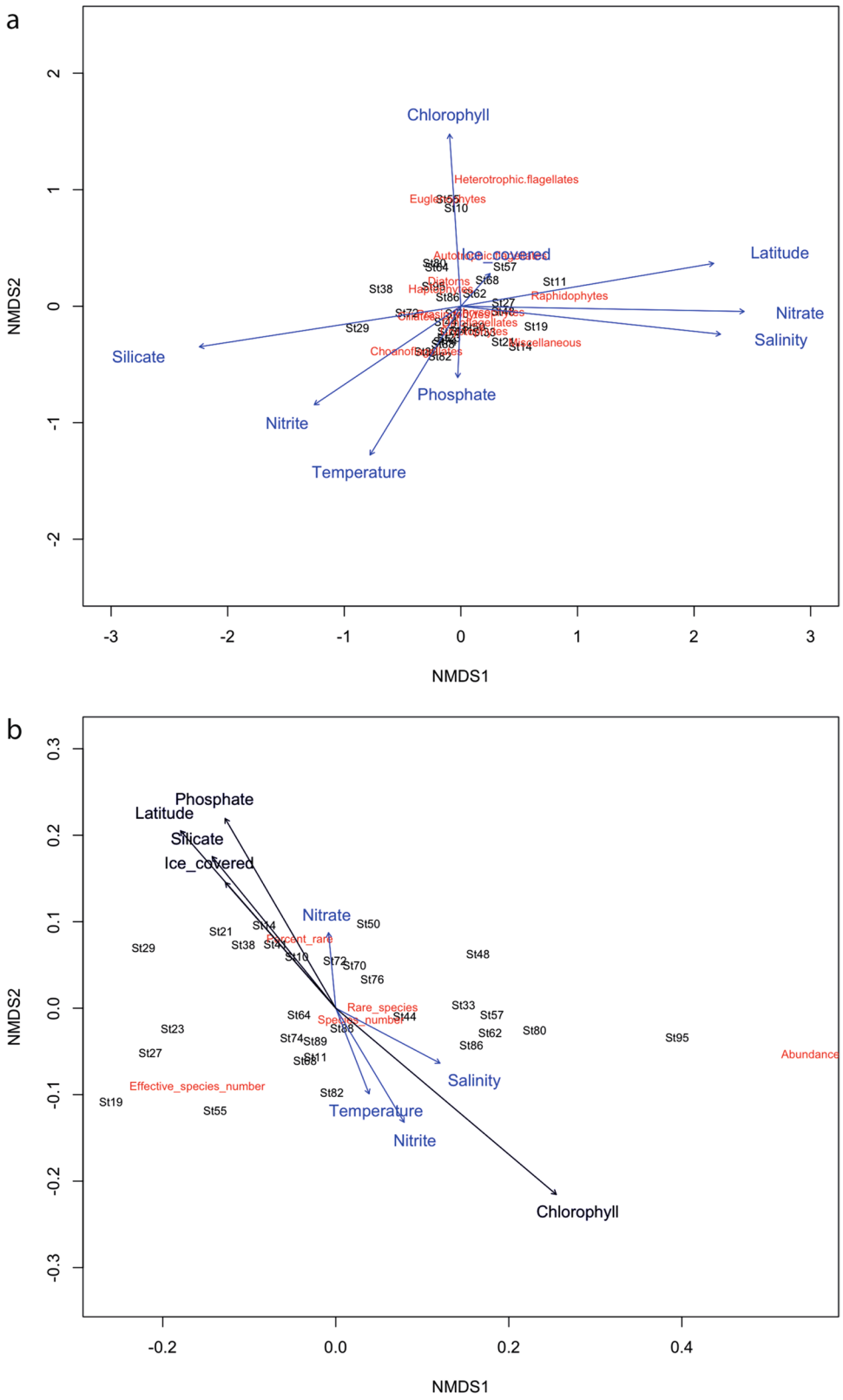

Fig. 4 Non-metric multidimensional scaling (NMDS) ordination plots with correlated environmental factors generated for (**a**) phytoplankton groups and surface stations, stress value = 0.11, and (**b**) diversity metrics and surface stations, stress value = 0.05

and haptophytes (Tables 3 and 4). In the surface samples, the maximum number of cells were found for species belonging to *Gyrodinium* and *Gymnodinium*, with ~ 2.0×10^4 cells l^{-1} at stations 68 and 91 (Table S2). *Heterocapsa* sp. and *Peridiniella danica* were occasionally observed in relatively large numbers as compared with

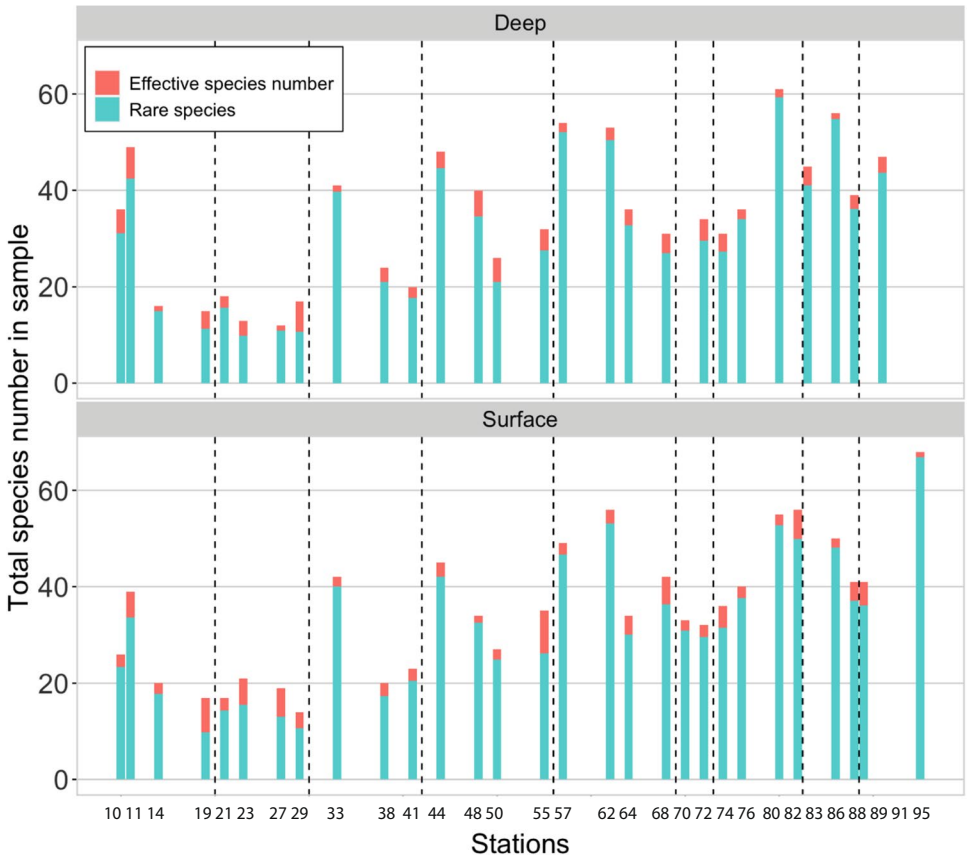

Fig. 5 Total number of species observed per sample as the sum of effective species numbers and rare species for each station from the surface and deeper samplings. Vertical dashed lines indicate transects 2a, 2b, 3, 4, 5, 6, 7, 8, and 9 (see Table 1 for details)

other dinoflagellates, while *Katodinium glaucum* was the most recurrent identifiable species, present at 18 stations (< 100 cells l^{-1}). Naked (unidentified) dinoflagellates in the size range 8–60 µm were spread over all stations up to ~ 1.6×10^4 cells l^{-1}. Thecate (unidentified) dinoflagellates occurred in different sizes and abundances, with up to 2.4×10^4 cells l^{-1} but slightly more frequently with lower latitudes and higher light intensities (towards the end of the expedition).

Species observed only south of 70° N

To reveal species with potential to establish further north if conditions change in their favor, we summarized all species only observed at stations below 70° N and at a minimum of three times. These species included the diatoms *Neodenticula seminae* in 6 samples, and *Ephemera planamembranacea*, *Leptocylindrus minimus*, *Rhizosolenia* cf. *hebetata*, *Thalassionema* sp., *Corethron* sp., *Cylindrotheca* sp., resting spores of *Chaetoceros socialis*, resting spores of *Thalassiosira* cf. *nordenskioeldii*, the dinoflagellate *Protoperidinium depressum*, the ciliate cf. *Leegaardiella sol*, colonies of choanoflagellates, and *Meringosphera* sp. Rare encounters in the samples included the dinoflagellate *Pronoctiluca spinifera*, which to our knowledge has not been observed in the Arctic region before this expedition.

Discussion

The Arctic region is negatively affected by climate change faster than any other ecosystem on Earth, and due to its early onset of climate effects, it may act as a model system for future changes of other ecosystems. Here, we demonstrated that micro- and nanoplankton community composition during early bloom conditions along the ice edge of Greenland consists of a highly diverse pool of species. The field campaign was conducted nearly two decades ago, providing an opportunity to use this dataset to reveal newly introduced species via shipping, currents, range expansions, or migration from southern warmer waters, as sea ice retreats and sea surface temperatures increase.

We observed more than 196 different species (taxa) of micro- and nanoplankton, which is within the range of what has been observed during Arctic summer (145 species, coastal Greenland, Krawczyk et al. 2015a; 153 species, Western Arctic, Wang et al. 2018), winter (145

species, Beaufort Sea, Niemi et al. 2011), and late spring (212 species, Yermak Plateau, Assmy et al. 2017). Herein, species number, observed species in each sample, varied between 12 and 68, which is in the upper range of the 7–12 observed by Niemi et al. (2011) and 10–30 by Assmy et al. (2017). The lower number of observed species in the samples by the mentioned studies can partly be related to different sampling volumes (50 and 250 ml, versus 1 L, respectively), but also differences between "under ice" and open water samplings. Even if it is challenging to compare studies, due to methodological variation, knowledge on species presence at a given time is still important as it may indicate an early introduction. Furthermore, comparisons among datasets are challenging due to continuous changes in nomenclature and the merging or splitting of species. One example is *Skeletonema costatum* where Sarno et al. (2005) introduced four new species with very similar morphology within the genus *Skeletonema*. In our dataset from 2002, we use *S. costatum*, a species recognized as cosmopolitan but rarely observed in the Arctic (Copepedia 2021). However, detecting change in phytoplankton communities relies on both species numbers and community structures (Dornelas et al. 2014; Hillebrand et al. 2018). Effective species numbers ranged from 1.0 to 8.8 (mean of 3.4), with no specific temporal or spatial variation and no correlation with number of observed species in a sample, rare species, or total abundance. Effective species numbers were in the same range as observed by Assmy et al. (2017) with a mean of ~ 5.4 (re-calculated by the present authors). Providing the total number of species alongside effective species number can be useful when describing the structure of an ecosystem since it will reveal the number of rare species.

Overall, about 88% of the species were considered rare species, and the number of rare species was positively correlated with both species number and total abundance, suggesting that a higher cell abundance in general involve higher number of species and more rare species. In addition, rare species and species numbers were negatively correlated with latitude, suggesting richer communities further south. Rare species have the potential to increase in abundance and their inclusion in monitoring studies can provide early indications of invasive species not yet established. They are also important under variable environmental conditions, where a decreased diversity can result in a less resilient ecosystem due to fewer species in each functional group under species loss (Snoeijs-Lejonmalm 2017). The Arctic ecosystem is undergoing major changes, not yet visible without a more detailed examination, and it is therefore of uttermost importance in future studies to also include quantification of rare species to determine if present day micro- and nanoplankton community already has less rare species as compared with two decades ago.

Until recently under-ice primary productivity has been underestimated due to the assumption of too low light intensities. However, massive blooms found under the sea ice indicated high productivity early in the spring, sometimes larger than in the open water (Arrigo et al. 2012; 2014; Arrigo and van Dijken 2015; Assmy et al. 2017), while Ardyna et al. (2011) observed higher Chl *a* concentrations with decreasing ice cover. Our measurements were performed during an early bloom, as indicated by generally high nutrient availability and only occasionally high biomass, in both ice covered and open waters (Chl *a*, Table 2). For example, stations like 80–82, 86, and 95 were sampled later in May and thereby had more developed blooms. This is similar to blooms observed north of Svalbard from the 25th of May and onwards, followed by a decrease in surface nitrate concentrations (Assmy et al. 2017). The number of species observed in each sample was correlated with the presence of ice, with a lower species number under the ice as compared with in the open water. One reason could be that under-ice algae often are dominated by specialists, e.g., species with a narrow range of environmental conditions they thrive in. The Arctic spring bloom, including ice-associated microalgae is subject for a mismatch in timing of carbon transfer to higher trophic levels (e.g., Søreide et al. 2010) and, thus, important to study for projecting future situations in timing, magnitude, and community composition.

Monitoring the establishment of potentially harmful non-native species and early shifts in community composition is important from an ecosystem management perspective, although it is not necessarily disadvantageous if newly introduced species serves a redundant function in the food web or occupy the same niche. As the sea ice declines, microplankton can travel with ballast water through the Arctic, with future projected routes from North America passing the west coast of Greenland and to Russia or Japan (Melia et al. 2016). Increased influence of Pacific water via the Arctic Ocean due to less sea ice and/or changed ocean circulation in the Arctic Ocean was exemplified by the diatom, *Neodenticula seminae* (Miettinen et al. 2013). During 1999 this species was observed in the Laborador Sea for the first time in 800,000 years (Reid et al. 2007). The reintroduction from the Pacific Ocean might be coupled to an extraordinary warm year in 1998 with more near-surface water transport from the Pacific to the Atlantic (Arrigo and van Dijken 2004; Jones et al. 2003; Poulin et al. 2010). We observed *N. seminae* in six samples collected between 65 and 68° N and sediment samples collected during 2006–2008 indicated an establishment of *N. seminae* all the way up to 79° N (Miettinen et al. 2013), which indicates an ongoing northward spread of the species since 1999. Since *N. seminae* may account for > 40% of the diatom assemblages in the sub-arctic Pacific (Shimada

et al. 2006) and usually dominate blooms in the Gulf of St. Lawrence (Sakshaug et al. 2009), this might reflect the future situation further north. The potential effect on the northern ecosystem is, however, still unknown but should be under observation.

Further, the diatom *Leptocylindrus minimus* was observed in samples collected at stations south of 70° N. This diatom has been associated with fish mortalities (Clement and Lambeye 1991) and is common in the Canadian Bay of Fundy (Martin et al. 2010), coastal waters in general (Horner 2002), and in Northern European seas (Kraberg et al. 2010). *L. minimus* was also observed at 64° N, SW Greenland, in samples from 2006 to 2010 (Krawczyk et al. 2015b). It has never, to our knowledge, been observed in the Arctic region (north of 70°). *L. minimus* is generally favored by high nitrate concentrations (Horner 2002; Alves-de-Souza et al. 2008), high temperature, and high salinity (Pizarra et al. 1997). Since nitrate was available at all stations herein except 95 (Table 2), future physical changes, e.g., elevated temperatures in this region, may govern its northward spread during spring-bloom conditions. Another example of a species observed for the first time in the Artic region to our knowledge was the heterotrophic dinoflagellate *Pronoctiluca spinifera* that generally thrives in eutrophic conditions replete with prey (Gomez 2013). Establishment of other introduced species can be expected with the ongoing changes, potentially affecting the existing phytoplankton communities by altering local food webs and species dynamics, with possible implications for carbon cycling through feeding patterns or altered primary productivity. Additional species only observed below 70° N (this study) included *Rhizosolenia* cf. *hebetata*; however, different varieties of *R. hebetata* were observed in sediment traps around 72°N already 1991–1992 (Kohly 1998). Later, *R. hebetata* (and varieties) was observed in West Spitsbergen waters around 79° N (2007 and 2010, Kubiszyn et al. 2014) and SW Greenland (2013, Krawczyk et al. 2018). Another example is *Ephemera planamembranacea*, a diatom observed in the Gulf of St. Lawrence, around 50° N (Bérard-Therriault et al. 1999), but also recorded from the Antarctic (Scott and Thomas 2005); thus, there is no a priori reason to believe it should not thrive in the Arctic. These are few examples to highlight the importance of more frequent sampling and/or to scrutinize existing datasets in order to monitor rapid changes in the basis of the Arctic food web.

Marine phytoplankton primary production is globally considered nitrogen limited (Moore et al. 2013). Concentrations of nitrate were herein replete for the phytoplankton during this early stage of the spring bloom except in station 95. This pattern is confirmed by Assmy et al. (2017) demonstrating a decrease in nitrate concentration later in the season for the region north of Svalbard. Silicate concentrations were > 2 µM except in station 58, having high diatom abundance and only 0.14-µM silicate, suggesting it was high enough for diatom frustule formation. In addition, phosphate concentrations were > 0.25 µM at all locations, and with the lowest concentration at the station with the highest Chl *a* concentration. The NMDS analyses suggested that a combination of high phosphate and silicate concentrations as well as high latitude and ice presence were associated with percent rare species and community composition in some of the stations (Fig. 4b). However, since nutrients were replete at almost all stations and both ice presence and latitude were rather negatively correlated with percent rare species, this combination of parameters does not provide any further insight as potential drivers of the community composition.

Further understanding of potential climate change effects on micro- and nanoplankton in the future Arctic seas is fundamental. As demonstrated herein, we already observed changes in the microplankton community due to warming of the region, with, e.g., species spreading from the North Pacific to the North Atlantic. We define a baseline of micro- and nanoplankton diversity two decades ago from which we may reveal changes and potential biodiversity losses in these communities. Since low diversity might affect the resilience of an ecosystem, a decrease in rare species could possibly make the ecosystem more vulnerable to changes. Indeed monitoring is needed for early warning of potential threats and to guide research and policy and management responses accordingly. By combining microscopy with molecular techniques, it may help to determine rare species as well as small size species (e.g., picoplankton), which may be of importance in terms of early introduction of non-native species. Although identifying and monitoring species abundance may come with a high cost, the costs of controlling already established and harmful organisms might be even higher.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12526-021-01204-w.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval No animal testing was performed during this study.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgements, if applicable. The cruise and sampling permits were administered by the Swedish Polar Secretariat.

Data availability The data is available from the authors upon request.

Authors' contributions AW performed sampling and collected the data during the expedition and was responsible for analyses and planning of the phytoplankton part of the field survey. MO processed and plotted the data and wrote a draft version of the manuscript. Both authors contributed during the writing process and have approved the final version of the manuscript.

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