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Summer and fall distribution of phytoplankton in relation to environmental variables in Labrador fjords, with special emphasis on *Phaeocystis pouchetii*

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ABSTRACT: Protist (>2 µm) taxonomic composition was investigated for the first time in 4 Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during summers 2007 and 2013, early fall 2010 and late fall 2009. Protist composition was significantly different from one season to another. Significant spatial differences in protist composition were found only during summer 2013. During summer 2007, the community was characterized by diatoms and a mixed assemblage of flagellates. In summer 2013, flagellates largely dominated the community, and an intense *Phaeocystis pouchetii* bloom was observed in Nachvak Fjord (18×10^6 cells l^{-1}). In autumn, the community was dominated by unidentified flagellates, prymnesiophytes and diatoms, in various proportions from early to late fall. From a summer situation characterized by stronger stratification, higher incident irradiance and depleted nutrients in surface waters, it evolved to an autumn situation characterized by decreasing air temperature and irradiance associated with an environmental forcing (e.g. weather) allowing cooling and greater vertical mixing of the water column. Combining our observations with those from the literature, we suggest the following annual succession in the Labrador fjord phytoplankton community: (winter) dinoflagellates and small flagellated cells — (spring) *Fragilariopsis* spp., *Chaetoceros* spp., *Thalassiosira* spp. and *Phaeocystis pouchetii* — (summer) *Chaetoceros* spp., *P. pouchetii* and *Chrysochromulina* spp. — (fall) *Gymnodinium*/*Gyrodinium* spp., *Chrysochromulina* spp. and other flagellates. Overall, the protist richness was 2 times higher in fall than in summer, the highest richness being observed in early fall, with 201 taxonomic entries, 72 genera and 131 species identified.

KEY WORDS: Taxonomic composition · Protists · Phytoplankton · Diatoms · *Phaeocystis* · Seasonal variability · Northeastern Canada · Labrador · Fjords

INTRODUCTION

Phytoplankton account for <1% of the photosynthetic biomass on Earth, but are responsible for nearly 50% of global net primary production (Winder & Sommer 2012). These key primary producers play a crucial role in climate regulation and biogeochemical cycling but also directly in aquatic ecosystems as they supply organic matter to higher trophic levels. All of these processes are critically dependent on phytoplankton taxonomic composition, and any change at the base of the marine food web can have

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repercussions on the entire ecosystem (Winder & Sommer 2012). Many studies have highlighted alterations in phytoplankton size structure and taxonomic composition due to increasing environmental changes (Moran et al. 2010, Hilligsoe et al. 2011, Marañón et al. 2012, Blais et al. 2017). Understanding the composition of the phytoplankton community and the variables influencing its dynamics are essential for a better prediction of the impacts of global warming on aquatic ecosystems.

In polar regions, the phytoplankton growth season is relatively short due to the low solar elevation in winter and thick sea-ice coverage. Subsequent seasonal differences in daily irradiance are large and thus have an important effect on community structure and succession. Many other environmental variables, such as stratification, nutrient inputs, water temperature and grazing pressure, also shape the dynamics of algal communities (Margalef 1978, Levasseur et al. 1984, Iversen & Seuthe 2011). In most arctic and subarctic ecosystems, the annual growth season of phytoplankton cells can be described as follows: in winter and early spring, low incident irradiance and sea-ice cover prevent any photosynthetic activity, and the community is dominated by nano-sized (2–20 µm) heterotrophic protists (Sherr et al. 2003, Terrado et al. 2008, Iversen & Seuthe 2011). Under these unfavourable conditions, some diatoms and dinoflagellates produce resting spores or cysts (Różańska et al. 2008) or become dormant in darkness (Smayda & Mitchell-Innes 1974, McMinn & Martin 2013). From April to mid-May, phytoplankton growth starts when warming and subsequent ice-melt lead to stratification of the water column, with the surface mixed layer becoming shallower than the critical depth (i.e. the critical depth hypothesis of Sverdrup 1953; reassessed by Behrenfeld & Boss 2014).

Although the upper water column generally contains abundant nutrients due to previous winter mixing (and regeneration), the algal community is not very active because light is still a limiting factor. This pre-bloom community is generally dominated by small phytoplankton composed of prasinophytes and chrysophytes (Hill et al. 2005). From late May, the spring phytoplankton bloom is triggered by the alternation between mixing and stratification, and by increases in daily irradiance and water temperature (Edwards & Richardson 2004). A compensation irradiance (i.e. the minimum irradiance required for net phytoplankton growth during spring) of 1.9 ± 0.3 mol quanta m^{-2} d^{-1} was proposed for Arctic waters (Tremblay et al. 2006). This estimate is similar to the critical values of 1.3 and 2.5 mol quanta m^{-2} d^{-1} for the onset of spring bloom in North Atlantic waters (35–75° N) (Siegel et al. 2002) and in the Labrador Sea (Lacour et al. 2015), respectively. Large centric diatoms, such as *Thalassiosira* spp. and *Chaetoceros* spp., as well as the prymnesiophyte *Phaeocystis pouchetii* (Hariot) Lagerheim, usually dominate these blooms (Gradinger & Baumann 1991, von Quillfeldt 2000, Lovejoy et al. 2002). During summer, when surface nutrients are depleted, the maximum production is usually observed at the subsurface, close to the nutracline (Martin et al. 2010) where the phytoplankton community is generally dominated by diatoms (Ardyna et al. 2011, Ferland et al. 2011, Simo-Matchim et al. 2016) and/or autotrophic nanoflagellates (Ardyna et al. 2017). In late summer and early fall, the decrease in water column stratification by surface cooling and wind mixing favours the supply of nutrients to surface waters. This nutrient replenishment promotes phytoplankton growth, and a fall bloom can possibly occur if, in addition, the irradiance in the euphotic zone is high enough to sustain algal photosynthetic activity (Ardyna et al. 2013, 2014). From mid-fall, light becomes a limiting factor for algae and thus terminates algal growth (Hegseth 1997, Garneau et al. 2007, Brugel et al. 2009). Under these conditions, the microbial food web predominates and the planktonic protist community is mainly composed of heterotrophic and mixotrophic flagellated cells.

Such coexistence of many phytoplankton species on only few resources illustrates the well-known 'paradox of the plankton' proposed by Hutchinson (1961), who asked why there are so many types of organisms in any one habitat, contrary to the principle of competitive exclusion stating that 2 species with identical ecological requirements cannot live in the same habitat at the same time (Gause 1932). The coexistence of different species (or taxonomic groups in our case) in the same habitat necessarily requires that they occupy different ecological niches. The niche concept was first introduced by Hutchinson (1957) who defined the fundamental niche as a multidimensional hypervolume describing the environmental and biological conditions under which an organism can survive and reproduce. The major ecological axes that define phytoplankton niches are the physical environment (water temperature and stratification), resources (light, macro- and micronutrients) and natural enemies (grazers and parasites) (Reynolds 2006, Litchman & Klausmeier 2008).

Despite the key role played by phytoplankton and other protists in the cycling of organic matter, the diversity of these crucial microorganisms has never, to our knowledge, been studied in the fjords along

the Labrador coast of Canada. The objectives of our study were (1) to describe the detailed taxonomic composition of phytoplankton in 4 Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during the transition from summer to fall, and (2) to assess the influence of environmental factors on the variability in phytoplankton communities. Understanding the factors that control species composition and dynamics is fundamentally important for a better prediction of the impact of environmental changes on marine polar ecosystems.

MATERIALS AND METHODS

Study area

The study region is located in Nunatsiavut in northern Labrador (Fig. 1). This vast region is on the eastern seaboard of Canada and extends between 56 and 60°N, along the Labrador Sea. Since 2007, several oceanographic campaigns have been conducted along the Labrador coast, especially in 4 fjords: Nachvak, Saglek, Okak and Anaktalak (Fig. 1), some undergoing natural climatic changes and others stressed by modern-day human activities. These fjords are highly influenced by both Atlantic and Arctic water masses, and they receive freshwater, nutrients and sediments from glaciers and rivers. Labrador fjords are nursing areas for a large number of fish stocks and are therefore important feeding grounds for seabirds and marine mammals (Allard & Lemay 2012). They are also heavily used by Labrador Inuit for hunting, harvesting and economic activities.

Located in the Torngat Mountains National Park, Nachvak is the northernmost fjord in this study (Fig. 1). This glaciated fjord is 45 km long by 2 to 4 km wide, gradually increasing in width eastward to Nachvak Bay, which opens to the Labrador Sea (Bell & Josenhans 1997). There are 4 successive basins, becoming increasingly deeper from west to east, with water depth ranging from 90 to 210 m separated by sills between 10 and 180 m below sea level (Richerol et al. 2012). The duration of the sea-ice cover is 6.6 mo yr^{-1} in Nachvak and 6.3 to 6.4 mo yr^{-1} in the other fjords (Brown et al. 2012), lasting from about mid-December to mid-July. Nachvak is a pristine fjord, considered a reference site to assess natural climatic and environmental variability of Nunatsiavut fjord ecosystems.

Saglek Fjord has been the site of a military radar station since 1953 as part of the Distant Early Warning Line (Fig. 1). This has led to extensive polychlorinated biphenyl (PCB) contamination in soil, sediments and the marine environment (Kuzyk et al. 2005a). Saglek Fjord is 65 km long by 2 to 14 km wide and comprises a succession of 7 basins; sills between 45 and 96 m below sea level separate these basins (Richerol et al. 2012).

Okak Bay is 50 km long (Fig. 1) and is occasionally used for travelling and harvesting by the Nain Inuit. The outer part of the bay is relatively shallow, about 45 to 50 m. The deepest basins are along the northern entrance, where average water depth reaches 200 m (Richerol et al. 2012). The southern entrance is narrow and shallow, bordered to the south by the Ubilik Peninsula and to the north by Okak Island.

Anaktalak Bay is long, narrow and straight, measuring 66 km long by 1 to 5 km wide (Fig. 1). Much of the outer part of the bay forms a large basin between 100 and 120 m deep that shallows to a sill at 85 m in the outer section of the bay (Richerol et al. 2012). Anaktalak Bay is the southernmost site in this study and is widely used for commercial activities by the Nain Inuit. Since 2005, the head of Anaktalak Bay harbours a nickel-copper-cobalt mine and concentrator operated by Vale NL (formerly Voisey's Bay Nickel Company).

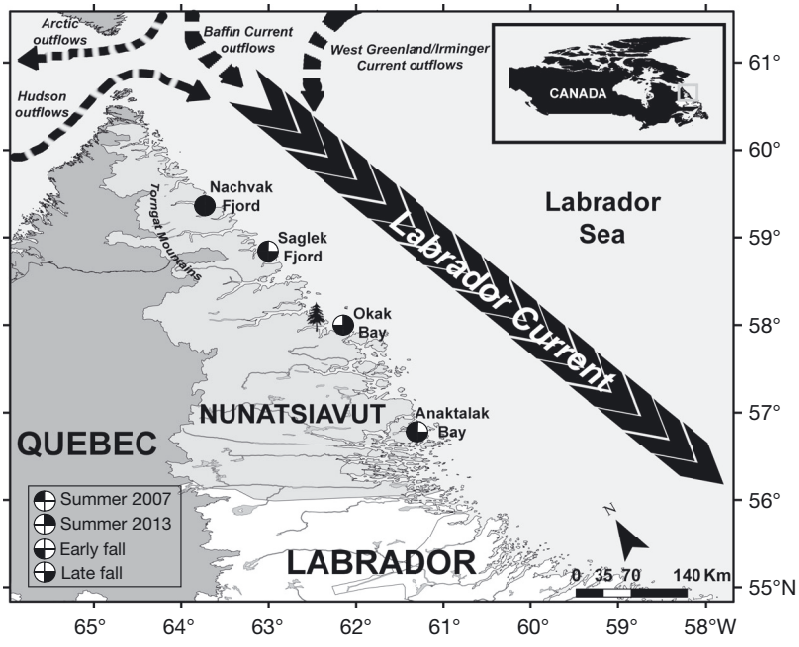

Fig. 1. Sampling periods and locations of Nachvak Fjord, Saglek Fjord, Okak Bay and Anaktalak Bay in Nunatsiavut, northern Labrador, Canada (adapted from Richerol et al. 2012)

For the sake of simplicity, Okak and Anaktalak bays will hereafter be considered 'typical fjords', just like Nachvak and Saglek. Nachvak and Saglek Fjords are located above 58° N, north of the tree line and within the Arctic ecoregion, while Okak and Anaktalak Fjords are situated between 56 and 58° N, south of the tree line and within the Subarctic ecoregion. The distance between the mouth of Nachvak and Anaktalak is ca. 330 km. In contrast to Nachvak and Okak, Saglek and Anaktalak are directly influenced by industrial and modern human activities. Detailed characteristics of the studied fjords can be found in Simo-Matchim et al. (2016).

Table 1. Codes of the samples collected in Labrador fjords

Fjord	Station	Position	Latitude (°N)	Longitude (°W)	Water depth (m)	Sample depth in the euphotic zone	Code
Nachvak	602	Inner	59°3.2′	63°52.1′	158	Surface	NIS
						Bottom	NIB
	600	Outer	59°5.3′	63°26.1′	207	Surface	NOS
						Bottom	NOB
Saglek	615	Inner	58°19.2′	63°32.5′	130	Surface	SIS
						Bottom	SIB
	617	Outer	58°30′	62°41.4′	139	Surface	SOS
						Bottom	SOB
Okak	630	Inner	57°28.3′	62°26.5′	51	Surface	OIS
						Bottom	OIB
	633	Outer	57°36.4′	61°53.8′	178	Surface	OOS
						Bottom	OOB
Anaktalak	624	Inner	56°25.2′	62°4.4′	71	Surface	AIS
						Bottom	AIB
	620	Outer	56°24′	61°13′	96	Surface	AOS
						Bottom	AOB

Sampling

Sampling was conducted from 31 July to 2 August 2007, 30 July to 1 August 2013, 24 to 27 October 2010 and 8 to 13 November 2009 onboard the Canadian research icebreaker CCGS 'Amundsen'. Table 1 presents the samples collected in the fjords during each period. Hereafter, the sampling periods are referred to as summer 2007, summer 2013, early fall and late fall, respectively; November 2009 was the period with the lowest water temperature and *in situ* irradiance (Tables 2 & 3). The average day length was 16.5 h during summer, 9.5 h in early fall and 8.3 h in late fall. The daily averaged precipitation (±SD) measured at Nain Airport in Labrador in July 2013 (4.0 ± 5.7 mm) was 3 times higher than in July 2007 (1.3 ± 1.4 mm) (http://climat.meteo.gc.ca).

Sampling was carried out at 2 stations (inner and outer) in each fjord. At each station, a downwelling photosynthetically active radiation (PAR, 400–700 nm) underwater profile was determined using a PNF-300 radiometer (Biospherical Instruments) to estimate the depth of the euphotic zone (Z_{eu}, 0.2% of surface irradiance, Knap et al. 1996). Incident PAR was measured at 10 min intervals with a 2π LI-COR sensor (LI-190SA) placed on an unshaded area of the foredeck.

A rosette sampler equipped with a conductivity, temperature, depth (CTD) probe (Sea-Bird Electronics SBE 911+), an *in situ* fluorometer (WETStar mini fluorometer model 9512008) and 12 l Niskin-type bottles (OceanTest Equipment, n = 24) was deployed to collect water samples at 2 depths (50% and 15 to 1% of surface irradiance). For simplicity, these 2 depths are hereafter respectively referred to as the surface (1–10 m) and the bottom layers (12–40 m) of the euphotic zone. Temperature, salinity and density (sigma-t, σ_t) were determined from CTD profiles. Subsamples for subsequent analyses were transferred from the Niskin-type bottles to 500 ml acid-washed Nalgene bottles (Knap et al. 1996). Water samples for nutrient concentrations were collected at 7 optical depths (100, 50, 30, 15, 5, 1 and 0.2% of surface irradiance), at 75 and 100 m in the aphotic zone.

Laboratory analyses

Nutrients

Triplicate samples for dissolved inorganic nutrients were filtered through Whatman GF/F glass-fibre filters (nominal pore size of 0.7 µm), and the filtrate was collected in 15 ml acid-washed polyethylene tubes. Nutrient samples were directly analysed or stored in a −80°C freezer for later analyses of nitrate plus nitrite (NO_3+NO_2), phosphate (PO_4) and silicic acid ($Si(OH)_4$) concentrations using a Bran-Luebbe 3 auto-analyser (method adapted from Grasshoff et al. 1999). A simple linear correction for the effect of varying salinity was applied for phosphate and silicic acid concentrations, as recommended by Grasshoff et al. (1999).

Table 2. Environmental conditions of the water column at the depth sampled in the surface layer of the euphotic zone in Nachvak, Saglek, Okak and Anaktalak fjords during summer 2007, summer 2013, early fall and late fall. Z_{eu}: euphotic zone depth; Z_m: surface mixed layer depth; Z_{nut}: nutracline depth; $\Delta\sigma_t$: stratification index; T: water temperature; S: salinity; E_z: daily *in situ* irradiance; NO_3+NO_2: nitrate plus nitrite; $Si(OH)_4$: silicic acid; PO_4: phosphate concentrations. The total abundance of protists >2 µm is also shown. Codes for samples are listed in Table 1

Code	Z_{eu} (m)	Z_m (m)	Z_{nut} (m)	$\Delta\sigma_t$ (kg m^{-3})	T (°C)	S	E_z (mol quanta m^{-2} d^{-1})	NO_3+NO_2 (µmol l^{-1})	$Si(OH)_4$ (µmol l^{-1})	PO_4 (µmol l^{-1})	Protist abundance (10^6 cells l^{-1})
Summer 2007											
NIS	29	6	5	2.21	1.4	30.6	20.27	0.14	1.63	0.18	2.68
NOS	44	31	3	1.43	2.5	31.1	23.83	1.26	3.54	0.24	1.59
SIS	83	12	11	1.93	2.2	30.7	13.48	0.52	0.48	0.46	0.71
SOS	45	10	13	1.90	3.1	30.2	14.38	0.49	0.76	0.36	1.88
AIS	32	11	16	3.21	5.3	28.2	16.46	0.10	2.43	0.17	1.19
AOS	31	23	11	2.65	5.8	29.3	16.19	0.25	0.42	0.23	1.66
Summer 2013											
NIS	35	9	36	2.76	2.3	29.3	25.96	0.93	10.38	0.35	0.49
NOS	34	65	22	1.03	1.5	31.4	19.04	0.61	3.95	0.37	2.58
OIS	18	3	11	3.59	4.2	26.2	20.44	0.32	16.11	0.12	2.12
OOS	53	3	15	1.68	3.0	30.3	18.89	0.07	1.51	0.16	0.87
Early fall											
NIS	54	3	24	1.55	2.3	30.7	3.20	2.59	4.79	0.81	2.3
NOS	27	6	26	0.90	2.7	31.4	2.54	4.25	6.38	0.78	1.01
SIS	60	10	19	1.35	2.1	30.4	3.09	2.02	4.19	0.45	2.3
SOS	36	18	18	0.65	2.6	31.4	2.70	2.03	5.08	0.68	1.69
OIS	34	4	18	0.85	1.9	29.9	3.26	2.02	5.77	0.73	1.62
OOS	51	39	39	0.43	3.2	31.7	3.90	1.86	3.92	0.68	0.76
AIS	47	25	5	0.19	2.7	30.3	3.75	4.64	6.64	0.94	0.33
AOS	22	17	10	0.44	3.5	31.1	0.60	1.21	2.77	0.40	0.56
Late fall											
NIS	13	72	17	0.45	−0.3	31.8	0.52	6.68	6.61	0.77	1.33
NOS	17	95	53	0.06	0.1	32.1	0.73	6.12	6.61	0.76	0.58
SIS	14	87	20	0.26	−0.1	32.0	0.43	5.16	7.58	0.92	0.67
OIS	20	7	13	0.07	0.9	31.8	0.25	4.95	7.46	0.85	0.31
AIS	16	34	8	0.12	1.2	30.8	2.12	3.08	6.12	0.62	0.47
AOS	34	26	45	0.65	0.4	31.9	2.80	2.81	3.92	0.49	0.55

Light microscopy analysis

Samples for the identification and enumeration of protist cells >2 µm were collected in 250 ml glass bottles and preserved in acidic Lugol's solution (Parsons et al. 1984). The bottles were stored in the dark at 4°C until analysis. Cells were identified to the lowest possible taxonomic rank using an inverted microscope (Wild Heerbrugg and Zeiss Axiovert 10) according to Utermöhl (1958). For each 10 or 50 ml settling chamber, at least 400 cells (accuracy ± 10%) were counted (Lund et al. 1958) over a minimum of 3 transects of 20 mm at a magnification of 400×. The main taxonomic references used to identify the protist cells were Tomas (1997), Bérard-Therriault et al. (1999) and Throndsen et al. (2007).

Calculations

The strength of the vertical stratification was estimated using 2 different indices: (1) the difference in density (σ_t) between 80 m (or the last sampled depth in a <80 m water column) and 2 m ($\Delta\sigma_t$, Tremblay et al. 2009), and (2) the maximum value of the Brunt–Väisälä frequency (N^2) measured in the upper water column (Tritton 1988). For the whole study period, there was a strong relationship between the vertical stratification index determined by $\Delta\sigma_t$ and N^2. Therefore, only $\Delta\sigma_t$ was considered in further analyses. The surface mixed layer depth (Z_m) was defined as the depth where the vertical gradient in density (σ_t) is >0.03 m^{-1} (de Boyer Montégut et al. 2004, Tremblay et al. 2009). The nutracline depth (Z_{nut}) was estimated to be where the vertical gradient of NO_3 con-

Table 3. Environmental conditions of the water column at the depth sampled in the bottom layer of the euphotic zone in Nachvak, Saglek, Okak and Anaktalak fjords during summer 2007, summer 2013, early fall and late fall. Abbreviations of environmental variables are defined in Table 2. The total abundance of protists >2 µm is also shown. Codes for samples are listed in Table 1

Code	T (°C)	S	E_z (mol quanta m^{-2} d^{-1})	NO_3+NO_2 (µmol l^{-1})	$Si(OH)_4$ (µmol l^{-1})	PO_4 (µmol l^{-1})	Protist abundance (10^6 cells l^{-1})
Summer 2007							
NIB	0.0	31.3	3.54	0.16	0.68	0.17	6.51
NOB	1.1	31.5	2.83	5.32	2.66	0.28	1.61
SIB	−0.5	31.8	4.06	2.35	1.36	0.65	0.67
SOB	0.5	31.4	1.61	1.32	0.76	0.33	2.22
AIB	−0.1	30.6	0.18	1.98	3.60	0.61	1.37
AOB	0.3	31.3	0.09	1.11	1.95	0.60	1.63
Summer 2013							
NIB	−0.3	31.6	4.29	1.41	4.35	0.55	21.7
NOB	1.2	31.5	4.44	1.03	3.12	0.39	2.47
OIB	1.0	30.0	7.09	0.25	10.46	0.26	3.08
OOB	1.9	30.8	5.21	0.34	0.66	0.25	0.62
Early fall							
NIB	2.2	31.6	0.89	6.86	5.02	1.01	1.43
NOB	2.6	31.6	0.40	3.61	5.58	1.00	0.45
SIB	1.3	31.7	1.00	2.70	4.65	0.72	0.67
SOB	2.6	31.4	0.58	1.95	4.89	0.69	0.77
OIB	1.1	31.3	0.53	1.88	5.15	0.90	1.02
OOB	3.1	31.7	1.16	1.67	3.45	0.67	0.91
AIB	2.7	30.3	1.31	3.54	6.08	0.91	0.37
AOB	3.5	31.2	0.06	1.45	2.71	0.44	0.49
Late fall							
NIB	0.2	32.1	<0.01	8.13	8.59	0.93	0.37
NOB	0.1	32.1	<0.01	5.97	6.78	0.79	0.56
SIB	0.4	32.1	<0.01	5.64	8.61	0.96	0.57
SOB	0.1	32.1	0.38	4.30	5.93	0.78	1.09
OIB	1.0	31.8	<0.01	4.83	7.16	0.77	0.22
AIB	1.9	31.0	<0.01	5.26	6.85	0.68	0.27
AOB	0.9	32.2	<0.01	2.87	3.54	0.52	0.53

centration (dNO_3/dZ) was highest. Daily incident downwelling irradiance (E) was calculated at each station. Daily irradiance at the sampling depths (E_z, mol quanta m^{-2} d^{-1}) was calculated using the equation of Lambert-Beer (Kirk 2011):

$$E_z = E \times \exp^{(-k_d \times Z)} \quad (1)$$

where k_d is the diffuse light attenuation coefficient (m^{-1}), and Z is the sampling depth (m).

Statistical analyses

A 4-way analysis of variance (ANOVA) was performed to assess significant differences in environmental variables between fjords (Nachvak, Saglek, Okak and Anaktalak), stations (inner and outer), depths (surface and bottom) and seasons (summer 2007, summer 2013, early fall and late fall). Prior to the ANOVA, all environmental variables were tested for normality of distribution and homoscedasticity of variance, using a Shapiro-Wilk test and residual diagrams, respectively. When required, a logarithmic or square-root transformation was applied to the data. The ANOVA was completed by a multiple comparison test of means (Tukey's honest significant difference [HSD] test for unequal sample sizes) or a Student's *t*-test. Pearson's correlation coefficient (r) was used to determine the relationship between 2 variables (Sokal & Rohlf 1995). These tests were carried out using JMP Pro version 11 software, and the estimation of variance components was done using the restricted maximum likelihood (REML) method.

A nonmetric multidimensional scaling (MDS) ordination of a Bray-Curtis similarity matrix coupled with a group-average cluster analysis was performed to identify groups of samples with similar taxonomic composition (Clarke & Warwick 2001), using PRIMER v6 and PERMANOVA+ software (Clarke & Gorley 2006). To reduce double zeros in the data matrix, only taxonomic entities that were present in more than 2 samples were included in the analyses. Before calculating the similarity matrix, the absolute abundance of each taxon was standardized (i.e. the abundance of each taxonomic entry was divided by the total cell abundance of the sample to obtain a relative value) and square-root transformed to reduce the influence of the most dominant taxa (Clarke & Warwick 2001). An analysis of similarities (1-way ANOSIM) was also performed on the Bray-Curtis similarity matrix to test whether the spatial and seasonal differences in taxonomic composition were significant. The pairwise R value gave an absolute measure of how separated the groups were on a scale of 0 (undistinguishable) to 1 (all similarities within groups are greater than similarities between groups) (Clarke & Warwick 2001). A

breakdown of species similarities (SIMPER) was used to determine which combination of taxa leads to the resulting groups (Clarke 1993).

A distance-based linear model permutation test (DistLM, McArdle & Anderson 2001) was performed to explore relations between environmental variables (water temperature, salinity, *in situ* irradiance, stratification index, euphotic zone depth, surface mixed layer depth, NO_3+NO_2, PO_4, and $Si(OH)_4$), and protist taxonomic groups (diatoms, dinoflagellates, chrysophytes, cryptophytes, dictyochophytes, euglenophytes, prasinophytes, prymnesiophytes, raphidophytes, unidentified flagellates, choanoflagellates, ciliates and heterotrophic protists other than choanoflagellates and ciliates). For each season, only taxonomic groups that were present in more than 2 samples were included in the model. Therefore, euglenophytes and heterotrophic protists were removed from the analysis in summer 2007, and dictyochophytes were excluded in summer 2013. The absolute abundance of each group was then standardized (by the total) and square-root transformed (Clarke & Warwick 2001). Before calculating the Bray-Curtis similarity matrix, a dummy value of 0.1 was added to protist abundances because we had some zeros in the matrix after pre-treating the data. After assessing normality of environmental variables, the natural logarithm transformation was applied when necessary to correct for skewness (Anderson et al. 2008). Analysis of multicollinearity revealed 5 high correlations between environmental variables: between water temperature and salinity ($r = -0.86$) in summer 2007; between nutracline depth and nitrate concentration ($r = 0.87$), water temperature and phosphate concentration ($r = -0.87$), phosphate and nitrate concentrations ($r = 0.92$) in summer 2013; and between silicic acid and phosphate concentrations ($r = 0.93$) in late fall. Nevertheless, we decided to keep all predictors in the model because we believe they are all important descriptors of ecological niches. All environmental variables were then normalized (i.e. for each entry, the mean value was subtracted and divided by the standard deviation) because they are on different scales with arbitrary origins (Clarke & Gorley 2006). For all seasons, the stepwise routine was run employing 999 permutations, except for early fall where the best routine was selected. The selection criterion was always Akaike's information criterion (AIC). A distance-based redundancy analysis plot (dbRDA, Anderson et al. 2008) from the DistLM analysis was used to visualize the final model. Four dbRDA plots were produced, one for each sampling season (summer 2007, summer 2013, early fall and late fall). The relationships between dbRDA coordinate axes and orthonormal variables (protist groups and environmental variables) were determined using multiple partial correlations (r_p). Finally, we ran a Bio-Env procedure, an analysis that identifies the optimal subset of environmental variables which best explains the biotic structure (Clarke & Ainsworth 1993). These ordinations were carried out using PRIMER v6 and PERMANOVA+ software (Clarke & Gorley 2006).

RESULTS

The environmental variables measured in Nachvak, Saglek, Okak and Anaktalak fjords during summers 2007 and 2013, early fall and late fall are presented in Tables 2 & 3. The ANOVA revealed significant spatial and seasonal differences in environmental variables (Table 4). Salinity was the only variable that significantly differed between fjords, stations, sampled depths and seasons. All other environmental variables were significantly different between seasons. In addition, significant differences between fjords and sampled depths were detected for water temperature and NO_3+NO_2, between fjords and stations for Z_m, between fjords for Z_{eu}, between stations and sampled depths for PO_4 and between sampled depths for E_z. Finally, Z_{nut}, $\Delta\sigma_t$ and $Si(OH)_4$ were significantly different between stations. Total protist abundances were significantly different only between sampling periods.

Physical environment

For the whole sampling period, maximum (5.8°C, Table 2) and minimum temperatures (–0.5°C, Table 3) were measured during summer 2007 in the surface layer of outer Anaktalak and in the bottom layer of inner Saglek, respectively. For the whole sampling period, the surface salinity was higher at the outer stations compared to the inner ones, especially in the 2 southernmost fjords (Okak and Anaktalak, Table 2). The surface layer of the euphotic zone (Z_{eu}) was warmer and less salty than the bottom layer (Fig. 2, Table 4). $\Delta\sigma_t$ was higher in both summers compared to early and late fall (Fig. 2, Table 2). Indeed, the upper water column of all fjords was well stratified during both summers and relatively well mixed in late fall (profiles not shown), as confirmed by the significant differences in $\Delta\sigma_t$ between seasons ($p < 0.0001$, Table 4). E_z was, on average, 6 times

Table 4. Summary of the ANOVA and subsequent tests for environmental and biological variables measured at the inner and outer stations of 4 Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during summers 2007 and 2013, early fall and late fall. Abbreviations of environmental variables are defined in Table 2. Numbers are p values; ns: not significant. For *a posteriori* multiple comparison, Tukey's HSD test and Student's *t*-test were used, where A > B > C

	Four-way ANOVA				Tukey or Student's test (α = 0.05)													
	Fjord	Station (In/Out)	Depth (Surf/Bot)	Season	Nachvak	Saglek	Okak	Anaktalak	In	Out	Surf	Bot	Summer 2007	Summer 2013	Early fall	Late fall
Z_{eu} (m)	<0.05	ns		<0.001	A, B	A	A, B	B					A	A, B	A	B
Z_m (m)	<0.05	<0.05		<0.0001	A	A, B	B	A, B	B	A			B	B	B	A
Z_{nut} (m)	ns	<0.01		<0.01					B	A			B	A, B	A, B	A
$\Delta\sigma_t$ (kg m^{-3})	ns	<0.01		<0.0001					A	B			A	A	B	C
T (°C)	<0.05	ns	<0.01	<0.001	B	A, B	A, B	A			A	B	A	A, B	A	B
S	<0.01	<0.01	<0.001	<0.0001	A	A, B	A, B	B	B	A	B	A	B, C	C	B	A
E_z (mol quanta m^{-2} d^{-1})	ns	ns	<0.0001	<0.0001							A	B	A	A	B	B
NO_3+NO_2 (µmol l^{-1})	<0.001	ns	<0.05	<0.0001	A	B	B	B			B	A	C	C	B	A
$Si(OH)_4$ (µmol l^{-1})	ns	<0.05	ns	<0.0001					A	B			B	A	A	A
PO_4 (µmol l^{-1})	ns	<0.05	<0.05	<0.0001					A	B	B	A	B	B	A	A
Protist abundance (10^6 cells l^{-1})	ns	ns	ns	<0.001									B	A	C	D

higher in the surface layer than in the bottom layer of Z_{eu} (Fig. 2, Tables 2 & 3). Due to the seasonal day length and sun elevation differences in high-latitude environments, E_z was higher during summer than in early fall and late fall (Fig. 2, Tables 2 & 3). In the 4 fjords and for the whole sampling period, $\Delta\sigma_t$ was negatively correlated with salinity ($r = -0.64$, $p < 0.0001$). Water temperature was positively correlated with E_z ($r = 0.46$, $p < 0.001$).

Nutrients

Nutrient concentrations showed large seasonal and spatial variability. NO_3+NO_2 concentrations were very low in the surface layer of Z_{eu} during both summers, but they increased in late fall (Fig. 3, Tables 2 & 3). NO_3+NO_2 increased with depth at all stations during both summers and at most stations of the 2 northernmost fjords (i.e. Nachvak and Saglek) during early and late fall. In contrast, their concentrations were relatively uniform throughout the water column of Okak and Anaktalak Fjords during early and late fall (profiles not shown). The deep waters of Nachvak and Saglek Fjords were richer in NO_3+NO_2 than those of Okak and Anaktalak. $Si(OH)_4$ and PO_4 concentrations showed similar variations to that of NO_3+NO_2. However, in summer 2007, in contrast to NO_3+NO_2 and $Si(OH)_4$, PO_4 was never depleted in the surface waters (up to 10 m, Simo-Matchim et al. 2016). A different pattern was observed in summer 2013, with NO_3+NO_2 and PO_4 almost depleted in the surface waters (up to 10 m), while surface $Si(OH)_4$ concentrations reached 10 to 16 µmol l^{-1} at inner stations of Nachvak and Okak (Table 2), suggesting high freshwater inputs from runoff in Nachvak and from the North River and Ikinet Brook in Okak. Higher surface $Si(OH)_4$ concentrations in Nachvak Fjord during summer 2013 were attributed to 3 times higher precipitation in July 2013 than in July 2007 (Fig. 3a,c). PO_4 concentrations were very similar in the surface and bottom layers of Z_{eu} (Fig. 3, Table 2 & 3).

Protist abundance and taxonomic composition

Surface layer protist (>2 µm) abundance ranged from 0.31 × 10^6 cells l^{-1} during late fall to 2.68 × 10^6 cells l^{-1} during summer 2007 (Table 2). In the bottom layer of Z_{eu}, protist abundance ranged from 0.22 to 21.7 × 10^6 cells l^{-1} during late fall and summer 2013, respectively (Table 3). In both layers, the minimum and maximum cell abundances were recorded at the

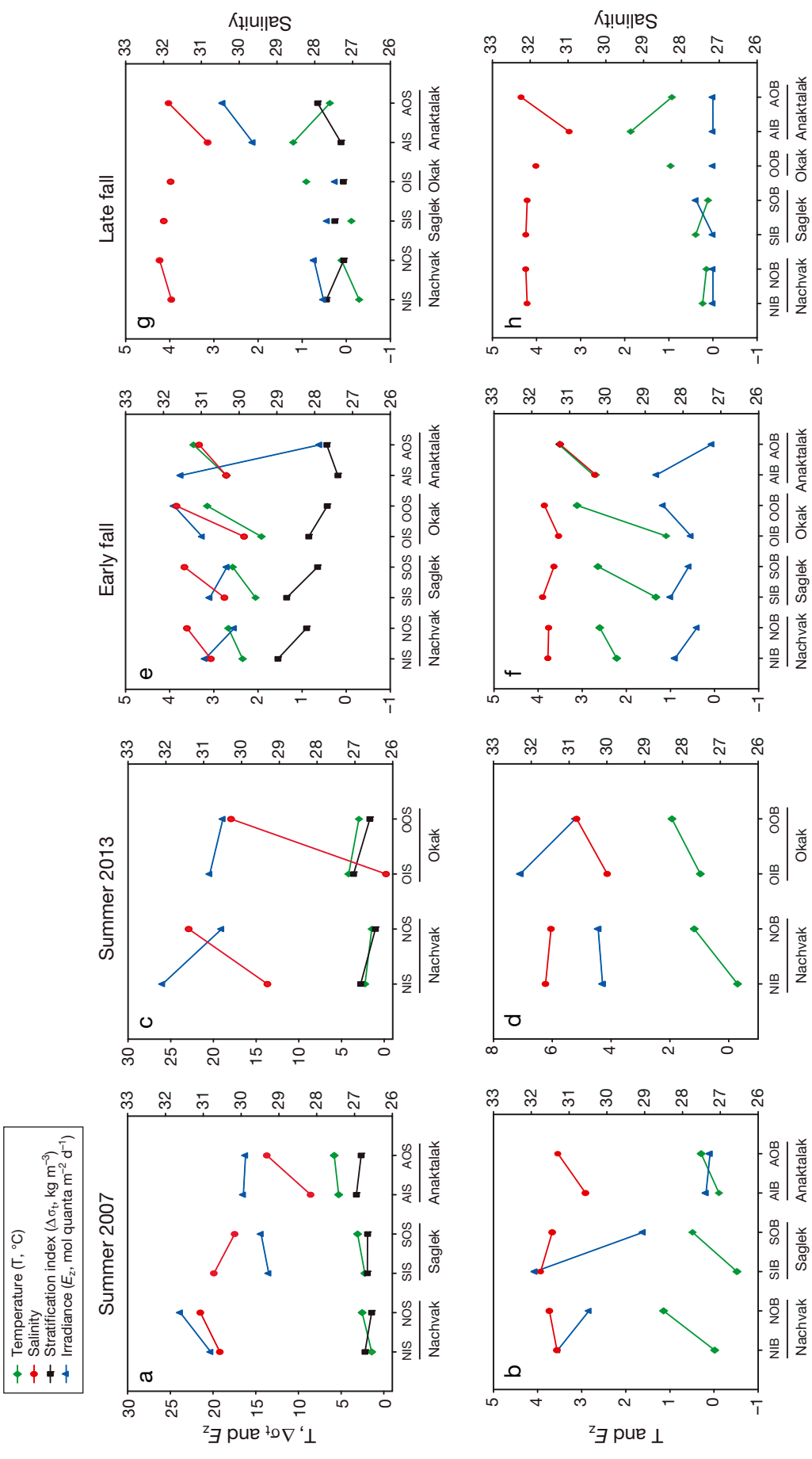

Fig. 2. Variations of water temperature (T), salinity and *in situ* irradiance (E_z) at the surface (top row) and bottom (bottom row) layers of the euphotic zone in Nachvak, Saglek, Okak and Anaktalak fjords during (a,b) summer 2007, (c,d) summer 2013, (e,f) early fall and (g,h) late fall. Variations of the stratification index ($\Delta\sigma_t$) of the upper water column are also shown. Codes for the samples are listed in Table 1. Note different scales for the *y*-axes

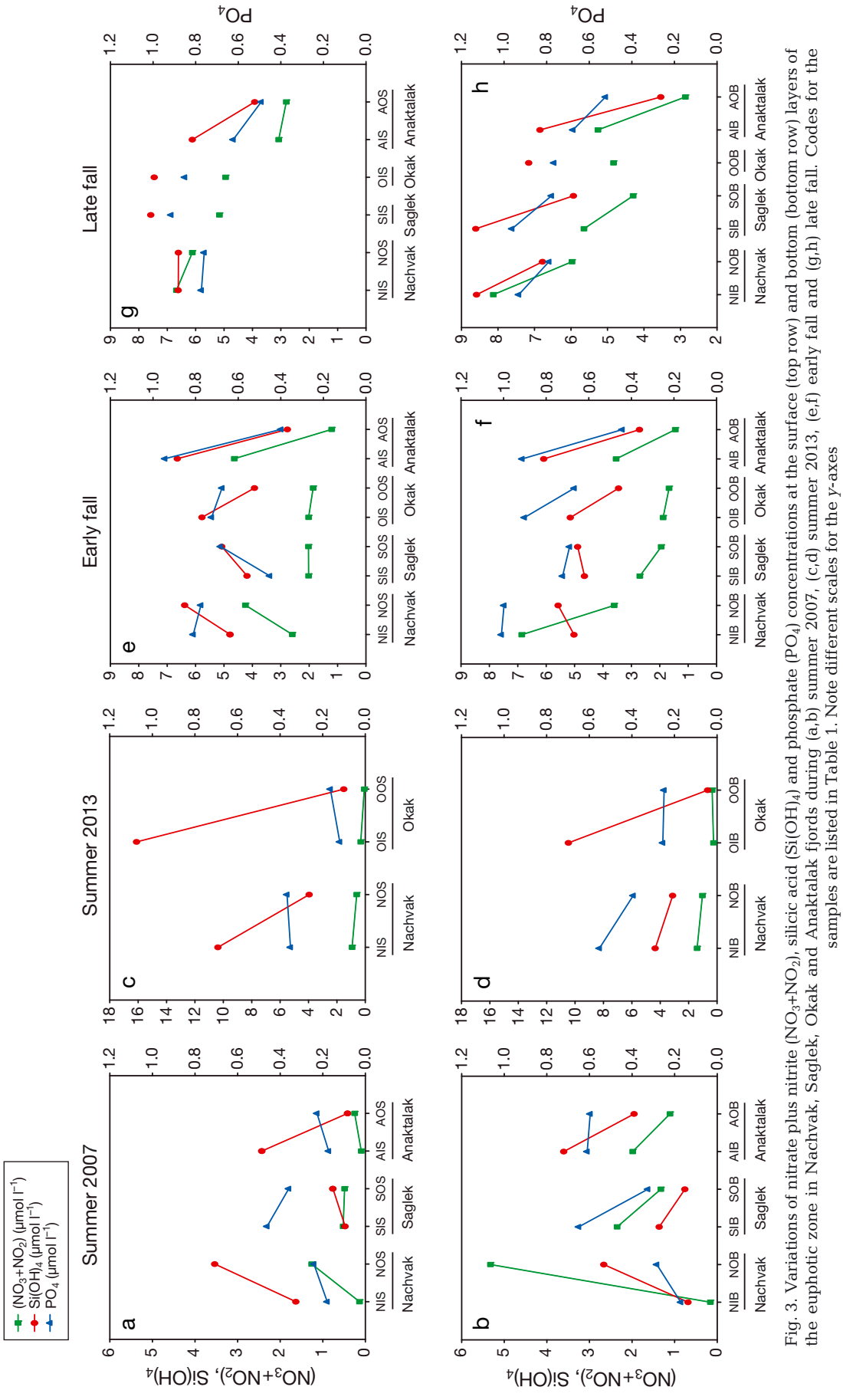

Fig. 3. Variations of nitrate plus nitrite (NO_3+NO_2), silicic acid ($Si(OH)_4$) and phosphate (PO_4) concentrations at the surface (top row) and bottom (bottom row) layers of the euphotic zone in Nachvak, Saglek, Okak and Anaktalak fjords during (a,b) summer 2007, (c,d) summer 2013, (e,f) early fall and (g,h) late fall. Codes for the samples are listed in Table 1. Note different scales for the *y*-axes

inner stations of Okak and Nachvak Fjords, respectively (Tables 2 & 3). During the fall periods, protists were more abundant in the surface layer than in the bottom layer of Z_{eu} (Tables 2 & 3).

The list of all planktonic protists recorded in the euphotic zone of Nachvak, Saglek, Okak and Anaktalak fjords during the whole sampling period is presented in Table S1 in the Supplement at www.int-res.com/articles/suppl/m572p019_supp.pdf. Among the fjords, the highest (200) and lowest (163) number of taxonomic entries were recorded in Nachvak and Okak, respectively (Table S1). However, the number of species, genera and taxonomic entries was not very different from one fjord to another. The maximum (201) and minimum (90) number of taxonomic entries were recorded during early fall and summer 2007, respectively (Table S1). In total, 131 species were reported for the whole sampling period; the number of species, genera and taxonomic entries was 2 times higher in fall than in summer (Table S1).

The taxonomic composition of the 4 fjord phytoplankton communities showed clear seasonal differences (Fig. 4). Spatial variations between fjords, stations and depths were less marked (Fig. 4). During summer 2007, the protist community was numerically dominated by diatoms and a mixed assemblage of flagellated cells (Fig. 4a). The numerically dominant taxa (and their mean abundances) were the centric diatoms *Chaetoceros gelidus* Chamnansinp, Li, Lundholm & Moestrup (210 × 10^3 cells l^{-1}) and *C. tenuissimus* Meunier (93 × 10^3 cells l^{-1}), the prymne-

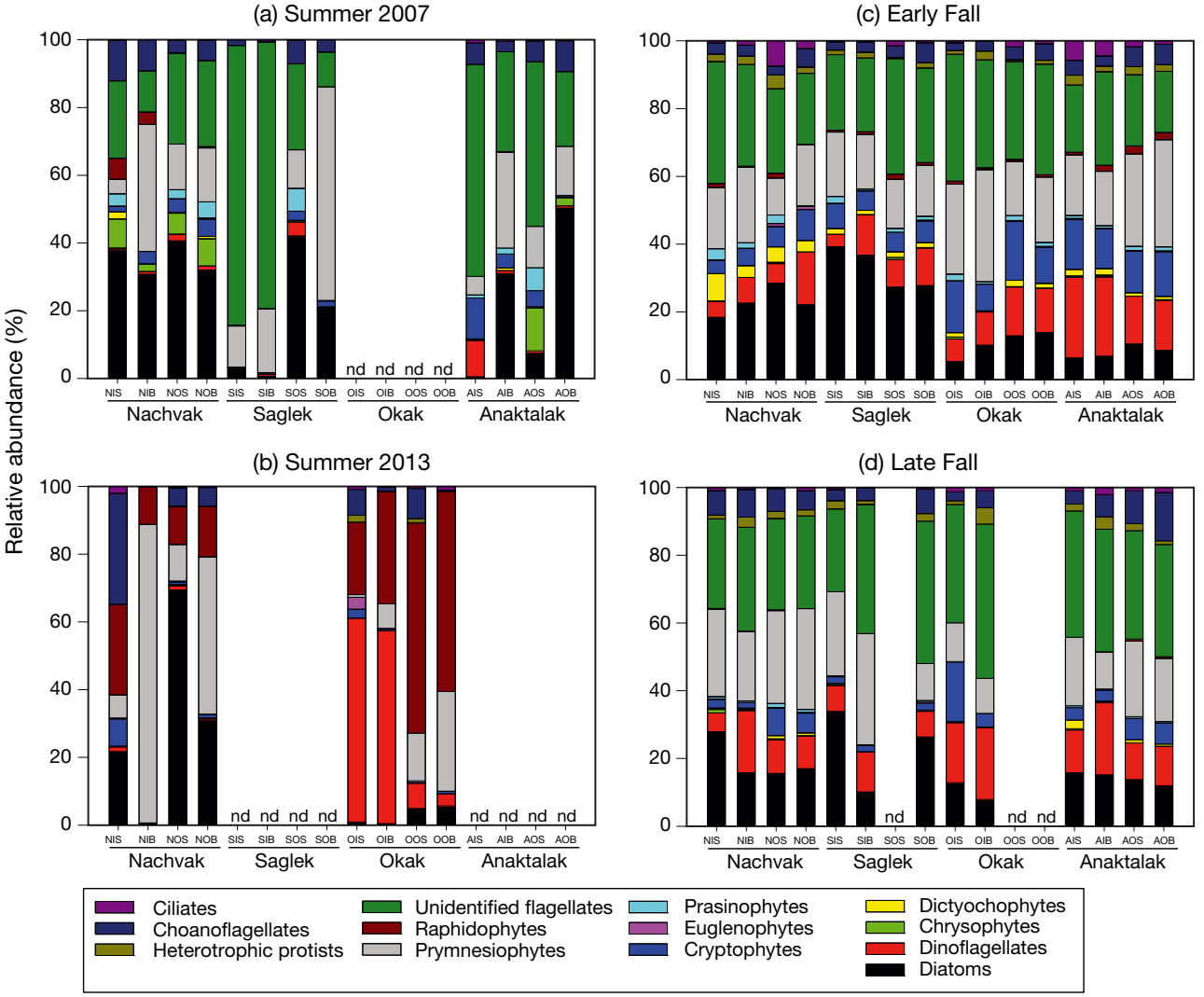

Fig. 4. Variations in the relative abundance of protist groups at the surface and bottom layers of the euphotic zone in Nachvak, Saglek, Okak and Anaktalak fjords during (a) summer 2007, (b) summer 2013, (c) early fall and (d) late fall. Codes for the samples are listed in Table 1; nd: no data available

siophytes *Chrysochromulina* spp. (≤5 µm, 142 × 10^3 cells l^{-1}) and *Phaeocystis pouchetii* (101 × 10^3 cells l^{-1}), unidentified flagellates (≤5 µm, 96 × 10^3 cells l^{-1}), unidentified Choanoflagellidea (≤5 µm, 104 × 10^3 cells l^{-1}) and the chrysophyte *Dinobryon balticum* (Schütt) Lemmermann (70 × 10^3 cells l^{-1}). *Chrysochromulina* spp. (≤5 µm) and unidentified Choanoflagellidea (≤5 µm) were observed in all summer 2007 samples (Table S1). Maximum abundances of *C. gelidus* (1.29 × 10^6 cells l^{-1}) and *P. pouchetii* (1.78 × 10^6 cells l^{-1}) were recorded in the bottom layer of Z_{eu} at inner Nachvak Fjord.

During summer 2013, Nachvak and Okak showed different phytoplankton communities (see Table 9, Figs. 4b & 5). An intense bloom of *P. pouchetii* (18 × 10^6 cells l^{-1}) and a more moderate one (1.21 × 10^6 cells l^{-1}) were observed in the bottom layer of inner and outer stations of Nachvak, respectively (Fig. 4b). In the sample from inner Nachvak, *Chaetoceros* spp. (≤20 µm) was the most abundant diatom, but its abundance did not exceed 3000 cells l^{-1}. In the sample from outer Nachvak, *Detonula confervacea* (Cleve) Gran (498 × 10^3 cells l^{-1}) and *Chaetoceros* spp. (≤20 µm, 120 × 10^3 cells l^{-1}) were the most abundant diatoms. In the surface sample of inner Nachvak, a higher proportion of choanoflagellates (mainly unidentified Choanoflagellidea, *Calliancantha natans* (Grøntved) Leadbeater and *Bicosta* spp.) was observed (Fig. 4b). Dinoflagellates (mostly *Gymnodinium/Gyrodinium* spp. [21–50 µm], *Amphidinium* cf. *kesslitzii* Schiller and *Heterocapsa rotundata* [Lohmann] Hansen) dominated the community in both samples of inner Okak (Fig. 4b). At outer Okak, unidentified flagellates (21–50 µm) were largely dominant.

During early and late fall, a well-mixed protist community was observed, with a slight numerical dominance of dinoflagellates, cryptophytes, ciliates and heterotrophic protists (Fig. 4c,d). In early fall, a weak (and nonsignificant) spatial variability was observed. The northernmost fjords of Nachvak and Saglek showed slightly higher relative abundances of diatoms (mainly *Arcocellulus cornucervis* Hasle, von Stosch & Syvertsen, *Chaetoceros* spp. [≤20 µm] and unidentified pennate diatoms [≤20 µm]), while the southernmost fjords of Okak and Anaktalak had higher relative abundances of *Chrysochromulina* spp. (≤5 µm), cryptophytes (mainly *Plagioselmis prolonga* var. *nordica* Novarino, Lucas & Morrall and unidentified Cryptophyceae [6–10 µm]) and dinoflagellates (mostly *H. rotundata*, *A.* cf. *kesslitzii* and *Gymnodinium/Gyrodinium* spp. [≤20 µm]). In late fall, both Nachvak and Saglek fjords showed higher relative abundances of prymnesiophytes (mainly *Chrysochromulina* spp. [≤5 µm]), while dinoflagellates (mainly *Gymnodinium/Gyrodinium* spp. [≤20 m] and *A.* cf. *kesslitzii*) were more numerous in Okak and Anaktalak Fjords. As in early fall, the most abundant diatoms were *A. cornucervis* and *Chaetoceros* spp. (≤20 µm).

Many protist taxonomic groups showed significant correlations with environmental variables (see Tables 5–8). During summer 2007, ciliates and various flagellate groups showed significant correlations with abiotic factors (Table 5). Of particular interest because of its numerical dominance in the bottom layer of the Z_{eu} during both summers, particularly in 2013, the prymnesiophyte *P. pouchetii* showed significant correlations with environmental factors only during summer 2007. It was positively

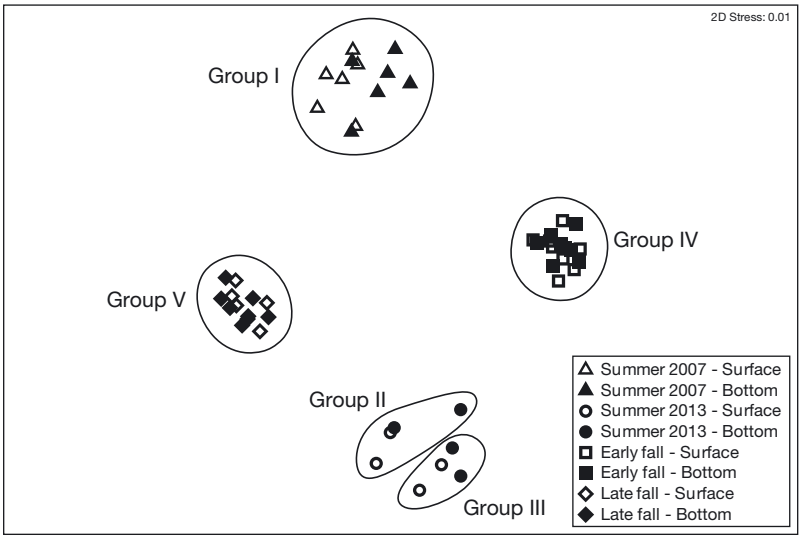

Fig. 5. Nonmetric multidimensional scaling (MDS) of the 49 samples collected in Nachvak, Saglek, Okak and Anaktalak fjords during summer 2007 (triangles), summer 2013 (circles), early fall (squares) and late fall (diamonds). Open symbols and closed symbols represent samples taken at the surface and bottom layers of the euphotic zone, respectively. Five groups of samples with similar taxonomic composition, as determined by the group-average clustering (at a similarity level of 40%), are super-imposed on the MDS

correlated with Z_m (r = 0.89, p < 0.05), water temperature (r = 0.87, p < 0.05) and NO_3+NO_2 (r = 0.86, p < 0.05). During summer 2013, more significant correlations were found (Table 6). In early fall, diatoms were significantly correlated with $\Delta\sigma_t$ while flagellate groups were related to other abiotic factors (Table 7). During late fall, more significant correlations were obtained, and only chrysophytes, cryptophytes and heterotrophic protists did not show significant links with environmental factors (Table 8).

Variability in protist taxa

In the euphotic zone, 5 groups of samples with taxonomically similar protists were assessed with the group-average cluster analysis superimposed on the MDS (Fig. 5). The global 1-way ANOSIM revealed significant differences between the 4 sampling periods (global R = 1, p < 0.001). The taxonomic composition was also significantly different between Nachvak and Okak fjords during summer 2013 (global R = 0.68, p < 0.05).

Group I was composed of all samples collected during summer 2007 and was represented by unidentified flagellates (37.2%), diatoms (24.8%) and prymnesiophytes (19.8%). The SIMPER analysis determined an average similarity of 42.4% between samples, and the main taxonomic entities whose combination leads to this group were unidentified flagellates (≤10 µm), the prymnesiophytes *Chrysochromulina* spp. (≤5 µm), unidentified Choanoflagellidea (≤5 µm) and the centric diatom *C. gelidus* (Table 9).

Group II was made up of all samples collected in Nachvak Fjord during summer 2013. This group was mainly represented by prymnesiophytes (38.1%), diatoms (30.5%) and raphidophytes (15.9%). The SIMPER determined an average similarity of 21.7% between samples, and uniden-

Table 5. Pearson's correlation coefficients between the abundance of protist taxonomic groups and environmental variables in Nachvak, Saglek, Okak and Anaktalak fjords during summer 2007. Samples were collected at the surface and bottom layers of the euphotic zone. Abbreviations of environmental variables are defined in Table 2. *p < 0.05, **p < 0.01, ***p < 0.001, ****p < 0.0001. For each season, only significant correlations are shown. Protist abbreviations are defined in Fig. 6

	Z_{eu}	Z_{nut}	T	S	E_z	PO_4
Dino				−0.73**		
Chryso		−0.69*				
Crypto	−0.69*			−0.63*		−0.65*
Prymnesio					−0.67*	
Un. flag	0.66*					
Choano	−0.83***					
Cil	−0.60*		0.60*	−0.81**	0.73*	

Table 6. As in Table 5, but for summer 2013

	Z_m	$\Delta\sigma_t$	T	S	E_z	NO_3+NO_2	$Si(OH)_4$	PO_4
Diat	0.84**	−0.73*						
Dino		0.73*		−0.74*			0.73*	
Chryso					0.97****			
Eugleno			0.71*	−0.96***			0.87**	
Prymnesio			−0.77*	0.75*	−0.73*			0.78*
Un. flag						−0.72*		
Choano					0.85**			
Het. protists			0.81*	−0.72*				−0.74*

Table 7. As in Table 5, but for early fall

	Z_m	Z_{nut}	$\Delta\sigma_t$	T	S	E_z
Diat			0.63**			
Dino	0.58*		0.77***			
Chryso					−0.55*	0.55*
Crypto	0.57*		−0.74**			
Eugleno				0.59*		
Prasino						0.55*
Un. flag		−0.50*				
Choano				0.69**		−0.51*

Table 8. As in Table 5, but for late fall

	Z_{eu}	Z_m	Z_{nut}	$\Delta\sigma_t$	T	E_z	$Si(OH)_4$	PO_4
Diat		0.56*			−0.57*			
Dino		−0.63*			0.77**			
Dictyocho						0.64*		−0.56*
Eugleno	0.58*		0.85***					
Prasino		0.59*	0.58*					
Prymnesio		0.64*			−0.60*			
Raphido				0.68*			−0.75**	−0.74**
Un. flag					0.56*			
Choano	0.55*			0.71**			−0.70**	−0.62*
Cil		−0.67*			0.67*			−0.57*

Table 9. Results of SIMPER analysis showing the breakdown of similarities within groups into contribution from each taxonomic entity. Protists are ordered by decreasing average contribution to a total of more than 70%

Main taxa	Contribution (%)
Group I (Summer 2007)	
Average similarity	42.4
Flagellates (≤5 µm)	42.9
Chrysochromulina spp. (≤5 µm)	10.9
Flagellates (6–10 µm)	8.4
Choanoflagellidea (≤5 µm)	6.2
Chaetoceros gelidus	4.2
Group II (Nachvak, Summer 2013)	
Average similarity	21.7
Flagellates (≤5 µm)	23.9
Phaeocystis pouchetii	19.2
Detonula confervacea	16.4
Chaetoceros spp. (≤5 µm)	6.8
Choanoflagellidea (≤5 µm)	5.3
Group III (Okak, Summer 2013)	
Average similarity	46.4
Flagellates (≤5 µm)	47.5
Heterocapsa rotundata	17.9
Flagellates (6–10 µm)	13.4
Group IV (Early fall)	
Average similarity	52.1
Flagellates (≤5 µm)	26.4
Chrysochromulina spp. (≤5 µm)	14.9
Arcocellulus cornucervis	7.4
Gymnodinium/*Gyrodinium* spp. (≤20 µm)	6.3
Plagioselmis prolonga var. *nordica*	4.3
Unidentified pennate diatoms (≤20 µm)	3.9
Flagellates (6–10 µm)	3.8
Heterocapsa rotundata	3.3
Prymnesiophyceae (≤5 µm)	3.1
Group V (Late fall)	
Average similarity	57.3
Flagellates (≤5 µm)	34.7
Chrysochromulina spp. (≤5 µm)	10.9
Gymnodinium/*Gyrodinium* spp. (≤20 µm)	8.5
Flagellates (6–10 µm)	5.8
Prymnesiophyceae (≤5 µm)	4.9
Amphidinium cf. *kesslitzii*	3.1
Chaetoceros spp. (≤20 µm)	3.0

tified flagellates (≤5 µm), the prymnesiophyte *P. pouchetii*, the centric diatoms *D. confervacea* and *Chaetoceros* spp. (≤5 µm) and unidentified Choanoflagellidea (≤5 µm) as the main taxa leading to Group II (Table 9).

Group III was composed of all samples collected in Okak in summer 2013 and was dominated by raphidophytes (43.9%) and dinoflagellates (32.1%). The average similarity between the samples was 46.4%, and unidentified flagellates (≤10 µm) and the dinoflagellate *H. rotundata* were the main taxa contributing to this group (Table 9).

Group IV was composed of all samples collected during early fall and was numerically represented by unidentified flagellates (27.2%), prymnesiophytes (20.1%) and diatoms (18.6%). The similarity between the samples was 52.1%, and the main taxa explaining this similarity were unidentified flagellates (≤10 µm), the prymnesiophytes *Chrysochromulina* spp. (≤5 µm) and unidentified Prymnesiophyceae (≤5 µm), the diatoms *A. cornucervis* and unidentified pennate diatoms (≤20 µm), the dinoflagellates *Gymnodinium*/*Gyrodinium* spp. (≤20 µm) and *H. rotundata*, and the cryptophyte *P. prolonga* var. *nordica* (Table 9).

Group V included all samples collected during late fall and was mostly composed of unidentified flagellates (33.5%), prymnesiophytes (20.5%) and diatoms (17.2%). The average similarity between the samples was 57.3%, and unidentified flagellates (≤10 µm), the prymnesiophytes *Chrysochromulina* spp. (≤5 µm) and unidentified Prymnesiophyceae (≤5 µm), the dinoflagellates *Gymnodinium*/*Gyrodinium* spp. (≤20 µm) and *A.* cf. *kesslitzii*, and the diatom *Chaetoceros* spp. (≤20 µm) were the main taxa explaining this group (Table 9).

Variability in protist taxonomic groups

For each season, the distance-based redundancy analysis (dbRDA) highlighted relationships between taxonomic groups of protists observed at both surface and bottom layers of Z_{eu}, and environmental variables (Fig. 6). Various ecological niches were observed for each sampling period. During summer 2007, the first 2 axes of the dbRDA explained 82.0% of the fitted variation (Fig. 6a). The first axis (dbRDA1) explained 55.2% of this variation and was strongly correlated with the euphotic zone depth (r_p = −0.87) (Fig. 6a). The second axis (dbRDA2) explained 26.8% of the variation and the main variables correlated to this axis were salinity (r_p = 0.70) and water temperature (r_p = −0.56). The dbRDA revealed clear differences in environmental conditions and protist group abundances between the surface and bottom layers of Z_{eu}. Diatoms, raphidophytes and choanoflagellates were more abundant in waters with a shallow euphotic zone and nutracline, whereas unidentified flagellates were more numerous in waters with a deep euphotic zone. Prymnesiophytes were abundant in salty, cold and low-lit waters in the bottom layer of Z_{eu}, whereas dinoflagellates and ciliates were associated with less salty, warm, stratified and well-lit waters. The other protist groups were linked to warm, well-lit, and PO_4-depleted waters. The Bio-

Env analysis identified salinity and euphotic zone depth, which combined explained 70% of the variability in protist groups during summer 2007.

During summer 2013, the first 2 axes of the dbRDA explained 78.2% of the fitted variation (Fig. 6b). The first axis (dbRDA1) explained 48.7% of this variation and was strongly correlated with $Si(OH)_4$ (r_p = 0.52), PO_4 (r_p = −0.50) and NO_3+NO_2 (r_p = −0.50). The second axis (dbRDA2) explained 29.5% of the fitted variation, and stratification index (r_p = −0.75) and *in situ* irradiance (r_p = 0.54) were the main variables explaining this axis. The dbRDA revealed clear differences in environmental conditions and protist groups between Nachvak and Okak fjords, with

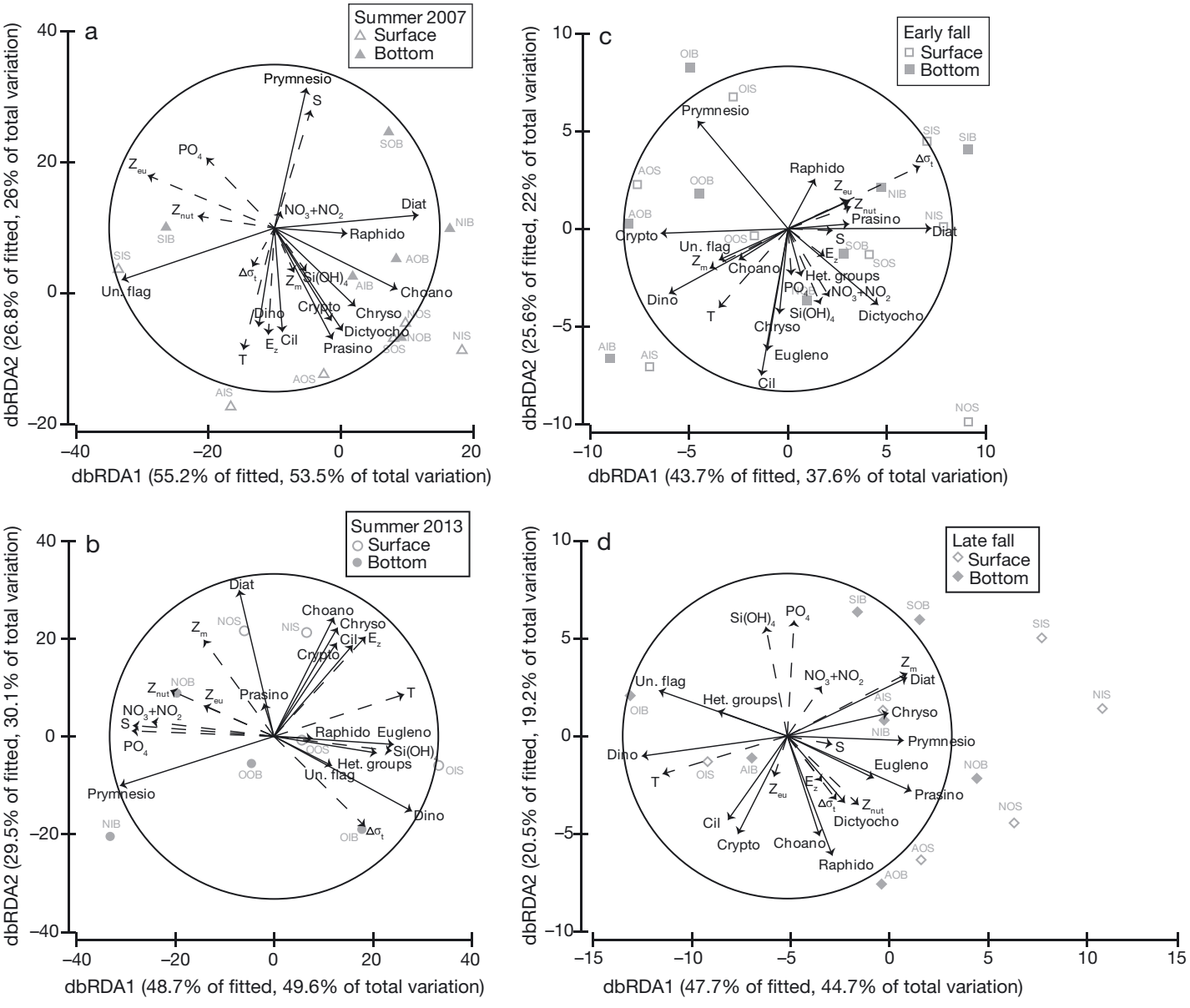

Fig. 6. Distance-based redundancy analysis (dbRDA) of samples collected in Nachvak, Saglek, Okak and Anaktalak fjords, showing taxonomic groups of protists (continuous lines) in relation to environmental variables (dotted lines) during (a) summer 2007, (b) summer 2013, (c) early fall and (d) late fall. The circle presents a vector overlay illustrating the contribution of protist taxonomic groups and environmental variables to the dbRDA axes. Codes and symbols in grey represent samples collected at the surface and bottom layers of the euphotic zone. Codes for samples are listed in Table 1. Abbreviations of environmental variables are defined in Table 2. Diat: diatoms; Dino: dinoflagellates; Chryso: chrysophytes; Dictyocho: dictyochophytes; Crypto: cryptophytes; Eugleno: euglenophytes; Prasino: prasinophytes; Prymnesio: prymnesiophytes; Raphido: raphidophytes; Un. flag: unidentified flagellates; Het. protists: heterotrophic protists; Choano: choanoflagellates; Cil: ciliates

Nachvak having colder and saltier waters, deeper surface mixed layer and nutracline, PO_4- and NO_3+NO_2-richer waters and higher abundances of diatoms and prymnesiophytes in the surface and bottom layer of Z_{eu}, respectively. Diatoms were associated with well-mixed waters with a deep surface mixed layer, whereas prymnesiophytes were associated with colder, more saline and NO_3+NO_2- and PO_4-rich waters. In contrast, dinoflagellates and unidentified flagellates were more abundant in well-stratified waters with a shallow nutracline and surface mixed layer. Euglenophytes and heterotrophic protists were associated with warm, fresher, $Si(OH)_4$-rich but NO_3+NO_2- and PO_4-depleted waters, whereas choanoflagellates, chrysophytes, ciliates and cryptophytes were linked to well-lit and relatively warm surface waters. The Bio-Env analysis selected 5 environmental variables: salinity, stratification index, *in situ* irradiance, PO_4 and NO_3+NO_2 which, when combined, explained 80% of the summer 2013 community.

For early fall, the first 2 axes of the dbRDA explained 69.3% of the fitted variation (Fig. 6c). The first axis (dbRDA1) explained 43.7% of this variation and was highly correlated with the stratification index (r_p = 0.68). Water temperature (r_p = −0.64) and $Si(OH)_4$ (r_p = −0.61) were strongly correlated with the second axis (dbRDA2), which explained 25.6% of the fitted variation. Diatoms and prasinophytes were more abundant in stratified waters, with a deep euphotic zone and nutracline, whereas dinoflagellates, cryptophytes and unidentified flagellates were linked with well-mixed waters with a deep surface mixed layer but shallow nutracline. Ciliates, euglenophytes and chrysophytes were associated with warm and nutrient-replete waters, whereas raphidophytes were related to colder and less-replete waters. Prymnesiophytes were more abundant under lower *in situ* irradiance and nutrient concentrations than dictyochophytes and heterotrophic protists. Water temperature, salinity, stratification index and $Si(OH)_4$ were the 4 variables identified by the Bio-Env, explaining 41% of the early fall protist community.

In late fall, the first 2 axes of the dbRDA explained 68.2% of the fitted variation (Fig. 6d). The first axis (dbRDA1) explained 47.7% of this variation and was correlated with surface mixed layer depth (r_p = 0.62) and water temperature (r_p = −0.59). The second axis (dbRDA2) explained 20.5% of the fitted variation, and $Si(OH)_4$ (r_p = 0.59) was the main variable explaining it. Diatoms, prymnesiophytes, chrysophytes, prasinophytes and euglenophytes were more abundant in cold waters with a deep surface mixed layer, whereas dinoflagellates, unidentified flagellates and heterotrophic protists were associated with warmer waters with shallower surface mixed layers. The other protist groups (i.e. raphidophytes, choanoflagellates, cryptophytes, dictyochophytes and ciliates) were more abundant in well-stratified waters with a deep nutracline and euphotic zone, and the lowest nutrient concentrations. The Bio-Env analysis revealed that the mixed layer depth alone explained 40% of the variability in protist groups. When combined with other environmental variables, the percentage of variation explained decreased.

DISCUSSION

This study highlighted a strong seasonality in the environmental variables of the Labrador fjords, allowing us to study the succession of the phytoplankton communities. Surprisingly, the phytoplankton taxonomic composition was not significantly different between the 4 fjords, even though variability in the abiotic factors is perceptible. The lack of significant spatial differences in protist composition could be explained by (1) the strong influence of Labrador Shelf waters on the studied fjords and (2) the relatively short distances between them (Fig. 1), causing some evenness in protist communities. Differences between fjords might have been better observed at the onset of the summer bloom, which was not possible during this study. However, in summer 2013, which was characterized by heavy precipitation, Nachvak and Okak fjords showed large taxonomic differences.

Summers 2007 and 2013

Both summer 2007 and 2013 protist communities were very different. During summer 2007, the community was mainly dominated by the silicon-requiring diatoms *Chaetoceros gelidus* and *C. tenuissimus*, the prymnesiophytes *Chrysochromulina* spp. (≤5 µm) and *Phaeocystis pouchetii,* and the chrysophyte *Dinobryon balticum*. These taxa were associated with nitrate- and silicic acid-depleted surface waters (Simo-Matchim et al. 2016). Summer diatoms and chrysophytes were associated with cooler and less saline surface waters, respectively. A similar pattern was also observed in the tide water glacial influenced-Godthåbsfjord (West Greenland), where diatoms were associated with cooler waters while *D. balticum* was related to low-saline surface waters (Krawczyk et al. 2015). During this period, the sum-

mer protist community was mainly dominated by unidentified flagellates (37.2%), diatoms (24.8%) and prymnesiophytes (19.8%), indicating a post-bloom intermediate situation between a diatom-based and a flagellate-based system (Fig. 4a). As nitrate and silicic acid were depleted in the surface waters, flagellates and less silicon-requiring algae, such as *P. pouchetii*, were favoured over diatoms. Similarly, Kubiszyn et al. (2014) noted a predominance of dinoflagellates (44%), diatoms (27%) and ciliates (13%) during summer along a longitudinal transect from the open sea to Kongsfjorden, West Svalbard.

Heavy precipitation coincided with our sampling performed in July 2013, resulting in high inputs of particles, dissolved silicon and possibly micronutrients in inner Nachvak surface waters coming from glaciers of the Torngat Mountains. A similar situation was also observed for Okak as a result of freshwater runoffs. This created a large horizontal nutrient gradient in surface waters between the inner and outer parts of these fjords (Table 2). During summer 2013, an intense bloom of *P. pouchetii* (18×10^6 cells l^{-1}; 83% of total protists >2 µm) occurred in the bottom layer of the euphotic zone in inner Nachvak where phosphate was abundant (0.55 µmol l^{-1}). In addition, *P. pouchetii* was 15 times less abundant (1.21×10^6 cells l^{-1}) but still represented almost 50% of the total protist community in the bottom layer of outer Nachvak. Blooms of *P. pouchetii* represent a recurrent phenomenon in Scandinavian fjords, as they have been observed at various locations such as in Balsfjord (Eilertsen et al. 1981), Kongsfjorden (Riebesell et al. 1995), Altafjord and Porsangerfjord (Eilertsen & Frantzen 2007). These blooms follow the sea ice retreat during summer, when meltwater-induced stratification reduces mixing depth and subsequently increases mean irradiance in the surface layer of the water column (Heimdal 1989, Marchant et al. 1991). Both Groups II and III, made up of the summer 2013 samples, were mainly composed of raphidophytes, prymnesiophytes and dinoflagellates. Although diatoms were relatively abundant in Group II, both communities in summer 2013 can nevertheless be seen as flagellate-based systems, as confirmed by the SIMPER analysis showing *P. pouchetii*, *H. rotundata* and unidentified flagellates as the main taxa leading to Groups II and III.

Phaeocystis pouchetii was abundant during both summers of this study: (1) in summer 2007 when diatom abundances were high and (2) in summer 2013 when diatoms were less abundant. Hansen & Eilertsen (2007) previously indicated a stochastic behaviour for *P. pouchetii*, i.e. it can be abundant at both high and low diatom abundances. In Scandinavian fjords, the interannual proportions between diatoms and *P. pouchetii* were variable (Throndsen & Heimdal 1976, Eilertsen et al. 1981, Lutter et al. 1989). Degerlund & Eilertsen (2010) showed that *P. pouchetii* has the ability to grow under silicic acid-depleted conditions and hence to be abundant throughout the bloom. In Norwegian fjords, Heimdal (1974) observed that *P. pouchetii* often co-occurred with *Chaetoceros* spp., whereas Eilertsen et al. (1989) reported that *Phaeocystis* spp. and the centric diatom *C. socialis* Lauder were the 2 dominant taxa during the spring bloom in these fjords. It should be appropriate at this point addressing the recent discovery of *C. gelidus* in Danish cold waters (Chamnansinp et al. 2013), which may have been previously misidentified in Scandinavian fjords as *C. socialis*, whose geographic distribution does not include polar/subpolar regions. However, such confirmation would mean revisiting all Scandinavian fjord samples for an accurate identification of *C. gelidus*.

A maximum of 101 taxa, 27 genera and 57 species were identified in Labrador fjords during both summers 2007 and 2013 (Table S1). The summer protist richness in Labrador fjords is comparable to West Spitsbergen fjords. In Hornsund and Kongsfjorden, 109 taxa, 31 genera and 61 species were recorded during summer 2002 (Wiktor & Wojciechowska 2005). However, the number of taxa in Labrador fjords during both summers (90 taxa in 2007 and 101 in 2013) was 2-fold higher than in Kongsfjorden, where a maximum of 51 taxa was reported during summers 2007, 2009 and 2010 (Kubiszyn et al. 2014).

During summers 2007 and 2013, NO_3+NO_2 was nearly depleted in the surface waters of most fjord stations (Table 2), suggesting that phytoplankton uptake was greater than supply. In addition, the molar ratios of NO_3+NO_2 to PO_4 and of NO_3+NO_2 to $Si(OH)_4$ in the surface waters ranged from 0.4 to 5.3 and from 0.02 to 1.08, respectively. These values are lower than the critical values of 16 and 1.1 of Redfield et al. (1963) and Brzezinski (1985), respectively. These results indicate that dissolved nitrogen was the nutrient in lowest availability for phytoplankton growth during summer. However, at stations with an $Si(OH)_4$ concentration lower than 2 µmol l^{-1}, diatoms were probably co-limited by dissolved silicon availability (see Simo-Matchim et al. 2016).

For the whole sampling period, the deep waters of Nachvak and Saglek fjords were richer in nutrients than those of Okak and Anaktalak fjords. This could explain the higher abundances of diatoms recorded at Nachvak and Saglek, whereas flagellates were more

abundant in Okak and Anaktalak. Although the ANOSIM did not reveal significant differences in protist taxonomic composition between the fjords, the spatial differences in nutrient concentrations could also explain why Nachvak Fjord had the highest number of taxa (200 taxa, Table S1) while the lowest richness was recorded in Okak Fjord (163 taxa, Table S1). This relation between marine protist diversity and nutrient richness has been previously reported in Arctic studies (Bluhm et al. 2011, Michel et al. 2012).

Early fall and late fall

Groups IV and V, respectively made up of early fall and late fall samples, were mainly composed of various proportions of unidentified flagellates and prymnesiophytes. Flagellates dominate the fall community since they have lower light requirements than diatoms (Takahashi et al. 1978, Harrison et al. 1983), whose photosynthetic activity can be limited by the low autumn irradiances. Moreover, motility and migration help them to override sedimentation and contribute to the assimilation of nutrients from deep layers (Estrada & Berdalet 1997). Since flagellates were far dominant in both Groups IV and V, we therefore qualify the fall protist community as a flagellate-based system. The community size structure as well as phytoplankton production support this idea by showing relatively high abundance of picophytoplankton (<2 µm) along with low production and biomass of large cells (Simo-Matchim et al. 2016).

For the whole sampling period, the highest protist richness was observed in early fall, with 201 taxa, 72 genera and 131 species recorded; it was 2-fold higher than in summer (Table S1). This supports the fact that both summer communities were mainly dominated by 2 groups (diatoms and prymnesiophytes), while in fall, we observed a mixed community showing higher occurrence percentages of various flagellate taxa (dictyochophytes, euglenophytes and prasinophytes; Table S1).

Seasonal variability in environmental forcing

Irradiance is an important factor for species composition in high-latitude ecosystems, and it was a major explanatory variable of our summer 2013 phytoplankton community. Irradiance largely influences the layer in which phytoplankton can be found within the water column. During summer, the high light intensities experienced by phytoplankton in the well-lit surface layer may sometimes be higher than their photoacclimation capacities, and thus expose them to photoinhibition processes. As a consequence, cells move downward in the water column, and their abundance in summertime is often higher in the bottom layer of the euphotic zone compared to the surface layer. This was the case in our study, where the total cell abundance averaged 1.26×10^6 cells l^{-1} in the surface layer and 2.06×10^6 cells l^{-1} in the bottom layer of the euphotic zone, where *in situ* irradiance was 6 times lower than in the surface layer (Tables 2 & 3). In addition to light avoidance, downward migration of phytoplankton is also related to nutrient limitation experienced in the surface layer of the water column (Gerbersdorf & Schubert 2011, Hall & Paerl 2011).

Water temperature was a major variable controlling the phytoplankton community in early fall. This finding was not surprising since the highest temperature averaged over the euphotic zone was recorded during early fall (data not shown). In early autumn, water masses, warmed up (during summer) and relatively stratified, are favourable for flagellated protists whose abundances become much higher compared to summer.

The surface mixed layer depth (Z_m) was the only explanatory variable of the late fall community. In late fall, the cooling of the surface layer associated with reduced irradiance and windy conditions contribute to weaken the stratification and to favour the deepening of the Z_m. Diehl et al. (2002) had previously noted that vertical mixing, by affecting the capacity of plankton cells to maintain their position within the water column, is a key variable that controls marine protist communities.

Annual protist succession

Although our sampling did not cover the whole phytoplankton growth season, we can however suggest a protist succession in Labrador fjords by combining our results with those from similar Scandinavian fjords. During winter in Kongsfjorden, Iversen & Seuthe (2011) noted a persistent microbial community dominated by small flagellates (2–5 µm). In Kobbefjord, the winter pelagic protist community was mainly composed of the dinoflagellate *Gymnodinium* spp. (>60%) (Mikkelsen et al. 2008). During the spring bloom in Kongsfjorden, the dominant species changed from April to May. The succession went from a *Fragilariopsis* spp.-dominated community in April to a *Chaetoceros* spp.-dominated community in

early May (Hodal et al. 2012). In the first half of May, *Thalassiosira* spp. dominated the community, and in the second half, *P. pouchetii* colonies were dominant (Hodal et al. 2012). In Altafjord and Porsangerfjord, the vernal phytoplankton community was dominated by *P. pouchetii*, the centric diatoms *Thalassiosira nordenskioeldii* Cleve and *C. socialis* (or *C. gelidus* as recently recorded in cold polar waters by Chamnansinp et al. 2013), and the pennate diatoms *Fragilariopsis oceanica* (Cleve) Hasle and *F. cylindrus* (Grunow ex Cleve) Frenguelli (Eilertsen & Frantzen 2007). In summer, higher abundances of dinoflagellates and *Emiliania huxleyi* (Lohmann) Hay & Mohler were recorded in both fjords. The fall bloom consisted of the same centric diatoms as above together with *P. pouchetii* (Eilertsen & Frantzen 2007). Based on these observations and our SIMPER analysis (Table 9), we suggest the following annual succession in the Labrador fjord protist community: dinoflagellates and small flagellated cells in winter — *Fragilariopsis* spp., *Chaetoceros* spp., *Thalassiosira* spp. and *P. pouchetii* in spring — *Chaetoceros* spp., *P. pouchetii* and *Chrysochromulina* spp. in summer — flagellates, *Gymnodinium/Gyrodinium* spp. and *Chrysochromulina* spp. in fall.

Distribution of *P. pouchetii* in Northern Hemisphere fjords

In a review on the main species characteristics of the phytoplankton spring bloom in Northeast Atlantic and Arctic waters (68–80° N), Degerlund & Eilertsen (2010) pointed out a tendency for *P. pouchetii* to increase in importance towards the north. They noticed a positive correlation between its abundance and latitude along the coast, confirming its northerly distribution. This finding corroborates our results, showing an increase in *P. pouchetii* abundance from the southernmost Anaktalak Fjord (56° N) to the northernmost Nachvak Fjord (59° N), where its abundance reached 18×10^6 cells l^{-1} in summer 2013. According to Degerlund & Eilertsen (2010), *P. pouchetii* was important at all locations of the Northeast Atlantic and the Arctic, but was most predominant in Altafjord and Porsangerfjord (northern Norway). Previous studies have also indicated its dominance in these areas, with large interannual variations in its abundance relative to diatoms (Throndsen & Heimdal 1976, Eilertsen et al. 1981, Lutter et al. 1989). *Phaeocystis pouchetii* was present at water temperatures between −1.7 and 9°C, and there was a weak trend towards lower abundances above 5°C. Schoemann et al. (2005) also reported that *P. pouchetii* was better adapted to cold temperatures below 5°C prevailing in arctic waters. This observation is in good agreement with our summer 2013 bloom of *P. pouchetii* which occurred in the bottom layer of the euphotic zone at Nachvak Fjord where the water temperature was −0.3°C. Various other studies in West Spitsbergen (Svalbard) also indicated that *P. pouchetii* was consistently recorded during summer (Wiktor & Wojciechowska 2005, Kubiszyn et al. 2014). During this study, we observed a linear relationship between *P. pouchetii* abundance and water temperature ranging from −0.5 to 5.8°C ($r = 0.87$, $p < 0.05$), showing that this prymnesiophyte is well-adapted to growth at ambient temperatures below 6°C (Schoemann et al. 2005, Degerlund & Eilertsen 2010).

Mechanisms behind *Phaeocystis* success

Several mechanisms could be responsible for the success of *P. pouchetii*: alternation between its colonial and flagellate stages (Schoemann et al. 2001), efficient nutrient uptake, high photosynthetic activity and reduced grazing (Schoemann et al. 2005).

The matrix in the *Phaeocystis* colonial stage can act as an energy and nutrient reservoir, giving a competitive advantage when resources (light and nutrients) are scarce or highly fluctuating (Veldhuis et al. 1991, Schoemann et al. 2001). Hamm (2000) suggested that the gel-like structure of the colony matrix could explain the general resistance of *Phaeocystis* to loss processes (colony degradation, cell lysis, viral infection, grazing, sinking, aggregation and sedimentation). The flagellated cells tend to be adapted to oligotrophic environments (Edvardsen & Imai 2006) and can persist in nutrient-poor waters.

Because of its small size and higher surface-to-volume ratio, *Phaeocystis* can outcompete diatoms under nutrient-poor conditions. Furthermore, its adaptation to light fluctuations and its ability to use organic phosphorus and sequester iron, an essential oligonutrient for algal growth, are other assets for its success (Schoemann et al. 2005). For instance, *Phaeocystis* is capable of rapid carbon incorporation at relatively low irradiances, while at high irradiances, photoinhibition may be less severe than in diatoms (Lancelot & Mathot 1987) or even absent (Verity et al. 1988). Davidson & Marchant (1992) also indicated that *Phaeocystis* might be able to adapt to a wide range of light climates. Cota et al. (1994) added that *Phaeocystis* can even survive a number of days

in dark waters and that it had a higher photosynthetic activity than diatoms since it can maintain its growth at low light levels. Moreover, Tortell et al. (2002) observed increased dominance of *Phaeocystis* relative to diatoms under low CO_2 conditions and suggested that CO_2 can possibly influence competition among species. Along with this finding, the CO_2 partial pressure at Nachvak Fjord during summer 2013 was very low, ranging from 230 to 300 µatm (B. Else pers. comm.) and coinciding with high *P. pouchetii* abundances and very low diatom abundances.

Data on *Phaeocystis* grazing are sometimes difficult to interpret, mostly due to the large size range of both life forms (free-living cells and colonies, ≈3–8 µm to 1.5–2 mm; Throndsen et al. 2007) and potential grazers (≈20 µm to cm). Due to their small size, single *Phaeocystis* cells are not efficiently grazed by mesozooplankton, but are often ingested by microzooplankton (e.g. crustaceans), ciliates and heterotrophic dinoflagellates (Nejstgaard et al. 2007). Most of the reported resistance of *Phaeocystis* to grazing could then be attributed to a size mismatch or to the mechanical hindrance caused by the presence of the mucilaginous matrix (Schoemann et al. 2005). Another reason is that zooplankton grazing can be taxon-specific. In the laboratory, the copepods *Acartia* spp. selected diatoms over *P. pouchetii* (Verity & Smayda 1989). Selective grazing of diatoms was also reported for krill (Haberman et al. 2003).

Despite many studies, the mechanisms responsible for diatom or *Phaeocystis* dominance during the phytoplankton bloom are still unclear and need further investigation. Having a diatom- or a *Phaeocystis*-dominated community entails many implications for the ecosystem. Diatom-dominated ecosystems are characterized by important primary production, high biomass of large cells and numerical dominance of nanophytoplankton (>2 µm). The herbivorous food web is predominant in such systems, with a large proportion of the production being transferred to higher trophic levels (Legendre & Rassoulzadegan 1995). In *Phaeocystis*-dominated systems, ungrazed and senescent cells are remineralized by heterotrophic bacteria, and most of the production flows through the microbial food web (Schoemann et al. 2005). Indeed, in Scandinavian fjords dominated by *P. pouchetii*, the structure and functioning of the community is influenced by dissolved organic carbon released by ungrazed colonies. This leads to the production of transparent exopolymer particles which enhance the formation of *Phaeocystis*-derived aggregates that are vertically exported out of the system (Reigstad et al. 2000).

CONCLUSION

This study was conducted in 4 Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during summers 2007 and 2013, early fall and late fall. Our results revealed a strong seasonality in the taxonomic composition of the phytoplankton community. However, despite large environmental differences between fjords, stations and sampled depths (surface and bottom layers of the euphotic zone), the protist taxonomic composition showed little spatial variability. Surprisingly, the protist richness was not much different between the 4 Labrador fjords. During summer 2007, diatoms (mainly *Chaetoceros gelidus* and *C. tenuissimus*) and a mixed assemblage of flagellated cells dominated the community. In summer 2013, flagellates were dominant, and an intense *Phaeocystis pouchetii* bloom was observed in the bottom layer of the euphotic zone in Nachvak Fjord (18×10^6 cells l^{-1}). The fall protist communities were mainly composed of unidentified flagellates and prymnesiophytes. The environmental factors mainly controlling the seasonal differences in protist taxonomic composition were different from summer to late fall. From a summer situation characterized by a stronger stratification, higher incident irradiance and depleted nutrients in surface waters, it evolved to an autumn situation characterized by decreasing air temperature and irradiance associated with an environmental forcing allowing a cooling and a higher vertical mixing of the water column. The highest protist richness was observed in early fall, with 201 taxa recorded, which was twice the summer richness.

This study provides the first data on protist spatial and seasonal variations in northeastern Canadian fjords. To date, published data on detailed protist distribution along the east coast of Canada are, to our knowledge, non-existent. This lack of knowledge is unfortunate, and while our contribution attempts to compensate for this weakness, it is also intended to pave the way for future, more in-depth investigations on protist dynamics. Whether our observations in Labrador fjords can be extrapolated to other fjords along Canada's east coast is yet to be confirmed by future studies. To determine a more precise annual succession in protist community, a sampling expedition in Labrador fjords should be conducted in late spring to assess whether phytoplanktom blooms occur under the sea ice as observed elsewhere in the Arctic (see Arrigo et al. 2012, Mundy et al. 2014, Assmy et al. 2017) and in the first half of July, immediately after the sea ice break-up. Moreover, in future investigations, it will be interesting to deter-

mine how protist taxonomic composition is affected by proto- and metazooplankton grazing throughout the seasons. Such knowledge is fundamental, especially in the actual era of climate change and Far North opening due to global warming. We have no doubt that these changes will increase natural and anthropogenic pressures on northern environments, and it therefore becomes crucial to continue monitoring these environments in order to better predict their response to such stresses.

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