

Microplankton succession in a SW Greenland tidewater glacial fjord influenced by coastal inflows and run-off from the Greenland Ice Sheet

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Abstract Studies of annual successions and inter-annual variations in sub-Arctic and Arctic microplankton assemblages are required in order to understand the structure and function of marine ecosystems. This study depicts the microplankton (>20 µm) structure in a sub-Arctic tidewater glacial fjord system, SW Greenland. The descriptions are based on monthly net hauls collected between January 2006 and December 2010. Two blooms, with distinctive species compositions, were identified across all years: a spring bloom and a summer/autumn bloom. In addition, the winter season—with weak stratification, deep tidal mixing, and dense coastal inflows—was characterised by a separate species composition at much lower abundance. Here, the highest variety of microplankton groups was recorded and represented by diatoms (*Chaetoceros* spp. and *Thalassiosira* spp.), silicoflagellates, dinoflagellates, and ciliates. During the spring bloom, species correlated with higher light intensities, i.e. haptophytes and diatoms (*Thalassiosira* spp. and *Fragilariopsis* spp.), dominated the microplankton assemblage. Among these, diatoms were also correlated with cooler and fresher waters influenced by

springtime melt. During the summer/autumn bloom, the microplankton assemblage was mainly represented by diatoms, such as *Chaetoceros* spp. ‘Low-saline’ chrysophytes were also present. The latter bloom coincides with elevated temperatures in the fjord and renewal of nutrients due to the onset of glacial meltwater run-off from the Greenland Ice Sheet. Our study shows a yearly recurrent succession of microplankton assemblages and that the annual succession is controlled primarily by ocean–fjord–glacier interactions.

Keywords Bloom dynamics · Freshwater run-off · Greenland Ice Sheet · Microplankton · Seasonal succession · Sub-Arctic tidewater glacier fjord system

Introduction

Microplankton (mainly phytoplankton) assemblages have been studied in various sub-Arctic and Arctic regions, but these studies are generally limited to the spring season (Quillfeldt 1996, 2001; Wassmann et al. 1999; Degerlund and Eilertsen 2010) and the summer season (Hasle and Heimdal 1998; Wiktor and Wojciechowska 2005; Kraberg et al. 2010). Diatoms and haptophytes are common in these blooms, with dinoflagellates observed later in the summer. Diatoms are mostly represented by *Chaetoceros* spp., *Thalassiosira* spp., and *Fragilariopsis* spp. (Quillfeldt 1996, 2001; Degerlund and Eilertsen 2010). According to Quillfeldt (2005), the pennate chain-forming *Fragilariopsis* spp. precede the centric genera (*Thalassiosira* and *Chaetoceros*) during the bloom. Among the centric forms, *Thalassiosira* spp. often appear prior to *Chaetoceros* spp. The commonly studied coastal sub-Arctic waters of

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southern Greenland and Iceland as well as the Arctic waters of northern Greenland, Svalbard, and the Arctic Ocean are characterised by a high abundance and diversity of diatoms (Grøntved and Seidenfaden 1938; Hasle and Heimdal 1998; Quillfeldt 2001; Jensen 2003; Degerlund and Eilertsen 2010). However, spring and summer bloom diatom assemblages vary depending on the seasonal sea ice cover (e.g. Quillfeldt 2001) and available light.

As one of the main primary producers, diatoms are also important due to their widespread distribution in the sub-Arctic and Arctic regions (Hasle and Syvertsen 1996; Quillfeldt 2001; Katsuki et al. 2009; Poulin et al. 2011). Along the coasts of Greenland, melting sea ice and glacial discharge influence the distribution, structure, and succession of diatoms and other phytoplankton assemblages inhabiting these coastal waters (Grøntved and Seidenfaden 1938; Gradinger and Baumann 1991; Quillfeldt 2001). Degerlund and Eilertsen (2010) stress that microplankton (i.e. phytoplankton) species characteristics should be related to hydrographic conditions, climate zone, distance from the coast, water depth (photic zone), and/or life cycle (e.g. spore formation). In broader high-latitude studies, these species–environment relationships are rather general due to time-limited and seasonally biased sampling. The lack of baseline information on species–environment relationships from time series thus likely prevents us from identifying changes that are more widespread. The ongoing MarineBasic-Nuuk long-term monitoring programme describes hydrography, chemistry, primary production, algal biomasses, and microplankton with larger meso-zooplankton composition in the outer sill region of Godthåbsfjord, SW Greenland, on a monthly basis (Juil-Pedersen et al. 2012). In this monitored sub-Arctic fjord system, light is available all year, including wintertime. The recorded annual time series show high planktonic diversity, particularly among diatoms, which seems to be characteristic of the Arctic and sub-Arctic sectors off West Greenland (Grøntved and Seidenfaden 1938; Smidt 1979; Thomsen 1982; Booth and Smith 1997; Poulsen and Reuss 2002).

This study aims to present the annual and seasonal successions of the microplankton assemblage based on monthly net hauls from the monitoring programme. We present the overall succession patterns, bloom dynamics, and distinct changes in species composition. The microplankton assemblage is described in relation to the studied area's hydrographic conditions. We hypothesise that physical variables strongly influence seasonal species composition in the sub-Arctic, glacier-influenced fjord environment. A detailed list of microplankton species is presented, providing a reference for future investigations in Greenland and comparative high-latitude studies.

Materials and methods

Study site

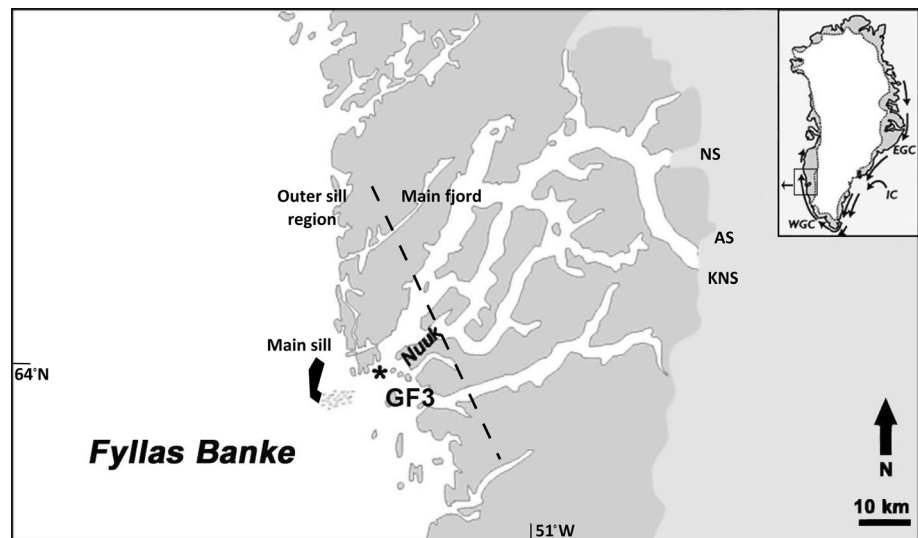
Godthåbsfjord is a 190-km-long sill fjord located in the SW Greenland and in direct contact with three tidewater outlet glaciers from the Greenland Ice Sheet, several river outlets, and (via the West Greenland continental shelf) the West Greenland Current (WGC) (Fig. 1). The fjord system is composed of a number of fjord branches and covers a surface area of ~ 2013 km², with a mean depth of ~ 260 m (maximum depths ~ 620 m). The main sill of the fjord (depth ~ 170 m) is located near the mouth of the fjord, where significant tidal forces (tidal range up to 4.6 m; Richter et al. 2011) modify the water masses entering and exiting the fjord. The main fjord has been divided into two regional domains: the outer sill region and the main fjord basin (Fig. 1).

Freshwater run-off from outlet glaciers and surrounding land during spring and particularly summer affects surface salinity distribution and creates a salinity gradient from the inner parts of the fjord to the outer shelf. Towards late summer/autumn, the hydrography of Godthåbsfjord is partly driven by a circulation mode triggered by subglacial freshwater discharge from tidewater outlet glaciers sending large volumes of subsurface meltwater into the inner parts of the fjord. During winter, regional dense coastal water and waters sourced in the WGC originating from the outer shelf region affect the deeper parts of the fjord system, setting up a density-driven circulation mode referred to as dense coastal inflow. A detailed hydrographic description of regional domains, water masses, freshwater, and circulation modes in Godthåbsfjord is provided by Mortensen et al. (2011, 2013, 2014).

Sampling

Microplankton samples were collected using net hauls at a station in the outer sill region of Godthåbsfjord (GF3; 64°07'N, 51°53'W; Fig. 1). Monthly pelagic samplings are performed as part of the MarineBasic-Nuuk programme, a component of the Greenland Ecosystem Monitoring Programme (www.g-e-m.dk). Our study uses data obtained in the period of 2006–2010. The monitoring programme included hydrographical data, such as water temperature, salinity, irradiance (PAR), and fluorescence, obtained by a SBE19plus CTD profiler equipped with a Seapoint Chlorophyll *a* (Chl *a*) Fluorometer and a Biospherical/Licor sensor. Water samples were collected using a Niskin water sampler at depths of 1, 5, 10, 15, 20, 30, and 50 m. For Chl *a*, 50–2000 ml of water from each depth was filtered through GF/C filters and extracted in 10 ml 96 %

Fig. 1 Map of the Godthåbsfjord system and the adjacent continental shelf and slope showing position of GF3 (star), main sill (black polygon), and regional domains (delimited by dashed line), with an overall scheme of the Greenland region circulation system. Relatively warm waters: IC Irminger Current; WGC West Greenland Current. Cold waters: EGC East Greenland Current. Three tidewater outlet glaciers are marked: NS Narsap Sermia, AS Akullersuup Sermia, KNS Kangiata Nunaata Sermia



ethanol for a minimum of 18 h. The samples were analysed on a fluorometer (TD-700, Turner Designs, USA) calibrated against a pure Chl *a* standard (Turner Designs). Water samples for nutrient analyses were pre-filtered through a GF/C filter and kept frozen ($-18\text{ }^{\circ}\text{C}$) prior to analysis. Phosphate (PO_4^{3-}) and silicate (SiO_2) concentrations were determined by spectrophotometric approach (Strickland and Parsons 1972; Grasshoff et al. 1983), while nitrate and nitrite ($\text{NO}_2^- + \text{NO}_3^-$) concentrations were measured by vanadium chloride reduction (Braman and Hendrix 1989). Primary production and zooplankton species composition were also considered during this study. Detailed information on water chemistry, nutrient concentration, and primary production is described in Juul-Pedersen et al. (2015) and on meso-zooplankton in Arendt et al. (2013).

Microplankton processing

Triplicate vertical hauls were taken monthly from 60 m to the surface using a 20- μm -mesh net. Each sample was transferred to an amber glass bottle and preserved with Lugol's iodine to a final concentration of 1 %. 2.5-ml subsamples were studied using plate-counting chambers (similar to Utermöhl chambers) and an inverted microscope (Nikon Eclipse TE 300 with Plan Fluor objectives). Differential illumination contrast was used to permit detailed structural analysis of cells. A two-step examination of each subsample was performed to obtain at least 500 cells: large, less-abundant cells were counted at low magnification (100 \times), and small, abundant cells were counted at higher magnification (400 \times or 600 \times with oil immersion for photographic identification; see Horner 2002). The number of cells (including colonies) in each subsample was

calculated by multiplying the number of individuals counted in photomasks (field of view) by the ratio of the whole chamber area to the area of the counted photomasks (for both lower and higher objective magnifications). Monthly cell counts were obtained by averaging the triplicate subsample counts, and percentage values were calculated for graphical illustration. The per cent species composition within the counted subsample represents the species composition within the entire sample.

Standard sample processing consisted of rinsing, then cleaning by hydrogen peroxide treatment, and finally mounting in Naphrax[®] for more accurate (species-level) identification of critical diatom species using a light microscope (LM). In addition, due to the mass chain formation of diatoms in May 2009, a more detailed study was performed using a scanning electron microscope (SEM).

Identification of microplankton species was based on Hasle and Syvertsen (1996), Hasle and Heimdal (1998), Quillfeldt (2001), Horner (2002), Throndsen et al. (2007), Hoppenrath et al. (2009), and Kraberg et al. (2010).

Data analysis

Multivariate analysis was used to explore the temporal patterns in species composition from net hauls. Relative abundances of all species in pooled replicates were square root-transformed, and Bray–Curtis similarities between samples (dates) were depicted through ordination by non-metric multidimensional scaling (nMDS) using the Primer v.6 software. The Bray–Curtis similarity between two samples, *j* and *k*, is defined as:

$$S_{jk} = 100 \left[1 - \frac{\sum_{i=1}^n |y_{ij} - y_{ik}|}{\sum_{i=1}^n (y_{ij} + y_{ik})} \right]$$

with y_{ij} and y_{jk} being the square root-transformed relative species abundances of species i in samples j and k , respectively. S ranges from 0 (no shared species) to 100 (identical samples).

Canonical correspondence analysis (CCA) was carried out to analyse the relationships between measured variables, i.e. salinity, temperature, PAR, Chl a , and nutrients (averaged values from 0 to 60 m) and microplankton species data with more than 0.2 % relative abundance. The statistical significance of relationships between species and variables was evaluated using permutation testing (1000 permutations) to calculate P values. This analysis was carried out using the XLSTAT program (www.xlstat.com).

Results

Hydrography

During winter and spring, the water column in the outer sill region of Godthåbsfjord was weakly stratified due to low freshwater run-off from land and deep tidal mixing (Fig. 2a). Low concentrations of Chl a , ranging from 0.05 to 0.2 $\mu\text{g l}^{-1}$, were recorded in the upper 60 m (averaged

values from 0 to 60 m water depth; Fig. 2c). The first phytoplankton bloom was typically observed from April to May, resulting in a peak in concentrations of Chl a , ranging from 0.5 to 9.5 $\mu\text{g l}^{-1}$ (averaged values from 0 to 60 m water depth; Fig. 2c). Strong deep tidally induced mixing in the outer sill region dispersed the bloom throughout the water column. Increased freshwater run-off from GrIS in the start of July strengthened water column stratification and produced a pycnocline within the upper 60 m, which could withstand strong tidal mixing in the outer sill region (Fig. 2). This stratification was maintained until September, when maximum surface water temperatures and minimum salinities were recorded above the pycnocline (Fig. 2a, b). From July to October, a second bloom was observed in the upper water column, showing a rise in concentrations of Chl a , ranging from 0.5 to 2.5 $\mu\text{g l}^{-1}$ (averaged values from 0 to 60 m water depth; Fig. 2c). Towards winter, the freshwater run-off decreased, resulting in increased surface salinities and weakening stratification.

Microplankton

Eleven taxonomic groups were identified (phylum to class, after Boxshall et al. 2013), i.e. Bacillariophyceae (diatoms), Haptophyta (haptophytes), Dictyochophyceae

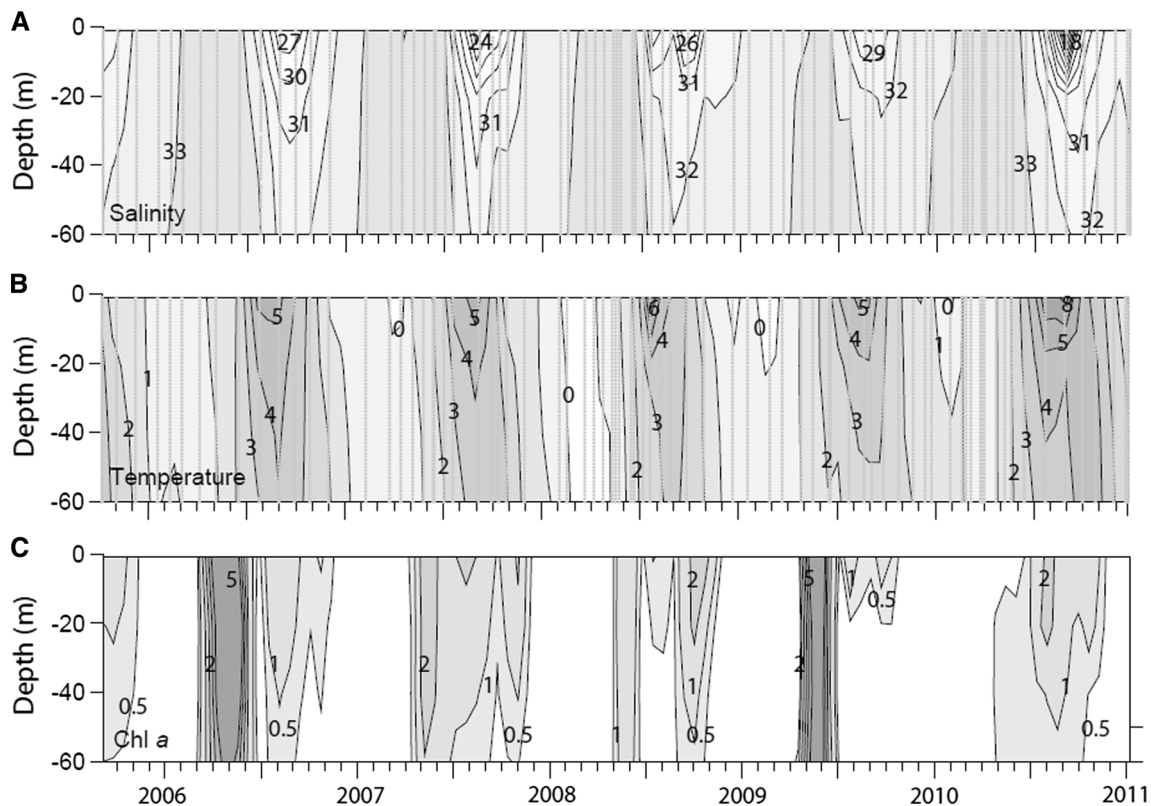


Fig. 2 Hydrographic measurements at GF3 from September 2005 to December 2010. Depth distribution of **a** salinity, **b** temperature ($^{\circ}\text{C}$), and **c** Chl a ($\mu\text{g l}^{-1}$) for the upper 60 m. Dotted lines represent sampling days, and depth of CTD casts and points represent water samples

(silicoflagellates), Dinoflagellata (dinoflagellates), Ciliophora (ciliates), Chrysophyceae (chrysophytes), Ebridaceae (ebridians), Chlorophyta, Heliozoa, and Radiolaria. Among these, 170 species were identified, mostly diatoms and 58 undetermined taxa (determined only to a generic level). In particular, haptophytes and many dinoflagellates were very difficult to identify in Lugol's fixed samples and were thus identified mainly to a genus level. A detailed list of all identified groups and species with affiliations is presented in Table 1. The microplankton assemblage from net hauls was generally dominated by diatoms, which occurred every month throughout the study period (annual average of 65.6–86.6 % in all years).

The nMDS plot for relative species abundances of microplankton shows a clustering of samples into three groups: winter (October–March), spring (April–May), and summer/autumn seasons (June–October) (Fig. 3). The following paragraphs describe the annual succession of major microplankton groups (i.e. diatoms, haptophytes, silicoflagellates, dinoflagellates, ciliates, and chrysophytes) for the three identified seasonal assemblage groups, including some deviations from a general recurring pattern. Seasonal microplankton assemblage composition (%) patterns are shown in Fig. 4 with a general scheme shown in Fig. 5.

Winter

Winter season in Godthåbsfjord was represented by four microplankton groups: diatoms, silicoflagellates, dinoflagellates, and ciliates. Diatoms were dominant in all years (average of 83.3 % in 2006–2010; Figs. 4, 5), represented by genus *Chaetoceros* (mainly *Chaetoceros decipiens* and *Chaetoceros convolutus*) and genus *Thalassiosira* (mainly *Thalassiosira antarctica* var. *borealis* and *Thalassiosira rotula*). In addition, *Thalassionema nitzschioides* showed a dominance pattern in early winter (i.e. October–December), while *Nitzschia frigida* occurred in late winter, prior to the spring blooms (Fig. 5). Silicoflagellates, mainly *Dictyocha speculum*, contributed significantly from January to March, with maxima in February 2006 (36.2 %; Fig. 4a) and February 2009 (9.8 %; Fig. 4d). The dinoflagellates were often present in winter months but generally in low relative abundances, except for the winters of 2009 (average of 7.6 %; Fig. 4d) and 2010 (average of 13.2 %; Fig. 4e). This group was mostly represented in winter by genus *Protoperdinium*. Ciliates, represented mainly by the tintinnids, i.e. *Favella serrata* and *Acanthostomella norvegica*, contributed significantly in winters 2009 and 2010 (average of 5.8 and 8.6 %, respectively; Fig. 4d, e).

Spring

Diatoms dominated the microplankton assemblage in spring and were complemented by haptophytes (Fig. 5). Haptophytes, represented by *Phaeocystis* sp., were mainly observed as solitary, non-motile cells and not as colonies, which might be an effect of fixation as fixatives are known to dissociate colonial cells from the colony matrix (A. Davidson, personal communication). The percentage of identified haptophytes may be biased as these cells are smaller than 20 µm, whereas the sampling method only accurately collects cells larger than 20 µm. Nevertheless, *Phaeocystis* sp. was observed during spring seasons with a maximum contribution recorded in April–May 2010 (average of 71.5 %; Fig. 4e). The year 2009 is an exception, with no haptophyte cells being observed in any samples (Fig. 4d). Diatoms showed highest relative abundances in April 2008 (98.6 %; Fig. 4c) and in April–May 2009 (average of 99.6 %; Fig. 4d). Spring 2008 was mainly represented by genus *Fragilariopsis*, i.e. *Fragilariopsis cylindrus* and *Fragilariopsis oceanica*, while spring 2009 was mainly represented by genus *Thalassiosira*, i.e. *Thalassiosira antarctica* var. *borealis*, *Thalassiosira nordenskiöldii*, *Thalassiosira rotula*, and *Thalassiosira angustilineata*. In May 2009, all of the above-listed *Thalassiosira* spp. appeared almost solely as long, massive chains together with a high relative abundance of resting spores of *T. antarctica* var. *borealis*. In contrast, spring 2010 revealed a low relative abundance of diatoms compared to previous years (i.e. average of 26.5 %; Fig. 4e).

Summer/autumn

Summer/autumn season was represented mainly by diatoms and occurrence of chrysophytes. Diatoms contributed most from July to October, reaching averages of over 85 % for each year studied (2006–2010; Figs. 4, 5). Highest relative abundances of this group were recorded in summer/autumn 2006 (average of 92.5 %; Fig. 4a) and summer/autumn 2010 (average of 91.4 %, excluding June—missing data; Fig. 4e). Diatoms were mainly represented by *Chaetoceros* spp. (Fig. 5), i.e. *Chaetoceros decipiens*, *Chaetoceros curvisetus*, and *Chaetoceros wighamii*. *Thalassionema nitzschioides* also showed importance during this season in all years (Fig. 5). Additionally, *Fragilariopsis cylindrus* and *Nitzschia frigida* were recorded in late summer/autumn 2010, unlike in the previous years studied. Another important algal species, *Dinobryon balticum* (chrysophytes), showed high relative abundances in June 2006 and June–July 2009 (averages of 16.2 and 22.8 % in Fig. 4a, d, respectively). *D. balticum* was primarily identified in colonies (i.e. >20 µm).

Table 1 List of all identified microplankton species (classified after Boxshall et al. 2013)

Group	Species
Bacillariophyceae	<i>Achnanthes groenlandica</i> (Cleve) Grunow <i>Achnanthes longipes</i> C. Agardh <i>Actinocyclus normanii</i> (Gregory) Hustedt <i>Actinocyclus</i> sp. <i>Amphora malectractata</i> Simonsen <i>Amphora marina</i> W. Smith <i>Amphora</i> sp. <i>Asteromphalus hyalinus</i> Karsten <i>Asteromphalus</i> sp. <i>Attheya septentrionalis</i> (Østrup) R.M. Crawford in R.M. Crawford, C. Gardner & Medlin <i>Aulacoseira</i> sp. <i>Bacterosira bathyomphala</i> (Cleve) Syvertsen <i>et</i> Hasle in Hasle & Syvertsen <i>Bacterosira</i> sp. <i>Bellerochea</i> sp. <i>Berkeleya rutilans</i> (Trentepohl ex Roth) Grunow <i>Ceratulina</i> sp. <i>Chaetoceros affinis</i> Lauder <i>Chaetoceros atlanticus</i> Cleve <i>Chaetoceros borealis</i> Bailey <i>Chaetoceros concavicornis</i> Mangin <i>Chaetoceros convolutus</i> Castracane <i>Chaetoceros costatus</i> Pavillard <i>Chaetoceros curvisetus</i> Cleve <i>Chaetoceros danicus</i> Cleve <i>Chaetoceros debilis</i> Cleve <i>Chaetoceros decipiens</i> Cleve <i>Chaetoceros diadema</i> (Ehrenberg) Gran <i>Chaetoceros bottnicus</i> var. <i>didyma</i> K.S. Mereschkowsky <i>Chaetoceros eibonii</i> Grunow <i>Chaetoceros fallax</i> Proseckina-Lavrenko <i>Chaetoceros furcellatus</i> Bailey <i>Chaetoceros mitra</i> (Bailey) Cleve <i>Chaetoceros simplex</i> Ostefeld <i>Chaetoceros socialis</i> Lauder <i>Chaetoceros</i> sp. <i>Chaetoceros wighamii</i> Brightwell <i>Cocconeis costata</i> Gregory <i>Cocconeis scutellum</i> Ehrenberg <i>Cocconeis</i> sp. <i>Corethron hystrix</i> Hensen <i>Coscinodiscus centralis</i> Ehrenberg <i>Coscinodiscus granii</i> Gough <i>Coscinodiscus</i> sp. <i>Cylindrotheca closterium</i> (Ehrenberg) J. Lewin & Reimann <i>Dactyliosolen fragilissimus</i> (Bergon) Hasle apud G.R. Hasle & Syvertsen <i>Dactyliosolen</i> sp. <i>Detonula confervacea</i> (Cleve) Gran <i>Detonula</i> sp.

Table 1 continued

Group	Species
	<i>Diploneis littoralis</i> (Donk) Cleve
	<i>Diploneis smithii</i> (Brébisson in W. Smith) P.T. Cleve
	<i>Diploneis</i> sp.
	<i>Donkinia</i> sp.
	<i>Entomoneis</i> sp.
	<i>Entomoneis subsalina</i> (Cleve) Krammer
	<i>Eucampia groenlandica</i> Cleve
	<i>Eucampia zodiacus</i> Ehrenberg
	<i>Fragilaria</i> sp.
	<i>Fragilaria striatula</i> Lyngbye
	<i>Fragilariopsis atlanticus</i> Paasche
	<i>Fragilariopsis cylindrus</i> (Grunow) Krieger in Helmke & Krieger
	<i>Fragilariopsis ocanica</i> (Cleve) Hasle
	<i>Fragilariopsis pseudonana</i> Hasle (Hasle)
	<i>Fragilariopsis reginae-jahniae</i> Witkowski, Lange-Bertalot <i>et</i> Metzeltin
	<i>Fragilariopsis</i> sp.
	<i>Gomphonemopsis</i> sp.
	<i>Grammatophora angulosa</i> Ehrenberg var. <i>islandica</i> (Ehrenberg) Grunow
	<i>Grammatophora arctica</i> Ehrenberg
	<i>Grammatophora arcuata</i> Ehrenberg
	<i>Grammatophora oceanica</i> Ehrenberg
	<i>Guinardia delicatula</i> Cleve (Hasle)
	<i>Guinardia</i> sp.
	<i>Gyrosigma arcuatum</i> (Donkin) Sterrenburg
	<i>Gyrosigma coelophilum</i> Okamoto, Nagumo, Tanaka & Inouye
	<i>Gyrosigma fasciola</i> (Ehrenberg) J.W. Griffith & Henfrey
	<i>Gyrosigma</i> sp.
	<i>Hyalinella lateripunctata</i> Witkowski, Lange-Bertalot & Metzeltin
	<i>Lauderia</i> sp.
	<i>Leptocylindrus danicus</i> Cleve
	<i>Leptocylindrus minimus</i> Gran
	<i>Leptocylindrus</i> sp.
	<i>Licmophora gracilis</i> (Ehrenberg) Grunow
	<i>Licmophora</i> sp.
	<i>Lyrella praetexta</i> (Ehrenberg) D.G.Mann in F.E. Round, R.M. Crawford & D.G. Mann
	<i>Melosira arctica</i> (Ehrenberg) Dickie
	<i>Melosira moniliformis</i> (Müller) Agardh
	<i>Melosira</i> sp.
	<i>Minidiscus</i> sp.
	<i>Navicula cancellata</i> Donkin
	<i>Navicula digitoradiata</i> (Gregory) Ralfs
	<i>Navicula directa</i> (W. Smith) Ralfs
	<i>Navicula distans</i> (W. Smith) Ralfs in Pritchard
	<i>Navicula granii</i> (Jørgensen) Gran
	<i>Navicula kariana</i> Grunow var. <i>frigida</i> (Grunow) Cleve <i>Navicula pelagica</i> Cleve
	<i>Navicula septentrionalis</i> (Grunow) Gran
	<i>Navicula</i> sp.
	<i>Navicula transitans</i> Cleve

Table 1 continued

Group	Species
	<i>Navicula vanhoeffenii</i> Gran
	<i>Nitzschia frigida</i> Grunow in Cleve & Grunow
	<i>Nitzschia hybrida</i> Grunow
	<i>Nitzschia longissima</i> (Brébisson) Ralfs in Pritchard
	<i>Nitzschia promare</i> Medlin
	<i>Nitzschia</i> sp.
	<i>Odontella aurita</i> Agardh
	<i>Paralia sulcata</i> (Ehrenberg) Cleve
	<i>Parlibellus delognei</i> (Van Heurck) Cox
	<i>Pauliella taeniata</i> Grunow
	<i>Pinnularia trevelyana</i> (Donkin) Rabenhorst
	<i>Plagiogramma staurophorum</i> (Gregory) Heiberg
	<i>Plagiotropis</i> sp.
	<i>Pleurosigma directa</i> Grunow
	<i>Pleurosigma normanii</i> Ralfs
	<i>Pleurosigma</i> sp.
	<i>Podosira</i> sp.
	<i>Porosira glacialis</i> (Grunow) Joergensen
	<i>Proboscia alata</i> (Brightwell) Sundström
	<i>Proboscia subarctica</i> K.Takahashi, R.W.Jordan & J.Pridle
	<i>Psammodiscus nitidus</i> (W. Gregory) F.E. Round & D.G. Mann
	<i>Pseudogomphonema kamtschaticum</i> (Grunow) L. K. Medlin
	<i>Pseudogomphonema</i> sp.
	<i>Pseudo-nitzschia</i> cf. <i>delicatissima</i> (Cleve) Heiden
	<i>Pseudo-nitzschia</i> cf. <i>seriata</i> f. <i>obtusa</i> (Hasle) Hasle
	<i>Pseudo-nitzschia</i> sp.
	<i>Pseudosolenia calcar-avis</i> (Schultze) B.G.Sundström
	<i>Rhabdonema arcuatum</i> (Lyngbye) Kützing
	<i>Rhizosolenia borealis</i> Sundström
	<i>Rhizosolenia hebetata</i> Bailey f. <i>hebetata</i>
	<i>Rhizosolenia</i> sp.
	<i>Rhizosolenia setigera</i> Brightwell
	<i>Rhizosolenia styliformis</i> Brightwell
	<i>Rhoicosigma</i> sp.
	<i>Rhoicosphenia genuflexa</i> (Kützing) Medlin
	<i>Rhopalodia arcuatum</i> (Lyngbye) Kützing
	<i>Skeletonema</i> cf. <i>grethae</i> Zingone & Sarno
	<i>Skeletonema</i> sp.
	<i>Striatella unipunctata</i> (Lyngbye) C. Agardh
	<i>Synedra gaillonii</i> (Bory de Saint-Vincent) Ehrenberg
	<i>Synedropsis hyperborea</i> (Grunow) Hasle, Medlin & Syvertsen
	<i>Synedropsis</i> sp.
	<i>Tabularia fasciculata</i> (C.A. Agardh) Williams & Round
	<i>Tabularia tabulata</i> (C.A. Agardh) Snoeijjs
	<i>Tabularia</i> sp.
	<i>Thalassionema nitzschioides</i> Grunow ex Hustedt
	<i>Thalassiosira angulata</i> (Gregory) Hasle
	<i>Thalassiosira anguste-lineata</i> (A.Schmidt) G.Fryxell & Hasle

Table 1 continued

Group	Species
	<i>Thalassiosira antarctica</i> Comber var. <i>borealis</i> Fryxell, Ducette <i>et</i> Hubbard
	<i>Thalassiosira bioculata</i> (Grunow) Østrup
	<i>Thalassiosira constricta</i> Gaardner
	<i>Thalassiosira delicatula</i> Ostenfeld
	<i>Thalassiosira gravida</i> Cleve
	<i>Thalassiosira hyalina</i> (Grunow) Gran
	<i>Thalassiosira hyperborea</i> var. <i>hyperborea</i> (Grunow) Hasle
	<i>Thalassiosira kushirensis</i> Takano
	<i>Thalassiosira minuscula</i> Krasske
	<i>Thalassiosira nordenskiöldii</i> Cleve
	<i>Thalassiosira rotula</i> Meunier
	<i>Thalassiosira</i> sp.
	<i>Thalassiothrix</i> sp.
	<i>Trachyneis</i> sp.
Ciliophora	<i>Acanthostomella norvegica</i> Kofoid & Campbell
	<i>Coxiella helix</i> (Claparède & Lachmann) Jørgensen
	<i>Dictyocysta elegans</i> Ehrenberg
	<i>Favella serrata</i> (Möbius) Jørgensen
	<i>Helicostomella fusiformis</i> (Meunier) Jørgensen
	<i>Helicostomella</i> sp.
	<i>Helicostomella subulata</i> (Ehrenberg) Jørgensen
	<i>Mesodinium rubrum</i> Lohmann
	<i>Lohmanniella oviformis</i> Leegaard
	<i>Parafavella denticulata</i> (Ehrenberg) Kofoid & Campbell
	<i>Salpingella acuminata</i> (Claparède & Lachmann) Jørgensen
	<i>Scuticociliata</i> sp.
	<i>Stenosemella</i> sp.
	<i>Stenosemella ventricosa</i> (Claparède & Lachmann) Jørgensen
	<i>Tintinopsis campanula</i> (Ehrenberg) Daday
	<i>Tintinopsis parvula</i> Jørgensen
	<i>Tintinopsis</i> sp.
Chlorophyta	<i>Pterosperma</i> sp.
Chrysophyceae	<i>Dinobryon balticum</i> (Schütt) Lemmermann
Dictyochophyceae	<i>Dictyocha speculum</i> Ehrenberg
Dinoflagellata	<i>Alexandrium</i> sp.
	<i>Amphidinium</i> sp.
	<i>Amylax triacantha</i> (Jørgensen) Sournia
	<i>Ceratium arcticum</i> (Ehrenberg) Cleve
	<i>Ceratium bucephalum</i> Cleve
	<i>Ceratium furca</i> (Ehrenberg) Claparède & Lachmann
	<i>Ceratium fusus</i> (Ehrenberg) Dujardin
	<i>Ceratium horridum</i> (Cleve) Gran
	<i>Ceratium lineatum</i> (Ehrenberg) Cleve
	<i>Ceratium</i> sp.
	<i>Dinophysis acuminata</i> Claparède & Lachmann
	<i>Dinophysis acuta</i> Ehrenberg
	<i>Dinophysis dens</i> Pavillard
	<i>Dinophysis skagii</i> Paulsen

Table 1 continued

Group	Species
	<i>Dinophysis norvegica</i> Claparède & Lachmann
	<i>Dinophysis odiosa</i> (Pavillard) Tai & Skogsberg
	<i>Dinophysis ovata</i> Claparède & Lachmann
	<i>Dinophysis rotundata</i> Claparède & Lachmann
	<i>Dinophysis</i> sp.
	<i>Ensiculifera</i> sp.
	<i>Gonyaulux</i> sp.
	<i>Gymnodinium</i> sp.
	<i>Gyrodinium</i> sp.
	<i>Peridiniella catenata</i> (Levander) Balech
	<i>Prorocentrum gracile</i> Schütt
	<i>Prorocentrum micans</i> Ehrenberg
	<i>Prorocentrum</i> sp.
	<i>Protoceratium reticulatum</i> (Claparède & Lachmann) Butschli
	<i>Protoperidinium</i> cf. <i>americanum</i> (Gran & Braarud) Balech
	<i>Protoperidinium bipes</i> (Paulsen) Balech
	<i>Protoperidinium</i> cf. <i>breve</i> Paulsen
	<i>Protoperidinium brevipes</i> (Paulsen) Balech
	<i>Protoperidinium</i> cf. <i>cerasus</i> (Paulsen) Balech
	<i>Protoperidinium</i> cf. <i>curtipes</i> (Jørgensen) Balech
	<i>Protoperidinium depressum</i> (Bailey) Balech
	<i>Protoperidinium</i> cf. <i>divergens</i> (Ehrenberg) Balech
	<i>Protoperidinium</i> cf. <i>granii</i> (Ostenfeld) Balech
	<i>Protoperidinium</i> cf. <i>meunieri</i> (Pavillard) Elbrächter
	<i>Protoperidinium</i> cf. <i>oblongum</i> (Aurivillius) Parke & Dodge
	<i>Protoperidinium</i> cf. <i>oceanicum</i> (VanHöffen) Balech
	<i>Protoperidinium ovatum</i> (Schütt) Balech
	<i>Protoperidinium pallidum</i> (Ostenfeld) Balech
	<i>Protoperidinium</i> cf. <i>pellucidum</i> Bergh
	<i>Protoperidinium</i> cf. <i>quarnerense</i> (Schröder) Balech
	<i>Protoperidinium</i> sp.
	<i>Protoperidinium steinii</i> (Jørgensen) Balech
	<i>Pyrophacus</i> sp.
Ebridiaceae	<i>Ebria tripartita</i> (Schumann) Lemmermann
Haptophyta	<i>Phaeocystis</i> sp.
Heliozoa	<i>Heliozoa</i> sp.
Radiolaria	Gen. et sp. nonident

Dinoflagellates also contributed significantly to the microp plankton assemblage in summer 2008 (average of 16.3 %; Fig. 4c), represented by *Protoperidinium brevipes* and *Peridiniella catenata*. The highest variety of species belonging to the dinoflagellate genera *Protoperidinium* was observed in September 2010, mainly consisting of *Protoperidinium* cf. *pellucidum*, *Protoperidinium brevipes*, and *Protoperidinium ovatum*.

Species–environment relationships

The environmental, species (>0.2 %), and sample values generated by CCA for axes 1 and 2 are plotted in Fig. 6. The measured variables used in this analysis are temperature, salinity, PAR, Chl *a*, and nutrients. The measured variables explain 48 % of the variance in species data with *P* value <0.0001. In contrast, nutrients show no statistical

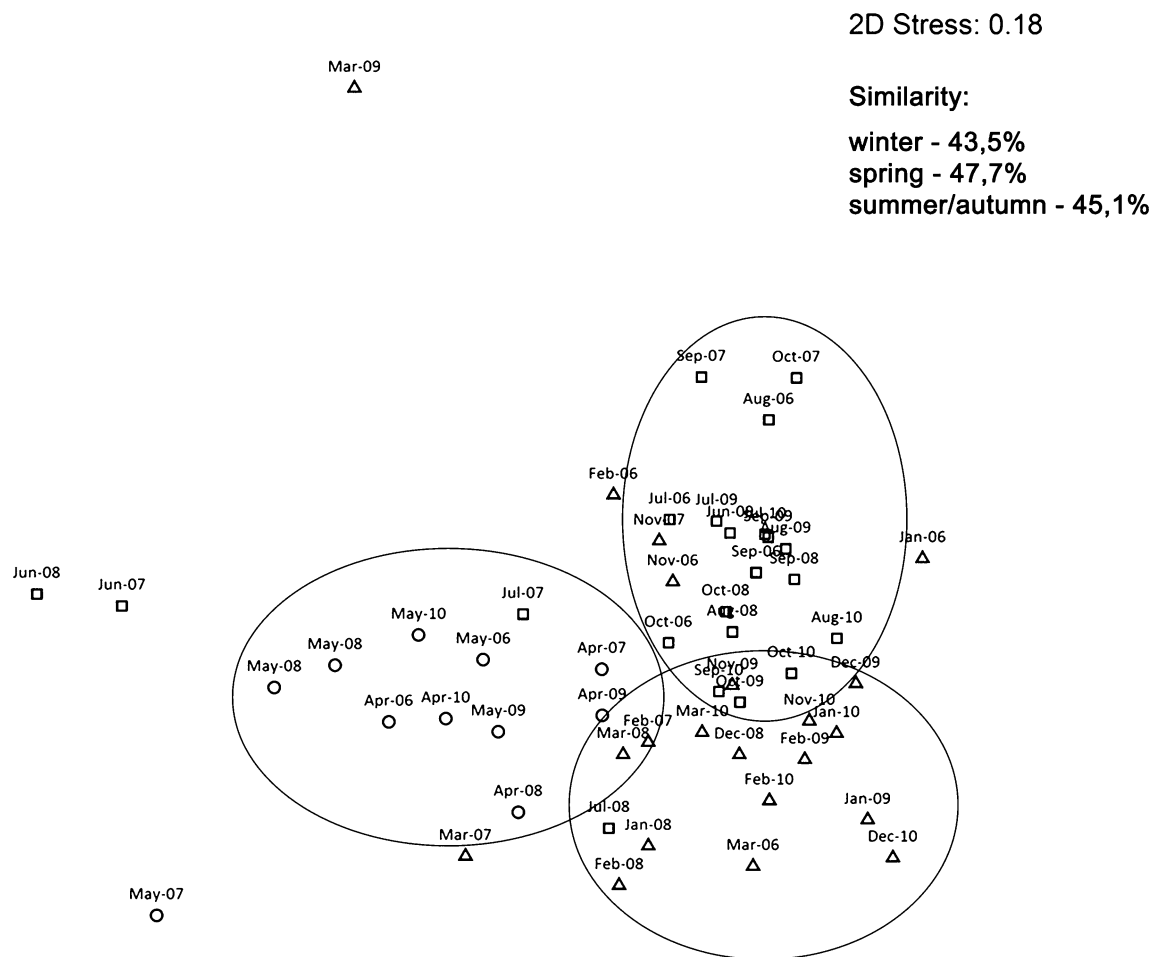


Fig. 3 Non-metric multidimensional scaling (nMDS) ordination for square root-transformed relative microplankton species abundance data for each sampling date, based on Bray–Curtis similarities. The distances between samples in the plot reflect their similarity in species composition. Samples are named according to month and year.

Different symbols are used to represent samples belonging to three marked seasons: *triangle*—winter (October–March); *circle*—spring (April–May); and *square*—summer/autumn (June–October). The figure gives similarity levels (%) between samples according to each season

significance in this study, with P value >0.06 . The combination of CCA axes 1 and 2 explains 51.7 % of the variance in microplankton data.

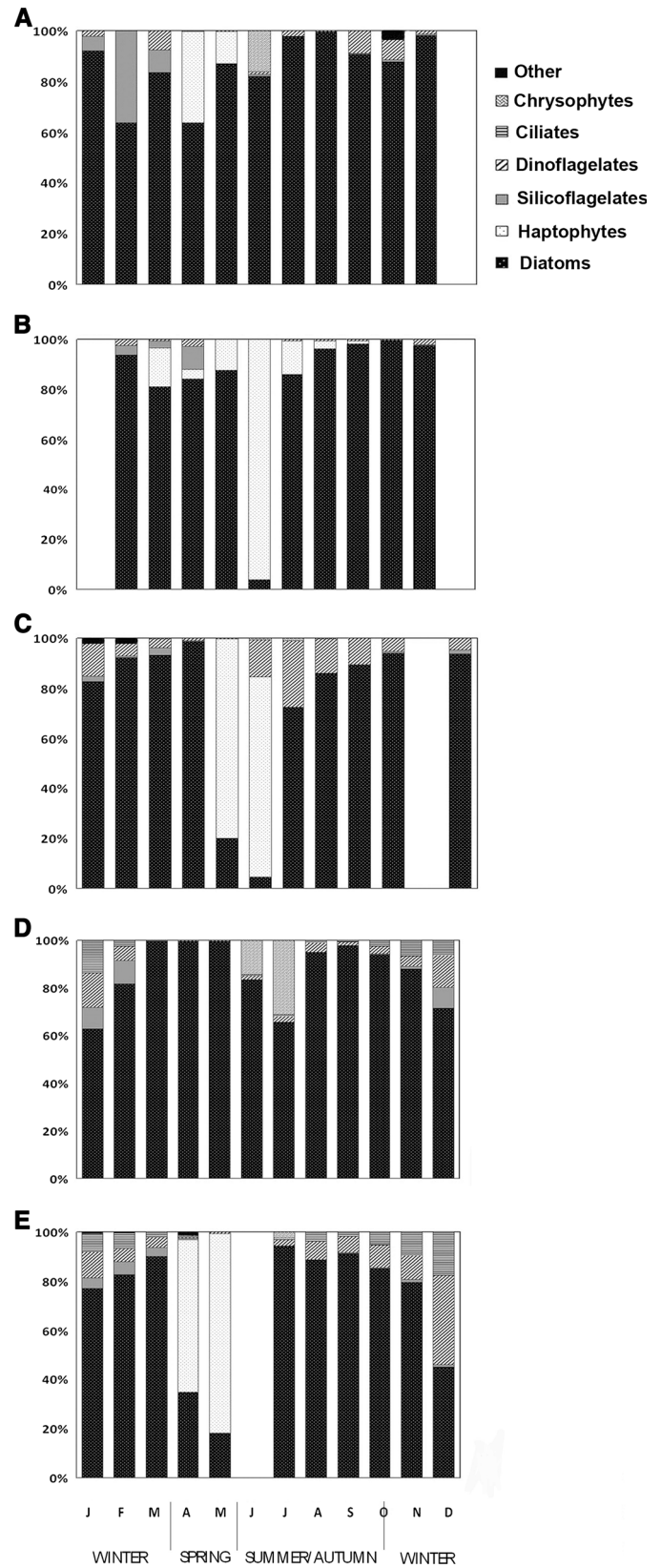
On the biplot, the direction of the variables' lines represents their approximate correlation to the ordination axis, other variables, and species. The correlation of variables with axes 1 and 2 indicates that PAR is positively correlated with axis 1, temperature is negatively correlated with axis 1, and salinity and Chl *a* are positively correlated with axis 2 (Fig. 6). A species' location along variables' lines presents its approximate weighted optima along each variable. Generally, silicoflagellates, dinoflagellates, and ciliates show preferences for more saline waters. Haptophytes and diatoms, such as *Thalassiosira* spp. and *Fragilariopsis* spp., are correlated with higher light intensities. *Thalassiosira* spp. and *Fragilariopsis* spp. are also correlated with cooler and fresher waters. Chrysophytes and diatom species *Nitzschia frigida* are associated with fresher waters. Diatoms,

such as *Chaetoceros* spp. and *Thalassionema nitzschioides*, are correlated with warmer waters, with the latter species also related to more saline waters (Fig. 6).

Discussion

The microplankton assemblage from net hauls reveals three seasonal groupings throughout the year, i.e. winter (October–March), spring (April–May), and summer/autumn (June–October) (Fig. 3). Spring and summer/autumn seasons depict separate blooms (i.e. peaks in phytoplankton biomasses; Fig. 2c), which are mainly produced by diatoms and the haptophyte *Phaeocystis* sp. The winter season, in contrast, shows the lowest phytoplankton biomasses, yet the highest microplankton diversity, represented by diatoms, silicoflagellates, dinoflagellates, and ciliates.

Fig. 4 Seasonal patterns of the microplankton assemblage composition (%) at GF3 in **a** 2006, **b** 2007, **c** 2008. The group ‘other’ includes ebridians, Chlorophyta, cyanobacteria, Heliozoa, and Radiolaria. All species used in this figure are listed in Table 1. Seasonal patterns of the microplankton assemblage composition (%) at GF3 in **d** 2009, **e** 2010. The group ‘other’ includes ebridians, Chlorophyta, cyanobacteria, Heliozoa, and Radiolaria. All species used in this figure are listed in Table 1



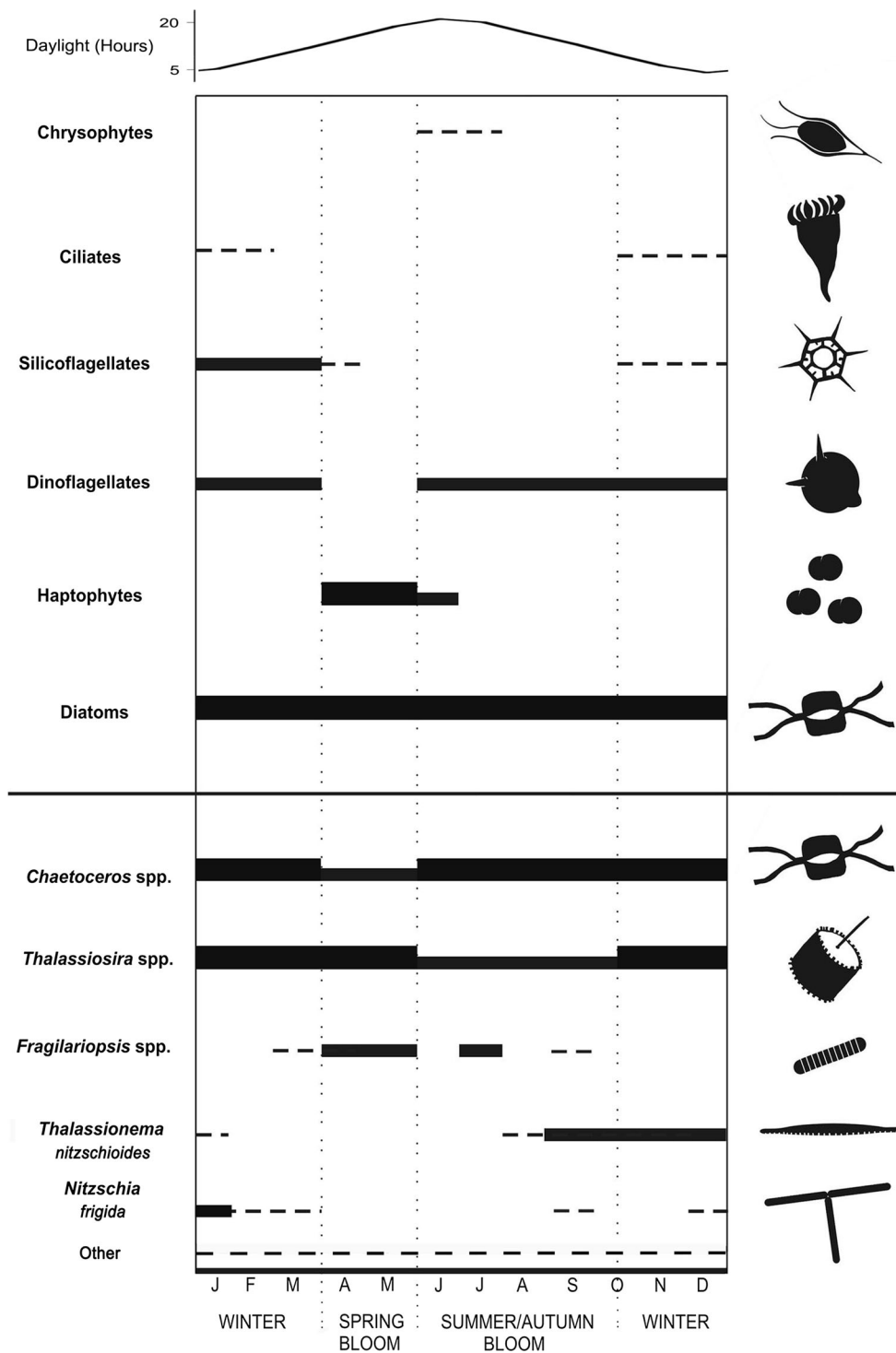


Fig. 5 Simplified graphical presentation of seasonal patterns of dominant microplankton groups (*above line*) and dominant diatom genera and species (*below line*) (>0.2%—see legend in Fig. 6 for particular species). These seasonal patterns are based on clustering

from Bray–Curtis similarities (averaged values from 2006 to 2010): *thick solid lines*—>20%, *solid lines*—20–5%, and *dashed lines*—<5%. Average daylight hours in Godthåb are plotted on top of the figure

Annual patterns

The established monthly sampling depicts two annual bloom patterns, but this may not give a full picture of the

beginning and/or end of blooms as bloom phases may vary in duration, usually lasting only a matter of weeks (e.g. Rat’kova and Wassmann 2002; Hill and Cota 2005). The two identified blooms were also observed and described in

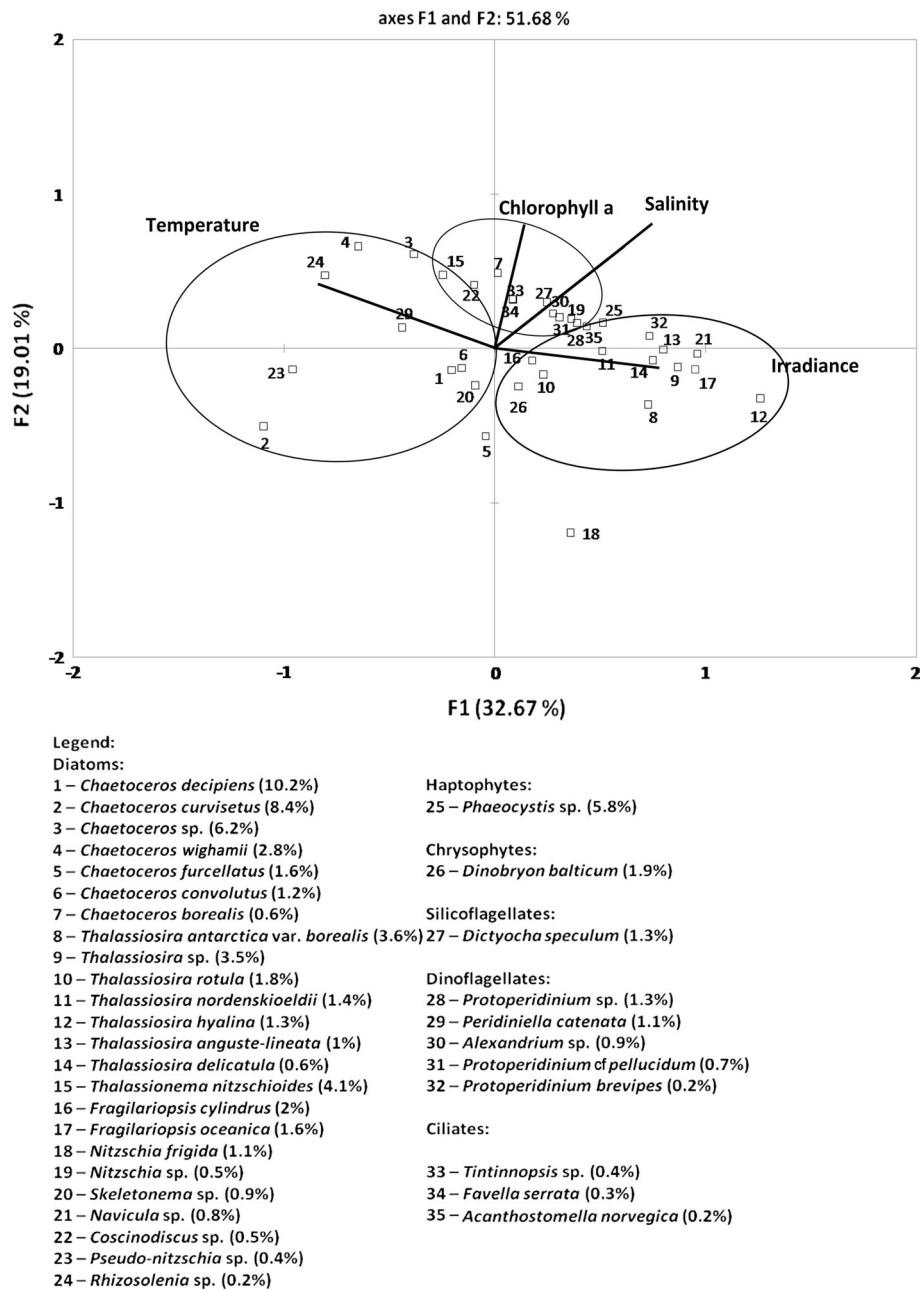


Fig. 6 Ordination diagram of the dominant microplankton species (>0.2 %) and variables, i.e. salinity, temperature, irradiance, and Chlorophyll *a* along the two CCA axes. Three groups of species can be identified: one influenced by higher water temperature (*cluster to*

the left), one influenced by higher salinity (*upper right cluster*), and one influenced by increased irradiance (*lower right cluster*). The legend gives average relative abundance of species calculated from all samples in *brackets*

previous planktonic studies from this sub-Arctic area (Smidt 1979; Arendt et al. 2013; Juul-Pedersen et al. 2015). Generally, all studied seasons and years are characterised by a dominance of diatoms, particularly the diatom genera *Chaetoceros* and *Thalassiosira* (Fig. 5). It should be noted that only diatoms were studied in greater detail using LM and SEM (mainly identified to a species level), while other potentially important microplankton groups, such as

haptophytes and dinoflagellates (mainly identified to a genus level), should be treated with caution (for a complete list of species and groups, see Table 1).

Seasonal succession

During winter, weak light conditions prevail in Godthåbsfjord, with a minimum day length of 4 h in December

(Fig. 5). Here, the diverse microplankton assemblage is represented by diatom species and genera showing variable environmental preferences: from fresher waters (*Nitzschia frigida*) to more saline waters (*Thalassionema nitzschioides*) and from cooler waters (*Thalassiosira* spp.) to warmer waters (*Chaetoceros* spp.). These affinities to variable temperatures and salinities indicated by dominant diatoms are linked to weaker water column stratification, typically observed in Godthåbsfjord during the winter season (Mortensen et al. 2011, 2013). This weak stratification, driven by low freshwater run-off and deep tidal mixing, is reinforced by dense coastal inflows pushing upper fjord waters outwards (Mortensen et al. 2011). These dense winter inflows are known to affect the basin waters in the inner fjord system as well (Smidt 1979). *T. nitzschioides* is reported in association with temperate waters of Atlantic origin, i.e. carried by the Irminger Current (Jiang et al. 2001) and the Atlantic–Norwegian Current (Koç Karpuz and Schrader 1990). Water at the sampling station (GF3) is influenced by waters of Atlantic origin found offshore in the WGC (see also Arendt et al. 2010; Juul-Pedersen et al. 2015) through intermediate and dense coastal inflows. In contrast, *N. frigida* is considered a cryophilic species common in sea ice edge blooms in the Arctic (Hasle and Heimdal 1998; Wiktor and Wojciechowska 2005; Degerlund and Eilertsen 2010; Poulin et al. 2011) and has been observed at the lower base of sea ice off the West Greenland coast (Jensen 2003). *N. frigida* has also been reported from Arctic sea ice during dark winter period (Niemi et al. 2011) as this species is known to be highly adapted to a wide range of light regimes (Poulin et al. 2011). Sea ice and glacial ice are present in the inner parts of Godthåbsfjord during winter, and both ice types pass through the sampling area in periodic bursts, affecting the sampled surface waters. Other microplankton groups associated with more saline waters are also significant during winter, i.e. silicoflagellates as well as dinoflagellates and ciliates during the last 2 years studied (2009–2010). In Arctic waters of the Canadian Beaufort Sea, diatoms (mostly *N. frigida*), dinoflagellates and ciliates, characterised both surface waters and bottom sea ice during dark winter period, showing a diverse winter community (Niemi et al. 2011), similar to that in the present study. In contrast, in the Atlantic-influenced coastal waters of Northern Europe, silicoflagellates are mainly found during late winter and spring, whereas dinoflagellates and ciliates are common during the summer season (Kraberg et al. 2010).

Spring bloom is the most pronounced annual bloom event in Godthåbsfjord with the exception of 2010, as described below. Highest phytoplankton biomasses are recorded during spring, favoured by increasing light intensities and incipient stratification inside the fjord due to an onset of freshwater input from snowmelt and melting of sea ice. The spring

microplankton assemblage is represented by species associated with higher light intensities, i.e. *Phaeocystis* sp. (2006–2008, 2010) and diatom genera such as *Thalassiosira* and *Fragilariopsis* (2006–2009) (Fig. 5). Species belonging to these diatom genera are also associated with cooler and fresher waters. *Fragilariopsis* spp. are typically considered species associated with sea ice and sea ice melt (Hasle and Syvertsen 1996; Quillfeldt 1996, 2001; Lovejoy et al. 2002). The outer parts of the Godthåbsfjord system remain largely free of sea ice, but during shorter periods (i.e. days to weeks), drifting and melting sea ice originating from the inner parts of the fjord system pass through the study area. This diatom genus thus seems to be better characterised as ‘directly and/or indirectly’ associated with sea ice, e.g. meltwater originating from sea ice. *Fragilariopsis* spp. recorded in Godthåbsfjord during spring seasons are therefore related to cold and freshwater in the surface layer (in common with *Fragilariopsis cylindrus* in Quillfeldt 2004), influenced by freshwater input from snowmelt as well as meltwater from sea ice. Generally, the haptophytes and diatoms dominant during spring blooms are also observed at most stations on the shelf outside the fjord (‘Fyllas Banke’) and in the central parts of Godthåbsfjord in May 2006 (Arendt et al. 2010). Furthermore, similar species compositions to the one observed in this study are typical of microplankton blooms reported farther north in Arctic regions (Quillfeldt 1996; Hasle and Heimdal 1998; Wiktor and Wojciechowska 2005; Degerlund and Eilertsen 2010).

During the initial part of the summer/autumn bloom (June–July; Fig. 5), colonies of chrysophyte *Dinobryon balticum* are found in association with fresher waters. *D. balticum* is regarded as preferring low-saline summer surface waters in Arctic regions (e.g. Hasle and Heimdal 1998; Keck et al. 1999). The summer months show a strong stratification of the water column in Godthåbsfjord driven by freshwater run-off from the GrIS. The summer/autumn bloom is mainly characterised by diatoms associated with warmer waters, i.e. *Chaetoceros* spp. and *Thalassionema nitzschioides*, corresponding with higher temperatures due to summer solar heating and air–sea heat exchange. *Chaetoceros* spp. dominate from July to October, and this diatom genus is the main contributor to the summer/autumn peak in biomass. This seasonal dominance of *Chaetoceros* spp. reflects the renewal of nutrients due to the onset of the major freshwater run-off from GrIS (see Mortensen et al. 2011). Generally, *Chaetoceros* spp. has been reported as the last successive stage (late summer) of the diatom growth season in West Greenland coastal waters (Grøntved and Seidenfaden 1938). Juul-Pedersen et al. (2015) show that the summer run-off is a key driver of the summer phytoplankton bloom in Godthåbsfjord, which, unlike in the classical Arctic pattern, compares to and in some years even exceeds the production in spring. Depending on various environmental factors (e.g.

freshwater input), a summer/autumn bloom might be a more pronounced event in the microplankton succession than the spring bloom, as recorded in 2010 (see below).

Inter-annual variations

Inter-annual variations in the dominant groups of the microplankton assemblage and bloom dynamics related to environmental conditions were observed during the study in Godthåbsfjord. We must note, however, that the monthly sampling procedure could have missed short-lived blooms (e.g. 1–2 weeks), which should not be interpreted as inter-annual variability.

In 2009, a distinct change in microplankton species composition was observed, one that was recorded only once throughout the entire study period (2006–2010). A complete absence of the significant component of spring blooms, the haptophyte *Phaeocystis* sp. (Fig. 4d), was accompanied by a mass occurrence of unusually long and massive chains of the diatom genus *Thalassiosira*, with almost no single cells (e.g. *Navicula* cf. *distans*). This change towards mass diatom chain formation may be explained by physiological adaptation to nutrient conditions. Only chains with specialised structures, such as spaces between cells (e.g. *Thalassiosira* spp.), can obtain a higher nutrient supply relative to solitary cells (Pahlow et al. 1997). Both high nutrient concentrations and high levels of turbulence are favourable for chain formation and survival (Pahlow et al. 1997). High nutrient levels were observed just prior to the spring bloom in 2009, with maximum nitrate plus nitrite (12.5 μM), phosphate (1.0 μM), and silicate (6.2 μM) concentrations (in Juul-Pedersen et al. 2010). Resting spores, particularly of the species *Thalassiosira antarctica* var. *borealis*, occurred simultaneously with the spring bloom (May 2009), which might be a response to rapid nutrient depletion towards the end of May (annual minima of 0.8, 0.1, and 0.8 μM for nitrate plus nitrite, phosphate, and silicate, respectively; Juul-Pedersen et al. 2010). The strong nutrient depletion during the 2009 spring bloom thus probably resulted from high nutrient uptake by chain-forming and spore-forming diatoms. Resting spores are often formed by certain species, e.g. *Thalassiosira antarctica* var. *borealis* (Quillfeldt 2001), when nutrients are nearing exhaustion. This mechanism ought to increase the species' survival potential by creating hibernating spores that sink to the sediment following the bloom and remain there until re-suspension (Hasle and Syvertsen 1996). These unusual trends observed in the microplankton assemblage in spring 2009 are possibly linked to an unusually long period of dense coastal inflow, which began in February and continued for at least 3 months (Mortensen et al. 2011; Rysgaard et al. 2012). This extensive inflow of dense coastal water continuously lifted nutrient-rich water

into the photic zone (above approximately 40 m), thereby influencing the zone in which the bloom occurs. We hypothesise that microplankton cells found in the nutrient-rich dense coastal waters were introduced to the surface layers prior to the spring bloom and may have produced the unusual species composition and succession observed in 2009. Another hypothesis is related to the single-cell stage of *Phaeocystis* sp., which might have been favoured by environmental conditions occurring prior to the 2009 spring bloom. Such a single-cell bloom could have been missed in the samples due to (1) cell size smaller than the mesh net size and/or (2) a possibly short-lived bloom occurring outside of the sampling scheme.

Nevertheless, *Phaeocystis* sp. reappeared in 2010, suggesting resilient microplankton species composition assemblages within these fjord systems. The absence of *Phaeocystis* sp. in spring 2009 and low relative abundance in spring 2006 coincide with the highest recorded phytoplankton biomass values (Fig. 2c and compare to Figs. 4, 5), probably linked to a higher contribution of diatoms during these two spring blooms compared with other years.

Phaeocystis spp. colonies and single cells have both been shown to be a food source for copepods (Nejstgaard et al. 2007), though they appear to represent a poor diet (Tang et al. 2011). In contrast, *Phaeocystis* spp. have been found to retain particular organic carbon within the pelagic to a greater extent relative to diatoms (Reigstad and Wassman 2007). The occurrence of *Phaeocystis* sp. in Godthåbsfjord is therefore important for the energy pathway through the food web, sustaining food for ciliates and likely the very abundant copepod within the fjord system, *Microsetella norvegica* (Arendt et al. 2013), which are thought to feed on particulate carbon aggregates (Koski et al. 2005, 2007).

In 2010, the most pronounced bloom event occurred in summer/autumn, as recorded by the late maximum peak in biomass. A similarly late annual peak in biomass (and primary production) has also been reported from previous annual surveys conducted during the relatively warm period of the 1950–1960s farther north, in Disko Bay, West Greenland (Andersen 1981). Summer/autumn 2010 in Godthåbsfjord (missing data for June; Fig. 4e) showed unusual occurrence of diatom species, typically inhabiting surface waters influenced by *inter alia* melting/drifting ice and/or snowmelt, i.e. *Fragilariopsis cylindrus* and *Nitzschia frigida* (Fig. 5). Exceptionally, high air temperatures in SW Greenland in 2010 contributed to markedly greater glacial ice melt (Mortensen et al. 2013). This resulted in a strong freshening of surface waters during summer, supported by the lowest surface salinity recorded throughout the study period (minimum of 18; Fig. 2a). The strong freshwater signal in summer 2010 was responsible for surface water properties suitable for the typically ice-

associated species. Additionally, a high variety of dinoflagellate genus *Protoberidinium* was observed in summer/autumn 2010, coinciding with the unusually late diatom bloom, possibly serving as a food source for these dinoflagellates. Dinoflagellates, coexisting with diatoms throughout the study period, have been shown to be important grazers of diatoms, such as the dominant genus *Protoberidinium* as well as the genera *Gymnodinium* and *Gyrodinium* (Hansen 1991; Bralewska and Witek 1995). These dinoflagellates typically occur at the peak of the diatom bloom or immediately after the bloom (e.g. Smetacek 1981; Tiselius and Kuylenstierna 1996; Juul-Pedersen et al. 2012).

In 2009–2010, dinoflagellates as well as predatory ciliates contributed significantly to the microplankton assemblage (Fig. 4d, e), which might be linked to the distinct changes recorded in the diatom bloom dynamics, i.e. mass chain formation in 2009 and pronounced summer/autumn bloom in 2010. Sherr et al. (1986) suggest that ciliates and dinoflagellates act as trophic intermediaries between small prey and larger predators. It is also known that ciliates, especially the tintinnids dominant in this study, feed on diatoms as well as build their shells by agglutinating particles suspended in the water column, e.g. leftovers of grazed diatom frustules, to their organic membranes (Karleskint et al. 2010).

Conclusions

The present paper highlights the importance of studying species–environment relationships at a temporal scale of months and multiple years in order to determine and identify key drivers for microplankton succession in sub-Arctic waters. In Godthåbsfjord, the annual succession patterns alongside measured biomasses confirm the existence of two blooms observed in previous studies. The more detailed seasonal patterns in microplankton succession reveal shifts from a high variety of microplankton groups, including small predators, in winter to predominantly phytoplankton during spring and summer/autumn blooms. Our study shows that species composition of microplankton assemblage is mainly influenced by physical variables such as salinity, temperature, and light, while chemical variables (nutrients) seem to be less decisive. Such detailed planktonic studies are extremely important in complex sub-Arctic systems such as Godthåbsfjord, where local and regional forces affect fjord circulation, e.g. local subglacial freshwater discharge from GrIS and large-scale circulation systems affecting dense coastal inflows. The ocean forcing via the West Greenland Current (WGC) versus a local freshwater input from GrIS subject to tidal mixing creates a highly productive system that is sensitive

to changing environmental conditions. An identified increased inflow of dense coastal water (2009) and increased freshwater input (2010) influenced physical and chemical water properties, which likely resulted in distinct changes in the microplankton assemblage structure during the observation period.

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