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Multivariate control of heterotrophic bacterial abundance and zooplankton grazing in Labrador fjords (northeastern Canada)

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ABSTRACT: This study was conducted in 4 Labrador fjords (Nachvak, Saglek, Okak, and Anaktalak) during the summers of 2007 and 2013, early fall 2010, and late fall 2009. Our results show that water temperature combined with the availability of nutrients and organic substrates are the main abiotic factors controlling the abundance of heterotrophic bacteria in Labrador fjords. Bacterivory also played a crucial role, with heterotrophic bacteria exerting a significant bottom-up control on the abundance of heterotrophic nanoflagellates ($r = 0.35$, $p < 0.05$) and ciliates ($r = 0.70$, $p < 0.01$). During summer 2013, the intrinsic phytoplankton growth rate varied between <0 and 0.64 d^{-1}, with a mean value of 0.36 d^{-1}. The herbivory rate was highly variable, ranging from 0.01 to 0.86 d^{-1}, with a mean value of 0.31 d^{-1}. Grazing mortality was 6-fold higher than phytoplankton growth rate. Mean phytoplankton growth and herbivory rates in Labrador fjords were comparable to the Barents and Bering seas. The intrinsic growth rate of total heterotrophic bacteria ranged between <0 and 0.68 d^{-1}, with a mean value of 0.30 d^{-1}. Bacterivory varied from 0.01 to 0.95 d^{-1}, with a mean of 0.30 d^{-1}. Mortality due to grazing was up to 2.3 times higher than total bacterial growth rate. This study improves our understanding of the factors influencing the dynamics of heterotrophic bacteria and indicates that herbivory and bacterivory exert substantial control on microbial communities in Labrador fjords.

KEY WORDS: Heterotrophic bacteria · Phytoplankton · Zooplankton · Growth · Grazing · Arctic · Canada · Labrador fjords

1. INTRODUCTION

Heterotrophic bacteria are key organisms in marine food webs, playing crucial roles in the control of carbon fluxes in the oceans. In coastal waters, heterotrophic bacteria can take up nearly 50% of the primary production (Robinson 2008). This organic matter is dissolved by various mechanisms and becomes accessible almost exclusively to heterotrophic bacteria and archaea (Ducklow & Carlson 1992). Labile dissolved organic carbon (DOC) is defined as the DOC fraction that can be decomposed by bacteria within a week or two (Søndergaard & Middelboe 1995). Many studies have indicated that temperature, labile DOC (Amon & Benner 1996, Azam & Malfatti 2007, Kirchman et al. 2009b), and nutrient concentrations (Guildford & Hecky 2000, Sala et al. 2002, Matz & Jürgens 2003) are the main bottom-up factors influencing bacterial dynamics in marine environments. In pelagic marine systems, various organic matter sources fulfill the bacterial DOC demand: phytoplankton exudation (Azam & Cho 1987, Kirchman et al. 1993), spontaneous autolysis of phytoplankton (van Boekel et al. 1992), viral lysis (Bratbak et al. 1992), excretion by

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herbivores (Nagata & Kirchman 1991), sloppy feeding by large zooplankton (Roy et al. 1989), and degradation of fecal material and other detritus (Jumars et al. 1989). Heterotrophic bacteria account for a large portion of total uptake of both phosphate and ammonium in marine systems (Kirchman 1994). Under limiting nutrient conditions, they may rival phytoplankton for the uptake of inorganic nutrients (phosphate, ammonium, and nitrate; Joint et al. 2002, Fouilland et al. 2007).

Nano- (2–20 µm) and micrograzers (20–200 µm) also have an important influence on microbial communities. Numerous authors have indicated that ciliates and phagotrophic dinoflagellates from ca. 12 to 200 µm in size are the main herbivores in planktonic food webs, whereas heterotrophic nanoflagellates (HNF; including choanoflagellates) and mixotrophic flagellates are key bacterial grazers (Gasol & Vaqué 1993, Nakamura 1994, Calbet & Landry 2004, Sherr et al. 2013, Lin et al. 2014).

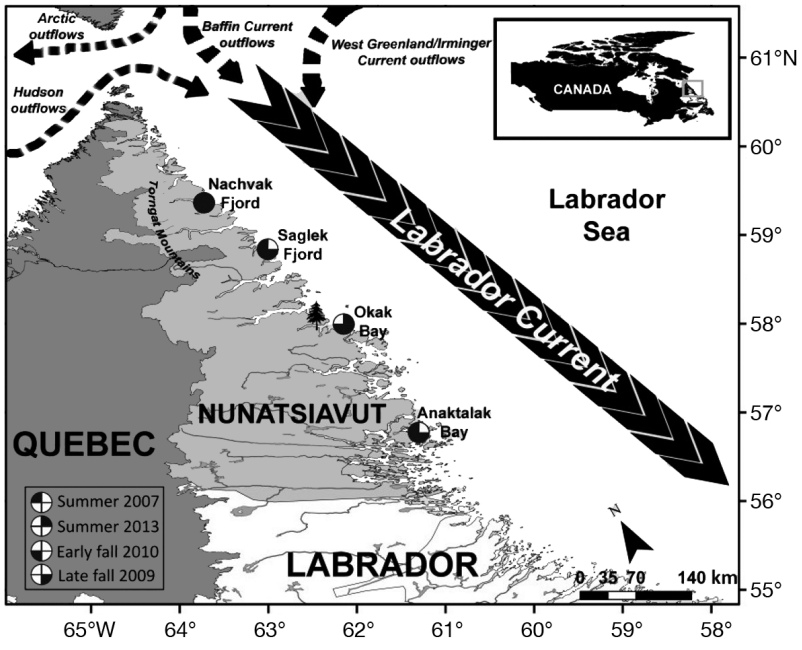

Fig. 1. Sampling periods and locations of Nachvak Fjord, Saglek Fjord, Okak Bay, and Anaktalak Bay in Nunatsiavut, northern Labrador (see Table 1) (adapted from Richerol et al. 2012)

There are no published data on the abundance dynamics of heterotrophic bacteria in fjords along the Labrador coast of Canada. In addition, no estimate of zooplankton grazing is available for this region. The objectives of our study were therefore to (1) assess the influence of water temperature, nutrients (phosphate and nitrate), DOC, and phytoplankton biomass on the abundance of heterotrophic bacteria in 4 Labrador fjords (Nachvak, Saglek, Okak, and Anaktalak) during summer and fall; (2) explore the relationship between HNF and heterotrophic bacteria; and (3) estimate herbivory and bacterivory rates.

2. MATERIALS AND METHODS

2.1. Study area

The study region is located in Nunatsiavut, on the eastern seaboard of Canada, between 46° and 60°N (Fig. 1). Four inlets, influenced by both Atlantic and Arctic water masses, were sampled: Nachvak, Saglek, Okak, and Anaktalak (Fig. 1). These 4 ecosystems are important environmental monitoring sites because they lie between regions undergoing significant changes (High Arctic; Arrigo et al. 2012) and others with more stable conditions (subarctic; Brown et al. 2012). They are strongly influenced to the north by climate change (including increased freshwater inflow from melting glaciers, changes in sea ice extent and volume, and warming of surface waters) and to the south by anthropogenic activities (e.g. mining, hydroelectric and tourism development, shipping, and aquaculture). Furthermore, because of the sill, which limits the renewal of water masses and consequently the supply of nutrients, primary production in fjords can be extremely variable. This scenario can lead to the development of a microbial community that is often different from other coastal estuaries (Archer et al. 2000, Zhou et al. 2005, Iversen & Seuthe 2011).

Located further north, in Torngat Mountains National Park, Nachvak Fjord is the study fjörd influenced by glaciers. Saglek Fjord has been the site of a military radar station since 1953 and so has high levels of polychlorinated biphenyl contamination in the soil, sediments, and marine environment (Kuzyk et al. 2005). Okak Bay is often used for travelling and harvesting by the Inuit. Anaktalak Bay is located further south and is widely used for economic activities by the Nain Inuit. A nickel mine and concentrator managed by Vale NL (formerly Voisey's Bay Nickel Company) has operated in Anaktalak Bay since 2005. The sea ice cover lasts ca. 6.6 mo yr^{-1} in Nachvak and ca. 6.3 to 6.4 mo yr^{-1} in the other inlets (Brown et al. 2012). A detailed description of the study area can be found in Simo-Matchim et al. (2016). For simplicity, Okak

and Anaktalak bays will hereafter be referred to as fjords.

2.2. Sampling

Samples were collected from 31 July to 2 August 2007, from 30 July to 1 August 2013, from 24 to 27 October 2010, and from 8 to 13 November 2009 onboard the Canadian research icebreaker CCGS 'Amundsen'. These sampling periods are referred to as summer 2007, summer 2013, early fall 2010, and late fall 2009, respectively. Sampling was conducted at an inner and outer station in each fjord. Table 1 presents the geographical position and sampling period for each station. At each station, an underwater profile of photosynthetically active radiation (PAR; 400–700 nm) was carried out using a PNF-300 radiometer (Biospherical Instruments) to estimate the depth of the euphotic zone (0.2% of surface irradiance; Knap et al. 1996). Incident PAR was measured every 10 min with a 2π LI-COR sensor (LI-190SA) placed in an unshaded zone of the foredeck.

Water samples were collected with a rosette sampler equipped with twenty-four 12 l Niskin-type bottles, a Sea-Bird Electronics SBE 911plus CTD probe for salinity and temperature measurements, and a chlorophyll fluorometer (WETStar mini fluorometer model 9512008). Samples were taken at 7 optical depths (95, 50, 30, 15, 5, 1, and 0.2% of surface light), at the subsurface fluorescence maximum (SCM) depth, and at 75 and 100 m in the aphotic zone for the determination of nutrients, DOC, chl *a*, primary production, and bacterial abundances. Water samples for the dilution experiments in 2013 and the determination of protist abundances were taken at 2 depths (50% of surface irradiance and 15 to 1% of surface irradiance), one of which was the SCM depth. Hereafter, these 2 depths are referred to as the surface and the bottom layers of the euphotic zone, respectively.

2.3. Laboratory analyses

2.3.1. Nutrients

Triplicate samples of dissolved inorganic nutrients were filtered on 0.7 µm Whatman GF/F filters and the filtrate collected in acid-washed polyethylene vials. Nutrient samples were directly analyzed or kept at −80°C for subsequent analyses of nitrate plus nitrite (NO_3 + NO_2), nitrite, phosphate, and silicic acid concentrations using a Bran-Luebbe 3 autoanalyzer (method modified from Grasshoff et al. 1999). A simple linear correction for the variation in salinity was performed for phosphate and silicic acid concentrations (Grasshoff et al. 1999).

2.3.2. DOC

In 2007 and 2009, seawater was filtered through precombusted (450°C for 5 h) 25 mm Whatman GF/F filters. The filtrate was collected in 5 ml Kimble brand borosilicate vials with Teflon-lined caps previously treated following the protocol of Burdige & Homstead (1994). The samples were then acidified (50 µl of 25% H_3PO_4) and kept in the dark at 4°C until analysis. DOC was determined using a Shimadzu TOC-5000A analyzer (Benner & Strom 1993).

In 2010 and 2013, the filtrate was collected in 9 ml Kimble brand vials previously treated as indicated above, acidified with 100 µl of 2 N HCl, and left in the dark at 4°C until analysis with a Shimadzu TOC-V_{CPN} analyzer (Benner & Strom 1993). Potassium

Table 1. Summary of station locations, water depths, and sampling periods in Nachvak, Saglek, Okak, and Anaktalak fjords. Dilution experiments were conducted only in Nachvak and Okak during summer 2013

Inlet	Stn	Position	Latitude (°N)	Longitude (°W)	Water depth (m)	Sampling period
Nachvak	602	Inner	59° 4.5′	63° 25.5′	158	Summer 2007 and 2013, early fall 2010, late fall 2009
	600	Outer	59° 2.6′	63° 52.5′	207	
Saglek	615	Inner	58° 16.4′	63° 31.5′	130	Summer 2007, early fall 2010, late fall 2009
	617	Outer	58° 30′	62° 41.3′	139	
Okak	630	Inner	57° 36′	61° 53.3′	51	Summer 2013, early fall 2010, late fall 2009
	633	Outer	57° 28.1′	62° 27′	178	
Anaktalak	624	Inner	56° 23.6′	61° 12.4′	71	Summer 2007, early fall 2010, late fall 2009
	620	Outer	56° 24.4′	62° 4.1′	96	

hydrogen phthalate was used to standardize DOC measurements. In addition, samples were regularly checked against low carbon (2 µM) and deep Sargasso Sea reference water (44–46 µM) every seventh sample. The mean DOC of 3 replicate injections of each sample had a 3% coefficient of variation.

2.3.3. Bacterial abundance

Duplicate subsamples were fixed with Grade I glutaraldehyde (Sigma; 0.1% final concentration) and stored in liquid nitrogen (–80°C) onboard the vessel until analysis by flow cytometry (Marie et al. 2005). Heterotrophic bacteria were stained with SYBR Green I (Invitrogen) and measured at 525 nm to detect low and high nucleic acid content (Belzile et al. 2008). Analyses were done with an Epics Altra flow cytometer (Beckman Coulter) equipped with Expo32 v1.2b software. The sample volume was quantified by weighing a subsample before and after analysis. Because archaea cannot be distinguished from bacteria using this protocol, bacterial abundances include both archaea and bacteria.

2.3.4. Protist identification and abundance

For the identification and enumeration of protist cells >2 µm, 200 ml subsamples were preserved in acidic Lugol's solution (Parsons et al. 1984). Samples were then kept in the dark at 4°C until analysis. Cells were identified to the lowest possible taxonomic level using an inverted microscope (Zeiss Axiovert 10) according to Lund et al. (1958). For each sample, a minimum of 400 cells (accuracy ±10%) and 3 transects were counted at magnifications of 200 and 400×. The main references used were Tomas (1997) and Bérard-Therriault et al. (1999).

2.3.5. Phytoplankton biomass

For chl *a* determination, duplicate 500 ml subsamples were filtered onto Whatman GF/F filters (total phytoplankton biomass: B_T, ≥0.7 µm) and onto 5 µm Nuclepore filters (biomass of large cells: B_L, ≥5 µm). Concentrations of chl *a* were measured onboard the vessel using a Turner Designs 10-AU fluorometer following 18 to 24 h of pigment extraction in 10 ml of 90% acetone at 4°C in the dark (Parsons et al. 1984). The biomass of small cells (B_S, 0.7–5 µm) was obtained by subtracting B_L from B_T.

2.3.6. Primary production

Primary production was determined using the ^{14}C-uptake method (Knap et al. 1996, Ferland et al. 2011) under simulated *in situ* conditions during summer 2013. One dark and 2 clear 500 ml Nalgene bottles were filled with seawater from each irradiance level. Each bottle was then inoculated with 20 µCi of $NaH^{14}CO_3$. In addition, 250 µl of 0.02 M 3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU; Legendre et al. 1983) was added to the dark bottle. Bottles were incubated in a Plexiglas deck incubator with flowing surface seawater (Mingelbier et al. 1994). After 24 h, 250 ml was filtered onto Whatman GF/F filters (referred to as total particulate phytoplankton production, P_T, ≥0.7 µm), and the remaining subsamples were filtered onto 5 µm Nuclepore filters (referred to as production of large cells, P_L, ≥5 µm). The filters were then acidified with 100 µl of 0.5 N HCl and left to evaporate overnight under a fume hood to remove any ^{14}C that had not been assimilated (Lean & Burnison 1979). Afterwards, 10 ml of Ecolume scintillation cocktail was added to each vial. The activity of each sample was measured using a Packard Tri-Carb 2900 TR liquid scintillation counter. Production rates of particulate organic carbon were determined according to Parsons et al. (1984). Production of small cells (P_S, 0.7–5 µm) was obtained by subtracting P_L from P_T.

2.3.7. Dilution experiments

Dilution experiments were conducted in summer 2013 following a method adapted from the 2-point dilution protocol of Landry & Hassett (1982). We did 3 different dilutions at the surface and bottom layers of the euphotic zone: a mixture of 25 to 55% whole seawater diluted with filtered seawater (FSW) from the same depth to which nutrients had been added (dilution D_1), unfiltered seawater (100%) with nutrient enrichment (dilution D_2), and unfiltered seawater (100%) without nutrient enrichment (dilution D_3). Nutrients were added in D_1 and D_2 because a previous study conducted in Labrador fjords indicated that phytoplankton are potentially nutrient limited (Simo-Matchim et al. 2016). Potassium nitrate, sodium phosphate, and sodium metasilicate were added to experimental bottles to yield concentrations of 5 µM nitrate, 0.33 µM phosphate, and 5 µM dissolved silicon; these concentrations are equivalent to the N:P Redfield (15–16; Redfield et al. 1963) and Si:N Brzezinski (1–2; Brzezinski 1985) molar ratios.

Seawater was gently transferred from Niskin bottles into 20 l carboys through silicone tubing. A 350 µm net was attached at the end of the tube to exclude large grazers. As the carboys were filled, care was taken to avoid bubbles in the tubing. All further steps were carried out under dim light. For dilution D_1, FSW was prepared by successive gravity filtration of seawater through a 5 µm cartridge and a 0.2 µm cartridge (Pall-Gelman Suporcap). Both cartridges were presoaked in 5% HCl for 8 h and abundantly rinsed with deionized water. Five liters of seawater were passed through the cartridges before collecting FSW for the dilutions. Afterwards, FSW was poured into a carboy, and seawater was gently added to yield the corresponding dilution (25 to 55%). Seawater was also collected in 2 other carboys for dilutions D_2 and D_3. Nutrients were added to dilutions D_1 and D_2, and the carboy content was gently mixed. Triplicate 2 l bottles were filled for each dilution using a silicone tube, starting from the unenriched dilution D_3. A 2 l bottle was also filled with FSW. During this process, the end of the silicone tube was always submerged to avoid bubbles. Because protists can lyse on contact with air (Gifford 1988), parafilm was placed on top of each bottle before securing the cap to minimize air bubbles. Prior to the dilutions, the bottles were wrapped with black screen to mimic the approximate *in situ* irradiance at the sampled depth. Bottles were incubated for 24 h in a Plexiglas deck incubator with flowing surface seawater. Temperature in the incubator was continually monitored.

Initial samples were taken directly from the carboy of the corresponding dilution for determination of nutrient and DOC concentrations, bacterial and protist cell (>2 µm) abundances, and chl *a* concentration. Initial samples of FSW were also taken. After the incubation, final samples were collected from all the 2 l bottles for determination of the variables previously listed. FSW was also analyzed to check if organisms were able to pass through the cartridges and if they multiplied during the incubation. Prior to experiments, all carboys, bottles, and silicone tubes were soaked overnight with 10% HCl and abundantly rinsed with deionized water. The silicone tubing was further rinsed with FSW and seawater just before filling the bottles. The Pall-Gelman Suporcap cartridge was filled with 0.01% HCl solution and kept at 4°C between experiments. It was rinsed with 10 l of distilled water and 2 l of seawater just before each experiment. Between experiments, all material was protected in plastic bags. Disposable polyethylene gloves were worn during the experimental setup. At all sampling stations, experiments were conducted immediately after collecting seawater except at inner Nachvak (Stn 602), where seawater was kept at 4°C for 9 h before starting the dilution because the previous station's incubation was still running.

Zooplankton grazing (g; d^{-1}) on phytoplankton (g_p) and heterotrophic bacteria (g_b) was estimated separately using the following equations (Sherr et al. 2013):

$$g = (k_1 - k_2) / (1 - x) \quad (1)$$

$$\mu = k_2 + g \quad (2)$$

where k_1 and k_2 are the apparent (or net) growth rates (d^{-1}) based on chl *a* concentration or bacterial abundance in dilutions D_1 (diluted seawater with added nutrients) and D_2 (undiluted seawater with added nutrients), respectively, and x is the fractional dilution. The intrinsic or instantaneous growth rate (μ; d^{-1}) of phytoplankton (μ_p) and that of heterotrophic bacteria (μ_b) were also estimated.

2.4. Calculations

At each station, temperature was averaged over the upper 100 m of the water column (or over the entire water column when water depth was <100 m). Bacterial abundances and nutrient and DOC concentrations were integrated over the upper 100 m of the water column (or the entire water column when depth <100 m) using the trapezoidal method (Knap et al. 1996), and phytoplankton production and biomass were integrated over the euphotic zone depth using the trapezoidal method. The intrinsic growth rates of phytoplankton and heterotrophic bacteria as well as zooplankton grazing rates on both communities were averaged to have one final value for each set of triplicate bottles.

2.5. Statistical analyses

Pearson's correlation coefficient (r) and model II linear regression (reduced major axis) were used to evaluate the relationship between 2 variables (Sokal & Rohlf 1995). These tests were carried out using SigmaPlot v12.5 software.

3. RESULTS

3.1. Environmental conditions

For the whole study period, the maximum temperature averaged in the upper 100 m of the water column

was recorded at outer Anaktalak (3.56°C) during early fall 2010, while the minima were noted at inner Nachvak (–0.22°C) during late fall 2009 and inner Saglek (–0.17°C) during summer 2007 (Table 2). Mean DOC concentrations ranged from 21 µM at inner Okak during late fall 2009 to 122 µM at outer Nachvak in summer 2007 (Table 2). Mean nutrient concentrations at the sampling stations generally increased from summer to late fall. For the whole study period, the northernmost fjords (Nachvak and Saglek) showed higher nutrient concentrations than the southernmost ones (Okak and Anaktalak; Table 2).

3.2. Phytoplankton biomass and production

Profiles of phytoplankton chl *a* biomass showed large spatial and seasonal differences in Labrador fjords (Fig. 2). Summer profiles were generally characterized by an SCM located between 10 and 30 m (Fig. 2a–d), whereas the fall profiles showed maximum chl *a* concentrations close to the surface (Fig. 2e–h). As with nutrients, the northernmost fjords (Nachvak and Saglek) showed higher chl *a* concentrations than the southernmost fjords (Okak and Anaktalak; Table 2, Fig. 2), except in summer 2007. Areal phytoplankton chl *a* biomass also showed large differences between fjords and seasons, with values ranging from 4.7 to 341 mg chl *a* m^{-2} during summer and from 8.8 to 125 mg chl *a* m^{-2} during fall (Table 2).

During summer 2013, total primary production ranged from 870 mg C m^{-2} d^{-1} at outer Okak to 4900 mg C m^{-2} d^{-1} at outer Nachvak (Fig. 3a). Total phytoplankton chl *a* biomass varied between 39 and 217 mg chl *a* m^{-2} at outer Okak and inner Nachvak,

Table 2. Environmental and biological conditions in Nachvak, Saglek, Okak, and Anaktalak fjords during summer 2007, summer 2013, early fall 2010, and late fall 2009 (see Table 1 for location of stations). *T*: water temperature averaged over the upper 100 m of the water column (or entire water column if water depth <100 m); DOC: dissolved organic carbon; $NO_3 + NO_2$: nitrate plus nitrite; $Si(OH)_4$: silicic acid; PO_4: phosphate concentrations; Chl *a*: integrated phytoplankton biomass; Total het. bacteria: integrated total heterotrophic bacterial abundance; HNA bacteria: percentage of high nucleic acid bacteria. Values were integrated over the upper 100 m of the water column (or entire water column if water depth <100 m). Mean integrated concentrations are given for DOC and nutrients. Mean integrated values were obtained by dividing integrated concentrations by 100 (when water depth was >100 m) or by the last depth sampled (water depth <100 m)

Stn	*T* (°C)	DOC (µM)	$NO_3 + NO_2$ (µM)	$Si(OH)_4$ (µM)	PO_4 (µM)	Chl *a* (mg m^{-2})	Total het. bacteria (10^{12} cells m^{-2})	HNA bacteria (%)
Summer 2007								
602	0.14	92.9	5.20	6.96	0.62	124.8	82.7	84.7
600	0.47	122.4	4.96	6.38	0.52	61.7	60.4	82.4
615	–0.17	66.5	4.77	5.85	0.82	4.7	13.9	71.4
624	2.16	88.2	1.93	3.67	0.49	66.6	86.4	85.2
Summer 2013								
602	0.02	78.2	5.82	8.23	0.88	340.8	63.7[a]	36.9[a]
600	1.02	68.2	4.13	5.86	0.73	222.6	111.1	61.0
630	2.05	72.9	2.38	6.16	0.53	43.2	7.5[a]	37.9[a]
633	0.83	78.2	2.83	4.94	0.6	41.5	40.5	56.8
Early fall 2010								
602	1.19	79.4	7.23	8.23	1.36	46.5	67.8	76.4
600	1.90	92.9	5.62	7.28	1.17	30.0	84.6	79.3
615	0.96	72.4	4.80	7.08	1.0	40.0	56.0	74.7
617	2.46	78.8	3.06	5.89	0.89	59.6	115.9	78.3
630	1.21	79.4	2.71	6.52	1.01	73.5	28.1	87.2
633	2.79	92.4	2.81	5.34	0.87	24.7	97.7	84.2
624	2.67	81.2	3.58	6.33	0.92	21.6	38.2	82.2
620	3.56	84.1	0.85	1.73	0.28	34.3	62.1	80.3
Late fall 2009								
602	–0.22	80.6	9.69	10.73	1.05	48.4	45.9	55.6
600	–0.07	82.9	6.95	8.03	0.84	37.2	57.0	52.4
615	–0.14	87.1	5.94	8.57	0.92	25.5	48.0	52.3
617	0.26	82.9	4.33	5.87	0.75	124.9	61.5	57.1
630	0.92	21.2	4.90	7.31	0.80	8.8	27.6	54.4
633	0.74	88.8	3.35	4.76	0.74	53.0	66.5	58.1
624	1.41	97.6	4.29	6.18	0.63	13.2	26.5	50.4
620	0.20	43.5	2.75	3.61	0.49	35.5	42.6	45.7

[a]Values calculated for the euphotic zone

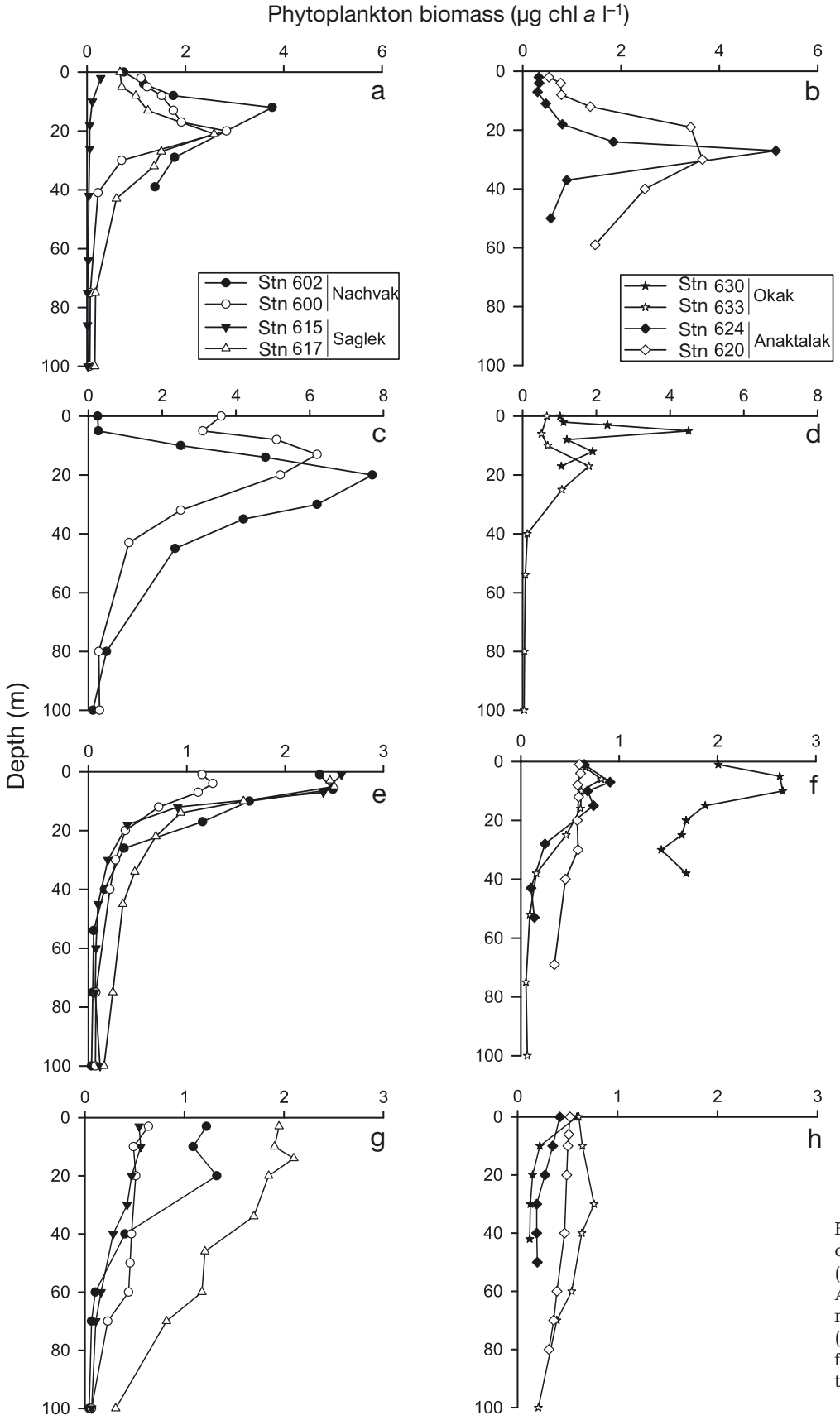

Fig. 2. Vertical profiles of chl *a* concentration in Labrador fjords (Nachvak, Saglek, Okak, and Anaktalak) during (a,b) summer 2007, (c,d) summer 2013, (e,f) early fall, and (g,h) late fall. Black symbols represent the inner stations and white symbols the outer stations

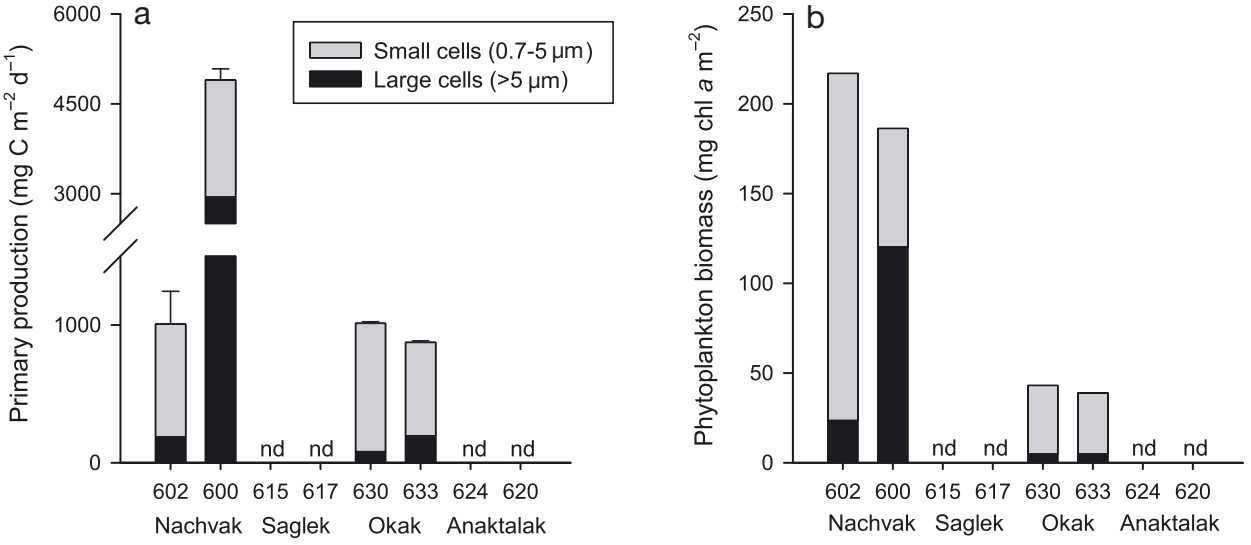

Fig. 3. Variations in (a) primary production and (b) phytoplankton chl *a* biomass at the inner and outer stations in Nachvak and Okak fjords during the summer 2013 grazing experiments. nd: no data available for Saglek and Anaktalak fjords. Production and biomass of small (0.7–5 µm) and large (>5 µm) cells were integrated from the surface down to the depth of 0.2% of surface irradiance. In (a), vertical lines represent the SD of the estimated rates

respectively (Fig. 3b). Production and biomass were mainly dominated by small phytoplankton cells (0.7–5 µm), except at outer Nachvak, where large phytoplankton (>5 µm) showed higher production and biomass (Fig. 3). The production:biomass (P_T:B_T) ratio ranged from 4.6 to 26.3 mg C mg chl a^{-1} d^{-1}. More details on phytoplankton dynamics in Labrador fjords during the whole study period can be found in Simo-Matchim et al. (2016).

3.3. Heterotrophic bacterial abundances

During the whole sampling period, cyanobacterial abundances were extremely low, making up <0.01 to 0.08% of the total (autotrophic plus heterotrophic) bacterial abundances (data not shown). Therefore, only heterotrophic bacteria were considered in the present study. Overall, the profiles of heterotrophic bacterial abundances (Fig. 4) followed those of phytoplankton chl *a* biomass (Fig. 2). The distribution of bacteria was vertically uniform at inner Saglek during summer 2007 and at most stations during late fall 2009 (Fig. 4a,g,h), while it showed large variations in other cases (Fig. 4b–f).

Areal heterotrophic bacterial abundances ranged from 7.5 × 10^{12} cells m^{-2} at inner Okak during summer 2013 to 116 × 10^{12} cells m^{-2} at outer Saglek during early fall 2010 (Table 2, Fig. 5b,c). During the whole study period, bacteria with high nucleic acid (HNA) content dominated the community at all stations, except at inner Nachvak (36.9%) and inner Okak (37.9%) during summer 2013 and outer Anaktalak (45.7%) during late fall 2009 (Table 2, Fig. 5b,d).

During summer 2013, areal abundances of total heterotrophic bacteria and HNA bacteria were positively correlated with NO_3 + NO_2 and phosphate (r = 0.96, $p < 0.05$ for each correlation). During late fall 2009, areal abundances of total bacteria and HNA bacteria were positively correlated with phytoplankton chl *a* biomass (r = 0.70, $p < 0.05$ and r = 0.72, $p < 0.05$, respectively). In addition, considering all stations and depths, total heterotrophic bacteria was positively correlated with water temperature during early fall 2010 (r = 0.33, $p < 0.001$) and late fall 2009 (r = 0.28, $p < 0.001$). No other significant correlation was found.

3.4. Heterotrophic protist community

During summer 2013, the heterotrophic protistan community in Nachvak and Okak was composed of ciliates, heterotrophic dinoflagellates, choanoflagellates, unidentified flagellates (<20 µm), and other heterotrophic groups. Ciliates were dominated by spirotrichs of the genera *Strombidium* Claparède & Lachmann, *Laboea* Lohmann and *Balanion* Wulff, and the choreotrichid *Lohmanniella oviformis* Leegaard. The main phagotrophic dinoflagellates were *Heterocapsa rotundata* (Lohmann) Hansen and *Gym-*

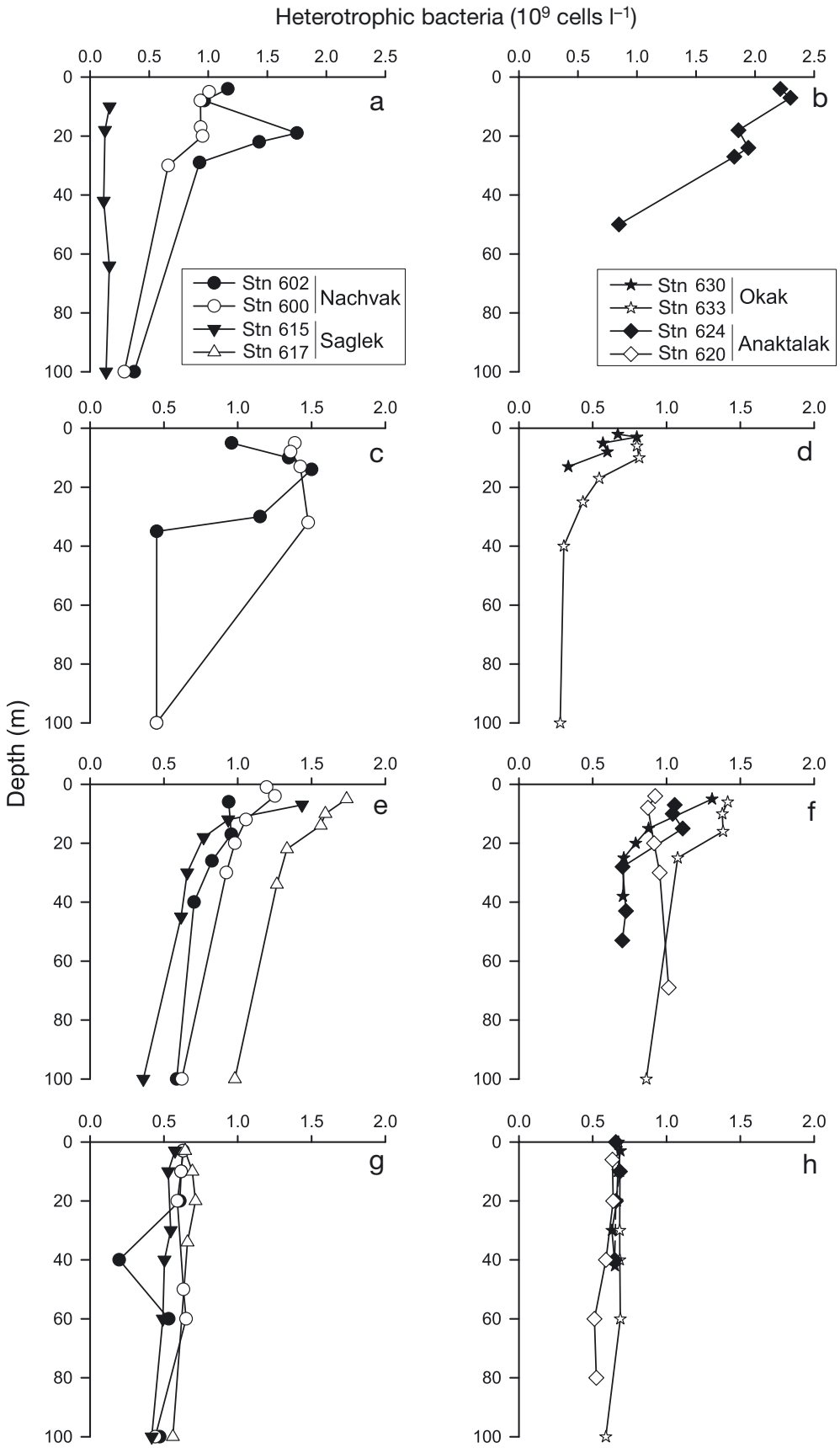

Fig. 4. Vertical profiles of the total abundance of heterotrophic bacteria in Labrador fjords (Nachvak, Saglek, Okak, and Anaktalak) during (a,b) summer 2007, (c,d) summer 2013, (e,f) early fall, and (g,h) late fall. Black symbols represent the inner stations and white symbols the outer stations

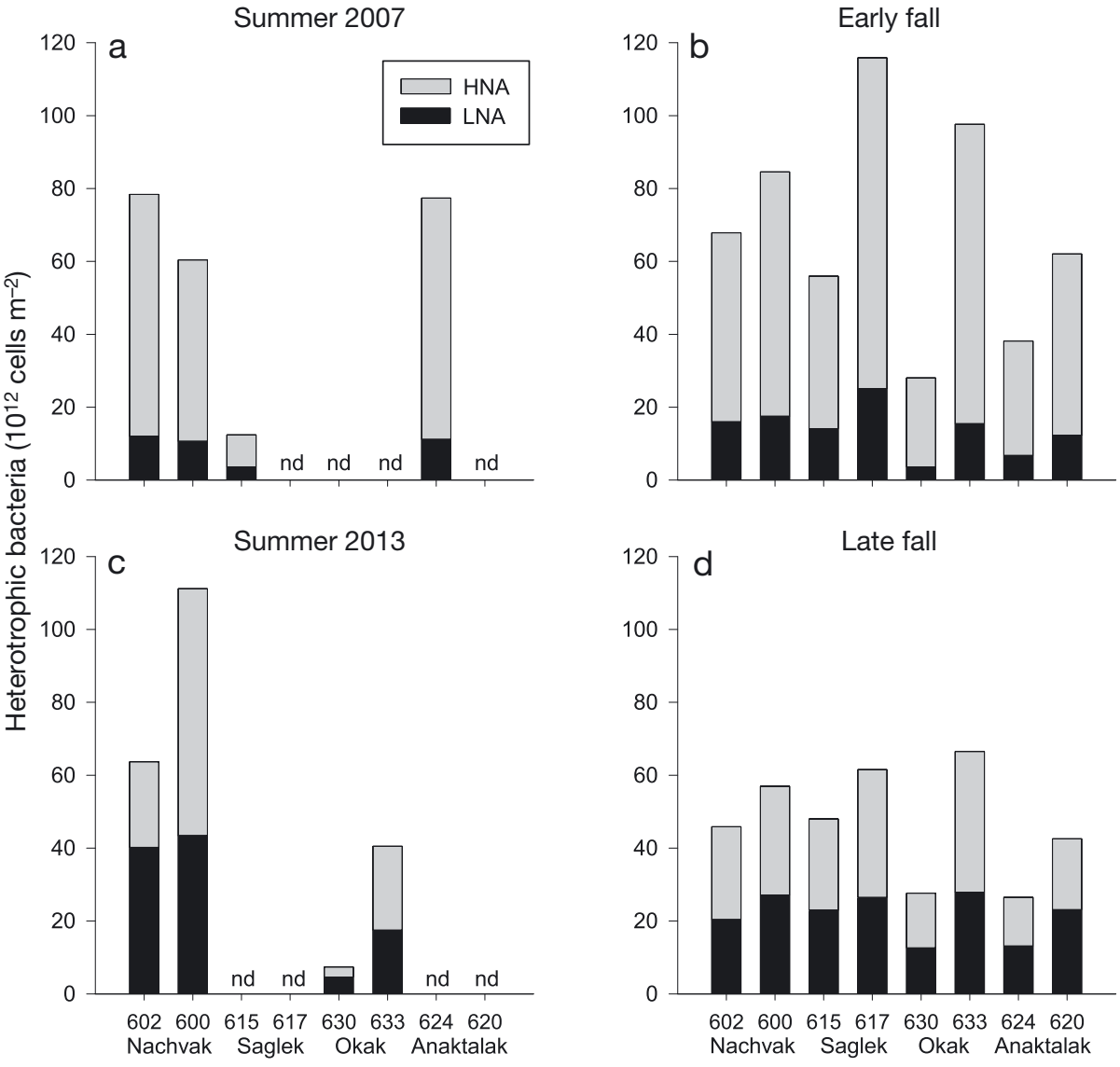

Fig. 5. Variations in total heterotrophic bacterial abundance at the inner and outer stations in Nachvak, Saglek, Okak, and Anaktalak fjords during (a) summer 2007, (b) summer 2013, (c) early fall, and (d) late fall. Abundances of bacteria with high nucleic acid (HNA) and low nucleic acid (LNA) content were integrated over the upper 100 m of the water column (or the entire water column if water depth was <100 m), except at Stns 602 and 630 during summer 2013, where they were integrated over the euphotic zone. nd: data not available

nodinium/*Gyrodinium* spp. Choanoflagellates were mainly represented by *Bicosta*, *Calliancantha*, *Diaphanoeca*, *Monosiga,* and *Parvicorbicula* species and some unidentified species (<20 µm). The other heterotrophic groups were dominated by *Leucocryptos marina* (Braarud) Butcher, *Meringosphaera mediterranea* Lohmann, *Notosolenus* sp. (sensu Bérard-Therriault et al. 1999), and *Telonema subtile* Greissmann. The thorough taxonomic composition of the protist community in Labrador fjords during summers 2007 and 2013, early fall 2010, and late fall 2009 is discussed in Simo-Matchim et al. (2017).

3.5. Relationships between phytoplankton, bacteria, and heterotrophic protists

Using data from the surface and bottom layers of the euphotic zone, we performed another correlation analysis. The abundance of heterotrophic bacteria was significantly correlated with phytoplankton chl *a* during summer 2013 ($r = 0.24$, $p < 0.05$), early fall 2010 ($r = 0.24$, $p < 0.001$), and late fall 2009 ($r = 0.14$, $p < 0.05$). In addition, they were also positively related to primary production ($r = 0.34$, $p < 0.001$) during early fall 2010. Choanoflagellate

abundances were significantly correlated with chl *a* during early fall 2010 (r = 0.43, p < 0.01) and late fall 2009 (r = 0.68, p < 0.001), whereas ciliates and dinoflagellates were correlated with chl *a* only during late fall 2009 (r = 0.55, p < 0.01 and r = 0.34, p < 0.05, respectively). For the whole study period, HNF abundances varied between 0.08 × 10^6 and 2.4 × 10^6 cells l^{-1}, while total heterotrophic bacterial abundances ranged from 0.11 × 10^9 to 2.3 × 10^9 cells l^{-1}. HNF showed a significant and positive linear relationship with total heterotrophic bacteria (Fig. 6). However, this relationship was not significant when tested separately for each sampling season. A significant correlation between total heterotrophic bacterial and ciliate abundances was also found during summer 2007 (r = 0.70, p < 0.01).

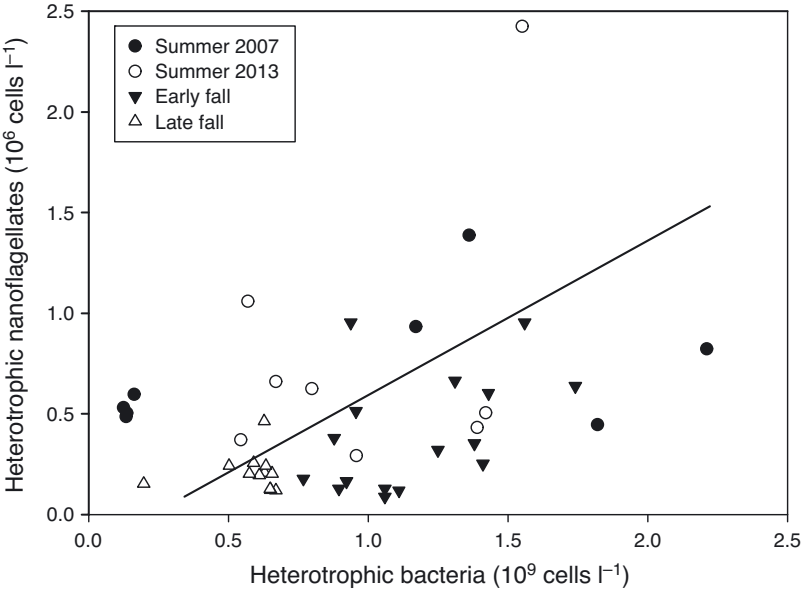

Fig. 6. Regression between heterotrophic nanoflagellate (HNF) abundance and total heterotrophic bacterial abundance in Nachvak, Saglek, Okak, and Anaktalak fjords during the whole study period (summers 2007 and 2013, early fall, and late fall). HNF include choanoflagellates and unidentified flagellates. The equation of the reduced major axis (model II) regression is $x_2 = (0.87/10^9\ x_1 - 0.33) \times 10^6$; r = 0.35, p < 0.05

3.6. Dilution assay results

Water temperature and $NO_3 + NO_2$ concentrations at the sampling depth as well as chl *a* concentrations and bacterial abundances in the undiluted seawater at the beginning of the experiments are presented in Tables 3 & 4. Although the difference was not significant, the net growth rate of phytoplankton was generally higher in bottles with nutrient enrichment (k_2) than in those without nutrient addition (k_3). Intrinsic phytoplankton growth rates (μ_p) varied between <0 and 0.64 d^{-1}, with a mean value of 0.36 d^{-1}. Herbivory (g_p) occurred at each station and sampling depth at a rate ranging from 0.01 to 0.86 d^{-1}, with a mean of 0.31 d^{-1}. Grazing mortality as a fraction of phytoplankton growth ranged from 0.04 to 5.6. The

Table 3. Summary of dilution experiments conducted on phytoplankton communities in Nachvak and Okak fjords during summer 2013. Water temperature (T) and nitrate plus nitrite ($NO_3 + NO_2$) concentration at the sampling depth; Chl *a*: initial phytoplankton chl *a* biomass in undiluted seawater; x: fractional dilution used in dilution D_1; k_1: chl *a*-based growth rate in dilution D_1 with nutrient enrichment; k_2 and k_3: chl *a*-based growth rate in dilutions D_2 and D_3 (undiluted seawater) with and without nutrient enrichment, respectively; μ_p: intrinsic phytoplankton growth rate; g_p: zooplankton grazing rate on algae; g_p:μ_p: ratio of grazing to growth rate. μ_p and g_p were calculated using k_1 and k_2. At each station, samples were collected at the surface (S) and bottom (B) layers of the euphotic zone. nd: not determined

Stn	Sampling depth (m)	T (°C)	$NO_3 + NO_2$ (µM)	Chl *a* (µg l^{-1})	x	k_1 (d^{-1})	k_2 (d^{-1})	k_3 (d^{-1})	μ_p (d^{-1})	g_p (d^{-1})	g_p:μ_p
Nachvak											
602-S	2	2.3	0.93	1.05	0.34	−0.80	−1.26	−1.34	<0	0.69	nd
602-B	20	−0.3	1.41	0.24	nd	nd	nd	nd	nd	nd	nd
600-S	2	1.5	0.61	5.04	0.45	0.63	0.61	0.13	0.64	0.03	0.04
600-B	13	1.2	1.03	2.5	0.45	0.19	0.18	0.05	0.19	0.01	0.07
Okak											
630-S	2	4.2	0.32	1.53	0.35	−0.92	−0.97	−1.02	<0	0.06	nd
630-B	5	1	0.25	4.74	0.55	0.17	−0.35	−0.52	0.39	0.39	1.00
633-S	2	3	0.07	0.86	0.25	0.38	0.29	−0.59	0.41	0.12	0.30
633-B	17	1.9	0.34	0.61	0.41	−0.20	−0.71	0.03	0.15	0.86	5.64

Table 4. Summary of dilution experiments conducted on heterotrophic bacterial communities in Nachvak and Okak fjords during summer 2013. Initial abundances of total and high nucleic acid bacteria in the undiluted seawater are shown. k_1: bacterial abundance-based growth rate in dilution D_1 with nutrient enrichment; k_2 and k_3: bacterial abundance-based growth rate in dilutions D_2 and D_3 (undiluted seawater) with and without nutrient enrichment, respectively; μ_b: intrinsic growth rate of heterotrophic bacteria; g_b: zooplankton grazing rate on bacteria; g_b:μ_b: ratio of grazing to growth rate. μ_b and g_b were calculated using k_1 and k_2. HNA: bacteria with high nucleic acid content; LNA: bacteria with low nucleic acid content. At each station, samples were collected at the surface (S) and bottom (B) layers of the euphotic zone. Sampling depths, fractional dilution, water temperature, and nitrate pus nitrite concentration at the sampling depth are indicated in Table 3. nd: not determined

Stn	Total heterotrophic bacteria						HNA bacteria						LNA bacteria					
	Abundance (10^6 cells l^{-1})	k_1 (d^{-1})	k_2 (d^{-1})	k_3 (d^{-1})	μ_b (d^{-1})	g_b (d^{-1})	g_b:μ_b	Abundance (10^6 cells l^{-1})	k_1 (d^{-1})	k_2 (d^{-1})	k_3 (d^{-1})	μ_b (d^{-1})	g_b (d^{-1})	g_b:μ_b	k_1 (d^{-1})	k_2 (d^{-1})	k_3 (d^{-1})	μ_b (d^{-1})	g_b (d^{-1})	g_b:μ_b
Nachvak																				
602-S	1340	−0.37	−0.29	−0.35	<0	nd	nd	1040	−0.47	−0.34	−0.38	<0	nd	nd	−0.12	−0.13	−0.33	<0	0.01	nd
602-B	1190	−0.43	−0.09	0.51	<0	nd	nd	861	−0.59	−0.15	0.67	<0	nd	nd	−0.14	0.05	0.25	<0	nd	nd
600-S	1180	0.08	−0.08	0.09	0.20	0.28	1.40	709	0.15	0.03	0.16	0.24	0.21	0.86	−0.01	−0.30	−0.03	0.23	0.53	2.30
600-B	995	0.08	−0.44	0.28	0.51	0.95	1.87	608	0.10	−0.60	0.34	0.68	nd	nd	0.05	−0.25	0.17	0.30	0.56	1.87
Okak																				
630-S	620	0.18	0.17	0.13	0.18	0	0	294	0.50	0.48	0.41	0.50	0.02	0.04	−0.16	−0.22	−0.2	<0	0.09	nd
630-B	258	0.01	0.13	0.30	<0	nd	nd	104	0.41	0.37	0.57	0.45	0.09	0.20	−0.26	−0.07	0.07	<0	nd	nd
633-S	776	0.04	0.34	0.43	<0	nd	nd	453	0.05	0.51	0.60	<0	nd	nd	0.03	0.03	0.13	0.02	nd	nd
633-B	354	0.12	0.38	0.38	<0	nd	nd	206	0.22	0.50	0.56	0.04	nd	nd	0.05	0.18	0.04	<0	nd	nd

highest intrinsic phytoplankton growth rate and the lowest herbivory rate were both observed at outer Nachvak (Table 3).

Contrary to phytoplankton, the net growth of heterotrophic bacteria was generally higher in bottles without nutrient enrichment (k_3) than in those with nutrient addition (k_2), although the difference was not significant. Under nutrient-limited conditions, heterotrophic bacteria seemed to increase in abundance much faster than phytoplankton. The intrinsic growth rates of heterotrophic bacteria (μ_b) varied between <0 and 0.68 d^{-1}, with a mean value of 0.30 d^{-1}. Bacterivory (g_b) varied from 0.01 to 0.95 d^{-1}, with a mean value of 0.30 d^{-1}. Grazing mortality as a fraction of heterotrophic bacteria growth ranged from 0 to 2.3. The highest intrinsic growth rate of heterotrophic bacteria and the highest bacterivory rate were both observed at the SCM in Nachvak Fjord (Table 4). In some cases, bacterial net growth (k_1) was lower in dilution D_1 than in the undiluted bottles (k_2 and k_3; Table 4), making calculation of the grazing rate impossible.

4. DISCUSSION

4.1. Multivariate control of bacterial growth

Warm, productive, chl *a*-rich waters favored the growth and accumulation of bacteria in the upper 100 m of the water column in Labrador fjords. This finding is in agreement with previous investigations and indicates a positive relationship between water temperature, resource availability, and bacterial abundances (Pomeroy et al. 1991, Pomeroy & Wiebe 2001). Although heterotrophic bacterial abundances did not show any significant relationship with DOC, they were positively correlated with chl *a* concentration. Bird & Kalff (1984) previously found that bacterial abundances are often well correlated with chl *a* concentration in marine systems. The absence of a direct relationship between bacteria and DOC is likely because bulk DOC concentration is a poor indicator of the concentration of labile DOC, which is readily available to bacteria. In our study, bacterial abundances were also positively correlated with phosphate concentrations. Because of the strong freshwater influence, heterotrophic bacteria in estuarine systems and fjords usually experience physiological phosphorus deficiency (Thingstad et al. 1993). This nutrient limitation could induce a higher reliance on DOC utilization by heterotrophic bacteria in

estuarine systems (Kritzberg et al. 2010). Thus, in Labrador fjords, water temperature and the supply of organic substrates and inorganic nutrients are the main abiotic factors controlling heterotrophic bacterial abundance. Our conclusions are corroborated by the results of Kirchman et al. (2009a,b), who identified the same factors as the main drivers controlling bacterial growth and activity in polar waters.

4.2. HNF are not the sole bacterial grazers

The 1:1000 ratio of HNF to bacteria calculated during our study is in perfect agreement with values reported in the literature (see Sanders et al. 1992). The positive and significant relationship we found between HNF and bacteria suggests bacterial control, i.e. a bottom-up control, on the nanograzers. This positive relationship has been reported in many studies (Sherr et al. 1984, Sanders et al. 1992, Lin et al. 2014). Despite being significant, the variance explained by our regression model is relatively low ($r = 0.35$), suggesting that other processes may exert tight control on bacteria and nanoflagellates. This weak relationship between HNF and heterotrophic bacteria is often reported in the literature, and 3 reasons were proposed by Gasol & Vaqué (1993) to explain it. First, organisms other than HNF are important predators of bacteria, and other loss processes (e.g. viral mortality) could be more important than predation. Second, HNF may prefer other carbon sources, such as picophytoplankton and labile DOC, to bacteria. Finally, significant top-down control on HNF by large ciliates, phagotrophic dinoflagellates, or small metazoans may limit their grazing pressure on bacteria. Although no estimates of bacterial mortality due to viruses are available for our study region, viruses in Labrador fjords are likely as active as in other polar systems. For instance, during summer in the southern Beaufort Sea, Payet & Suttle (2013) estimated that 1.4 to 29% of the bacterial standing stock was removed daily by viral lysis. Furthermore, Wells & Deming (2006) reported that bacterial mortality caused by viruses in Franklin Bay (Amundsen Gulf) could be at least twice that caused by grazers.

4.3. Growth and grazing rates

Mean intrinsic phytoplankton growth rate in Labrador fjords (0.36 d^{-1}) was very similar to that in the Barents Sea (0.32 d^{-1}; Verity et al. 2002) and the Bering Sea (0.35 and 0.47 d^{-1}; Table 5) during summer. Summer herbivory averaged 0.31 d^{-1} in Labrador fjords and was comparable to the Barents Sea (0.24 d^{-1}; Table 5) and the Bering Sea (0.27 and 0.43 d^{-1}; Table 5). The phytoplankton grazing rate we found was similar to the mean value of 0.41 d^{-1} estimated by Calbet & Landry (2004) in subpolar oceanic regions. However, the mean algal growth and zooplankton grazing rates we calculated were much higher than those reported by Sherr & Sherr (2009) in the western Arctic Ocean under similarly low water temperatures (Table 5). Interestingly, for all the regions presented in Table 5, including Labrador

Table 5. Growth rates of phytoplankton and total heterotrophic bacteria as well as zooplankton grazing rates in Arctic/subarctic regions during summer. Unless otherwise indicated, grazing experiments were conducted using the dilution method. Mean ± SD or range is indicated for each parameter

Region	Temperature (°C)	Growth rate (d^{-1})	Grazing rate (d^{-1})	Grazing:growth[a] (%)	Reference
Phytoplankton					
Western Arctic Ocean	−0.4 ± 2.0	0.11 ± 0.13	0.06 ± 0.05	27 ± 33	Sherr & Sherr (2009)
Barents Sea	−0.2 – 7.4	0.32 ± 0.13	0.24 ± 0.11	77 ± 8	Verity et al. (2002)
Bering Sea	6.6 ± 0.9	0.47 ± 0.15	0.27 ± 0.14	58 ± 31	Liu et al. (2002)
Bering Sea	6.8 ± 1.8	0.35 ± 0.30	0.13 ± 0.09	49	Strom & Fredrickson (2008)
Bering Sea	11.1 ± 1.1	0.53 ± 0.21	0.43 ± 0.28	90 ± 56	Olson & Strom (2002)
Labrador fjords	1.7 ± 0.8	0.36 ± 0.20	0.31 ± 0.35	4 – 564	This study
Bacterioplankton					
Central Arctic Ocean	−1 to <1	0.03 – 0.09	0.002 – 0.009[b]	4 – 22	Sherr et al. (1997)
Resolute Passage	−1 to <1	0.62 – 1.02	0.76 – 0.88	86 – 93	Anderson & Rivkin (2001)
Labrador fjords	−0.3 – 4.2	<0 – 0.68	0 – 0.95	0 – 187	This study

[a]Grazing rate × (growth rate)$^{-1}$ × 100
[b]Grazing method: uptake of fluorescent-labeled bacteria

fjords, the phytoplankton Q_{10} value ranged from 1.5 to 2.0, indicating a likely temperature dependence of algal growth rates in cold waters (Eppley 1972).

Overall, phytoplankton growth responded positively to nutrient addition: chl *a*-based growth rates were generally higher with added nutrients (k_2) than without (k_3). However, the increase in phytoplankton growth due to nutrient addition did not compensate for grazing losses. Indeed, our results show that summer protist herbivory can be 6 times higher than the maximum intrinsic growth of algae (Table 3), indicating that zooplankton prey heavily on algae. To support this high grazing pressure during summer 2013, we estimated the export of biogenic carbon out of the euphotic zone in Labrador fjords using the model of Tremblay et al. (1997) based on phytoplankton size structure. Apart from outer Nachvak (Stn 600), where half of the production was potentially exported out of the euphotic zone, less than 20% of total primary production at the other 3 locations was vertically exported (data not shown). This could indicate that a large part of the primary production is grazed by herbivores in Labrador fjords rather than being exported to greater depths.

There are only a few direct measurements of bacterivory in the Arctic, and even fewer studies used the dilution method as we did (Table 5). In Labrador fjords, the addition of FSW to dilutions seems to have affected bacterial growth. Indeed, net bacterial growth rates (k) were usually higher in dilution D_1 than in dilutions D_2 and D_3. This biased result could be explained by the fact that the addition of whole seawater to FSW can lead to modified grazer behavior (Moigis 2006), changes in bacterial community composition (Agis et al. 2007), and enrichment of organic and inorganic nutrients (Ferguson et al. 1984). The rates of bacterioplankton growth and mortality due to zooplankton grazing in Labrador fjords were similar to values reported in Resolute Passage but much higher than those estimated in the central Arctic Ocean (Table 5). Bacterivorous zooplankton activity ranged from nil to nearly twice the total bacterial growth, implying that grazing is an important factor controlling bacterial abundance during summer. Many previous studies corroborate our findings and indicate that grazing and viral lysis are important causes of bacterial mortality (Proctor & Fuhrman 1990, Sherr & Sherr 1994, Suttle 2007). Because our study provides the first data on zooplankton grazing in Labrador fjords, whether our estimates of herbivory and bacterivory can be extrapolated to other seasons and years must still be confirmed by future investigations.

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