Université du Québec
à Rimouski

VARIABILITÉ SPATIALE ET SAISONNIÈRE DES COMMUNAUTÉS PHYTOPLANCTONIQUES ET BACTÉRIENNES DES FJORDS SUBARCTIQUES DE LA CÔTE EST DU CANADA

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PAR

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À mes parents bien-aimés,
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RÉSUMÉ

Dans les fjords de la Scandinavie, du Groenland et de la côte ouest du Canada, diverses études ont montré que la dynamique des communautés planctoniques est fortement influencée par la stratification de la colonne d'eau, le régime lumineux et la disponibilité des nutriments. De telles observations sont cependant difficiles à valider pour les fjords subarctiques de la côte est du Canada, particulièrement les fjords du Labrador, car la dynamique du plancton n'y avait encore jamais été étudiée. Devant ce manque de connaissances et sachant la rapidité des changements climatiques auxquels sont assujettis les milieux polaires, il devenait impératif d'acquérir de telles données, d'autant plus que la réponse des communautés planctoniques face au réchauffement climatique est déterminante pour l'ensemble des maillons des réseaux trophiques. C'est dans ce contexte que s'insère cette thèse dont l'objectif central était de déterminer la variabilité spatiale et saisonnière des communautés phytoplanctoniques et bactériennes des fjords de Nachvak, Saglek, Okak et Anaktalak pendant l'été 2007, l'été 2013, le début de l'automne 2010 et la fin de l'automne 2009.

La production primaire, la biomasse chlorophyllienne et l'exportation verticale du carbone organique particulaire ont présenté une variabilité saisonnière très marquée, les plus fortes valeurs ayant été observées pendant l'été. La communauté estivale a été principalement dominée par le nanophytoplancton (2-20 μm) tandis que la communauté automnale a présenté de plus fortes abondances de picophytoplancton (<2 μm). L'analyse de la contribution relative du petit et du gros phytoplancton à la production totale a permis de suggérer que la production primaire est préférentiellement retenue dans la zone euphotique au lieu d'être exportée vers les profondeurs. Les variations saisonnières dans la production et la biomasse phytoplanctonique ainsi que dans l'exportation du carbone ont été principalement attribuables à la stratification de la colonne d'eau et à la durée de l'éclairement journalier. Étonnamment, la dynamique du phytoplancton n'a pas présenté de différences significatives d'un fjord à l'autre. Nos résultats ont également permis de déterminer qu'en raison de la fonte tardive du couvert de glace, le bloom pélagique a lieu pendant l'été dans les fjords du Labrador, et non au printemps comme couramment observé dans les fjords de la Scandinavie et du Groenland.

Pendant l'été 2007, la communauté a été dominée par les diatomées et un assemblage mixte de flagellés. À l'été 2013, les flagellés ont nettement dominé la communauté et un bloom important du prymnésiophyte *Phaeocystis pouchetii* (jusqu'à 18×10^6 cellules l^{-1}) a été observé dans le fjord de Nachvak. À l'automne, la communauté a été dominée par les flagellés non identifiés, les prymnésiophytes et les diatomées, leurs abondances respectives variant du début de l'automne à la fin de l'automne. Les principales variables environnementales responsables de ces différences significatives dans la composition

taxonomique des protistes étaient la température et la salinité de l'eau, l'intensité de la stratification, l'éclairement journalier et la profondeur de la couche de mélange de surface. En combinant nos résultats à ceux de la littérature, nous avons suggéré la succession annuelle suivante dans la communauté des protistes: (hiver) dinoflagellés et autres flagellés ─ (printemps) *Fragilariopsis* spp., *Chaetoceros* spp., *Thalassiosira* spp. et *Phaeocystis pouchetii* ─ (été) *Chaetoceros* spp., *P. pouchetii* et *Chrysochromulina* spp. ─ (automne) flagellés, *Gymnodinium/Gyrodinium* spp. et *Chrysochromulina* spp. Nous avons également pu dresser la toute première liste de protistes planctoniques des fjords du Labrador, en précisant l'abondance relative et le pourcentage d'occurrence de chaque taxon identifié. Avec plus de 200 taxons recensés, cette liste de protistes est sans conteste la plus complète de la littérature sur les fjords polaires.

La température de l'eau et la biomasse chlorophyllienne ont significativement influencé l'abondance des bactéries hétérotrophes pendant l'été 2013, le début de l'automne et la fin de l'automne. Pour l'ensemble de la période d'étude, une relation positive et significative a été trouvée entre l'abondance des nanoflagellés hétérotrophes et celle des bactéries hétérotrophes. À l'été 2013, le taux de croissance intrinsèque du phytoplancton a varié entre <0 jr^{-1} et 0,64 jr^{-1}, avec une moyenne de 0,36 jr^{-1}. Le taux de broutage par le microzooplancton a été très variable, allant de 0,01 à 0,86 jr^{-1}, avec un taux moyen de 0,31 jr^{-1}. La mortalité due au broutage a été jusqu'à six fois plus élevée que la croissance du phytoplancton. Les taux de croissance du phytoplancton et de broutage par le microzooplancton dans les fjords du Labrador ont été comparables aux valeurs dans les mers de Barents et de Béring. Cette thèse de doctorat présente les toutes premières données sur les communautés planctoniques des fjords subarctiques du Labrador, données qui serviront de référence pour les études futures et qui permettront de mieux prédire les réponses du plancton face aux perturbations environnementales naturelles et anthropiques.

Mots-clés : Production et biomasse phytoplanctoniques, structure de taille, composition taxonomique, protistes, bactéries hétérotrophes, broutage, Arctique, Canada, Labrador, fjords subarctiques

ABSTRACT

In fjords of Scandinavia, Greenland, and of the west coast of Canada, various studies tend to show that the dynamics of plankton communities is strongly influenced by the stratification of the water column, the light regime and the nutrient availability. Such observations are however difficult to validate for subarctic fjords of the east coast of Canada, especially Labrador fjords, because plankton dynamics had never been studied there. Faced with this lack of knowledge and knowing the speed of climate change experienced by polar environments, it became imperative to acquire such data, especially as the answer of plankton communities facing global warming is determinant for all the food web links. This thesis fits in this context and the central objective was to determine the spatial and seasonal variability of phytoplankton and bacteria communities in Nachvak, Saglek, Okak and Anaktalak fjords during summer 2007, summer 2013, early fall 2010 and late fall 2009.

Primary production, chlorophyll biomass and vertical export of particulate organic carbon showed a marked seasonal variability, the highest values being observed during summer. The summer community was mainly dominated by nanophytoplankton (2-20 μm) while the fall community presented higher abundances of picophytoplankton (<2 μm). The analysis of the relative contribution of small and large phytoplankton to total production allowed to suggest that primary production was preferentially retained in the euphotic zone rather than being exported to greater depths. The seasonal variations of phytoplankton production and biomass, as well as carbon export were mainly due to the stratification of the water column and the duration of daily light. Surprisingly, phytoplankton dynamics did not show any significant difference from one fjord to another. Our results also revealed that the pelagic bloom occurs during summer in Labrador fjords and not in spring as usually observed in fjords of Scandinavia and Greenland. This is explained by the late sea-ice break-up in Labrador fjords.

During summer 2007, the community was dominated by diatoms and a mixed assemblage of flagellates. In summer 2013, flagellates clearly dominated the community and an important bloom of the prymnesiophyte *Phaeocystis pouchetii* (up to 18×10^6 cells l^{-1}) was observed at Nachvak Fjord. During fall, the community was dominated by unidentified flagellates, prymnesiophytes and diatoms, their respective abundances varying from early fall to late fall. The main environmental variables responsible for these significant differences in protist taxonomic composition were water temperature and salinity, the strength of stratification, the daily light and the depth of the surface mixed layer. By combining our results to those from the literature, we suggested the

following annual succession in the protist community: (winter) dinoflagellates and other flagellates ─ (spring) *Fragilariopsis* spp., *Chaetoceros* spp., *Thalassiosira* spp. and *Phaeocystis pouchetii* ─ (summer) *Chaetoceros* spp., *P. pouchetii* and *Chrysochromulina* spp. ─ (fall) flagellates, *Gymnodinium/Gyrodinium* spp. and *Chrysochromulina* spp. We were also able to draw the very first list of planktonic protists in Labrador fjords, indicating the relative abundance and the occurrence percentage of every taxon identified. With more than 200 taxa reported, this list of protists is without contest the most complete of the literature on polar fjords.

Water temperature and chlorophyll biomass significantly influenced the abundance of heterotrophic bacteria during summer 2013, early fall and late fall. For the whole sampling period, a positive and significant relationship was found between the abundance of heterotrophic nanoflagellates and that of heterotrophic bacteria. During summer 2013, the intrinsic growth rate of phytoplankton varied between <0 d^{-1} and 0.64 d^{-1}, with a mean of 0.36 d^{-1}. Microzooplankton grazing rate was very variable, ranging from 0.01 to 0.86 d^{-1}, with a mean rate of 0.31 d^{-1}. Mortality due to grazing was up to six times higher than phytoplankton growth. Phytoplankton growth and microzooplankton grazing rates in Labrador fjords were comparable to values in the Barents Sea and the Bering Sea. This doctoral thesis presents the very first data on the plankton communities of subarctic Labrador fjords, data which will be used as reference for future studies and which will help to better predict plankton responses to natural and anthropogenic environmental disturbances.

Keywords: Phytoplankton production and biomass, size structure, taxonomic composition, protists, heterotrophic bacteria, grazing, Arctic, Canada, Labrador, subarctic fjords

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LISTE DES ABRÉVIATIONS, DES SIGLES ET DES ACRONYMES

^{14}C	Carbone-14
ANOSIM	Analysis of similarities
ANOVA	Analysis of variance
B_L	Biomass of large phytoplankton
B_S	Biomass of small phytoplankton
B_T	Total phytoplankton biomass
CCGS	Canadian Coast Guard Ship
CDOM	Colored dissolved organic matter
Chl *a*	Chlorophyll *a*
Choano	Choanoflagellidea
Chryso	Chrysophyceae
Cil	Ciliates
Crypto	Cryptophyceae
CTD	Conductivity, temperature, depth
dbRDA	Distance-based redundancy analysis
DCMU	3-(3,4-dichlorophenyl)-1,1-dimethylurea
Diat	Diatoms

Dictyocho	Dictyochophyceae
Dino	Dinophyceae
DistLM	Distance-based linear model
DOC/COD	Dissolved organic carbon/Carbon organique dissous
DOC_L	Labile dissolved organic carbon
Eugleno	Euglenophyceae
Euk. Pico	Eukaryotic picophytoplankton
FRQNT	Fonds de recherche du Québec - Nature et Technologies
H. prot	Heterotrophic protists
Het. groups	Heterotrophic groups
HNA	High nucleic acid
HNF	Heterotrophic nanoflagellates
ICES	International Council for the Exploration of the Sea
IPCC	Intergovernmental Panel on Climate Change
LNA	Low nucleic acid
MDS	Multidimensional scaling
Micro	Microplankton
MZP	Microzooplankton
Nano	Nanophytoplankton
NSERC	Natural Sciences and Engineering Research Council of Canada

O. flag	Other flagellates
P:B	Production:Biomass
PAR	Photosynthetically active radiation
PC	Principal component
PCA	Principal component analysis
PCB	Polychlorinated biphenyl
P-E	Photosynthesis-irradiance
Picocyano	Picocyanobacteria
P_L	Production of large phytoplankton
PNF	Profiling natural fluorescence
POC/COP	Particulate organic carbon/Carbone organique particulaire
POC_E	Particulate organic carbon exported
Prasino	Prasinophyceae
Prymn, Prymesio	Prymnesiophyceae
P_S	Production of small phytoplankton
P_T	Total particulate phytoplankton production
PUA	Polyunsaturated aldehydes
Raphido	Raphidophyceae
SADCP	Ship-mounted acoustic Doppler current profiler
SCM	Subsurface chlorophyll maximum

SIMPER	Similarity percentages
Un. flag	Unidentified flagellates

LISTE DES SYMBOLES

$(NO_3+NO_2)_{0\text{-}Zeu}$	Nitrate plus nitrite integrated over the euphotic zone
$(NO_3+NO_2)_{0\text{-}Zm}$	Nitrate plus nitrite integrated over the surface mixed layer
$(PO_4)_{0\text{-}Zeu}$	Phosphate integrated over the euphotic zone
$(PO_4)_{0\text{-}Zm}$	Phosphate integrated over the surface mixed layer
$(Si(OH)_4)_{0\text{-}Zeu}$	Silicic acid integrated over the euphotic zone
$(Si(OH)_4)_{0\text{-}Zm}$	Silicic acid integrated over the surface mixed layer
$\Delta\sigma_t$	Stratification index
CO_2	Carbon dioxide/Dioxyde de carbone
E	Daily incident downwelling irradiance
$E_{0\text{-}Zeu}$	Daily irradiance averaged in the euphotic zone
E_Z	Daily irradiance at the sampling depth
g	Microzooplankton grazing rate
H_2O	Water/Eau
k_d	Diffuse light attenuation coefficient
N^2	Brunt–Väisälä frequency
NO_2	Nitrite

NO_3+NO_2	Nitrate plus nitrite
O_2	Dioxygen/Dioxygène
P^B	Chlorophyll *a* specific photosynthetic rate at irradiance E
P^B_o	Chlorophyll *a* specific photosynthetic rate at zero irradiance
P^B_s	Light-saturated maximum photosynthetic rate without photoinhibition
PO_4	Phosphate
S	Salinity
S_{eu}	Salinity averaged in the euphotic zone
$Si(OH)_4$	Silicic acid
T	Water temperature
T_{eu}	Water temperature averaged in the euphotic zone
Z	Water column depth
Z_{eu}	Euphotic zone depth
Z_m	Surface mixed layer depth
Z_{nutr}, Z_{nut}	Nitracline depth based on NO_3 gradient concentrations
α^B	Initial slope (photosynthetic efficiency) of the P-E curve
β^B	Photoinhibition parameter
μ	Phytoplankton intrinsic growth rate

INTRODUCTION GÉNÉRALE

Les producteurs primaires jouent un rôle clé dans les écosystèmes marins car ils fournissent la matière organique nécessaire à la croissance des organismes des niveaux trophiques supérieurs. Contrairement aux autres milieux côtiers et du fait des conditions environnementales particulières qui y prévalent, les fjords présentent une richesse et une diversité spécifiques réduites (Becker 1994). Ces spécificités biologiques les rendent d'autant plus sensibles aux perturbations induites par les changements climatiques. La convention cadre des Nations Unies sur les changements climatiques (IPCC 2007) définit les changements climatiques comme des perturbations qui sont attribuées directement ou indirectement à une activité humaine altérant la composition de l'atmosphère mondiale et qui viennent s'ajouter à la variabilité naturelle du climat observée au cours de périodes comparables. Les écosystèmes polaires sont les plus sévèrement touchés par les changements climatiques (Moline et al. 2008, Post et al. 2009) et ils subissent des perturbations environnementales sans précédent (Arrigo et al. 2008). Ainsi, les milieux arctiques connaissent une diminution accélérée de l'étendue et de l'épaisseur de la glace de mer (Stroeve et al. 2007, Kwok et al. 2009), un dégel précoce et un gel tardif de la glace (Markus et al. 2009) et une intensification du cycle hydrologique (Peterson et al. 2006, Serreze et al. 2006). Ces perturbations environnementales majeures affectent considérablement l'équilibre fragile des réseaux trophiques et elles expliquent en grande partie les bouleversements de la dynamique des communautés planctoniques de l'océan Arctique (Li et al. 2009, McLaughlin & Carmack 2010). Cependant, leurs répercussions sur le plancton des régions côtières arctiques notamment les fjords du Labrador, sont peu connues.

Cycle de la production primaire pélagique dans l'Arctique

La production primaire désigne la synthèse de la matière organique via le processus de photosynthèse par des organismes dits autotrophes. Elle traduit la vitesse à laquelle se forme, par unité de temps, une quantité donnée de matière organique, à partir de composés inorganiques et d'un apport d'énergie. La photosynthèse nécessite du carbone inorganique dissous sous forme de gaz carbonique (CO_2) et elle se déroule selon l'équation suivante de Falkowski & Raven (2007) :

$$CO_2 + H_2O \rightarrow CH_2O + O_2$$

où CH_2O est la molécule de base des hydrates de carbone tels que les glucides.

Toute vie sur terre dépend directement ou indirectement de la production primaire. Les organismes assurant la production primaire sont aussi appelés producteurs primaires et ils sont à la base de toute chaîne alimentaire. En milieu aquatique, la production primaire est réalisée par les cellules algales qui se développent principalement dans les couches supérieures de la colonne d'eau (qui reçoivent suffisamment de lumière) mais aussi dans la glace de mer. Dans le premier cas, on parle de production primaire pélagique (réalisée par le phytoplancton) et dans le second cas, il s'agit de la production primaire sympagique (réalisée par les algues de glace). On distingue aussi la production primaire brute et la production primaire nette. Cette dernière est obtenue en soustrayant la respiration cellulaire à la production brute.

Selon la source d'azote supportant la production primaire, on distingue également la production nouvelle et la production régénérée. Lorsque le mélange vertical est suffisamment puissant pour injecter dans la zone euphotique les nutriments issus des couches profondes, la production primaire soutenue par ces nutriments d'origine allochtone et particulièrement le nitrate, est dite nouvelle (Dugdale & Goering 1967, Eppley & Peterson 1979). La production nouvelle peut également être entretenue par d'autres sources allochtones d'azote notamment l'apport atmosphérique d'ammonium, de nitrate, d'ammoniac et d'azote organique dissous (Paerl 1985, Legendre & Gosselin 1989,

Prospero et al. 1996) ainsi que par la fixation d'azote moléculaire atmosphérique (N_2) par les cyanobactéries diazotrophes (Carpenter & Romans 1991). Par contre, lorsque la stratification de la colonne d'eau est très importante, empêchant tout réapprovisionnement de la zone euphotique en nutriments issus du fond, la production primaire est dite régénérée car soutenue par des sources autochtones d'azote telles que l'ammonium, régénéré *in situ* par les bactéries hétérotrophes (Dugdale & Goering 1967, Eppley & Peterson 1979).

Du fait des conditions extrêmes des hautes latitudes (lumière, température, stratification, couvert de glace), la production primaire est très variable d'une saison à l'autre mais aussi d'une région à l'autre (Carmack & Wassmann 2006). La production primaire arctique est fortement influencée par la quantité de lumière reçue par le phytoplancton et par la disponibilité des nutriments (Tremblay & Gagnon 2009). D'une manière générale, plus on s'éloigne des côtes, plus la production primaire diminue en raison de la baisse subséquente des concentrations en nutriments. Cela permet de distinguer les milieux côtiers eutrophes de l'océan profond généralement oligotrophe (Chavez et al. 2002). De plus, au fur et à mesure qu'on approche des pôles, la production primaire pélagique diminue tandis que la production sympagique augmente (Gosselin et al. 1997).

Pendant l'hiver, de loin la saison la plus longue de l'année, lorsque le rayonnement solaire est très faible (voir nul pendant la nuit polaire) et la couverture de glace et de neige très épaisse, la production primaire est négligeable (Olli et al. 2002, Forest et al. 2008). Par conséquent, l'exportation verticale de la matière vers les couches profondes est également très faible. Sous ces conditions défavorables, les dinoflagellés et certaines diatomées produisent des formes de résistance (spores ou kystes) ou entrent en dormance. Au fur et à mesure que la saison avance, l'éclairement journalier et la fonte de la neige (et de la glace) augmentent et favorisent le réchauffement progressif de l'eau. Cependant, malgré les fortes concentrations de nutriments dans la colonne d'eau (issus du mélange hivernal et de la régénération), la production primaire pélagique reste encore faible car limitée par les faibles intensités lumineuses.

Au printemps, le bloom est déclenché par l'alternance entre les épisodes de stabilisation-déstabilisation de la colonne d'eau, ainsi que par l'augmentation de l'éclairement journalier et de la température de l'eau. Cette période de floraison est caractérisée par une production primaire et une biomasse chlorophyllienne élevées (Wassmann & Reigstad 2011). Un pic dans l'exportation verticale de carbone accompagne également le bloom printanier (Olli et al. 2002, Reigstad et al. 2008) qui est majoritairement associé à une production nouvelle dominée par les cellules de grande taille (≥5 μm) telles que les diatomées. Aux hautes latitudes, le cycle de croissance du phytoplancton et par conséquent la période du bloom (printemps, été ou automne) dépendent fortement de la durée du couvert de glace (Simo-Matchim et al. 2016). Ainsi, dans les fjords du Labrador, recouverts de glace du 11 décembre jusqu'au 16 juillet environ (durée moyenne sur la dernière décennie; Service canadien des glaces, Environnement Canada 2015), le pic de croissance du phytoplancton a lieu pendant l'été (Simo-Matchim et al. 2016). En effet, la disparition tardive de la glace de mer dans les fjords du Labrador empêche le déclenchement d'un bloom au printemps, puisque les fjords sont encore recouverts de glace. Ce bloom estival dans les fjords du Labrador diffère de l'habituel bloom printanier qui est quasi la norme dans les fjords de Norvège, du Svalbard et du Groenland, qui sont pour la plupart libres de glace beaucoup plus tôt.

Dans le cycle classique de production primaire avec un bloom printanier, l'été est caractérisé par des eaux très pauvres en nutriments et fortement stratifiées. En effet, le bloom a épuisé les nutriments en surface et le réchauffement estival des eaux empêche le réapprovisionnement en nutriments issus de la couche profonde. Sous ces conditions post-bloom, la communauté phytoplanctonique est dominée par les cellules de petite taille telles que les flagellés et la production régénérée est dominante (Lochte et al. 1993, Sieracki et al. 1993, Hill & Cota 2005).

À l'automne, le refroidissement de la couche de surface couplé aux vents forts affaiblit la stabilité verticale de la colonne d'eau et favorise l'injection de nutriments dans la couche de surface. Lorsque cet enrichissement en nutriments coïncide avec des intensités

lumineuses dans la zone euphotique suffisamment élevées, alors il est possible qu'un bloom automnal survienne (Ardyna et al. 2013, 2014, Simo-Matchim et al. 2016). Avec l'avancement de la saison, la lumière devient de nouveau un facteur limitant la production primaire et cela met fin au cycle de croissance du phytoplancton (Garneau et al. 2007, Brugel et al. 2009). Sous ces conditions, les flagellés hétérotrophes et mixotrophes dominent la communauté.

Devenir de la production primaire

La matière organique produite dans la couche de surface peut avoir deux destinées, soit elle est recyclée sur place, soit elle est exportée. L'exportation peut se faire vers les profondeurs (exportation verticale) ou vers un autre écosystème (exportation horizontale). Le devenir de la production primaire est déterminé par la structure de l'écosystème et les principaux facteurs qui interviennent sont la taille du phytoplancton, le broutage, la sédimentation ou la rétention du gros phytoplancton, l'agrégation du petit phytoplancton et l'accumulation ou la sédimentation de ces agrégats cellulaires (Fig. 1).

Selon Klein et al. (2002), la quantité de carbone organique particulaire (COP) exporté hors de la zone euphotique dans un système à l'état d'équilibre est fonction du *f*-ratio qui est le ratio de la production nouvelle à la production primaire totale. Le *f*-ratio donne ainsi un indice sur le potentiel d'exportation du système et il est estimé à partir de la structure de taille des communautés phytoplanctoniques (Tremblay et al. 1997). Plus les cellules sont de grande taille, plus le potentiel d'exportation du carbone est élevé et vice versa (Fig. 1). Aux hautes latitudes, le flux de COP est caractérisé par une forte saisonnalité (Wiedmann et al. 2016). La disponibilité des nutriments, la dynamique du phytoplancton et du zooplancton fluctuent tout au long de l'année (Węsławski et al. 1991, Rat'kova & Wassmann 2002, Leu et al. 2011), entraînant une grande variabilité des principaux contributeurs au flux vertical de COP que sont les agrégats cellulaires, les pelotes fécales et la neige marine (Turner 2002, 2015). En période de dégel, les algues de glace contribuent aussi significativement à

l'exportation verticale, lorsque les cellules sont libérées dans la colonne d'eau (Tremblay et al. 1989, Arrigo et al. 2014).

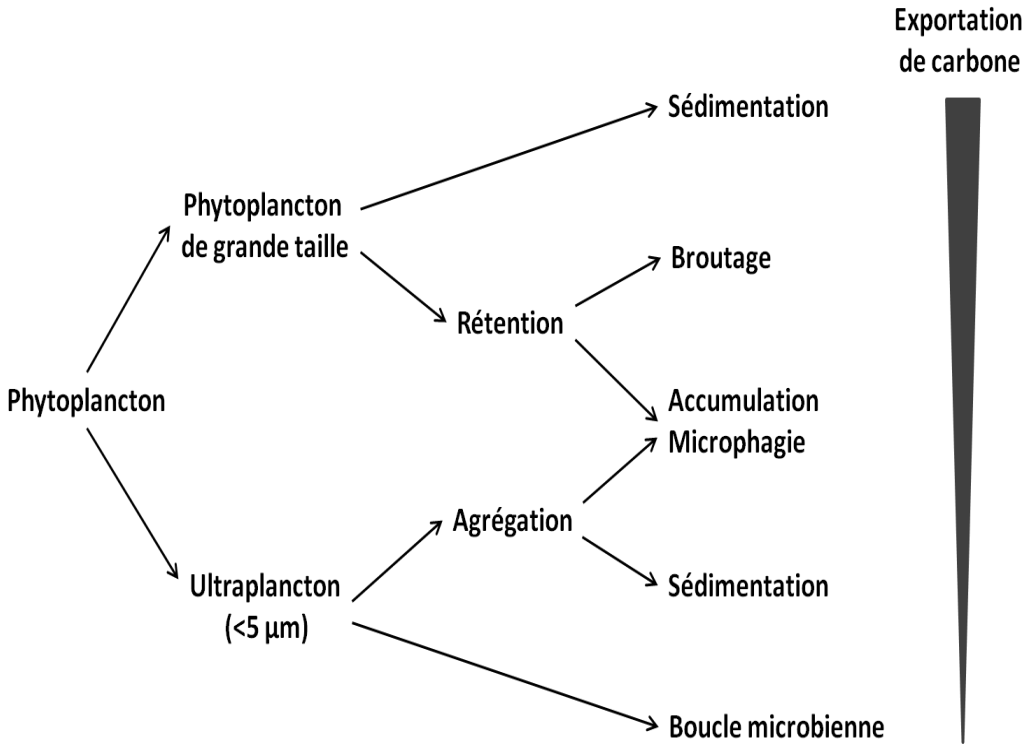

Fig. 1. Modèle de bifurcation de l'exportation de carbone biogène en fonction de la taille du phytoplancton et des caractéristques de l'environnement. Redessinée d'après Legendre & Le Fèvre (1989)

La dominance du bloom par tel ou tel autre taxon revêt une grande importance pour l'exportation du carbone. Par exemple, les floraisons algales dominées par les taxons de grande taille tels que les diatomées peuvent entraîner une forte sédimentation de la biomasse (Wassmann et al. 1991, Thompson et al. 2008). De plus, les diatomées sénescentes ou en dormance ont une grande vitesse de sédimentation (Rynearson et al.

2013), et certains taxons libèrent des substances exopolymériques qui contribuent à la formation des agrégats cellulaires (Kiørboe et al. 1994, Thornton 2002) et de la neige marine (Lampitt et al. 2001), augmentant ainsi l'exportation verticale de carbone. Par contre, lorsque le bloom est dominé par le prymnésiophyte *Phaeocystis pouchetii*, comme observé quelques fois dans les fjords de la Scandinavie (Degerlund & Eilertsen 2010), alors le scénario est tout autre. En effet, même présent en forte abondance dans la colonne d'eau, la contribution de *P. pouchetii* au flux vertical de carbone est faible car il ne favorise pas la formation des agrégats cellulaires (Reigstad et al. 2000, Reigstad & Wassmann 2007). Selon Reigstad et al. (2000), quelle que soit la composition taxonomique de la communauté phytoplanctonique, l'exportation de carbone n'est forte que si le contrôle « top-down » notamment le broutage par le microzooplancton est faible. Les processus de broutage sont abordés plus loin dans cette introduction.

Production primaire et changements climatiques

L'évolution de la production primaire globale face aux changements climatiques est un sujet de controverse au sein de la communauté scientifique. D'un côté, les observations satellitaires et *in situ* ainsi que les modèles climatiques prédisent une diminution de la production primaire dans l'océan mondial (Polovina et al. 2008, Boyce et al. 2010, 2011, Steinacher et al. 2010). De l'autre côté, diverses études suggèrent plutôt une augmentation de la production primaire globale (Behrenfeld 2011, Chavez et al. 2011, McQuatters-Gollop et al. 2011, Tauscher & Oschlies 2011).

Ce manque d'unanimité persiste également pour les régions polaires. Ainsi, dans l'océan Arctique, certaines études sont en faveur d'une augmentation de la production primaire (Carmack & Chapman 2003, Lee & Whiteledge, 2005, Doney 2006, Arrigo et al. 2008, Pabi et al. 2008, Zhang et al. 2010) qui serait principalement due à (1) l'allongement de la période libre de glace, qui aura pour conséquence d'accroître les intensités lumineuses reçues par le phytoplancton et de prolonger la saison de production (Fig. 2) et (2) la fréquence plus accrue des remontées d'eaux profondes riches en nutriments. Au contraire,

d'autres études avancent que le réchauffement climatique favorisera l'adoucissement des eaux de surface (Rabe et al. 2011, Morison et al. 2012), ce qui abaissera la productivité des milieux arctiques. En effet, l'accroissement des températures conduira à l'augmentation des apports d'eau douce, ce qui renforcera la stratification haline des masses d'eau et favorisera des conditions d'oligotrophie en diminuant le flux de nutriments dans la zone euphotique (Behrenfeld et al. 2006, Tremblay et al. 2006, Li et al. 2009, 2013, McLaughlin & Carmack 2010). De plus, les apports d'eau de fonte, riche en matière organique dissoute et particulaire, pourraient augmenter la turbidité de l'eau et atténuer davantage la lumière disponible pour les cellules algales.

Force est de constater que la plupart des perturbations attribuables aux changements climatiques rapportées par la littérature portent sur la production et la biomasse phytoplanctoniques. Très peu d'études ont été menées concernant les effets de ces changements sur la structure de taille et la composition taxonomique du phytoplancton arctique. Également, on sait très peu sur comment les changements liés au climat affecteront la succession saisonnière des protistes des hautes latitudes. Ces lacunes tiennent principalement au fait que les études *in situ* demeurent limitées dans l'Arctique, entraînant un manque de représentativité de la complexité réelle de cette région. En effet, les conditions extrêmes de l'Arctique induisent un coût élevé des expéditions scientifiques, et la présence de glace limite fortement le déploiement des instruments d’échantillonnage et l'acquisition des données sur le terrain. Heureusement, depuis les dernières années, des moyens considérables pour la recherche en Arctique ont été mis sur pied et de nombreux programmes comme le Réseau ArcticNet ont pu être créés. ArcticNet a pour objectif principal d'étudier les changements climatiques dans l'Arctique canadien côtier afin de contribuer au développement et à la diffusion des connaissances nécessaires à l'élaboration de stratégies d'adaptation.

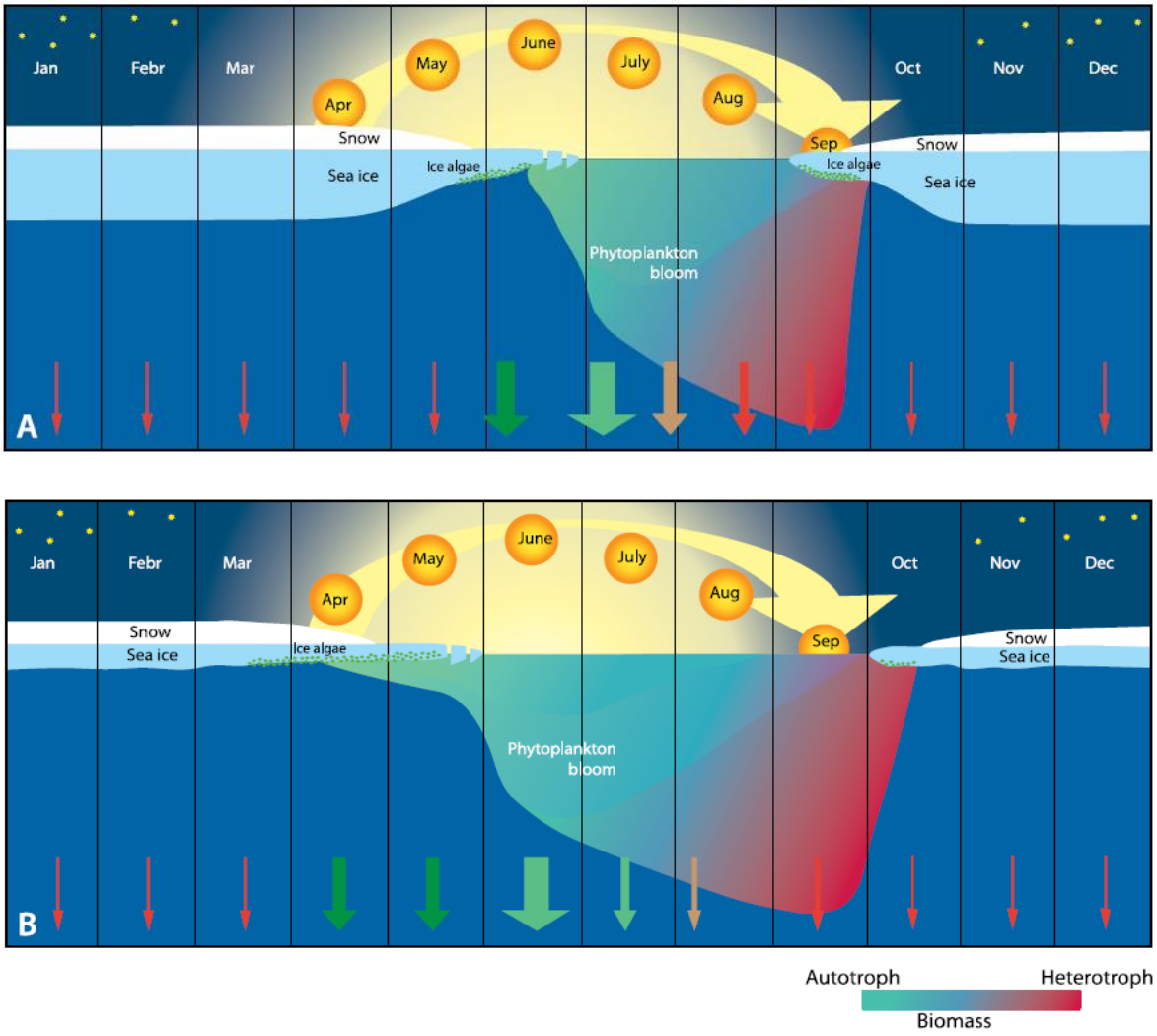

Fig. 2. Saisonnalité du développement du phytoplancton et de l'exportation verticale de carbone (A) dans les conditions climatiques actuelles et (B) dans un scénario de réchauffement climatique entraînant une plus longue période libre de glace. Le gradient du vert au rouge indique le passage d'une biomasse autotrophe à une biomasse hétérotrophe. L'épaisseur et la couleur des flèches verticales illustrent respectivement l'intensité et la composition du flux de matière organique exportée hors de la zone euphotique. Vert sombre : carbone dérivé des algues de glace; vert clair : carbone dérivé du phytoplancton; rouge et orange : détritus organiques (provenant de la matière organique particulaire non vivante). Modifiée de Wassmann & Reigstad (2011)

Contrôle environnemental des communautés planctoniques

En milieu pélagique, trois types de facteurs régulent la dynamique des communautés planctoniques : les facteurs ascendants ou « bottom-up », les facteurs descendants ou « top-down » et les facteurs « sideways » (Kirchman 2008, Mostajir et al. 2012). Les facteurs ascendants font référence aux ressources telles que la lumière, les nutriments et la matière organique, qui affectent plus le taux de croissance des organismes que leur biomasse. Bien que la température soit généralement présentée comme un facteur ascendant, Moran et al. (2010) recommandent de la considérer séparément car elle n'est pas une ressource pouvant être épuisée. Les facteurs descendants sont représentés par l'ensemble des pressions qui conduisent à des prélèvements de biomasse. Ils incluent la mortalité (par autolyse et lyse virale), le broutage, l'advection et la sédimentation. Les facteurs « sideways » quant à eux désignent les différentes interactions intra- et interspécifiques comme la compétition, l'allélopathie et la syntrophie.

Succession écologique des communautés planctoniques

Les travaux fondamentaux de Margalef (1978, 1997), Margalef et al. (1979), Legendre & Le Fèvre (1989) et Legendre & Rassoulzadegan (1995) ont contribué à établir les théories sur l'écologie du phytoplancton. Plusieurs modèles ont mis en évidence les relations entre la turbulence, la concentration en nutriments et les caractéristiques physiologiques du phytoplancton (Margalef et al. 1979, Legendre & Rassoulzadegan 1995, Cullen et al. 2002). Ainsi, selon le fameux « Mandala » de Margalef et al. (1979), la succession écologique va d'une communauté dominée par les diatomées dans les eaux bien mélangées et riches en nutriments à une communauté dominée par les flagellés dans les eaux stratifiées et pauvres en nutriments (Fig. 3).

Dans le même ordre d'idées, Margalef (1978) a distingué les espèces à stratégie adaptative r de celles à stratégie adaptative K (Fig. 3). La stratégie r se retrouve chez des

espèces généralistes telles que les diatomées dont le taux de mortalité est élevé. Elle est associée à une forte turbulence, une richesse en éléments nutritifs, une faible compétition pour les ressources et une faible efficacité énergétique. Par contre, la stratégie K est rencontrée chez des espèces plus spécialistes à taux de mortalité faible, notamment les flagellés. Elle est liée à des milieux peu turbulents et pauvres en nutriments, avec une forte compétition pour les ressources et une efficacité énergétique élevée.

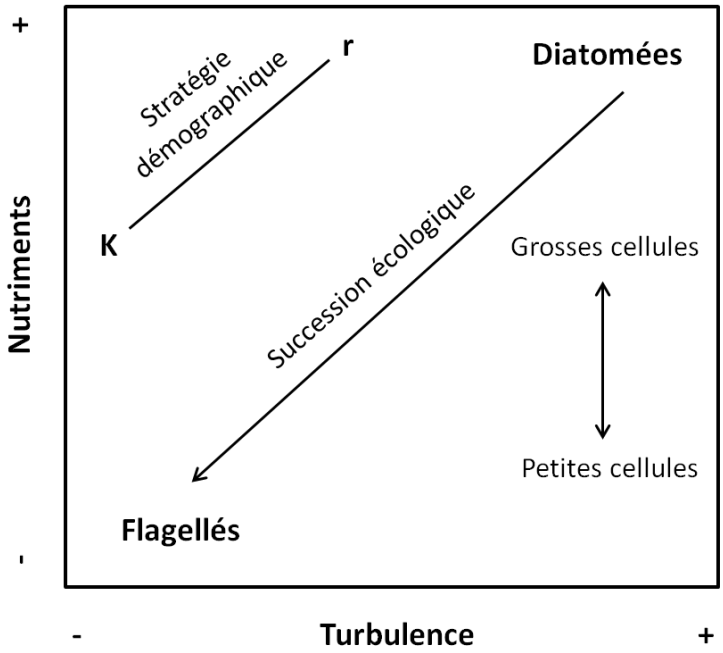

Fig. 3. Représentation schématique du « Mandala » de Margalef et al. (1979) mettant en relation la turbulence, la concentration en nutriments et la succession écologique du phytoplancton. Modifiée de Margalef et al. (1979)

Adapté du « Mandala » de Margalef et al. (1979), le modèle de Cullen et al. (2002) permet de distinguer quatre régimes phytoplanctoniques ayant chacun des propriétés biologiques bien définies entre autres par la biomasse, l'activité physiologique, la structure de taille et la composition taxonomique de la communauté. En contrôlant le

réapprovisionnement des nutriments dans la couche de surface, l'intensité de la stratification détermine en partie le régime phytoplanctonique dominant. Intervient aussi le rapport surface : volume des cellules, qui est un élément clé de leur réponse aux apports de nutriments. Ainsi, dans les écosystèmes très turbulents et riches en éléments nutritifs, la croissance du gros phytoplancton (≥5 μm) est favorisée au détriment des plus petites cellules. Ce régime phytoplanctonique est généralement caractérisé par une production primaire et une biomasse algale élevées. Il favorise le développement du réseau trophique herbivore, dominé par les diatomées et caractérisé par un transfert important de la production primaire vers les niveaux trophiques supérieurs (Legendre & Le Fèvre 1989, Kiørboe 1993) et une exportation considérable de la matière organique particulaire vers les profondeurs. Dans les milieux peu turbulents et moins riches en nutriments, les petites cellules (0,7-5 μm), du fait de leur rapport surface : volume élevé, assimilent mieux les faibles teneurs en nutriments que les grosses cellules. Dans de tels systèmes, les flagellés sont très abondants, de même que les bactéries hétérotrophes. Par conséquent, le réseau trophique prédominant est la boucle microbienne au sein de laquelle la production primaire est contrôlée par la régénération des nutriments, permettant un fonctionnement autosuffisant. Une faible proportion de la production primaire est transférée vers les niveaux trophiques supérieurs et l'exportation en profondeur est négligeable.

Bactéries des hautes latitudes

Dans le Domaine des bactéries, on distingue les cyanobactéries qui sont des procaryotes photosynthétiques et les bactéries hétérotrophes qui dépendent de la matière organique. De la même façon, on distingue également les bactéries libres et les bactéries fixées (sur la matière particulaire). Les bactéries libres sont plus petites que les bactéries fixées mais elles constituent l'essentiel de la biomasse bactérienne dans les eaux côtières. Dans l'ensemble de cette thèse, le terme « bactéries » renvoie à tous les procaryotes (Bactéries et Archées) puisque la méthode de dénombrement utilisée (la cytométrie en flux) ne permet pas de les différencier.

Cyanobactéries

Bien que l'importante contribution des cyanobactéries à la production primaire polaire ait été soulignée (Vézina & Vincent 1997, Vincent 2000), il n'en demeure pas moins que ces procaryotes autotrophes sont très souvent rapportés comme absents ou très peu abondants dans les milieux marins des hautes latitudes (Gradinger & Lens 1995, Brown & Bowman 2001, Bano & Hollibaugh 2002, Melnikov et al. 2002). Dans les rares études où les cyanobactéries ont été dénombrées, leur présence a été associée à une intrusion d'eau douce (Waleron et al. 2007, Blais et al. 2012). Cependant, les travaux de Van Hove et al. (2008) dans des fjords arctiques ont révélé que les cyanobactéries sont beaucoup plus abondantes en milieu polaire qu'on ne le croyait. En effet, des abondances de cyanobactéries pouvant aller jusqu'à 25×10^6 cellules l^{-1} ont été rapportées dans le fjord de Disraeli sur la côte nord de l'île d'Ellesmere où la température de l'eau n'excédait pas -0.25°C. Les apports d'eau douce étant très importants dans les fjords du Labrador, il n'est pas exclu que les cyanobactéries y atteignent aussi de fortes abondances.

Bactéries hétérotrophes

Les bactéries hétérotrophes sont une composante clé des réseaux trophiques marins et elles jouent un rôle central dans les flux océaniques de carbone (Nagata 2008). Leur métabolisme est fortement influencé par la température de l'eau, la disponibilité du carbone organique dissous labile (Amon & Benner 1996, Azam & Malfatti 2007, Kirchman et al. 2009b) et la concentration des nutriments notamment le phosphate (Cotner et al. 1997, Guildford & Hecky 2000, Sala et al. 2002, Matz & Jürgens 2003). La température exerce une influence à la fois directe sur la physiologie des organismes planctoniques et indirecte à travers la stratification des masses d'eau et l'accès aux ressources nutritives. En milieu aquatique, le carbone organique se présente sous forme dissoute (carbone organique dissous, COD) et particulaire (carbone organique particulaire, COP). La majeure partie du carbone organique des milieux marins se trouve sous forme dissoute, le COP ne

représentant qu'environ 10% du total. Le COD est défini ici comme étant la fraction du carbone organique qui passe à travers un filtre Whatman GF/F ayant une porosité nominale de 0,7 µm. La fraction de la matière organique qui est dégradée par les bactéries hétérotrophes en une à deux semaines est dite labile (Sondergaard & Middelboe 1995). Le COD labile représente moins d'un pourcent du COD total des océans, mais sa dégradation par les bactéries peut constituer une voie importante des flux d'énergie, de carbone et de nutriments dans les milieux pélagiques.

Suivant leur contenu en acide nucléique, on distingue les bactéries à contenu en acide nucléique élevé (high nucleic acid : HNA) et celles à contenu en acide nucléique faible (low nucleic acid : LNA). Considérer le contenu en acide nucléique comme un indice de l'activité bactérienne ne fait pas l'unanimité au sein de la communauté scientifique. Pour certains auteurs (Gasol & del Giorgio 2000, Lebaron et al. 2001, Seymour et al. 2004), les bactéries HNA seraient plus actives et auraient un taux de croissance plus élevé que les bactéries LNA. Par contre, d'autres études montrent que les bactéries LNA seraient tout aussi actives que les bactéries HNA (Zubkov et al. 2004, Longnecker et al. 2005). En l'état actuel des connaissances, affirmer que les bactéries HNA sont plus actives ou que celles LNA sont tout bonnement inactives ou mortes est une vision trop simpliste (Bouvier et al. 2007) qui devrait être reconsidérée.

Broutage par le microzooplancton

Maillon central des réseaux trophiques pélagiques, le microzooplancton englobe par définition les ciliés, les flagellés et les dinoflagellés hétérotrophes de taille <200 µm (Sherr & Sherr 2002, Calbet & Landry 2004). Ces protistes phagotrophes sont généralement classés en deux catégories : les bactérivores et les herbivores (Sherr & Sherr 1994). La bactérivorie désigne la prédation sur les cyanobactéries et les bactéries hétérotrophes, alors que l'herbivorie renvoit au broutage du phytoplancton eucaryote. De nombreuses études ont relevé que la pression de broutage exercée par le microzooplancton a une forte influence

sur le devenir de la production et de la biomasse phytoplanctoniques dans l'océan global (Olson & Strom 2002, Calbet & Landry 2004, Leising et al. 2005). Par exemple, dans diverses régions océaniques, Sherr & Sherr (1994) ont noté qu'une proportion importante (≥50%) de la production primaire journalière était consommée par le microzooplancton. Au début de l'été dans la mer de Barents, Verity et al. (2002) ont observé que les taux de croissance du phytoplancton et de broutage par le microzooplancton étaient étroitement liés et que les pertes dues au broutage représentaient 64 à 97% de la croissance algale. Dans les eaux côtières de l'archipel canadien, 73% de l'abondance du microzooplancton était constituée par les dinoflagellés hétérotrophes qui ont d'ailleurs exercé une forte prédation sur les diatomées (Bursa 1961). Dans la baie de Disko (ouest du Groenland) et à Young Sound, un fjord au nord-est du Groenland, de nombreux ciliés et dinoflagellés hétérotrophes ont été identifiés comme les principaux brouteurs du phytoplancton (Hansen et al. 1999, Levinsen et al. 1999, Rysgaard et al. 1999, Levinsen & Nielsen 2002). Contrairement aux ciliés qui ingèrent des proies <20 μm, les dinoflagellés hétérotrophes sont capables de consommer des organismes de taille très variée, allant des procaryotes <1 μm aux chaînes de diatomées de plus de 200 μm (Sherr & Sherr 1994). En outre, il a été prouvé que même les dinoflagellés autotrophes sont capables de prédation. Bockstahler & Coats (1993) ont notamment rapporté le broutage des diatomées par trois espèces de dinoflagellés responsables de marées rouges dans la baie de Chesapeake. Jacobsen (1993) a également retrouvé des vacuoles digestives dans plusieurs espèces de dinoflagellés autotrophes.

Les nanoflagellés (<20 μm) peuvent consommer une très grande proportion et parfois l'entièreté de la production bactérienne (Sherr et al. 1989, Capriulo et al. 1991, Sanders et al. 1992). Toutefois, des discordances (« mismatch ») entre la production bactérienne et le broutage par les flagellés hétérotrophes ont été plusieurs fois rapportées. Elles ont été attribuées entre autres au fait que (1) en plus des flagellés hétérotrophes, d'autres protistes tels que les ciliés et les flagellés mixotrophes sont aussi d'importants bactérivores (Sherr & Sherr 1994) et (2) la lyse virale est également une cause majeure de mortalité du bactérioplancton (Proctor & Fuhrman 1990). Très longtemps considérés comme étant

uniquement des bactérivores, on sait aujourd'hui que les nanoflagellés consomment également le phytoplancton eucaryote. En effet, Sherr & Sherr (1994) ont indiqué que les autotrophes de taille <1 μm sont principalement broutés par les flagellés <5 μm tandis que les producteurs dont la taille oscille entre 1 et 10 μm sont majoritairement consommés par les flagellés de 5 à 20 μm.

Du fait des températures extrêmes qui prévalent dans l'Arctique, on pourrait s'attendre à ce que les taux de croissance du phytoplancton et des bactéries hétérotrophes ainsi que le taux de broutage par le microzooplancton soient inférieurs aux autres régions océaniques. Cette idée est d'ailleurs soutenue par la compilation de Sherr et al. (2013) qui comparent le taux de broutage du microzooplancton entre diverses régions océaniques pendant l'été, et concluent que dans l'ensemble, les valeurs sont plus faibles pour les régions arctiques. En effet, le taux de broutage du microzooplancton a été de 0,06 jr^{-1} dans la partie ouest de l'océan Arctique (Sherr et al. 2009), de 0,24 jr^{-1} dans la mer de Barents (Verity et al. 2002), de 0,13 à 0,43 jr^{-1} dans la mer de Béring (Liu et al. 2002, Olson & Strom 2002, Strom & Fredrickson 2008) contre 0,39 à 0,50 jr^{-1} dans les régions tropicales et tempérées (Calbet & Landry 2004).

Particularités des fjords

Selon Syvitski & Shaw (1995), un fjord est un estuaire profond, situé en haute latitude, qui s’est formé à la suite du retrait des glaciers et des fluctuations relatives du niveau de la mer lors de la dernière glaciation. Un fjord peut également être défini comme une vallée glaciaire inondée et très profonde, aux berges en pente très raide, et dont l’embouchure est généralement barrée par un seuil peu profond formé par une moraine.

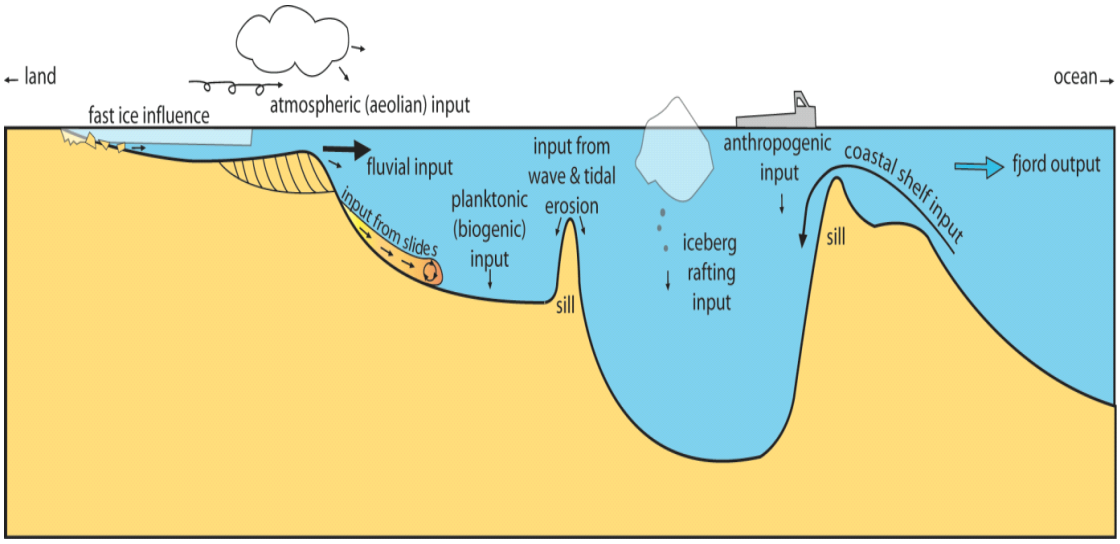

Fig. 4. Illustration des caractéristiques physiques des fjords. Tirée de Brown et al. (2012) d'après Syvitski & Shaw (1995)

Le volume total d'eau dans l'ensemble des fjords du monde avoisine $1{,}4 \times 10^{14}$ m^3, ce qui équivaut au volume total d'eau contenue dans les lacs (Syvitski et al. 1987). Les fjords sont généralement longs et étroits avec un apport d'eau douce à l'amont et un seuil à l'entrée qui limite les échanges entre les eaux profondes du fjord et les eaux à l'extérieur du fjord (Fig. 4). Semblables aux fjords, les fjards sont des baies profondes créées par action glaciaire et envahies par la mer. Cependant, contrairement à un fjord, un fjard n'a pas de seuil frontal limitant les échanges d'eau.

Les fjords sont d'un grand intérêt scientifique en raison de leurs particularités (profondeur de l'eau, profondeur du seuil, salinité, stratification, apports d'eau douce et de sédiments, régime climatique, influence anthropique, etc.). Du fait de la présence d'un seuil limitant la circulation des masses d'eau, il peut arriver que la couche d'eau profonde ne soit renouvelée que de façon périodique, ce qui entraîne des conséquences au niveau de la productivité. En effet, selon le temps de résidence des masses d'eau qui influence en partie la concentration des nutriments, la production primaire des fjords peut être extrêmement

variable. Cela favorise le développement d'une faune et d'une flore marines différentes de celles des autres milieux côtiers (De Ladurantaye et al. 1984, Archer et al. 2000, Zhou et al. 2005, Iversen & Seuthe 2011).

Problématique : pourquoi s'intéresser aux fjords du Labrador ?

Situés sur la côte est du Canada, les fjords du Labrador sont des zones importantes pour l'alimentation et la reproduction des mammifères marins comme les baleines, les phoques et les ours polaires. Les communautés inuites dépendent également des fjords du Labrador pour la chasse, les déplacements et les activités commerciales (Allard & Lemay 2012). Ces écosystèmes fragiles sont fortement influencés au nord par les changements climatiques (notamment l'augmentation des apports en eau provenant de la fonte des glaciers, le changement de la période de gel et de dégel de la glace de mer et le réchauffement des eaux de surface) et au sud par les activités anthropiques (par exemple le développement minier, hydroélectrique et touristique, le transport maritime et l'aquaculture). Au nord de la limite des arbres, au-dessus du 58^{e} parallèle, sont situés les fjords de Nachvak et de Saglek (Fig. 5). Un peu plus au sud, entre le 56^{e} et le 58^{e} parallèle, se trouvent les baies d'Okak et d'Anaktalak (Fig. 5). Ces quatre écosystèmes constituent d'importants sites de surveillance environnementale car ils se situent entre des régions subissant des changements notables (Haut-Arctique; Arrigo et al. 2012) et d'autres aux conditions plus stables (subarctique; Brown et al. 2012).

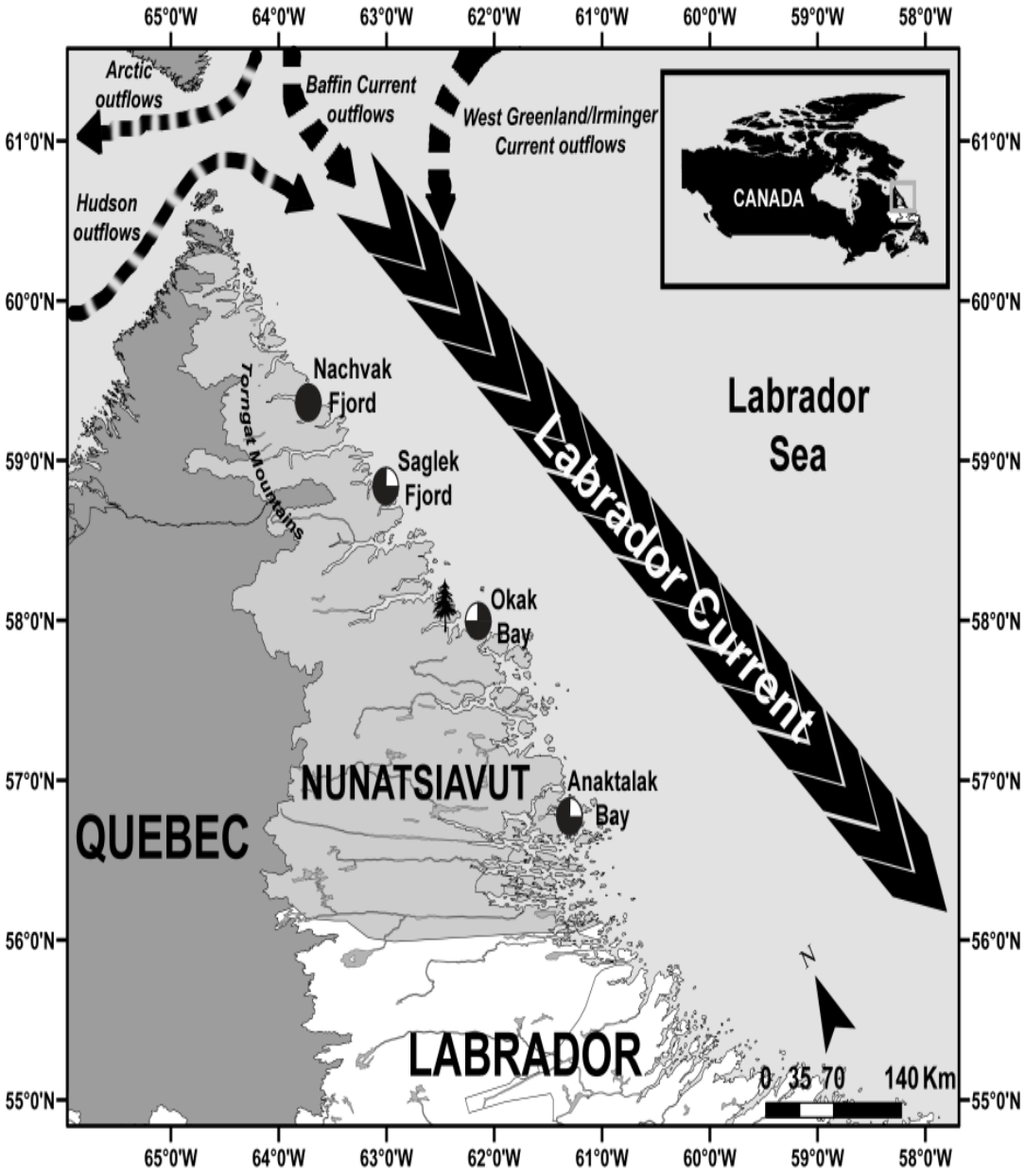

Fig. 5. Localisation des fjords de Nachvak et de Saglek, et des baies d'Okak et d'Anaktalak dans le Nunatsiavut au nord du Labrador. Modifiée de Richerol et al. (2012)

Quoiqu'extrêmement importants pour les communautés locales et les mammifères marins, les fjords du Labrador restent encore très peu étudiés et mal connus des scientifiques. Les seules études qui y ont été menées jusqu'à présent ont porté sur la pollution chimique (Kuzyk et al. 2005a, 2005b, Brown et al. 2009, 2013, 2015) et la paléocéanographie (Richerol et al. 2012, 2014). À notre connaissance, la dynamique des communautés planctoniques des fjords du Nunatsiavut n'avait encore jamais été étudiée. Les résultats de cette thèse permettront donc de mieux comprendre et de documenter l'écologie, la structure et le fonctionnement des communautés phytoplanctoniques et bactériennes des fjords du Labrador, mais aussi leurs réponses face aux perturbations environnementales naturelles et anthropiques.

Objectifs de recherche

L'objectif central de cette thèse est de déterminer la variabilité spatiale et saisonnière des communautés phytoplanctoniques et bactériennes, pendant l'été et l'automne, dans les fjords du Labrador, à couvert de glace saisonnier. Les éléments de réponse à cet objectif central sont apportés dans les trois articles de recherche (chapitres 1 à 3) issus de cette thèse.

Le premier chapitre traite des variations spatiales et saisonnières de la production et de la biomasse du petit (0,7-5 μm) et du gros phytoplancton (≥5 μm) et de l'exportation potentielle du carbone biogène hors de la zone euphotique. La structure de taille [pico (<2 μm), nano (2-20 μm) et micro (≥20 μm)] du phytoplancton et les principaux groupes taxonomiques de la communauté sont également abordés. Le dernier volet de ce chapitre fait le lien entre les variations de la dynamique du phytoplancton et les conditions environnementales. Les hypothèses testées dans ce chapitre sont : (1) la production et la biomasse du phytoplancton, de même que l'exportation de carbone augmentent le long du gradient latitudinal et elles sont plus élevées à l'été qu'à l'automne, (2) le microphytoplancton est plus abondant pendant l'été alors que le pico- et le

nanophytoplancton sont plus abondants pendant l'automne et (3) les variations saisonnières dans la dynamique du phytoplancton sont principalement influencées par le régime lumineux, la stratification verticale de la colonne d'eau et la disponibilité des éléments nutritifs.

Le second chapitre décrit de façon très détaillée la composition taxonomique des communautés estivale et automnale et propose une possible succession annuelle de protistes dans les fjords du Labrador. Une section spéciale de ce chapitre a été consacrée à *Phaeocystis pouchetii*, particulièrement abondant dans les comptages de l'été. La liste exhaustive de l'ensemble des entités taxonomiques identifiées pendant toute la période d'étude a également été dressée. L'abondance relative et le pourcentage d'occurrence de chaque taxon y ont été minutieusement indiqués. Il importe de préciser que cette liste de protistes planctoniques est la toute première à être dressée pour les fjords du Labrador. En outre, avec plus de 200 taxons identifiés, cette liste est, à notre connaissance, la plus complète de la littérature portant sur les fjords des hautes latitudes et il va sans dire qu'elle servira de référence pour d'autres études dans le domaine.

Le troisième chapitre porte sur trois principaux objectifs : (1) l'influence de la température de l'eau et de la disponibilité de la matière organique labile sur l'abondance et l'activité potentielle des bactéries hétérotrophes, (2) la relation entre l'abondance des bactéries et celle des nanoflagellés hétérotrophes et (3) l'estimation du taux de broutage du phytoplancton par le microzooplancton. Ces objectifs ont permis de tester les hypothèses suivantes : (1) plus la température de l'eau et la concentration de la matière organique labile sont élevées, plus les bactéries hétérotrophes sont abondantes et actives, (2) l'abondance des bactéries est inversement proportionnelle à celle des nanoflagellés hétérotrophes et (3) dans les fjords du Labrador, le taux de broutage par le microzooplancton serait proche de 0,41 jr^{-1}, valeur moyenne estimée dans les régions océaniques polaires par Calbet & Landry (2004)

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CHAPITRE 1

VARIATIONS SAISONNIÈRES DE LA DYNAMIQUE DU PHYTOPLANCTON DANS LES FJORDS DU NUNATSIAVUT (LABRADOR, CANADA) ET LEURS RELATIONS AVEC LES CONDITIONS ENVIRONNEMENTALES

Ce premier article scientifique, intitulé « Seasonal variations of phytoplankton dynamics in Nunatsiavut fjords (Labrador, Canada) and their relationships with environmental conditions » a été corédigé par moi-même, les professeurs Michel Gosselin, Yves Gratton et Jean-Éric Tremblay, ainsi que par la professionnelle de recherche Marjolaine Blais. Il a été publié dans le numéro d'avril 2016 de la revue *Journal of Marine Systems*.

En tant que premier auteur, ma contribution à ce travail fut l'essentiel de la recherche portant sur la production primaire, la biomasse chlorophyllienne, la structure de taille et la composition taxonomique du phytoplancton. J'ai également participé aux sorties en mer, aux analyses en laboratoire et au traitement statistique des résultats. De plus, j'ai rédigé l'article. Le professeur Michel Gosselin, second auteur, a fourni l'idée originale. Il a grandement contribué à la définition de la problématique, l'élaboration du plan d'échantillonnage et la révision de l'article. Marjolaine Blais a réalisé les mesures de production primaire, elle a apporté son aide aux autres analyses de laboratoire et elle a aidé à structurer l'article. Les professeurs Yves Gratton et Jean-Éric Tremblay ont respectivement fourni les données physiques et celles de nutriments, et ils ont participé à la révision de l'article.

Les résultats de cet article ont été présentés à plusieurs conférences nationales et internationales: l'assemblée annuelle de Québec-Océan en novembre 2012 à Montréal, la réunion scientifique annuelle d'ArcticNet en décembre 2012 à Vancouver et la *Gordon*

Research Conference en mars 2013 à Ventura aux États-Unis. Ces résultats ont également été présentés pendant le concours de vulgarisation scientifique *Ma thèse en 180 secondes* organisé dans le cadre du 81^{e} congrès de l'ACFAS en mai 2013 à Québec. Une capsule vidéo de ma prestation à ce concours est disponible à partir du lien suivant: https://www.youtube.com/watch?v=maOLntr-e7c.

RÉSUMÉ

La dynamique du phytoplancton et son contrôle environnemental ont été étudiés dans quatre fjords du Labrador (Nachvak, Saglek, Okak et Anaktalak) pendant l'été, le début de l'automne et la fin de l'automne. La production primaire et la biomasse chlorophyllienne ont été mesurées à sept profondeurs optiques, incluant celle du maximum de subsurface de chlorophylle *a* (SCM). L'abondance du phytoplancton, la structure de taille et la taxonomie ont été déterminées au SCM. L'analyse en composantes principales et le cadrage multidimensionnel non métrique ont permis d'analyser les relations entre la production, la biomasse et la composition taxonomique de la communauté en lien avec les variables environnementales. Nous avons observé une variabilité saisonnière marquée, avec des différences significatives dans la structure et le fonctionnement des communautés phytoplanctoniques pendant l'été et l'automne. Étonnamment, la production primaire et la biomasse chlorophyllienne n'ont pas été significativement différentes d'un fjord à l'autre. Les plus fortes valeurs de production primaire (1730 mg C m^{-2} jr^{-1}) et de biomasse chlorophyllienne (96 mg chl *a* m^{-2}) ont été mesurées pendant le bloom estival, et ces valeurs élevées indiquent que les fjords du Labrador sont des écosystèmes très productifs. La communauté estivale a présenté des abondances de nanophytoplancton (2-20 μm) relativement élevées tandis que la communauté automnale a été caractérisée par une production primaire et une biomasse chlorophyllienne faibles ainsi que des abondances relativement élevées de picophytoplancton (<2 μm). Pendant toute la période d'étude, la faible valeur de carbone potentiellement exporté hors de la zone euphotique (≤31% de la production primaire totale) suggère que la production phytoplanctonique est principalement broutée par le microzooplancton au lieu d'être exportée vers le fond. Pendant l'été, nous avons observé une communauté mixte de diatomées et de flagellés tandis qu'à l'automne, la communauté a été largement dominée par les flagellés. Les variations saisonnières de la dynamique du phytoplancton ont été principalement contrôlées par l'intensité de la stratification verticale et par les grandes différences dans la durée du jour dues à la localisation nordique des fjords du Labrador. Cette étude documente pour la toute première fois la structure et le fonctionnement des communautés phytoplanctoniques dans les fjords du Labrador et fournit les bases essentielles pour les recherches futures et pour la surveillance des changements environnementaux dans les régions côtières arctiques et subarctiques.

Mots-clés : Production et biomasse phytoplanctoniques, structure de taille, composition taxonomique, variations saisonnières, Arctique, Canada, Labrador, fjords

SEASONAL VARIATIONS OF PHYTOPLANKTON DYNAMICS IN NUNATSIAVUT FJORDS (LABRADOR, CANADA) AND THEIR RELATIONSHIPS WITH ENVIRONMENTAL CONDITIONS

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ABSTRACT

We assessed phytoplankton dynamics and its environmental control in four Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during summer, early fall and late fall. Primary production and chlorophyll *a* (chl *a*) biomass were measured at seven optical depths, including the depth of subsurface chl *a* maximum (SCM). Phytoplankton abundance, size structure and taxonomy were determined at the SCM. Principal component analysis and non-metric multidimensional scaling were used to analyze relationships between production, biomass and community composition in relation to environmental variables. We observed a marked seasonal variability, with significant differences in phytoplankton structure and function between summer and fall. Surprisingly, primary production and chl *a* biomass were not significantly different from one fjord to another. The highest values of primary production (1730 mg C m^{-2} d^{-1}) and chl *a* biomass (96 mg chl *a* m^{-2}) were measured during the summer bloom, and those high values indicate that Labrador fjords are highly productive ecosystems. The summer community showed relatively high abundance of nanophytoplankton (2–20 μm) while the fall community was characterized by low primary production and chl *a* biomass as well as relatively high abundance of picophytoplankton (<2 μm). The low value of carbon potentially exported out of the euphotic zone throughout the study (≤31% of total primary production) suggests that phytoplankton production was mainly grazed by microzooplankton rather than being exported to greater depths. We observed a mixed assemblage of diatoms and flagellates in summer, whereas the fall community was largely dominated by flagellates. Seasonal variations in phytoplankton dynamics were mainly controlled by the strength of the vertical stratification and by the large differences in day length due to the northerly location of Labrador fjords. This study documents for the very first time phytoplankton structure and function in Labrador fjords, and provides an essential foundation for further research and for monitoring environmental changes in arctic and subarctic coastal areas.

Keywords: Phytoplankton production and biomass, size structure, taxonomic composition, seasonal variations, Arctic, Canada, Labrador, fjords

1.1 Introduction

Primary producers play a key role in oceans by supplying organic matter to higher trophic levels, including zooplankton, fish larvae and benthic animals. Due to their low number of trophic links, polar marine ecosystems are particularly sensitive to any changes in primary production (Rysgaard et al. 2003, Grebmeier et al. 2006, Wassmann et al. 2011). Arctic and subarctic marine environments are changing as evidenced by the decrease in sea-ice thickness and extent (Kwok et al. 2009), the early melt and late freeze-up (Markus et al. 2009), and the enhancement of the hydrological cycle (Peterson et al. 2006). These environmental changes have already altered the production and taxonomic composition of marine phytoplankton in offshore areas of the Canadian High Arctic (Li et al. 2009, Arrigo & van Dijken 2011, Tremblay et al. 2011), but little is known about their impact on particular nearshore environments like fjords.

Fjords are long and narrow inlets carved by glacier ice. Typical fjords have deep muddy basins separated by rock sills and are surrounded by tall, steep sidewalls. Contrariwise, shallow, irregularly shaped inlets with gently sloping sidewalls and large intertidal zones are usually called fjards. Some fjords have sills at the mouth, others do not. In silled fjords, where tidal and wind mixing are weak, the rate of deep-water exchange tends to be slow, and permanent or temporary stagnant conditions may develop in the bottom layer (Skei et al. 2003). Such a characteristic influences many environmental factors including temperature, salinity, nutrient concentrations and oxygen level. Consequently, organisms evolving in fjord-type estuaries have to deal with conditions that can be very different from the adjacent sea, and environmental control of phytoplankton dynamics might thus be specific to a particular fjord. Here, we compare the dynamics of phytoplankton in two fjords (Nachvak and Saglek) and two bays (Okak and Anaktalak) located in northern Labrador (Fig. 1).

In Scandinavian fjords, typical annual primary production rates range from 110 to 140 g C m^{-2} $year^{-1}$, with about 60% occurring after the spring bloom in March and April (Aure et al. 2007). In Kongsfjorden, a high-latitude fjord in Svalbard, Hodal et al. (2012)

found that diatoms are the most important phytoplankton group during the spring bloom, although the nanoflagellate *Phaeocystis pouchetii* often co-occurs as single cells or colonies (Eilertsen et al. 1981). Apart from the vernal bloom, the phytoplankton community is dominated by cells <10 μm (Seuthe et al. 2011). Iversen & Seuthe (2011) found that the microbial food web dominated the community in stratified water masses of Kongsfjorden in July and September. During winter, they also observed the persistence of the microbial community (Iversen & Seuthe 2011). Such data are lacking for most fjords in eastern Canada, including the Labrador fjords.

Labrador fjords are nursery areas for a large number of fish stocks, and they are therefore important feeding grounds for seabirds and marine mammals (Allard & Lemay 2012). Labrador Inuits also depend on these inlets for their hunting, harvesting, and economic activities. Despite their intensive use and ecological importance for a large number of marine organisms, Labrador fjords have been little studied. Very little is known about basic features such as the structure, the function and the composition of phytoplankton, and its seasonal distribution patterns in these fjords. To date, only few studies have been carried out in these fjords, and those were focused on chemical pollution (e.g., Kuzyk et al. 2005a, 2005b, Brown et al. 2009, 2013, 2015) and paleoceanography (e.g., Richerol et al. 2012, 2014). The objectives of our study were therefore (1) to describe the variabilities of primary production, of the biomass of small (0.7-5 μm) and large (≥5 μm) phytoplankton cells, of biogenic carbon export and of the phytoplankton size structure and community composition in four Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during summer, early fall and late fall, and (2) to assess the influence of environmental factors on the structure and function of phytoplankton communities. To our knowledge, this is the first study on phytoplankton dynamics in Nunatsiavut fjord ecosystems, with the ultimate aim of providing a reference point for future monitoring of environmental changes in arctic and subarctic coastal areas. Such knowledge is essential for a better understanding of the ecological status of these fjords as well as for their sustainable use and to predict their response to climate change.

1.2 Materials and methods

1.2.1 Study area

Our study region is located in Nunatsiavut (meaning "Our Beautiful Land") in the northern part of Labrador. This region is located on the eastern seaboard of Canada and extends between 56°N and 60°N along the Labrador Shelf. Shelf waters inshore of the cold and salty Labrador Current have temperatures below 4°C and salinities less than 34 (Khatiwala et al. 2002). The temperature and moisture regimes are dominated by north–south transgressions of cold dry arctic air and warm moist atlantic air masses (Hare & Hay 1974). The cold Labrador Current, which brings arctic water southward along the coast of Labrador, has a significant influence on the local climate (Engstrom & Hansen 1985).

In summer, the mean air temperature along the coast is around 10°C, while inland it can reach 16°C. These conditions are reversed during winter, when mean temperatures are around 3°C along the coast and warmer than inland temperatures (Short & Nichols 1977, Ullah et al. 1992). The mean annual precipitations in Labrador vary from 750 mm in the north to 960 mm in the south. Snowfall is relatively heavy, with annual amounts ranging from 390 cm to 480 cm (Ullah et al. 1992). Over the last ten years, the region has been ice-covered from about 11 December to 2–16 July (Canadian Ice Service, Environment Canada 2015).

The general characteristics of the studied fjords and bays are described in Brown et al. (2012). Temperature and salinity contours are presented in Figures 2 and 3 for summer, early fall and late fall. Nachvak, the northernmost fjord in this study, is located in the Torngat Mountains National Park Reserve (Fig. 1a). It is also the only "classical" fjord, being long and narrow with only one access to the ocean. Nachvak Fjord is 45 km long and 2 to 4 km wide, gradually increasing in width eastward to Nachvak Bay, which opens to the Labrador Sea (Bell & Josenhans 1997). There are four 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. Nachvak Fjord receives freshwater and sediments from Palmer River, and Nachvak, Kogarsok and Ivitak brooks (Anderson 1988). From 2000 to 2009, the sea-ice cover lasted, on average, about one week longer in Nachvak Fjord compared to the three other fjords (see Brown et al. 2012). The average annual sediment load to the basins ranges between 1.1 and 3.2 kg s^{-1} (Kahlmeyer 2009). Nachvak is a pristine fjord, considered as a reference site to assess natural climatic and environmental variability of Nunatsiavut fjord ecosystems.

Saglek Fjord is 65 km long and 2 to 14 km wide. The width increases eastward to Saglek Bay, which opens to the Labrador Sea. Saglek Fjord is wider than Nachvak. The fjord has been the site of a military radar station since 1953 as part of the DEW (Distant Early Warning) Line (Fig. 1b). This led to extensive polychlorinated biphenyl (PCB) contamination in soil, sediments, and the marine environment (Kuzyk et al. 2005a, Brown et al. 2013, 2015). The temperature (Fig. 2b) and salinity (Fig. 3b) contours start near the southern shore of Saglek Bay while the inner fjord is located between stations 613 and 615. The sidewalls are generally steep, extending up to more than 800 m above sea level. There is a succession of seven basins, with water depths ranging from 80 to 256 m and increasing from west to east. Sills between 45 and 96 m below sea level separate these basins (Brown et al. 2012). Saglek Fjord receives freshwater and sediments mainly from Nachvak, North Arm and Southwest brooks (Anderson 1988). The average annual sediment entering the basins ranges between 0.5 and 12 kg s^{-1} (Kahlmeyer 2009).

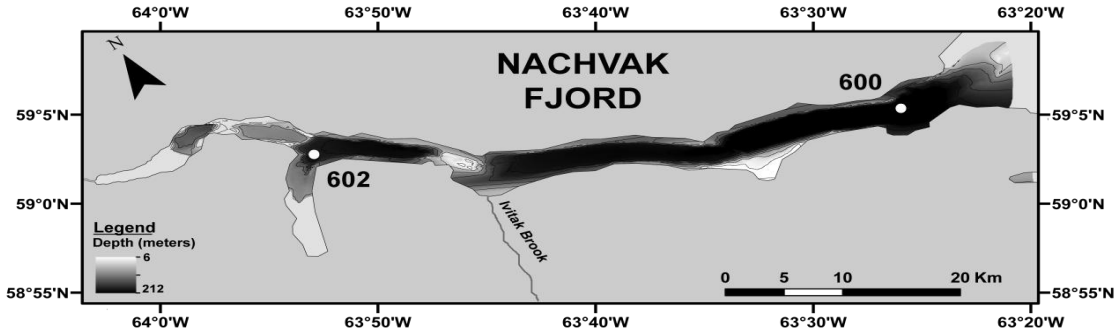
Okak Bay is a 50 km-long, irregularly shaped fjard (Fig. 1c) which is occasionally used for travel and harvesting by the Inuits from the town of Nain. The head of the bay is relatively shallow, about 45 to 50 m. The deepest basins are along the northern entrance, where water depth average reaches 200 m. Temperature (Fig. 2c) and salinity (Fig. 3c) contours are from a section close to the north shore and begin north of Okak Island (see Fig. 1c). The inner bay is found between stations 630 and 632. The southern entrance is narrow and shallow, bordered to the south by Ubilik Peninsula and to the north by Okak

Island (Brown et al. 2012). The freshwater inputs come from North and Sipukat rivers, and Siugak and Ikinet brooks (Anderson 1988).

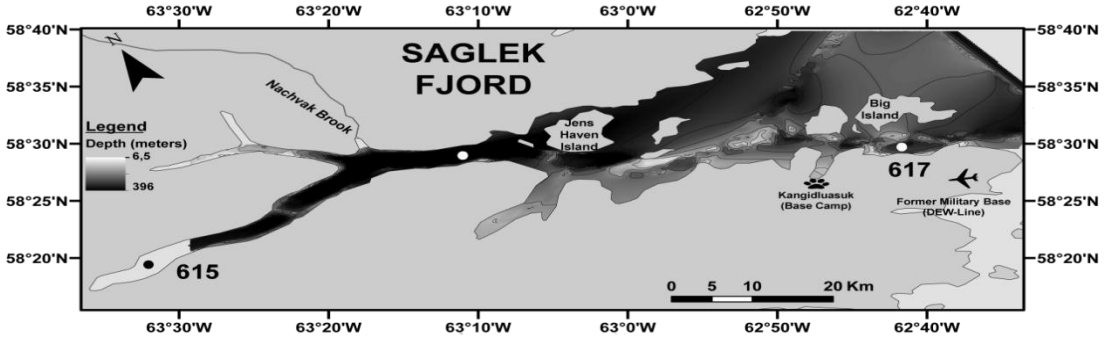
Anaktalak Bay is a long, narrow, straight fjard of 66 km long and 1 to 5 km wide (Fig. 1d). Much of the bay forms a large basin between 100 and 120 m deep that shallows to a sill at 85 m depth in the outer section of the bay. There are many channels and islands, and the contours of temperature (Fig. 2d) and salinity (Fig. 3d) are more similar to those found in an open estuary than to the other fjords (see Section 3.1). The average annual sediment load ranges between 0.04 and 0.45 kg s^{-1}. Anaktalak Bay is the southernmost site of this study and is widely used for commercial activities by the Nain Inuits. Since 2005, the head of Anaktalak Bay has been the site of a nickel-copper-cobalt mine and concentrator operated by Vale NL (formerly Voisey's Bay Nickel Company). Because the treated effluents from the mine are directly discharged into the bay, Nunatsiavut communities are concerned with the potential environmental impacts of mining activities and associated shipping operations in Anaktalak Bay.

For the sake of simplicity, Okak and Anaktalak bays will be considered, from here on, as typical fjords, just as Nachvak and Saglek fjords. These four Labrador fjords are important sites for ecosystem monitoring because they are located between regions undergoing significant changes (High Arctic) and others with more stable conditions (subarctic). 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°N and 58°N, south of the tree line and within the subarctic ecoregion. Moreover, in contrast to Nachvak and Okak fjords, Saglek and Anaktalak fjords are directly influenced by industrial and modern-day human activities.

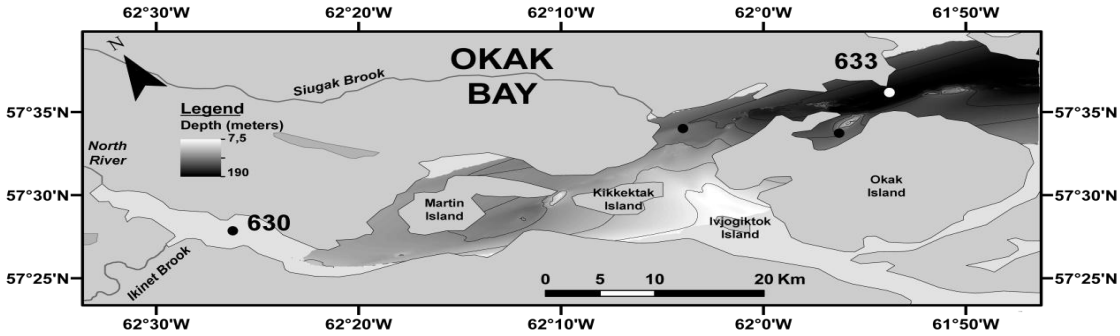
a


64°0'W
63°50'W
63°40'W
63°30'W
63°20'W
N
NACHVAK
FJORD
600
602
59°5'N
59°0'N
58°55'N
Ivitak Brook
Legend
Depth (meters)
6
212
0 5 10 20 Km

b


63°30'W
63°20'W
63°10'W
63°0'W
62°50'W
62°40'W
58°40'N
58°35'N
58°30'N
58°25'N
58°20'N
N
SAGLEK
FJORD
Nachvak Brook
Jens
Haven
Island
Big
Island
617
Kangidluasuk
(Base Camp)
Former Military Base
(DEW-Line)
615
Legend
Depth (meters)
6,5
396
0 5 10 20 Km

c


62°30'W
62°20'W
62°10'W
62°0'W
61°50'W
57°35'N
57°30'N
57°25'N
N
OKAK
BAY
633
Siugak Brook
Legend
Depth (meters)
7,5
190
North
River
Martin
Island
Kikkektak
Island
Ivjogiktok
Island
Okak
Island
630
Ikinet Brook
0 5 10 20 Km

d

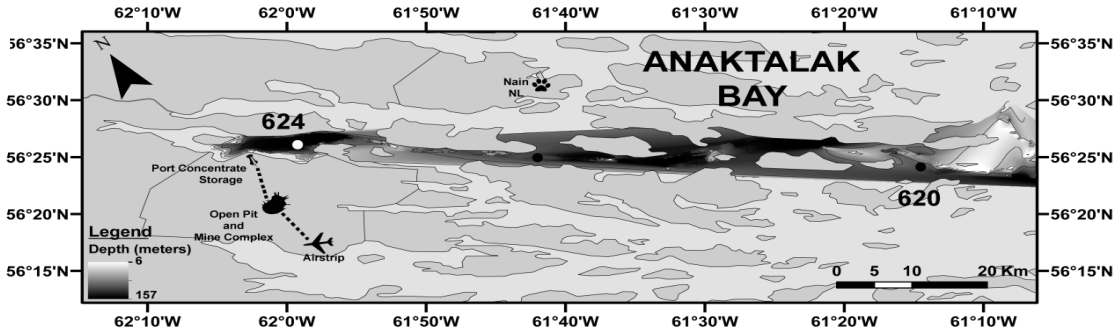

62°10'W
62°0'W
61°50'W
61°40'W
61°30'W
61°20'W
61°10'W
56°35'N
56°30'N
56°25'N
56°20'N
56°15'N
N
ANAKTALAK
BAY
Nain
NL
624
620
Port Concentrate
Storage
Open Pit
and
Mine Complex
Airstrip
Legend
Depth (meters)
6
157
0 5 10 20 Km

Fig. 1. Maps of (a) Nachvak Fjord, (b) Saglek Fjord, (c) Okak Bay and (d) Anaktalak Bay showing the location of the sampling stations (adapted from Richerol et al. 2012)

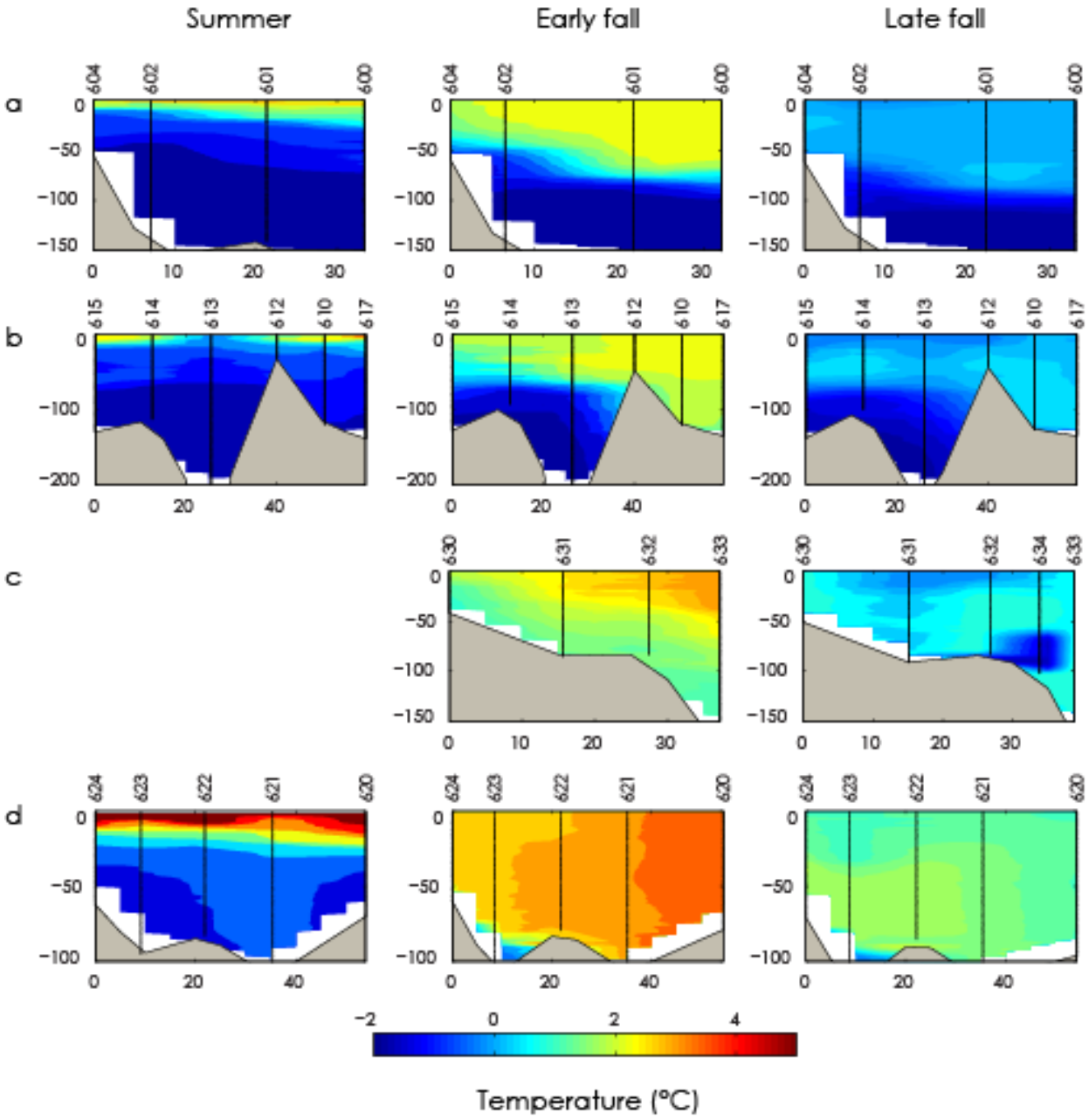


Fig. 2. Temperature contours for Labrador fjords from north (top) to south (bottom): (a) Nachvak, (b) Saglek, (c) Okak and (d) Anaktalak. Each row of panels is from the same fjord. The columns are arranged by season: summer, early fall and late fall from left to

right. Vertical lines indicate the location of the sampling stations, which are identified by their numbers

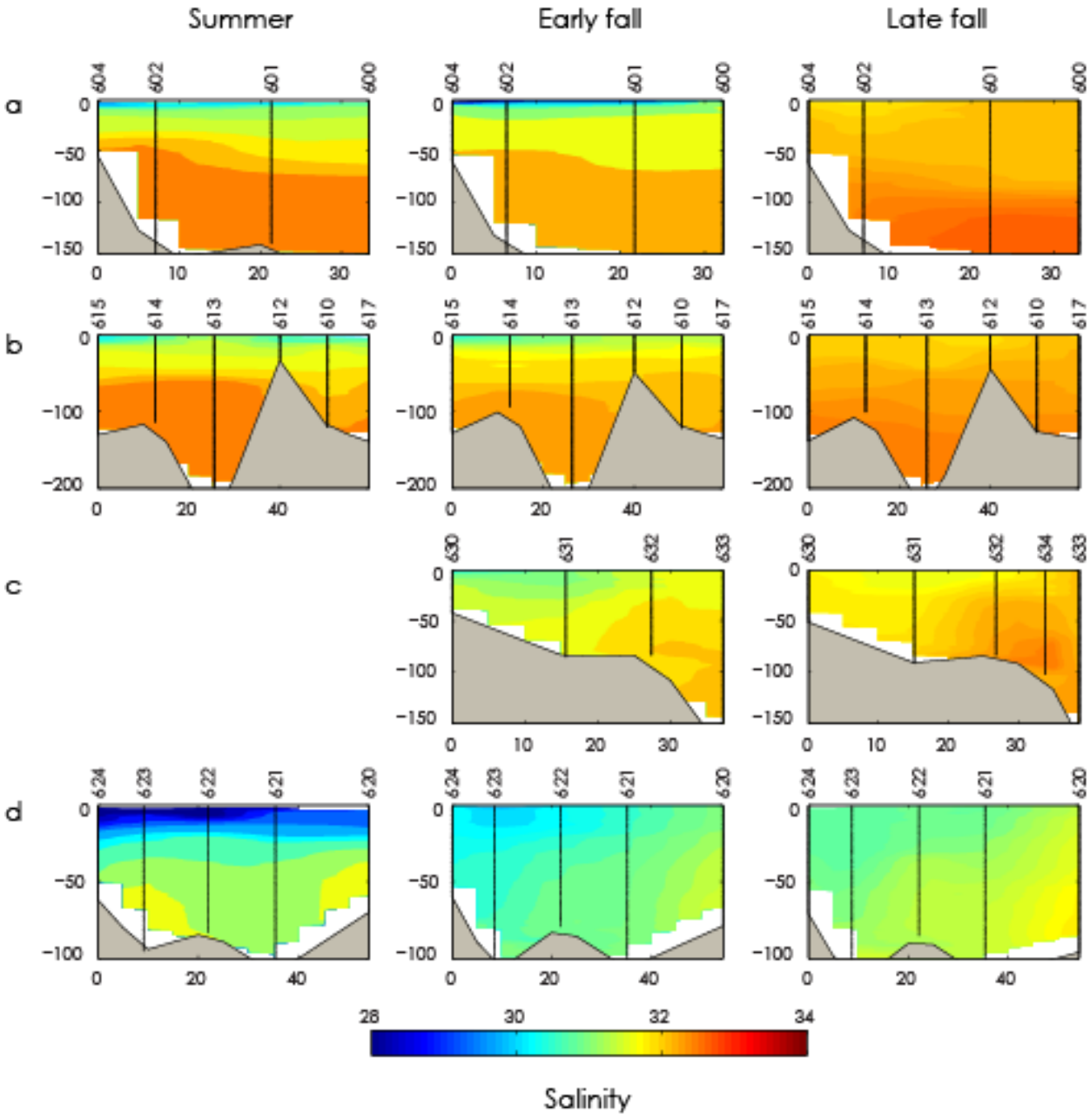


Fig. 3. Salinity contours for Labrador fjords from north (top) to south (bottom): (a) Nachvak, (b) Saglek, (c) Okak and (d) Anaktalak. Each row of panels is from the same fjord. The columns are arranged by season: summer, early fall and late fall from left to

right. Vertical lines indicate the location of the sampling stations, which are identified by their numbers

1.2.2 Sampling

Sampling was conducted onboard the CCGS *Amundsen* from 31 July to 2 August 2007, 24 to 27 October 2010 and 8 to 13 November 2009. Hereafter, these sampling periods are referred to as summer, early fall and late fall, respectively. Apart from Okak Fjord, which was not sampled during summer, all the other fjords were sampled during all three periods.

At each fjord, biological sampling was carried out at two stations furthest apart from each other referred to as the inner and the outer stations. At each station, a vertical profile of irradiance (PAR: photosynthetically active radiation, 400–700 nm) was performed with a PNF-300 radiometer (Biospherical Instruments) and used to estimate the depth of the euphotic zone (Z_{eu}, 0.2% of surface irradiance; Knap et al. 1996). The diffuse light attenuation coefficient (K_d, m^{-1}) in the euphotic zone was determined by the slope of a linear regression between the natural logarithm of underwater PAR and depth, and when not possible, from the Secchi disk depth using the conversion factor of 1.44 (Holmes 1970). Downwelling incident PAR was measured every 10 min with a 2π LI-COR sensor (LI-190SA) placed on an unshaded area of the foredeck.

A rosette sampling unit equipped with a CTD (Conductivity, Temperature and Depth) probe (Sea-Bird Electronics SBE 911+), an *in situ* fluorometer (WETStar mini fluorometer model 9512008), and 24 12 L Niskin-type bottles (OceanTest Equipment) was deployed to measure water temperature, salinity and *in vivo* chlorophyll fluorescence from the surface down to about 10 m from the bottom. The ship also carries a 150 kHz Ship-mounted Acoustic Doppler Current Profiler (SADCP).

Water samples were collected at seven optical depths (95, 50, 30, 15, 5, 1 and 0.2% of surface irradiance), as well as at the subsurface chlorophyll *a* (chl *a*) maximum (SCM) depth, and at 75 m and 100 m in the aphotic zone. Subsamples for subsequent analyses

were transferred from the Niskin-type bottles to acid-washed Nalgene bottles (Knap et al. 1996).

1.2.3 Laboratory analyses

Nutrients

Triplicate samples for dissolved inorganic nutrients were filtered through Whatman GF/F glass-fiber filters (nominal pore size of 0.7 μm), and the filtrate was collected in 15 ml acid-washed polyethylene tubes. Nutrient samples were directly analyzed or stored in a -80°C freezer for later analyses of nitrate plus nitrite (NO_3+NO_2), nitrite (NO_2), phosphate (PO_4) and silicic acid ($Si(OH)_4$) concentrations using a Bran-Luebbe 3 autoanalyzer (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).

Primary production

Primary production was estimated by the ^{14}C-assimilation method (Knap et al. 1996, Ferland et al. 2011) using *in situ* simulated incubations during summer and early fall. In late fall, production rate was determined from photosynthesis-irradiance (P-E) curves (method adapted from Morán & Estrada 2001).

For the ^{14}C on-deck incubations, two light and one dark 500 ml Nalgene polycarbonate bottles were filled with seawater from each light level and then inoculated with 20 μCi of $NaH^{14}CO_3$. The dark bottle contained 250 μl of 0.02 M 3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU; Legendre et al. 1983). Bottles were incubated for 24 hours, generally starting in the morning (Mingelbier et al. 1994), in a plexiglas deck incubator under simulated *in situ* conditions with running surface seawater. At the end of the incubation period, 250 ml were filtered onto Whatman GF/F glass-fiber filters (referred to as total particulate phytoplankton production: P_T, ≥0.7 μm) and the remaining

subsamples were filtered onto 5 μm Nuclepore polycarbonate membrane filters (referred to as production of large phytoplankton 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 incorporated (Lean & Burnison 1979). Subsequently, 10 ml of Ecolume scintillation cocktail was added to each vial. The activity of each sample was determined using a Packard Tri-Carb 2900 TR liquid scintillation counter. Production rates of particulate organic carbon were calculated according to Parsons et al. (1984). Production of small phytoplankton (P_S, 0.7–5 μm) was obtained by subtracting P_L from P_T.

Concerning P-E curves, photosynthetic parameters were determined using the ^{14}C-assimilation method. At each station, water samples were taken from two depths: at 50% of surface irradiance and at the SCM (or at 15% surface irradiance when SCM was not present). At each depth, 200 μCi of $NaH^{14}CO_3$ were added to 850 ml of seawater. Fourteen sterile polystyrene tissue culture flasks (Corning), previously refrigerated, were filled with 50 ml of the prepared solution. Twelve of these bottles were placed in a Babin-type incubator (Babin et al. 1994) and exposed to various irradiances ranging from 20 to 800 μmol quanta m^{-2} s^{-1}. The temperature in the incubator was kept as close as possible to that of the upper water layer. In the two other flasks, 25 μl of 0.02 M DCMU was added, and they were stored in darkness to determine the dark fixation of ^{14}C (Legendre et al. 1983). In order to determine P_T and P_L at both depths of a station, these operations were repeated four times: twice at the depth of 50% surface irradiance and twice at the SCM. After 3 to 5 hours of incubation, the content of each bottle was filtered onto the corresponding filter (Whatman GF/F glass-fiber filters for P_T and 5 μm Nuclepore polycarbonate membrane filters for P_L). Each filter was placed in a 20 ml polyethylene scintillation vial, acidified with 100 μl of 0.5 N HCl and then treated the same way as for the ^{14}C on-deck incubation method. P-E curves were fit using non-linear least-squares regressions (using Statistica) to the following model adapted from Lewis & Smith (1983):

$$P^B = P^B_s \left[\left(1 - e^{-\alpha^B E / P^B_s} \right) e^{-\beta^B E / P^B_s} \right] - P^B_o$$

where P^B [mg C (mg chl *a*)$^{-1}$ h^{-1}] is the photosynthetic rate at irradiance E, P^B_s [mg C (mg chl *a*)$^{-1}$ h^{-1}] is the light-saturated maximum photosynthetic rate without photoinhibition, P^B_o [mg C (mg chl *a*)$^{-1}$ h^{-1}] is the photosynthetic rate at zero irradiance, α^B [mg C (mg chl a)$^{-1}$ h^{-1} (μmol quanta m^{-2} s^{-1})$^{-1}$] is the initial slope (photosynthetic efficiency) of the P-E curve and β^B [mg C (mg chl a)$^{-1}$ h^{-1} (μmol quanta m^{-2} s^{-1})$^{-1}$] is the photoinhibition parameter. The superscript B indicates chl *a* normalization.

The photosynthetic parameters, the profiles of chl *a* and PAR, and the hourly incident irradiance were used to estimate the daily integrated primary production in the euphotic zone using the trapezoidal method (Knap et al. 1996). The photosynthetic parameters of the samples taken as close as possible to the surface were assumed to be representative of the phytoplankton assemblages in the surface layer down to the beginning of the SCM. Those from the SCM were assumed to be representative of the phytoplankton assemblages from this level of the water column down to the limit of the euphotic zone.

Phytoplankton biomass

For size-fractionated chl *a* determination, duplicate 500 ml subsamples were filtered onto Whatman GF/F glass-fiber filters (total phytoplankton biomass: B_T, ≥0.7 μm) and onto 5 μm Nuclepore polycarbonate membrane filters (biomass of large phytoplankton: B_L, ≥5 μm). Another 500 to 1000 ml subsample was filtered onto 20 μm silk mesh (biomass of phytoplankton ≥20 μm). Concentrations of chl *a* were measured onboard the ship using a Turner Designs 10-AU fluorometer after 18 to 24 hours of pigment extraction in 10 ml of 90% acetone at 4°C in the dark (acidification method of Parsons et al. 1984). The biomass of small phytoplankton cells (B_S, 0.7–5 μm) was obtained by subtracting B_L from B_T.

Flow cytometry analysis

At each station, pico- (<2 μm) and nano- (2–20 μm) phytoplankton abundances were determined at the SCM (or at 15% surface irradiance when SCM was not present). Subsamples were fixed with 0.1% final concentration glutaraldehyde Grade I (Sigma), stored in liquid nitrogen onboard the ship and kept frozen at -80°C before analysis (Marie et al. 2005). Cells were counted using an EPICS ALTRA flow cytometer (Beckman Coulter) equipped with a 488 nm laser (15 mW output). Microspheres (1 μm, Fluoresbrite plain YG, Polysciences) were added to each subsample as an internal standard. Cyanobacteria and photosynthetic eukaryotes were differentiated in orange fluorescence from phycoerythrin (575 ± 20 nm) and red fluorescence from chlorophyll (675 ± 10 nm). Pico- and nanophytoplankton were discriminated based on forward scatter calibration with known-size microspheres. Microplankton (≥20 μm) abundance was determined from microscopic counts.

Light microscopy analysis

Samples for the identification and enumeration of eukaryotic cells >2 μm were collected at the SCM (or at 15% surface irradiance when SCM was not present). They were preserved in acidic Lugol's solution (Parsons et al. 1984) and stored in the dark at 4°C until analysis. Cells were identified to the lowest possible taxonomic rank using an inverted microscope (Wild Herbrugg) according to Lund et al. (1958). For each sample, a minimum of 400 cells (accuracy ± 10%) and three transects were counted at magnifications of 200× and 400×. The main taxonomic references used to identify the cells were Tomas (1997) and Bérard-Thérriault et al. (1999).

1.2.4 Vertical export of biogenic carbon

The quantity of particulate organic carbon potentially exported (POC_E) out of the euphotic zone was calculated using the equation of Klein et al. (2002):

$$\mathbf{POC_E = P_T \times \textit{f}\text{-ratio}}$$

where *f*-ratio is the ratio of new to total production. The *f*-ratio was estimated from the size structure of the phytoplankton community using the empirical relationship of Tremblay et al. (1997):

$$\textit{f}\text{-ratio} = 0.04 + (0.74 \times (P_L/P_T)),\ r^2 = 0.80$$

1.2.5 Calculations

Water temperature and salinity were averaged over the euphotic zone and will hereafter be referred to as T_{eu} and S_{eu}, respectively. The strength of vertical stratification was estimated using two different indices: (1) the difference in density (sigma-t [σ_t]) between 80 m (or the last sampled depth in <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 stratification index determined by $\Delta\sigma_t$ and N^2 ($r = 0.82$, $p < 0.0001$). Therefore, only $\Delta\sigma_t$ was considered in further analyses. The surface mixed layer (Z_m) was defined as the depth where the vertical gradient in sigma-*t* between two successive depths is >0.03 kg m^{-4} (threshold gradient method: Thomson & Fine 2003, Tremblay et al. 2009). The nutricline depth (Z_{nutr}) was estimated to be where the vertical gradient of NO_3^- concentration (dNO_3^-/dz) was highest. Daily incident downwelling irradiance (E) was calculated at each station. Daily irradiance averaged in the euphotic zone ($E_{0\text{-}Zeu}$ in mol quanta m^{-2} day^{-1}) was calculated using the equation of Riley (1957):

$$E_{0\text{-}Zeu} = E \times (1 - e^{-k_d \times Zeu}) / (k_d \times Z_{eu})$$

where k_d is the diffuse light attenuation coefficient (m^{-1}) and Z_{eu} is the depth of the euphotic zone (defined at 0.2% of surface irradiance).

Using the trapezoidal method (Knap et al. 1996), phytoplankton production and biomass were integrated over the Z_{eu}. Nutrient concentrations were integrated over the Z_{eu} and the Z_m.

1.2.6 Statistical analyses

To have a complete design and avoid missing values, we performed three different analyses of variance (ANOVA 1, 2 and 3) (Sokal & Rohlf 1995). (1) For primary production and carbon export, a two-way ANOVA was used to test for significant differences between the outer stations of three fjords (Nachvak, Saglek and Anaktalak) and three seasons (summer, early fall and late fall). (2) For phytoplankton chl *a* biomass and all environmental variables, a three-way ANOVA was performed to assess significant differences between three fjords (Nachvak, Saglek and Anaktalak), stations (inner and outer), and three seasons (summer, early fall and late fall). (3) For all environmental and biological variables, another three-way ANOVA was conducted to test differences between all four fjords (Nachvak, Saglek, Okak and Anaktalak), stations (inner and outer), and two seasons (early fall and late fall). ANOVAs were completed by a multiple comparison test of means (Tukey's Honesty Significant Difference test for unequal sample sizes) or by Student's *t*-test (if only two groups). All the results were then combined in a single table. Prior to ANOVA, all environmental and biological variables were tested for normality 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. Pearson's correlation coefficient (r) was used to determine the relationship between two variables (Sokal & Rohlf 1995). A principal component analysis (PCA) was performed to evaluate the relationships among environmental variables [T_{eu}, Z_{eu}, $E_{0\text{-}Zeu}$, $\Delta\sigma_t$,

$(NO_3+NO_2)_{0\text{-}Zeu}$, $(PO_4)_{0\text{-}Zeu}$, $(Si(OH)_4)_{0\text{-}Zeu}$,], size fractions of particulate phytoplankton production (P_S and P_L), and chl *a* biomass (B_S and B_L). These tests were carried out using JMP version 10.0.0 software and the estimation was done using the Restricted Maximum Likelihood (REML) method.

A non-metric multidimensional scaling (MDS) ordination of a Bray-Curtis similarity matrix coupled with a group-average cluster analysis was performed to identify groups of stations with similar taxonomic composition (Clarke & Warwick 2001) using PRIMER v6 software (Clarke & Gorley 2006). The relative abundance of each taxonomic group was square-root transformed and used to calculate the similarity matrix. An analysis of similarities (one-way ANOSIM) was also performed to test whether 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).

1.3 Results

The environmental and biological variables measured in Nachvak, Saglek, Okak and Anaktalak fjords during summer, early fall and late fall are summarized in Tables 1 to 4. ANOVAs revealed significant spatial and seasonal differences in environmental variables (Table 5). T_{eu}, Z_{nutr} and $(PO_4)_{0\text{-}Zeu}$ were significantly different between fjords, stations and seasons; S_{eu}, $E_{0\text{-}Zeu}$, $(NO_3+NO_2)_{0\text{-}Zeu}$ and $(Si(OH)_4)_{0\text{-}Zm}$ were significantly different between fjords and seasons; and Z_m, $\Delta\sigma_t$, $(NO_3+NO_2)_{0\text{-}Zm}$, $(PO_4)_{0\text{-}Zm}$ and $(Si(OH)_4)_{0\text{-}Zeu}$ showed significant differences only between seasons. Primary production (i.e., P_T, P_S and P_L) and potential carbon export were significantly different only among seasons. Z_{eu} and chl *a* biomass (i.e., B_T, B_S and B_L) did not show any significant difference between fjords, stations or seasons (Table 5).

1.3.1 Physical environment

According to temperature and salinity contours, the upper water column of the fjords was well stratified in summer, with a warm and less saline surface layer (Figs. 2 and 3, left column). Anaktalak presented a much warmer (Fig. 2d and Fig. S1b in Supplementary data) and fresher (Fig. 3d and Fig. S2b in Supplementary data) surface layer. The bottom layer (>50 m) was cold (Fig. S1a) and salty (Fig. S2a) in the two northernmost fjords (Nachvak and Saglek). In early fall (Figs. 2 and 3, middle column), the surface layer of Nachvak and Saglek was thicker, warmer (Fig. S1c) and less saline (Fig. S2c). The vertical structures of the two southernmost fjords (Okak and Anaktalak) were almost salt-wedge-like (Fig. S2d). Anaktalak was still much warmer and fresher than the three other fjords. Some stations were well stratified while others were well mixed (Figs. S1c, d and S2c, d). In late fall, all the fjords were well mixed (Fig. S1e, f), with salinities around 32, except at the head of Anaktalak where the salinity was around 31 (Fig. S2e, f).

Surface temperature decreased progressively from summer to late fall in all fjords (Figs. 2 and S1). However, Z_{eu} was warmer in early fall than during the two other seasons (Table 1). Indeed, the highest temperature of the euphotic zone (T_{eu}) was recorded at the outer station of Anaktalak during early fall (3.4°C; Table 1) while the lowest value was registered at the inner station of Saglek in late fall (-0.2°C; Table 1). Overall, T_{eu} was higher in Okak and Anaktalak fjords. During summer and early fall, T_{eu} was generally higher at the outer stations compared to their inner counterparts (Table 1). For the whole sampling period, the surface salinity was higher at the outer stations than at the inner ones, especially in the two southernmost fjords (Figs. 3 and S2).

Although Z_{eu} did not show significant differences between fjords, station positions along the fjord and seasons (Tables 1 and 5), it was always deeper than Z_m and Z_{nutr} during summer and early fall, but shallower than Z_m and Z_{nutr} at the two northernmost fjords and at the outer station of Okak during late fall. Z_m was shallower during summer and early fall than during late fall (Table 1). Z_m was generally deeper than Z_{nutr} during the late fall period

(Table 1). Z_{nutr} was deeper in Nachvak and Saglek than in Anaktalak. It was also deeper at the outer stations compared to their inner counterparts (Table 1). During summer, $E_{0\text{-}Zeu}$ was higher in Nachvak than in Saglek and Anaktalak (Table 1). The stratification index of the water column ($\Delta\sigma_t$) was higher in summer than during early and late fall (Table 1). It was positively correlated with $E_{0\text{-}Zeu}$ ($r = 0.81$, $p < 0.0001$) and negatively correlated with S_{eu} ($r = -0.57$, $p < 0.01$).

Table 1. Environmental variables of stations sampled in Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during summer, early fall and late fall. T_{eu}: water temperature averaged over the depth of the euphotic zone (Z_{eu}); S_{eu}: salinity averaged over Z_{eu}; Z: water column depth; Z_m: surface mixed layer depth; Z_{nutr}: nitracline depth calculated using NO_3 concentrations; $E_{0\text{-}Zeu}$: daily irradiance averaged over Z_{eu}; $\Delta\sigma_t$: stratification index

Fjord	Station	Position	T_{eu} (°C)	S_{eu}	Z (m)	Z_{eu} (m)	Z_m (m)	Z_{nutr} (m)	$E_{0\text{-}Zeu}$ (mol quanta m^{-2} day^{-1})	$\Delta\sigma_t$ (kg m^{-3})
Summer										
Nachvak	602	Inner	0.2	31.2	158	29	6	5	7.65	2.21
	600	Outer	0.7	31.5	207	44	31	3	7.74	1.43
Saglek	615	Inner	-0.3	31.9	130	83	12	11	4.57	1.93
	617	Outer	0.4	31.5	139	45	10	13	4.62	1.90
Anaktalak	624	Inner	2.0	29.5	71	32	11	16	5.74	3.21
	620	Outer	3.3	30.2	96	31	23	11	5.80	2.65
Early fall										
Nachvak	602	Inner	1.7	31.6	158	54	3	24	1.02	1.55
	600	Outer	2.5	31.7	207	27	6	26	1.02	0.90
Saglek	615	Inner	1.2	31.7	130	60	10	19	1.03	1.35
	617	Outer	2.6	31.7	139	36	18	18	1.03	0.65
Okak	630	Inner	1.3	31.3	51	34	4	18	1.31	0.85
	633	Outer	3.0	31.7	178	51	39	39	1.30	0.43
Anaktalak	624	Inner	2.7	30.4	71	47	25	5	1.52	0.19
	620	Outer	3.4	31.1	96	22	17	10	0.30	0.44
Late fall										
Nachvak	602	Inner	0.0	31.9	158	13	72	17	0.35	0.45
	600	Outer	0.1	32.1	207	17	95	53	0.35	0.06
Saglek	615	Inner	-0.2	32.0	130	14	87	20	0.26	0.26
	617	Outer	0.2	32.1	139	42	90	49	0.49	0.13
Okak	630	Inner	0.9	31.8	51	20	7	13	0.91	0.07
	633	Outer	0.7	32.1	178	21	103	31	0.49	0.01
Anaktalak	624	Inner	1.2	30.8	71	16	34	8	0.51	0.12
	620	Outer	0.6	31.9	96	34	26	45	0.53	0.65

1.3.2 Nutrients

Nutrient distributions were influenced by water column stratification (Figs. 4, S1, and S2). Surface nitrate concentrations increased from summer to late fall (Fig. 4). Nitrate increased with depth at all stations during summer (Fig. 4a, b) and at most stations of the two northernmost fjords (Nachvak and Saglek) during early and late fall (Fig. 4c, e). In contrast, its concentration was relatively uniform throughout the water column of Okak and Anaktalak fjords during early and late fall (Fig. 4d, f). The deep waters of Nachvak and Saglek fjords (Fig. 4a, c, e) were richer in nitrate than those of Okak and Anaktalak (Fig. 4b, d, f). Silicic acid and phosphate concentrations showed similar variations to those of nitrate (data not shown). But, in contrast to nitrate and silicic acid, phosphate was never exhausted in the surface waters during summer. In Nachvak and Saglek, Z_{eu} was richer in nitrate and phosphate than in Anaktalak (Table 2, Fig. 4). Silicic acid concentrations integrated in the Z_m were higher in Nachvak than in Anaktalak (Table 2). The mean integrated NO_3+NO_2, PO_4 and $Si(OH)_4$ concentrations in Z_{eu} and in Z_m were lower during summer compared to late fall (Table 2). Nitrite (NO_2) made up 5.8%, 9.0% and 6.4% of the total NO_3+NO_2 integrated over Z_{eu} during summer, early fall and late fall, respectively.

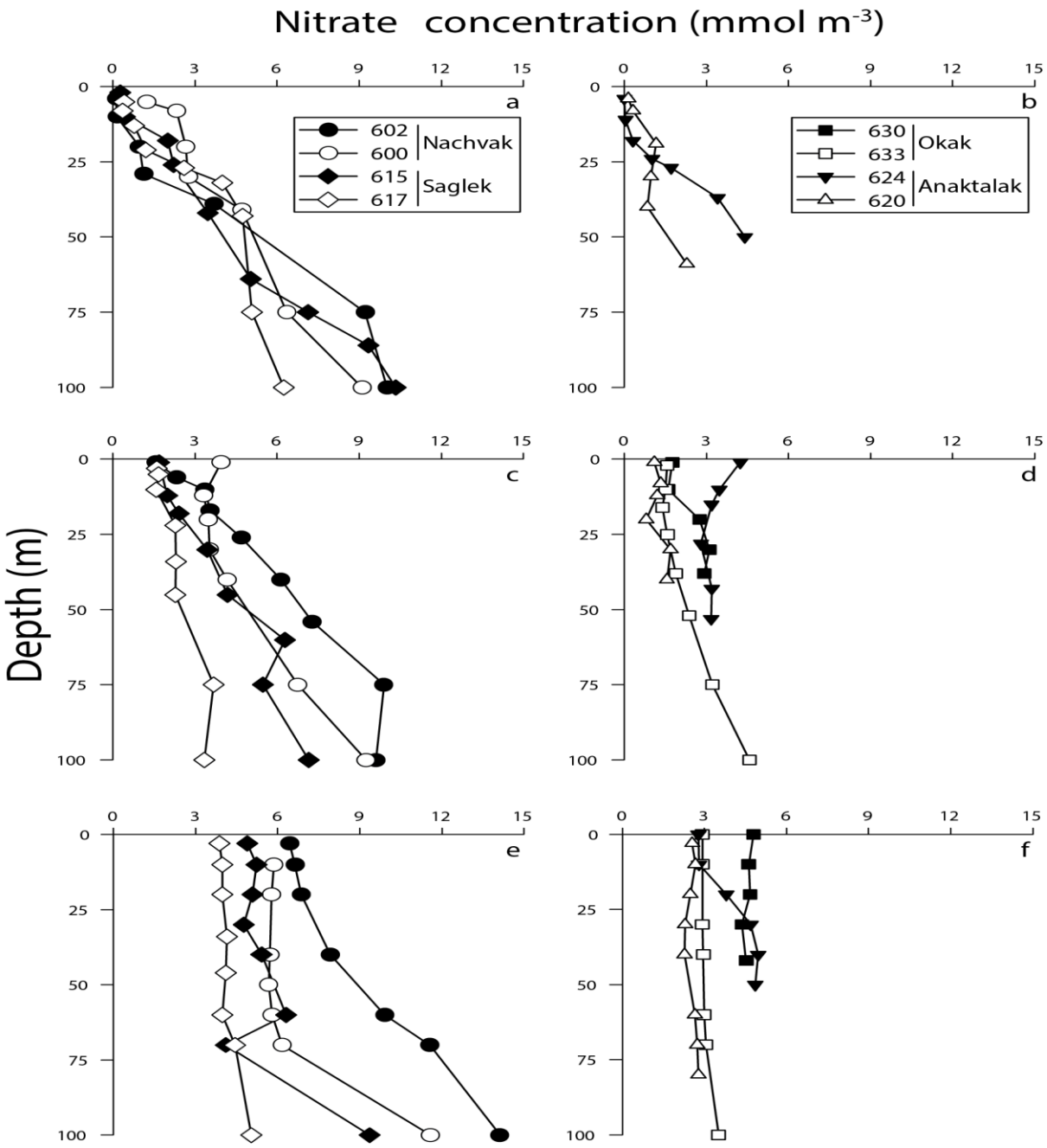


Fig. 4. Nitrate profiles for Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during (a, b) summer, (c, d) early fall and (e, f) late fall. Black symbols represent the inner stations and white symbols the outer stations

Table 2. Nutrient concentrations (mmol m^{-3}) of stations sampled in Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during summer, early fall and late fall. Mean integrated concentrations in the euphotic zone (Z_{eu}) and the surface mixed layer depth (Z_m) are given for nitrate plus nitrite (NO_3+NO_2), silicic acid ($Si(OH)_4$) and phosphate (PO_4)

Fjord	**Station**	**Position**	**NO_3+NO_2 0-Zeu**	**$Si(OH)_4$ 0-Zeu**	**PO_4 0-Zeu**	**NO_3+NO_2 0-Zm**	**$Si(OH)_4$ 0-Zm**	**PO_4 0-Zm**
Summer								
Nachvak	602	Inner	0.75	1.52	0.33	0.14	1.40	0.18
	600	Outer	4.03	5.28	0.44	2.72	3.74	0.33
Saglek	615	Inner	3.93	4.39	0.75	0.82	0.93	0.49
	617	Outer	3.44	4.42	0.63	0.55	0.80	0.30
Anaktalak	624	Inner	1.13	2.34	0.40	0.12	1.96	0.19
	620	Outer	0.79	1.08	0.38	0.70	0.88	0.33
Early fall								
Nachvak	602	Inner	5.40	6.08	1.12	1.75	6.25	0.61
	600	Outer	3.83	5.80	0.95	4.25	6.38	0.78
Saglek	615	Inner	3.73	5.81	0.86	2.15	4.35	0.53
	617	Outer	2.42	5.17	0.77	2.16	4.94	0.70
Okak	630	Inner	2.71	6.52	1.01	2.02	5.77	0.73
	633	Outer	2.02	4.05	0.74	2.02	4.05	0.74
Anaktalak	624	Inner	3.58	6.33	0.92	3.73	6.22	0.89
	620	Outer	1.36	2.88	0.46	1.33	2.84	0.45
Late fall								
Nachvak	602	Inner	6.87	6.62	0.78	9.69	10.73	1.05
	600	Outer	6.09	6.63	0.76	6.95	8.03	0.84
Saglek	615	Inner	5.37	7.69	0.92	5.94	8.57	0.92
	617	Outer	3.86	5.36	0.70	4.33	5.87	0.75
Okak	630	Inner	5.00	7.51	0.82	5.14	7.65	0.79
	633	Outer	3.23	4.66	0.73	3.49	4.94	0.59
Anaktalak	624	Inner	3.33	5.60	0.59	4.06	5.99	0.61
	620	Outer	2.69	3.70	0.47	2.76	3.80	0.48

1.3.3 Primary production and phytoplankton chl *a* biomass

Depth-integrated values of primary production showed a steep decrease from summer to late fall (Table 3, Fig. 5a-c). During summer, outer stations were extremely productive (P_T >1000 mg C m^{-2} day^{-1}), with production rates decreasing from the northernmost to the southernmost fjord (Fig. 5a). On average, summer P_T was five-fold and ten-fold larger than in early fall and late fall, respectively (Table 3, Fig. 5a-c). In early fall, P_T ranged from 33.4 mg C m^{-2} day^{-1} at outer Anaktalak to 338 mg C m^{-2} day^{-1} at inner Saglek (Table 3, Fig. 5b). During late fall, the highest (140 mg C m^{-2} day^{-1}) and lowest (6 mg C m^{-2} day^{-1}) P_T values were recorded at outer Okak and inner Saglek, respectively (Table 3, Fig. 5c). In early fall, the landward stations of all fjords were more productive than their seaward counterparts (Table 3, Fig. 5b). The reverse tendency was observed in late fall, except at Nachvak Fjord (Table 3, Fig. 5c). Throughout the study, small phytoplankton cells (0.7–5 µm) accounted for most of the primary production (Fig. 5a-c). P_T, P_S and P_L were significantly different among the sampling seasons, with the highest values being measured in summer (Tables 3 and 5); no other significant difference was found. P_T, P_S and P_L were positively correlated with $E_{0\text{-}Zeu}$ ($r = 0.55$, $p < 0.01$; $r = 0.51$, $p < 0.05$; $r = 0.59$, $p < 0.01$; respectively). P_S was also significantly correlated with $(PO_4)_{0\text{-}Zm}$ and $(Si(OH)_4)_{0\text{-}Zm}$ ($r = -0.43$, $p < 0.05$ for both correlations). P_T showed significant positive linear regressions with both $E_{0\text{-}Zeu}$ and $\Delta\sigma_t$ (Fig. 8a, b). However, its relation with T_{eu} was significant only during early fall (Fig. 8c).

Subsurface chlorophyll *a* (chl *a*) maxima were observed at most stations during summer. In early and late fall, the highest chl *a* concentrations were generally observed near the surface (data not shown). The chl *a* biomass integrated over Z_{eu} showed a general (but not significant) decrease from summer to late fall (Tables 3 and 5, Fig. 5d-f), with the exception of outer Saglek which had higher concentrations in late fall (Fig. 5f) than during the two other sampling periods (Fig. 5d, e).

Table 3. Primary production, chlorophyll *a* (chl *a*) biomass and biogenic carbon export at stations sampled in Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during summer, early fall and late fall. P_T: total phytoplankton production integrated over the euphotic zone (Z_{eu}); P_L/P_T: ratio of production by large phytoplankton (≥5 μm) to total phytoplankton production; B_T: total phytoplankton biomass integrated over Z_{eu}; B_L/B_T: ratio of biomass of large phytoplankton (≥5 μm) to total phytoplankton biomass; POC_E/P_T: ratio of particulate organic carbon potentially exported (POC_E) out of the Z_{eu} to P_T. The standard deviation is given for P_T in summer and early fall, and for B_T in summer. nd means no data available

Fjord	Station	Position	P_T (mg C m^{-2} day^{-1})	P_L / P_T (%)	B_T (mg chl *a* m^{-2})	B_L / B_T (%)	POC_E / P_T (%)
Summer							
Nachvak	602	Inner	nd	nd	83.6 ± 0.01	70.4	nd
	600	Outer	1727 ± 38.4	49.7	55.3 ± 0.01	62.4	40.8
Saglek	615	Inner	nd	nd	4.56 ± 0.08	14.3	nd
	617	Outer	1600 ± 60.2	27.0	57.0 ± 0.71	39.9	24.0
Anaktalak	624	Inner	nd	nd	57.0 ± 5.27	55.7	nd
	620	Outer	1145 ± 32.8	29.2	96.5 ± 1.86	70.9	25.6
Early fall							
Nachvak	602	Inner	224 ± 6.17	15.2	44.6	29.1	15.2
	600	Outer	111 ± 4.90	13.9	20.6	31.7	14.3
Saglek	615	Inner	338 ± 20.6	24.8	36.6	56.2	22.4
	617	Outer	228 ± 15.6	21.5	45.5	60.4	19.9
Okak	630	Inner	264 ± 3.08	24.8	73.5	64.5	22.3
	633	Outer	141 ± 10.6	11.9	21.5	28.8	12.8
Anaktalak	624	Inner	47.8 ± 0.97	11.8	21.6	28.3	12.7
	620	Outer	33.4 ± 1.79	16.2	17.6	34.5	16.0
Late fall							
Nachvak	602	Inner	96.8	47.9	40.9	57.5	39.5
	600	Outer	23.8	18.1	20.5	45.9	17.4
Saglek	615	Inner	6.42	9.5	13.6	54.5	11.1
	617	Outer	138	19.1	81.3	74.7	18.1
Okak	630	Inner	74.4	49.5	7.33	37.3	40.5
	633	Outer	140	46.6	27.5	50.2	38.5
Anaktalak	624	Inner	30.0	6.5	9.32	88.8	8.84
	620	Outer	57.2	10.7	19.7	18.3	11.9

Table 4. Phytoplankton community structure and composition in Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during summer, early fall and late fall. Cells were counted at the subsurface chlorophyll maximum (SCM) depth (or at 15% surface irradiance when SCM was not present). Picocyano: picocyanobacteria; Euk. pico: eukaryotic picophytoplankton (<2 μm); Nano: nanophytoplankton (2–20 μm); Micro: microplankton (≥20 μm); Diat: diatoms; Dino: dinoflagellates; Prymn: prymnesiophytes; Crypto: cryptophytes; O. flag: other flagellates (includes chlorophytes, chrysophytes, dictyochophytes, euglenophytes, prasinophytes, raphidophytes and unidentified flagellates); H. prot: heterotrophic protists (comprises choanoflagellates, ciliates and other heterotrophic cells). nd means no data available

Fjord	Station	Position	Community structure (%)				Total (>0.2 µm) (10^6 cells l^{-1})	Community composition (%)						Total (>2 µm) (10^6 cells l^{-1})
			Pico-cyano.	Euk. pico.	Nano.	Micro.		Diat.	Dino.	Prymn.	Crypto.	O. flag.	H. prot.	
Summer														
Nachvak	602	Inner	0.01	28.2	68.3	3.44	11.6	31.8	0.8	36.9	3.6	17.7	9.2	6.62
	600	Outer	0.14	74.1	22.3	3.51	8.12	32.0	1.2	16.0	5.1	39.6	6.1	1.61
Saglek	615	Inner	3.08	22.1	74.8	0.02	0.74	0.7	0.6	18.9	0.0	79.2	0.6	0.67
	617	Outer	0.09	71.6	28.2	0.08	6.33	24.0	0.4	60.4	1.7	10.0	3.5	2.31
Anaktalak	624	Inner	0.74	53.6	45.3	0.41	9.53	31.1	0.9	28.1	4.2	32.2	3.5	1.38
	620	Outer	0.20	45.2	52.4	2.13	4.30	56.3	0.6	12.7	0.3	21.8	8.3	1.86
Early fall														
Nachvak	602	Inner	9.39	81.6	8.3	0.77	7.44	22.6	7.6	22.3	5.1	35.4	7.0	1.43
	600	Outer	10.9	81.5	7.2	0.36	7.11	22.1	15.5	18.0	9.2	25.7	9.6	0.45
Saglek	615	Inner	33.6	57.7	8.5	0.18	3.81	36.7	12.0	16.1	5.7	24.4	5.1	0.67
	617	Outer	16.5	76.5	6.9	0.07	12.0	27.7	11.1	15.0	6.3	31.8	8.0	0.77
Okak	630	Inner	65.3	28.0	6.6	0.19	5.62	10.2	9.8	33.1	7.9	33.5	5.6	1.02
	633	Outer	6.59	86.2	7.1	0.10	9.34	13.9	13.1	19.3	10.7	36.1	6.9	0.91
Anaktalak	624	Inner	2.87	91.8	5.2	0.14	12.3	6.9	23.5	16.1	11.7	32.8	9.1	0.37
	620	Outer	14.8	76.2	8.9	0.11	6.32	8.6	14.9	31.6	13.2	22.7	9.0	0.49
Late fall														
Nachvak	602	Inner	11.2	71.4	16.5	0.96	0.78	15.8	18.4	20.5	1.7	31.8	11.8	0.37
	600	Outer	6.90	73.9	18.4	0.75	1.97	17.0	9.6	29.8	5.8	29.4	8.4	0.56
Saglek	615	Inner	8.65	59.9	30.9	0.55	1.03	10.1	11.8	32.8	1.9	38.4	5.0	0.57
	617	Outer	5.03	77.4	15.8	1.75	2.68	26.3	7.6	10.9	2.0	43.3	9.9	1.09
Okak	630	Inner	6.96	83.5	9.3	0.24	1.83	7.9	21.3	10.3	4.0	45.7	10.8	0.22
	633	Outer	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd
Anaktalak	624	Inner	10.5	73.4	15.5	0.57	1.38	15.2	21.4	10.9	3.3	37.0	12.3	0.27
	620	Outer	7.57	76.8	15.1	0.47	2.73	11.9	11.7	18.6	6.2	34.8	16.8	0.53

In summer, biomass was generally dominated by large cells (≥5 μm, B_L) (Fig. 5d). However, in early and late fall, it was mainly due to small cells (0.7–5 μm, B_S) at about half of the stations (Fig. 5e, f). The ANOVA revealed no significant difference in chl *a* biomass (Table 5). B_S and B_L were positively correlated with $E_{0\text{-}Zeu}$ ($r = 0.46$, $p < 0.05$; $r = 0.51$, $p < 0.05$; respectively) and with $\Delta\sigma_t$ ($r = 0.59$, $p < 0.01$; $r = 0.46$, $p < 0.05$; respectively). Furthermore, B_S was negatively correlated with $(NO_3+NO_2)_{0\text{-}Zm}$ and $(PO_4)_{0\text{-}Zm}$ ($r = -0.45$, $p < 0.05$; $r = -0.44$, $p < 0.05$; respectively), while B_L was negatively correlated with $(Si(OH)_4)_{0\text{-}Zeu}$ ($r= -0.45$, $p < 0.05$).

Overall, for the whole sampling period, the production per unit biomass, i.e., the P:B ratio of small cells was twice that of large cells (15.5 mg C mg chl a^{-1} day^{-1} versus 7.05 mg C mg chl a^{-1} day^{-1}). The P:B ratio of total phytoplankton (small plus large cells) was nearly seven times larger in summer than in late fall (23.7 mg C mg chl a^{-1} day^{-1} versus 3.38 mg C mg chl a^{-1} day^{-1}).

The potential export of particulate organic carbon (POC_E) out of the euphotic zone showed very similar patterns to both P_T and P_L (Fig. 5a-c and g-i). The proportion of P_T potentially exported out of the euphotic zone was, on average, 31% during summer, 19% in early fall, and 28% during late fall (Table 3). The ANOVA showed significant difference in POC_E only between seasons (Table 5). POC_E was up to one order of magnitude larger during summer than during early and late fall (Fig. 5g-i).

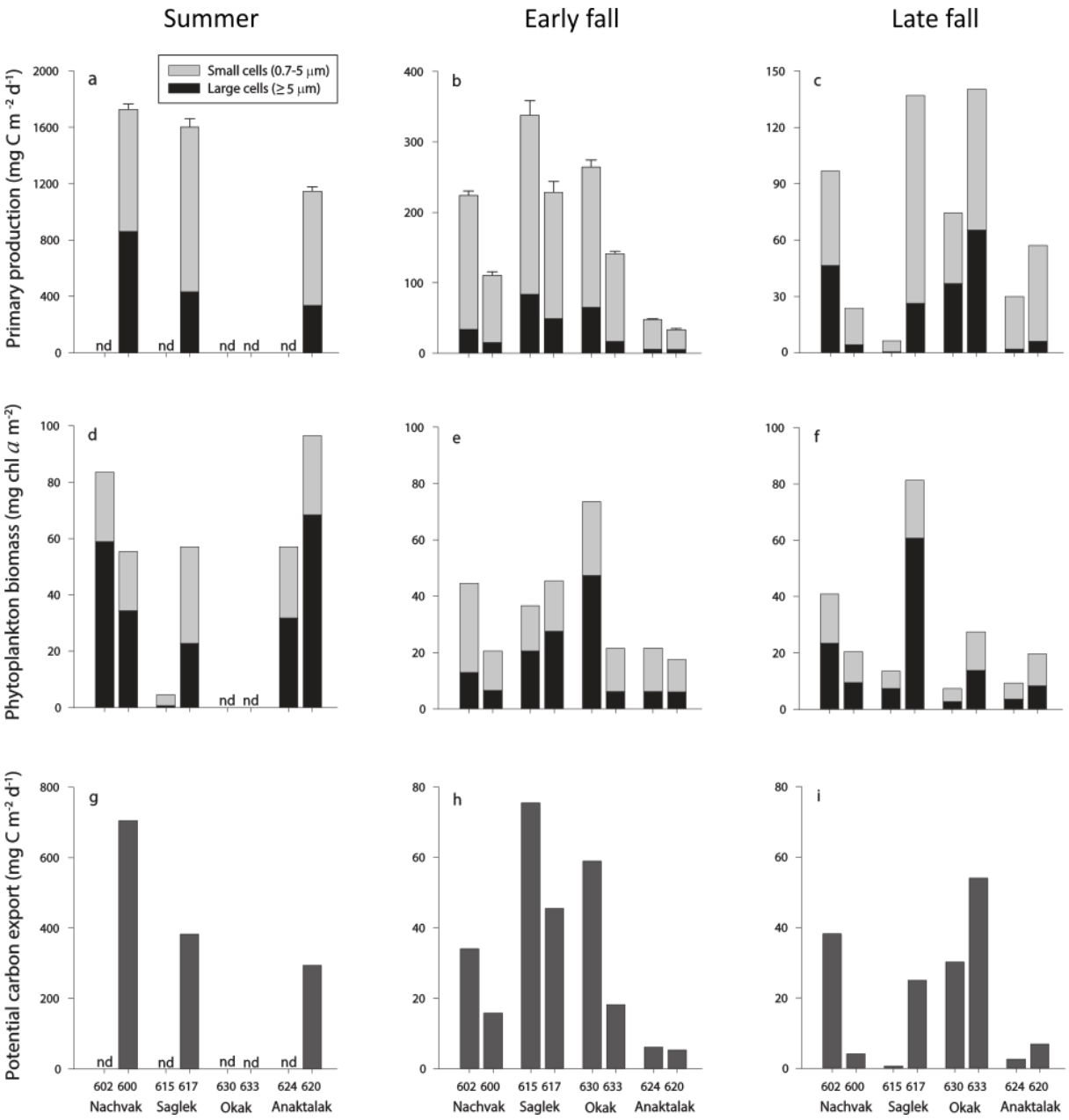


Fig. 5. Variations in (a–c) primary production, (d–f) phytoplankton chlorophyll *a* biomass, and (g–i) potential carbon export out of the euphotic zone in Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during (a, d, g) summer, (b, e, h) early fall and (c, f, i) late fall. Production and biomass of small (0.7–5 µm) and large (≥5 µm) cells were integrated from the surface to 0.2% of surface irradiance. In (a) and (b), vertical lines represent the standard deviation of the estimated rates. nd means no data available

Table 5. Summary of the analysis of variance (ANOVA) and subsequent tests for environmental and biological variables measured at the inner and outer stations of Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during summer, early fall and late fall. Variable abbreviations are defined in Tables 1–3. ns means not significant. For a *posteriori* multiple comparison Tukey tests: A > B > C

	ANOVA					Tukey test or Student's t-test ($\alpha \leq 0.05$)								
	Fjord	Station (In/Out)	Season	Fjord × Season	Station × Season	Nachvak	Saglek	Okak	Anaktalak	Station In	Station Out	Summer	Early fall	Late fall
Environmental variable														
T_{eu} (°C)	< 0.001	< 0.01	< 0.0001	0.01 < p < 0.05	ns	B	B	A,B	A	B	A	B	A	C
S_{eu}	< 0.01	ns	0.01 < p < 0.05	ns	ns	A	A	A,B	B			B	A,B	A
Z_{eu} (m)	ns	ns	ns	ns	ns									
Z_m (m)	ns	ns	< 0.0001	< 0.01	ns							B	B	A
Z_{nutr} (m)	0.01 < p < 0.05	< 0.0001	< 0.0001	< 0.01	< 0.0001	A	A	A,B	B	B	A	C	B	A
$E_{0\text{-}Zeu}$ (mol quanta m^{-2} day^{-1})	< 0.01	ns	< 0.0001	< 0.01	ns	A	B	A,B	B			A	B	C
$\Delta\sigma_t$ (kg m^{-3})	ns	ns	< 0.001	0.01 < p < 0.05	ns							A	B	B
$(NO_3+NO_2)_{0\text{-}Zeu}$ (mmol m^{-3})	0.01 < p < 0.05	ns	0.01 < p < 0.05	ns	ns	A	A	A,B	B			B	A,B	A
$(Si(OH)_4)_{0\text{-}Zeu}$ (mmol m^{-3})	ns	ns	0.01 < p < 0.05	ns	ns							B	A,B	A
$(PO_4)_{0\text{-}Zeu}$ (mmol m^{-3})	0.01 < p < 0.05	0.01 < p < 0.05	< 0.01	ns	ns	A	A	A,B	B	A	B	B	A	A
$(NO_3+NO_2)_{0\text{-}Zm}$ (mmol m^{-3})	ns	ns	< 0.01	ns	ns							B	B	A
$(Si(OH)_4)_{0\text{-}Zm}$ (mmol m^{-3})	0.01 < p < 0.05	ns	< 0.001	ns	ns	A	A,B	A,B	B			B	A	A
$(PO_4)_{0\text{-}Zm}$ (mmol m^{-3})	ns	ns	< 0.01	ns	ns							B	A	A
Biological variable														
P_T (mg C m^{-2} day^{-1})	ns	/	< 0.001	/	/							A	B	B
P_S (mg C m^{-2} day^{-1})	ns	/	< 0.001	/	/							A	B	B
P_L (mg C m^{-2} day^{-1})	ns	/	0.01 < p < 0.05	/	/							A	B	B
B_T (mg chl *a* m^{-2})	ns	ns	ns	ns	ns									
B_S (mg chl *a* m^{-2})	ns	ns	ns	ns	ns									
B_L (mg chl *a* m^{-2})	ns	ns	ns	ns	ns									
POC_E (mg C m^{-2} day^{-1})	ns	/	0.01 < p < 0.05	/	/							A	B	B

1.3.4 Phytoplankton community structure and composition

At the SCM, the lowest total phytoplankton (>0.2 µm) abundances were observed in late fall compared to the two other sampling periods (Table 4). In summer, total phytoplankton abundance ranged from 0.74×10^6 cells l^{-1} at inner Saglek to 11.6×10^6 cells l^{-1} at inner Nachvak. During early fall, it ranged from 3.81×10^6 cells l^{-1} at inner Saglek to 12.3×10^6 cells l^{-1} at inner Anaktalak. During late fall, the lowest (0.78×10^6 cells l^{-1}) and highest (2.73×10^6 cells l^{-1}) abundances of total phytoplankton were found at inner Nachvak and outer Anaktalak, respectively (Table 4). For the whole sampling period, the algal community was numerically dominated by picoeukaryotes (<2 µm; Table 4, Fig. 6a-c), except at the inner stations of Nachvak and Saglek fjords and the outer station of Anaktalak, where nanophytoplankton (2–20 µm) were dominant during summer (Table 4, Fig. 6a). However, picocyanobacteria dominated the community at the inner station of Okak Fjord during early fall (Table 4, Fig. 6b). During summer, their abundance at many stations seemed to be under the limit of detection of the flow cytometer (≈ 10 cells ml^{-1}; Table 4). Picocyanobacteria were more abundant during early fall compared to late fall (Table 4; Fig. 6b, c), probably due to the warmer temperatures of the early fall period. They made up on average 0.43%, 10.6% and 7.5% of the total picophytoplankton abundance during summer, early fall and late fall, respectively. The relative abundance of nanophytoplankton (2–20 µm) was higher in late fall than in early fall (Table 4; Fig. 6b, c). For the whole sampling period, the relative abundance of microplankton was always very low (<4% of the total phytoplankton abundance; Table 4, Fig. 6a-c).

The abundance of picocyanobacteria was correlated only with $(Si(OH)_4)_{0\text{-}Zeu}$ ($r = 0.44$, $p < 0.05$) and that of picoeukaryotes was correlated with T_{eu} ($r = 0.47$, $p < 0.05$); there was no significant correlation with any other environmental variables. Nanophytoplankton abundance was negatively correlated with S_{eu} ($r = -0.46$, $p < 0.05$) and with all nutrient concentrations integrated over Z_{eu} and Z_m (r ranging from -0.68 to -0.49, $p < 0.01$). It was also positively correlated with $E_{0\text{-}zeu}$ and $\Delta\sigma_t$ ($r = 0.76$, $p < 0.0001$;

$r = 0.65$, $p < 0.01$; respectively). Microplankton was correlated with $E_{0\text{-}zeu}$, $(Si(OH)_4)_{0\text{-}Zeu}$, and $(Si(OH)_4)_{0\text{-}Zm}$ ($r = 0.75$, $p < 0.0001$; $r = -0.51$, $p < 0.05$; $r = -0.53$, $p < 0.05$; respectively).

During summer, the algal community (>2 µm) was numerically dominated by diatoms, prymnesiophytes and other flagellates (Fig. 6d); the latter group includes chlorophytes, chrysophytes, dictyochophytes, euglenophytes, prasinophytes, raphidophytes and unidentified flagellates. In early and late fall, a different community composition was observed (Fig. 6e, f), with higher relative abundances of dinoflagellates, cryptophytes and heterotrophic protists (Table 4), the latter being composed of choanoflagellates, ciliates and other heterotrophic cells (e.g., *Telonema subtile*).

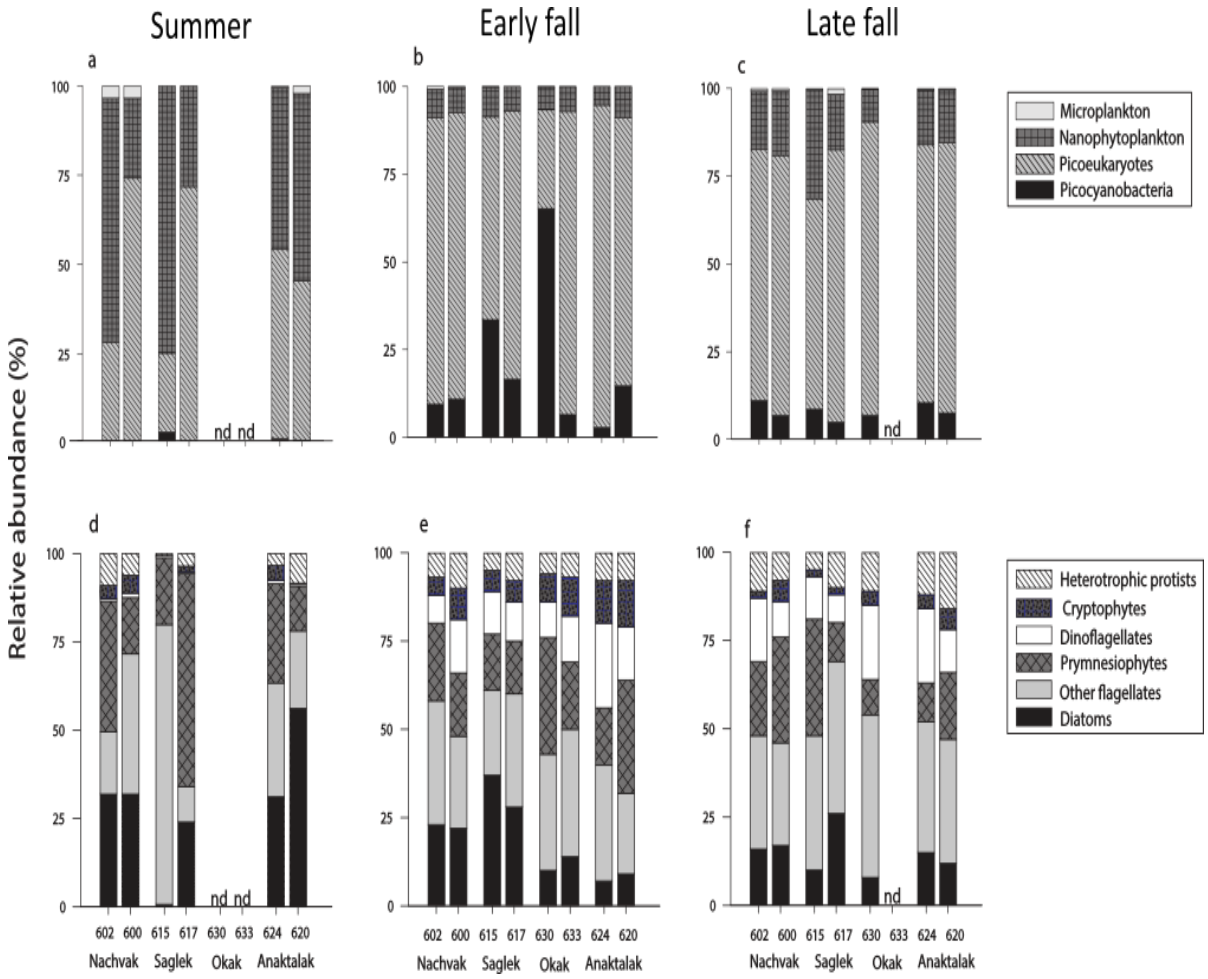


Fig. 6. Variations in the relative abundance of (a-c) picocyanobacteria (<2 μm), photosynthetic picoeukaryotes (<2 μm), nanophytoplankton (2–20 μm) and microplankton (≥20 μm), and of (d-f) six protist groups (diatoms, dinoflagellates, prymnesiophytes, cryptophytes, other flagellates and heterotrophic protists) at the subsurface chlorophyll maximum (SCM) depth (or at 15% surface irradiance when SCM was not present) in Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during (a, d) summer, (b, e) early fall and (c, f) late fall. Other flagellates comprise chlorophytes, chrysophytes, dictyochophytes, euglenophytes, prasinophytes, raphidophytes and unidentified flagellates. Heterotrophic protists include choanoflagellates, ciliates and other heterotrophic cells. nd means no data available

1.3.5 Multivariate analyses

The principal component analysis (PCA) highlighted relationships between the distribution of P_S, P_L, B_S, B_L and environmental variables (Fig. 7). The first two principal components explained 68.1% of the total variance. Principal component 1 (PC1) explained 52.7% of the total variability and was highly correlated with $E_{0\text{-}zeu}$, $\Delta\sigma_t$, P_S, P_L, B_S, B_L and with all nutrients integrated over Z_{eu} (Table 6). PC1 seems to capture the observed seasonal variability in production and nutrient inventories in Labrador fjords, associating well-lit, highly stratified and productive water masses with low nutrient concentrations. Principal component 2 (PC2) explained 15.4% of the variance. T_{eu}, Z_{eu}, nitrogenous and silicon nutrient inventories and P_L contributed to this axis (Table 6). PC2 seems to reflect the variability between inner and outer stations during early fall. Indeed, higher P_L (Fig. 5b) values were associated with colder (Fig. S1c, d) and nutrient-repleted (Fig. 4c, d) waters located at inner sites (Tables 1–3).

For the whole study period, the group-average cluster analysis performed on samples collected at the SCM identified six groups of stations with similar taxonomic composition (Fig. 9). The one-way ANOSIM revealed that the season-to-season taxonomic differences between groups of stations were significant (global $R = 0.45$, $p < 0.001$). No other significant difference was found among fjords or among stations. Groups I to IV were composed of all samples collected during summer whereas groups V and VI were made up of fall samples. Dinoflagellates, which were rarely present during summer, were always present in the fall samples (Fig. 6d, e, f). Group I, which included three stations, was mainly composed of diatoms (32%), mixed flagellate classes (30%) and prymnesiophytes (27%). Groups II, III, and IV were each composed of only one station. Group II was dominated by prymnesiophytes (60%) and diatoms (24%). Groups III and IV were mostly composed of diatoms (56%) and mixed flagellate classes (79%), respectively. Group V was made up of all samples collected in early fall and half of those collected in late fall. This group was numerically dominated by mixed flagellate classes (32%) and prymnesiophytes

(23%). Group VI, which consisted of four late fall samples, was mostly composed of mixed flagellate classes (42%), diatoms (17%) and dinoflagellates (17%).

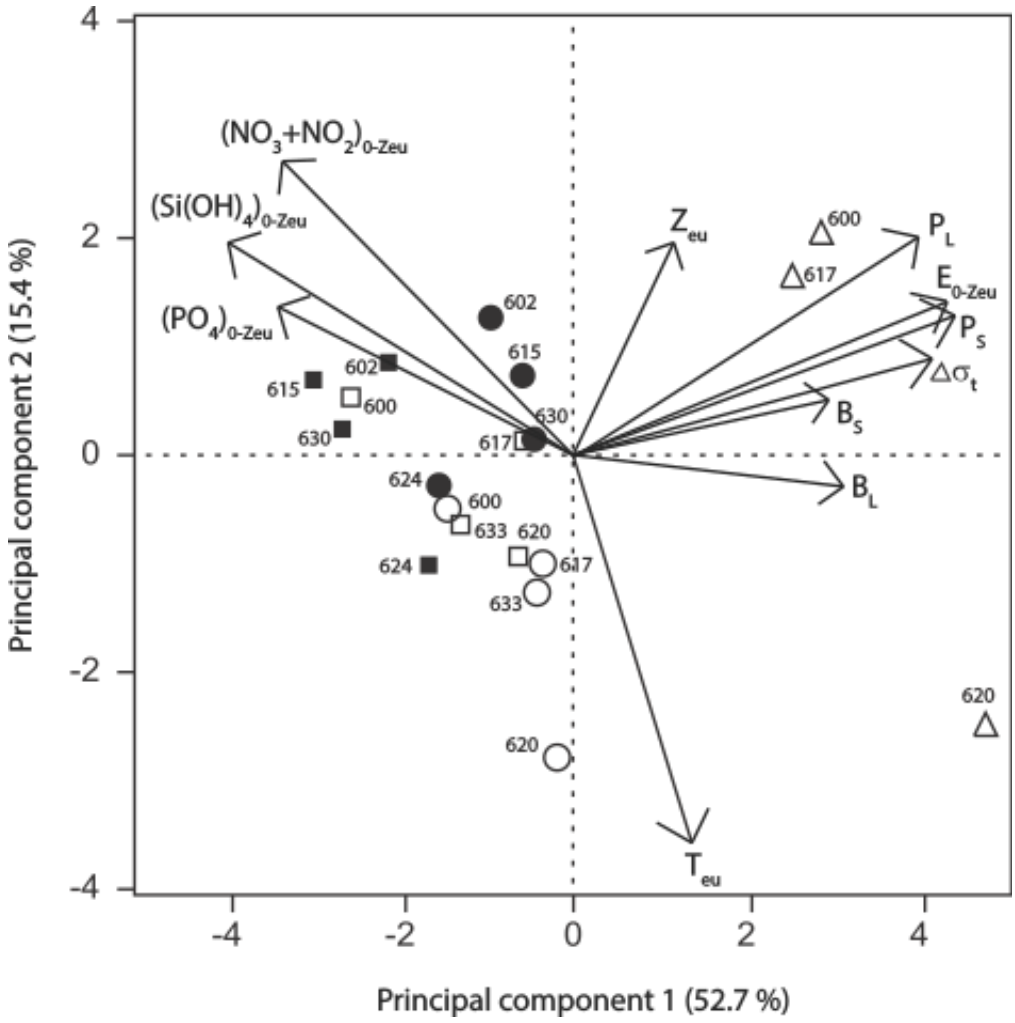


Fig. 7. Principal components analysis (PCA) of stations sampled in Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during summer (triangles), early fall (circles) and late fall (squares). Black symbols represent the inner stations and white symbols the outer stations. Variable abbreviations are defined in Tables 1–3

Table 6. Factor coordinates of the variables used in the principal component analysis (PCA). Variable abbreviations are defined in Tables 1–3. Significant factor coordinates are in bold

Variable	**PC 1**	**PC 2**
T_{eu}	0.29	**-0.75**
Z_{eu}	0.24	**0.41**
$E_{0\text{-}Zeu}$	**0.91**	0.30
$\Delta\sigma_t$	**0.87**	0.19
$(NO_3+NO_2)_{0\text{-}Zeu}$	**-0.70**	**0.57**
$(Si(OH)_4)_{0\text{-}Zeu}$	**-0.84**	**0.41**
$(PO_4)_{0\text{-}Zeu}$	**-0.71**	0.29
P_S	**0.93**	0.27
P_L	**0.84**	**0.43**
B_S	**0.62**	0.11
B_L	**0.65**	-0.06

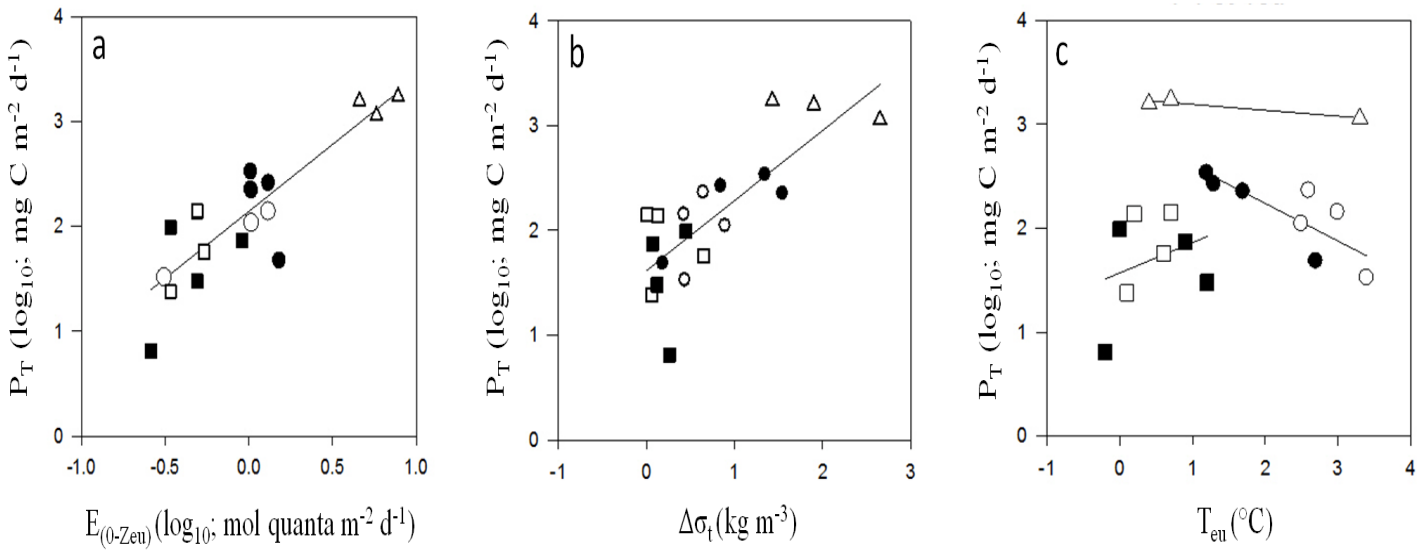


Fig. 8. Relationships between total particulate primary production and (a) the mean irradiance in the euphotic zone, (b) the stratification index, and (c) the temperature averaged over the euphotic zone in Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during summer (triangles), early fall (circles) and late fall (squares). Black symbols represent the inner stations and white symbols the outer stations. The regression slopes are shown: (a) $\log_{10}(y) = 1.28 \log_{10}(x) + 2.14$, $r^2 = 0.73$, $p < 0.0001$; (b) $\log_{10}(y) = 0.66\,x + 1.61$, $r^2 = 0.58$, $p < 0.0001$; (c) Summer: $\log_{10}(y) = -0.06\,x + 3.25$, $r^2 = 0.91$, $p > 0.05$; Early fall: $\log_{10}(y) = -0.36\,x + 2.96$, $r^2 = 0.64$, $p < 0.05$; Late fall: $\log_{10}(y) = 0.29\,x + 1.57$, $r^2 = 0.09$, $p > 0.05$. Variable abbreviations are defined in Tables 1 and 3

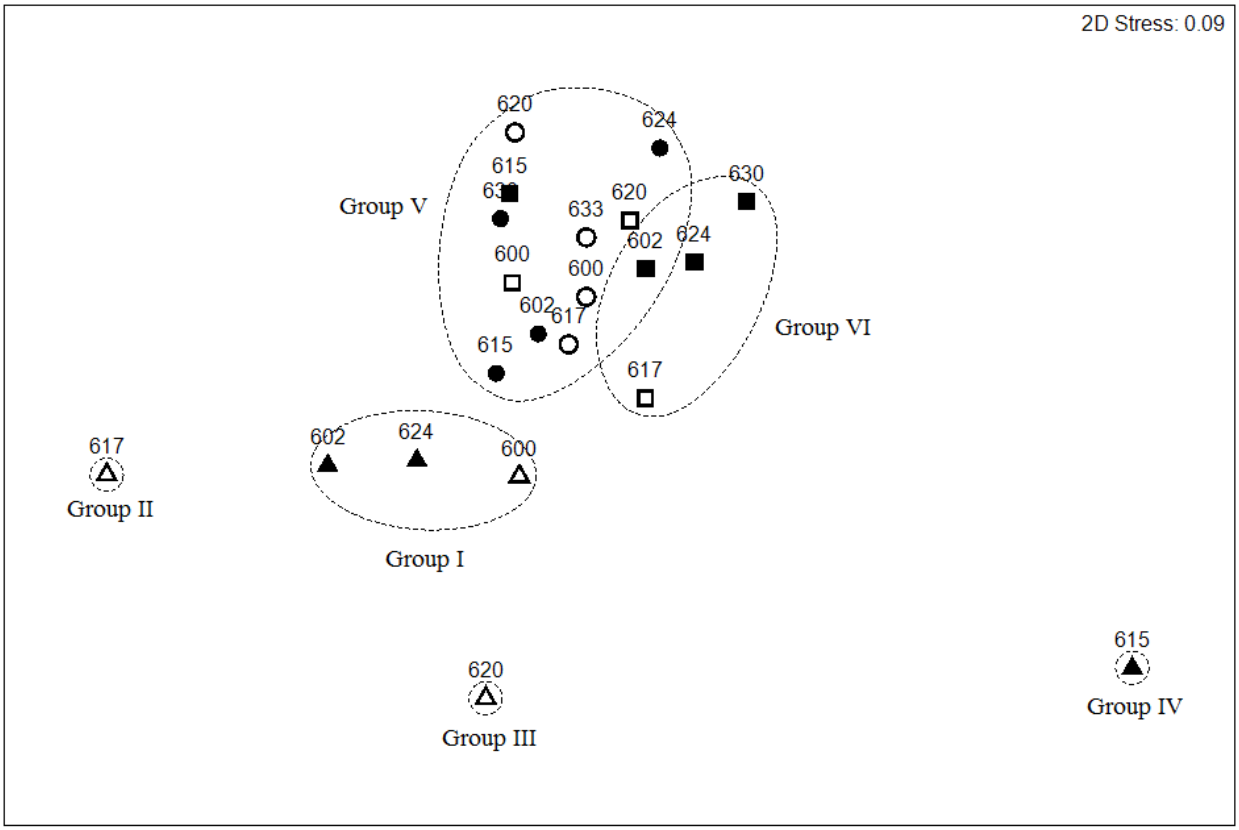


Fig. 9. Non-metric multidimensional scaling (MDS) of stations sampled in Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during summer (triangles), early fall (circles) and late fall (squares). Black symbols represent the inner stations and white symbols the outer stations. The six groups of stations with similar taxonomic composition as determined by the group-average clustering (at a similarity level of 88%) are superimposed on the MDS. Samples for taxonomic composition analysis were collected at the subsurface chlorophyll maximum (SCM) depth (or at 15% surface irradiance when SCM was not present

1.4 Discussion

1.4.1 Summer

Bloom stages

The group-average cluster analysis (Fig. 9) enabled us to distinguish three distinct phytoplankton assemblages during summer in Labrador fjords: a diatom-based system (group III), a flagellate-based system (group IV) and an intermediate system (groups I and II) in transition between diatom-based and flagellate-based systems. These assemblages show the different stages of the summer bloom in Labrador fjords.

The diatom-based system (group III), observed at outer Anaktalak, was mainly composed of centric diatoms (56%) with *Chaetoceros* being the most abundant genus. This station was also characterized by high primary production (>1000 mg C m^{-2} day^{-1}), and the biomass of large cells (68 mg chl *a* m^{-2}) was 2.4 times higher than that of small cells (28 mg chl *a* m^{-2}). This strongly supports the occurrence of an ongoing summer diatom bloom at this station. The flagellate-based system observed at inner Saglek (group IV) was composed of different flagellate classes (79%). The low nutrient concentrations in the surface mixed layer (Table 2), the extremely low total chl *a* biomass (4.56 mg m^{-2}; Table 3) and the low relative abundance of diatoms (0.7%; Table 4) observed at this station suggest that a bloom occurred earlier in the season.

Labrador fjords: Highly productive systems

The summertime P_T (1145 to 1727 mg C m^{-2} day^{-1}) and chl *a* biomass (5 to 96 mg chl *a* m^{-2}) in Labrador fjords fell in the range of values reported in other subarctic fjords (Table 7). For example, in Gullmar Fjord, P_T values around 1400 to 1600 mg C m^{-2} day^{-1} were measured during summer (Lindahl et al. 1998), and Juul-Pedersen et al. (2015) reported maximum P_T of 1383 mg C m^{-2} day^{-1} in the outer part of

Godthåbsfjord (SW Greenland) which is ice-free throughout the year (Meire et al. 2015). However, our summertime P_T was much higher than in some subarctic Swedish and Norwegian fjords (Table 7). In Lysefjord, P_T was around 350 mg C m^{-2} day^{-1} in June (Aure et al. 2007). In Byfjord and Kungsbackafjord, values of 892 mg C m^{-2} day^{-1} (Söderström et al. 1976) and 500 mg C m^{-2} day^{-1} (Olsson & Olundh 1974) were reported in August. Interestingly, the P_T measured in Labrador fjords in early August, about two weeks after the sea-ice cover melt (1727 mg C m^{-2} day^{-1}; Table 7), was similar to values measured during the spring and summer blooms (maxima of 1743 mg C m^{-2} day^{-1} in late April/early May and of 1383 mg C m^{-2} day^{-1} in July) in Godthåbsfjord (Juul-Pedersen et al. 2015). In addition, the P_T in Labrador fjords was similar to the Hudson Strait, where P_T ranged from 1132 to 1549 mg C m^{-2} day^{-1} in summer (Ferland et al. 2011). Based on these comparisons, the summer P_T in Labrador fjords (>1000 mg C m^{-2} day^{-1}) is thus consistent with a highly productive subarctic ecosystem.

Subsurface chlorophyll maxima (SCM) were observed in the stratified and nitrate-poor surface waters of Labrador fjords during summer. SCM is a common feature in ice-free arctic waters during late summer and early fall (Martin et al. 2010, Ardyna et al. 2013), and it usually corresponds to the late stage of a bloom. In summer, when stratification is strong and nutrients are exhausted in the upper layer, the SCM is located in the transition zone, close to the pycnocline, between the warm surface layer and the cold deep layer. During fall, windy conditions and subsequent increased mixing are responsible for the shallowness of the SCM.

Table 7. Range or mean of total primary production and chlorophyll (chl *a*) biomass in Northern Hemisphere fjords. Maximum production values are indicated for Godthåbsfjord and Indian Arm. Values were integrated over the euphotic zone or over the upper water column (ranging from 20 m to 50 m). nd means no data available. Note: Due to large interannual variations of climatic and hydrographic conditions, the sea-ice cover in the fjords is highly variable from year to year, and this table gives only an indication of what is usually observed. Hence, information on sea-ice cover and glaciers presented here should be interpreted cautiously

Fjord	Latitude (°N)	Primary production ($mg\ C\ m^{-2}\ day^{-1}$)	Chl*a* ($mg\ m^{-2}$)	Period	Bloom	Reference
Svalbard						
Kongsfjorden•,*	78.5	30-1850	1-52	April-May	April/May	Hodal et al. 2012
Kongsfjorden•,*	78.5	4-445	nd	March-September	April	Iversen & Seuthe 2011
Greenland						
Young Sound•,*	74.0	64	nd	July	Mid-July	Rysgaard et al. 1996
Young Sound•,*	74.0	1-280	nd	June-August	Mid-July	Rysgaard et al. 1999
Kobbefjord•	64.0	10-4200	nd	April-June	May	Mikkelsen et al. 2008
Godthåbsfjord*	64.1	1739 (max)	nd	May		Arendt et al. 2010[a]
Godthåbsfjord*	64.1	1-97	nd	January-March	April/May, July/August	Juul-Pedersen et al. 2015
Godthåbsfjord*	64.1	134-1743	nd	April-June	April/May, July/August	Juul-Pedersen et al. 2015
Godthåbsfjord*	64.1	74-1383	nd	July-September	April/May, July/August	Juul-Pedersen et al. 2015
Godthåbsfjord*	64.1	2-178	nd	October-December	April/May, July/August	Juul-Pedersen et al. 2015
Norway						
Ullsfjord	69.5	3028	44-134	April	April	Archer et al. 2000[b]
Balsfjord	69.3	3246	54-222	April	April	Archer et al. 2000[b]
Fjord Malangen	69.2	2093	54-108	April	April	Archer et al. 2000[b]
Lysefjord	59.0	350	20-70	June		Aure et al. 2007
Faroe Islands						
Kaldbaksfjord•	62.0	700-3400	200-600	April-October	May	Gaard et al. 2010
Sweden						
Gullmar Fjord•	58.0	600-1200	nd	March-May		Lindahl et al. 1998
Gullmar Fjord•	58.0	1400-1600	nd	June-August		Lindahl et al. 1998
Gullmar Fjord•	58.0	600-1600	nd	September-November		Lindahl et al. 1998
Byfjord•	58.0	308-892	nd	August-October		Söderström et al. 1976[c]
Kungsbackafjord•	57.4	180-793	nd	April-October		Olsson & Olundh 1974[c]
Scotland						
Loch Ewe	57.8	210-650	nd	May-July	May	Davies 1975[d]
Canada						
Labrador fjords•	56-60	1145-1727	5-96	July-August	July/August	This study
Labrador fjords•	56-60	33-338	18-73	October		This study
Labrador fjords•	56-60	6-140	7-81	November		This study
Jervis Inlet	50.0	84-1700	nd	January-December	April	Timothy & Soon 2001
Howe Sound	49.5	0.04-5302	nd	January-December	April/May, September	Stockner et al. 1977
Indian Arm	49.4	6640 (max)	nd	January-December	April/May, September	Stockner & Cliff 1979[e]
Saanich Inlet	48.6	94-3000	nd	January-December	April	Timothy & Soon 2001
Saguenay Fjord•	48.3	0.86-166	nd	May-October	July	Côté & Lacroix 1979

• Indicates seasonally ice-covered fjords.

* Indicates fjords in direct contact with glaciers.

[a] Gross primary production was estimated by the ^{14}C-assimilation method using *in situ* incubations (for 2 h during mid-day).

[b] Gross primary production was measured from changes in total CO_2.

[c] Reviewed in Matthews & Heimdal (1979).

[d] Reviewed in Burrell (1988).

Nutrient limitation

In summer, nitrate was completely depleted in the upper 10 m of the water column (Fig. 4a, b), indicating that phytoplankton uptake was greater than nitrate resupply to the surface layer. Hence, further phytoplankton production was likely limited by dissolved inorganic nitrogen in this layer. This is confirmed by the seasonal average of the NO_3:PO_4 molar ratio (range: 1.7 to 8.9 in the euphotic zone), which was lower than the Redfield value of 16:1 (Redfield et al. 1963) in all fjords and sampling seasons. Moreover, the seasonal average of the NO_3:$Si(OH)_4$ molar ratio (range: 0.4 to 1.0 in the euphotic zone) was lower than the Brzezinski value of 1:1.1 (Brzezinski 1985), suggesting that silicic acid was also a limiting nutrient. Silicic acid concentration in summer was generally below 2 mmol m^{-3} in the surface mixed layer (Table 2); this concentration is within the range of reported values for the affinity constant of diatoms for dissolved silicon (K_s = 0.8 to 3.4 mmol m^{-3}; Paasche 1973, Azam & Chisholm 1976). It thus appears that diatoms had already reduced silicic acid concentrations to levels that limited their abundance. Therefore, diatoms were co-limited by nitrogen and silicic acid, the latter nutrient being essential for frustule formation.

Since nitrate was completely depleted (Fig. 4a, b) and silicic acid was reduced to low concentration in the surface layer (Table 2), small phytoplankton cells, because of their low surface-to-volume ratio, were able to outcompete larger cells like diatoms. In the northernmost inlets (Nachvak and Saglek fjords), the replenishment of nitrate from a depth of 25 m is explained by diffusion, vertical mixing and nitrogen regeneration or by its lower assimilation by algal cells since *in situ* irradiance can be a limiting factor for phytoplankton production in the deeper part of the euphotic zone.

Similar results were found in other Northern Hemisphere fjords such as Lysefjord (Aure et al. 2007), Kaldbaksfjord (Gaard et al. 2010) and Jervis and Saanich inlets (Timothy & Soon 2001), where phytoplankton production and biomass were also limited by nutrient supply. Interestingly, this nitrogen limitation of Labrador fjord-type estuaries is also common to arctic shelf seas such as Baffin Bay (Garneau et al. 2007, Tremblay et al.

2009, Ardyna et al. 2011) and Hudson Bay (Ferland et al. 2011, Lapoussière et al. 2013). One could have expected a different pattern since phosphorus is usually the limiting nutrient in freshwater (Brett et al. 2000, Elser et al. 2007).

1.4.2 Fall

During early fall, the P_T in Labrador fjords (33 to 338 mg C m^{-2} day^{-1}) was comparable to values reported in October at the subarctic Byfjord (308 mg C m^{-2} day^{-1}; Söderström et al. 1976) and at Jervis Inlet (310 mg C m^{-2} day^{-1}; Timothy & Soon 2001). Labrador fjords were as productive as the Beaufort Sea (mean of 64 mg C m^{-2} day^{-1}) and the Canadian Arctic Archipelago (mean of 122 mg C m^{-2} day^{-1}) during early fall (Ardyna et al. 2011). Their production was also similar to Hudson Bay, where P_T ranged from 70 to 435 mg C m^{-2} day^{-1} during early fall (Lapoussière et al. 2013). For the late fall period, we consider our P_T results (6 to 140 mg C m^{-2} day^{-1}) to be similar to the values in Jervis and Saanich inlets, both of which are seasonally ice-free fjords (155 and 160 mg C m^{-2} day^{-1}, respectively; Table 7; Timothy & Soon 2001).

During fall, the community was mainly composed of different flagellate classes (32% for group V and 42% for group VI). It is well known that flagellates have lower light requirements than diatoms (Takahashi et al. 1978, Harrison et al. 1983), and therefore they easily dominate the community during this period of the year. Takahashi et al. (1978) also argued that their motility may help them remain near the surface, when strong autumnal winds and subsequent mixing of water column cause other cells to sink. Degerlund & Eilertsen (2010) observed that prymnesiophytes tend to dominate in weakly stratified and more saline water masses. This conclusion agrees well with prymnesiophytes being the second dominant taxonomic group during early fall (23% in group V). In group VI, dinoflagellates (17%) were mainly from the *Gymnodinium/Gyrodinium* complex, and these taxa were likely heterotrophic. These two flagellate-based systems were characterized by a

relatively high abundance of picophytoplankton as well as low production and biomass of large cells.

Possible bloom in early fall?

The high chl *a* biomass (integrated over the euphotic zone) measured at inner Okak Fjord in early fall (73.5 mg chl *a* m^{-2}) suggests that a fall bloom of large phytoplankton cells (≥5 μm) may occur in northern Labrador fjords. Indeed, the contribution of large cells to total biomass reached 65% at this station (Table 3). The occurrence of a fall bloom at inner Okak is likely since the average irradiance over the euphotic zone (1.3 mol quanta m^{-2} day^{-1}; Table 1) is equal to the critical value (1.3 ± 0.3 mol quanta m^{-2} day^{-1}) required for the onset of net phytoplankton growth in North Atlantic waters (35–75°N; Siegel et al. 2002). Furthermore, we consider that the average irradiance in Okak Fjord is similar to the value of 1.9 ± 0.3 mol quanta m^{-2} day^{-1} required for bloom initiation in the Arctic Ocean (Tremblay et al. 2006, Garneau et al. 2007). Fall blooms and the mechanisms underlying them are less frequent in the literature. Generally, they are believed to occur when enhanced mixing in fall, which entrains nutrient-rich water to the mixed layer, coincides with sufficiently high irradiance (Dutkiewicz et al. 2001, Findlay et al. 2006, Ardyna et al. 2014).

Light limitation in late fall

The seasonal decrease of the P:B ratio, a good indicator of phytoplankton photosynthetic performance, is largely attributed to the seasonal decline in irradiance, as confirmed by the significant correlation between the P:B ratio of small ($r = 0.95$, $p < 0.001$) and that of large ($r = 0.78$, $p < 0.001$) cells with $E_{0\text{-}Zeu}$. Aguilera et al. (2002) previously indicated that the photosynthetic performance of algal cells was influenced by the seasonal changes in solar radiation.

Due to the northerly location of Labrador fjords, the seasonal differences in daily irradiance are large (Table 1). According to Sverdrup's critical depth model, net primary production is possible once phytoplankton receives enough light for positive growth (Sverdrup 1953). In late fall, the average irradiance in the euphotic zone was very low, ranging from 0.26 to 0.91 mol quanta m^{-2} day^{-1} (Table 1). Even though nutrients were replenished in the water column, these low light levels terminated the productive season.

Impacts of weak stratification

As the season advances, stratification weakens with the reduction in freshwater runoff from surrounding lands and glaciers (Eilertsen et al. 1981). This enhances nutrient transport from deep-water layers through vertical mixing, which is one of the key variables that controls the growth of phytoplankton cells within the water column (Diehl et al. 2002). Indeed, mixing processes are usually accompanied by changes in light and nutrient availability (Winder & Sommer 2012), and they can also affect the capacity of algal cells to maintain their vertical position in the surface water. In accordance with this idea, we argue that the seasonal decrease in stratification probably reached an extent where the mixing depth was greater than the critical depth, a condition when water column respiration would be greater than photosynthesis, thus preventing an increase in phytoplankton biomass (Sverdrup 1953).

Fjords are stratified chiefly as a result of melting snow and ice as well as freshwater runoff from rivers and land. These inputs induce changes in the physical and chemical properties of the water column (e.g., temperature, salinity, nutrient concentrations, euphotic zone and surface mixed layer depths) and thus play an important role in phytoplankton dynamics. Strong autumnal winds also enhance vertical mixing of the water column and thus reduce stratification.

So, what precisely controls stratification in Labrador fjords? For the whole sampling period, $\Delta\sigma_t$ was significantly correlated with S_{eu} and $E_{0\text{-}Zeu}$. Fresher and well-lit water

masses were more stratified. The correlation between $\Delta\sigma_t$ and T_{eu} was not significant, suggesting that the temperature range observed throughout our study (-0.2 to 3.4°C; Table 1) was too small to noticeably affect vertical stratification, which was mainly controlled by the salinity gradient caused by freshwater inputs. This situation is typical of Northern Hemisphere fjords (Keck et al. 1999, Rysgaard et al. 2003).

1.4.3 Potential carbon export

Throughout the study period, the low percentage of particulate organic carbon potentially exported out of the euphotic zone (POC_E, ≤31%) suggests that a large part of the primary production was efficiently retained in the euphotic zone or grazed by microzooplankton rather than being exported to greater depths (Tremblay et al. 1997). In agreement with these ideas, Juul-Pedersen et al. (2006) estimated that 83% of the phytoplankton-based POC was retained in the upper 50 m of the water column in Disko Bay (West Greenland) in June. Despite the lack of vertical flux observations in our study, we believe that such high retention could also occur in Labrador fjords during summer, since the integration depth (50 m) used by Juul-Pedersen et al. (2006) falls in the range of our summer euphotic zone depths (Table 1). The authors also indicated that the loss rate of phytoplankton-based POC due to grazing in Disko Bay averaged 18% day^{-1} while the loss rate due to sedimentation was about 4% day^{-1} (Juul-Pedersen et al. 2006). Arendt et al. (2010) furthermore noted that protozooplankton actively feed on algae in Godthåbsfjord. Similarly, Archer et al. (2000) found that microzooplankton grazed up to 68% of the primary production during the spring bloom in Norwegian fjords. Since our sampling occurred while there was an ongoing summer bloom, it is likely that the POC_E we measured was lower than it would have been few days earlier. Even in the late stage of the bloom, the fjords were still highly productive, and they are thus likely to have supported a large herbivorous community during the peak stage of the bloom. Indeed, the Labrador coast is known for its great whale watching from May to September, strongly supporting that high primary productivity is transferred to the higher trophic levels.

1.4.4 Size structure of phytoplankton community

For the whole sampling period, picophytoplankton cells were consistently the most abundant at almost all stations. The positive correlation of picophytoplankton abundance with T_{eu} clearly indicates a direct effect of temperature on the growth rate of small algal cells. Factors responsible for warmer water temperatures may thus favour higher abundances of picophytoplankton. This finding is in agreement with Tremblay et al. (2009), who noted that picophytoplankton abundance increases with water temperature throughout the Arctic for a temperature range of -2 to 5°C.

Several studies have focused on picophytoplankton in Kongsfjorden, but most of them did not distinguish between picocyanobacteria and picoeukaryotes (e.g., Wang et al. 2009, Iversen & Seuthe 2011) as we did. While cyanobacteria are generally thought not to be abundant in polar marine waters, they accounted for a large fraction of total phytoplankton cells in Okak Fjord during early fall (up to 65%; Table 4). Van Hove et al. (2008) previously noted a cyanobacteria abundance of 25×10^6 cells l^{-1} in fluorescence microscopy counts from Disraeli Fjord (northern coast of Ellesmere Island), where water temperature was -0.25°C. We hypothesize that cyanobacteria in Labrador fjords may have an allochthonous origin and were brought by freshwater inflow. Similar observations were made in the Beaufort Sea, where cyanobacteria were also related to freshwater inputs (Waleron et al. 2007, Blais et al. 2012).

Nanophytoplankton were more abundant during summer and showed a significant positive correlation with both $E_{0\text{-}Zeu}$ and $\Delta\sigma_t$. This can be explained by the fact that stratification traps cells in the upper layer, where they are exposed to higher irradiance. A negative correlation was also found between nanophytoplankton and both salinity and nutrient inventories, indicating that nanophytoplankton was a major consumer of dissolved nutrients in stratified surface waters.

Throughout the study period, the relative abundance of microplankton (≥20 μm) was very low (<4% of the total cell abundance) in all fjords. However, size-fractionated chl *a*

data revealed that microphytoplankton made up from 4 to 49% of the total chl *a* biomass during summer. This indicates that the microphytoplankton size-class was likely composed of chain-forming and/or colonial species larger than 20 µm. This finding is similar to observations from Saanich Inlet where chl *a* biomass was dominated by microphytoplankton during spring and summer periods (Grundle et al. 2009). Its predominance was attributed to high nutrient concentrations or to frequent nutrient resupply.

1.4.5 Latitudinal gradient

The variability along the latitudinal gradient was not marked, and the northernmost fjords (Nachvak and Saglek) were not significantly different from the southernmost fjords (Okak and Anaktalak). Compared to the other three locations, phytoplankton dynamics were not significantly different in Nachvak Fjord, the only fjord which receives freshwater and sediments from a glacier-fed river (Ivitak Brook) draining the south-central part of the fjord catchment (Brown et al. 2012). Finally, primary production and biomass showed no clear differences between the inner and the outer stations of the fjords. Differences between fjords probably could have been better observed at the onset of the summer bloom. The surface waters of Anaktalak Fjord were clearly warmer than those of the other fjords (Figs. 2d and S1b), and the bloom may have started earlier and lasted longer in Anaktalak relative to the other fjords.

1.4.6 Pollution

There was no significant difference in phytoplankton production and biomass between pristine inlets (Nachvak and Okak) and those where anthropogenic activities occur (i.e., extensive PCB contamination in Saglek and mining activities and associated shipping operations in Anaktalak; see Section 2.1). Previous studies in Saglek Fjord have indicated negative impacts of PCB on the survival and reproductive success of benthic invertebrates,

fishes, seabirds and marine mammals (Kuzyk et al. 2005a, 2005b, Brown et al. 2009, 2013, 2015). It is noteworthy to mention that algal cells were not considered in these studies, so the effects of contaminants and abiotic stressors on pelagic lower trophic levels are still unknown in this environment. Since this is the first report on phytoplankton dynamics in Labrador fjords, there is no baseline study that would allow us to compare the data obtained from Saglek and Anaktalak to data collected prior to these anthropogenic ecosystem alterations.

Metals constitute an important group of abiotic stressors for marine algae that elicit stress responses such as the production of reactive oxygen species (Ramesh et al. 2015). In Chañaral Bay (Chile), copper mining activities have led to high marine sediment accumulations that have caused reduced light penetration and high mortalities among algae, marine invertebrates, and fishes (Castilla & Nealler 1978). In a productive system such as Saglek Fjord, small phytoplankton, with its large surface-to-volume ratio, may dominate the particulate organic matter and become an efficient sorbent matrix for hydrophobic organic contaminants **(**HOC, which include PCB), and thus be an important entry for these compounds into marine food webs (Magnusson & Tiselius 2010). These observations call for more studies on the role of planktonic communities on the potential transfer of contaminants to higher trophic levels in Labrador fjord systems.

1.4.7 Other drivers of productivity in fjord systems

The factors controlling the magnitude of primary production in fjord systems are numerous and include not only nutrient availability, irradiance and water column stability, as already mentioned, but also more complex variables such as bathymetry, sea-ice cover, hydrographic conditions and freshwater runoff (Juul-Pedersen et al. 2015, Meire et al. 2015, Murray et al. 2015). Although published literature on physical oceanography of Labrador fjords is nonexistent, the factors listed above undoubtedly control phytoplankton dynamics and largely explain the differences in productivity shown in Table 7.

Sea-ice cover

It is interesting to note that the highest primary production rates (>2000 mg C m^{-2} day^{-1}) were observed in seasonally ice-free fjords located in High Arctic Norway (i.e., Ullsfjord, Balsfjord and Fjord Malangen) and in southern British Columbia (Canada; i.e., Howe Sound, Indian Arm and Saanich Inlet; Table 7). The subarctic Kaldbaksfjord (Faroe Islands) is the only seasonally ice-covered fjord showing very high production rates (Table 7). The lowest summer P_T values (Table 7) were reported in Young Sound, which is a High Arctic glacial fjord on the northeast coast of Greenland that is ice covered for 9-10 months per year (from October to June; Murray et al. 2015), and in the Saguenay Fjord (Québec, Canada), which is the southernmost fjord in the Northern Hemisphere and ice covered from January to April.

The sea-ice cover controls the light level experienced by phytoplankton in the water column. In this way, it partly determines the onset of the bloom and the number of blooms occurring in northern ecosystems. Indeed, our study revealed a single summer pelagic bloom in Labrador fjords instead of two blooms as sometimes observed in Greenlandic fjords (in spring and summer; Glud et al. 2000, Riisgaard et al. 2014, Juul-Pedersen et al. 2015; Table 7), Norwegian fjords (in spring and summer; Wasmann 1983, Keck et al. 1999, Wasmann et al. 2000), and fjords on the west coast of Canada (in spring and fall; Stockner et al. 1977, Stockner & Cliff 1979; Table 7). Because Labrador fjords are ice covered from mid-December to mid-July, the onset of a pelagic spring bloom is unlikely to happen. With climate warming, a feasible scenario is that Labrador fjords could be ice-free weeks earlier, and a spring bloom may occur in the future. Although the high chl *a* biomass noted at inner Okak during early fall (73.5 mg chl *a* m^{-2}; Table 3) suggests the occurrence of a possible fall bloom in Labrador fjords, this observation still needs to be confirmed by further studies.

Hydrography

Labrador fjords are located between 56° and 60°N and are seasonally ice covered. Therefore, their hydrography should be, in theory, more similar to the hydrography of Norwegian or Swedish fjords than to the other fjords listed in Table 7, as Greenlandic fjords which are mostly glacier fjords. The Labrador Sea is bounded by strong currents: the West Greenland and Labrador currents to the east (Lazier 1979), narrow and strong currents trapped on the continental slopes of Greenland and Labrador to the north and west, and the Atlantic Current or North Atlantic drift to the south (Lazier 1980). The Labrador Current flows southward and carries colder water to Labrador fjords compared to Norwegian fjords such as Kongsfjorden, which receives warm Atlantic water from the West Spitsbergen Current (Hodal et al. 2012). Moreover, contrary to Swedish fords, which are either within a bay (Gullmar Fjord and Kungsbackafjord) or inland (Byfjord), the mouths of Labrador fjords are all located on the Labrador Shelf.

The properties of the Labrador Current have been known to vary significantly over the past years (Yashayaev 2007). On average, the temperature on the Labrador Shelf is below 0°C while salinity varies between 32 and 34 (Yashayaev 2007). For the whole sampling period, all outer stations of the Labrador fjords (stations 600, 617, 633, and 620; Table 1) had salinities around 32 below 25 m (Fig. S2 in Supplementary data). The temperatures below 25 m were more variable: they were below 0°C in summer (Fig. S1 in Supplementary data) when the stratification is very strong. During summer, the tides at Nain (56.3°N, close to Anaktalak Fjord) were of the mixed semi-diurnal variety, with a maximum range of 2.5 m at the spring tide. The raw (unprocessed) Ship-mounted Acoustic Doppler Current Profiler (SADCP) eastward currents (almost aligned with the fjord) observed at outer Anaktalak Fjord on 20 October 2007 varied between 0.3 and -0.3 m s^{-1}, showing a dominant M_2 semi-diurnal tidal signal. The SADCP currents observed at the mouth of the three other fjords were of the same order. These observations, along with the salinity structure in late fall (Figs. 3 and S2), strongly suggest a penetration of shelf waters into Labrador fjords. Unfortunately, the residual currents are still poorly known.

Freshwater inflow

Freshwater discharge largely influences primary production by transporting coloured dissolved organic matter (CDOM), particles and nutrients into the fjords. These inputs have opposite effects on productivity: while nutrients stimulate primary production, CDOM and particles increase light attenuation and subsequently limit primary production. In Young Sound and Godthåbsfjord, light was strongly attenuated in the upper 5 m by particles associated with glacial discharge of melt water (Murray et al. 2015). In the Saguenay Fjord, about 80% of light attenuation in the euphotic zone is due to CDOM (Xie et al. 2012, Zhang & Xie 2015), and this contributes to explain the low primary production (Table 7). Côté & Lacroix (1979) previously observed a marked relation between the thickness of the euphotic zone and freshwater inputs to the Saguenay Fjord. They measured a negligible P_T in May and June (10 mg C m^{-2} day^{-1}) along with a very shallow euphotic zone (≤5.5 m). The maximum value reported (166 mg C m^{-2} day^{-1}; Table 7) was measured in July, when the euphotic zone depth never exceeded 10 m.

1.5 Conclusion

This study was conducted in four Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during summer, early fall and late fall. It builds our knowledge of phytoplankton structure and function in these fjords and reports for the very first time values of primary production, chl *a* biomass and potential carbon export as well as phytoplankton cell abundances and taxonomic composition. Our results revealed a clear seasonal variability in phytoplankton structure and function, which were mainly influenced by the light regime, stratification strength and nutrient supply. Surprisingly, despite significant differences in environmental factors, no significant spatial difference in biological variables was found, neither among the fjords nor the sampling stations. Our analysis showed that Labrador fjords are highly productive ecosystems. However, it is likely that our sampling did not cover the period of maximum phytoplankton production. In

order to determine the complete production cycle of phytoplankton, a sampling expedition to Labrador fjords should be conducted in the first half of July, immediately after the sea-ice break-up. This will ensure that the summer bloom in the pelagic community is fully sampled. Indeed, because Labrador fjords are ice-free from mid-July (to mid-December), the outburst of pelagic algal cells does not take place in spring but rather in July. Moreover, in future investigations, it would be interesting to evaluate vertical export (with moored, sequential sediment traps) and grazing by proto- and metazooplankton to confirm our hypothesis that primary production is efficiently retained in the upper euphotic zone under current climate conditions. Being the first to characterize phytoplankton dynamics in Labrador fjords, our study is instrumental in assessing the response of these unique ecosystems to anthropogenic and climate changes.

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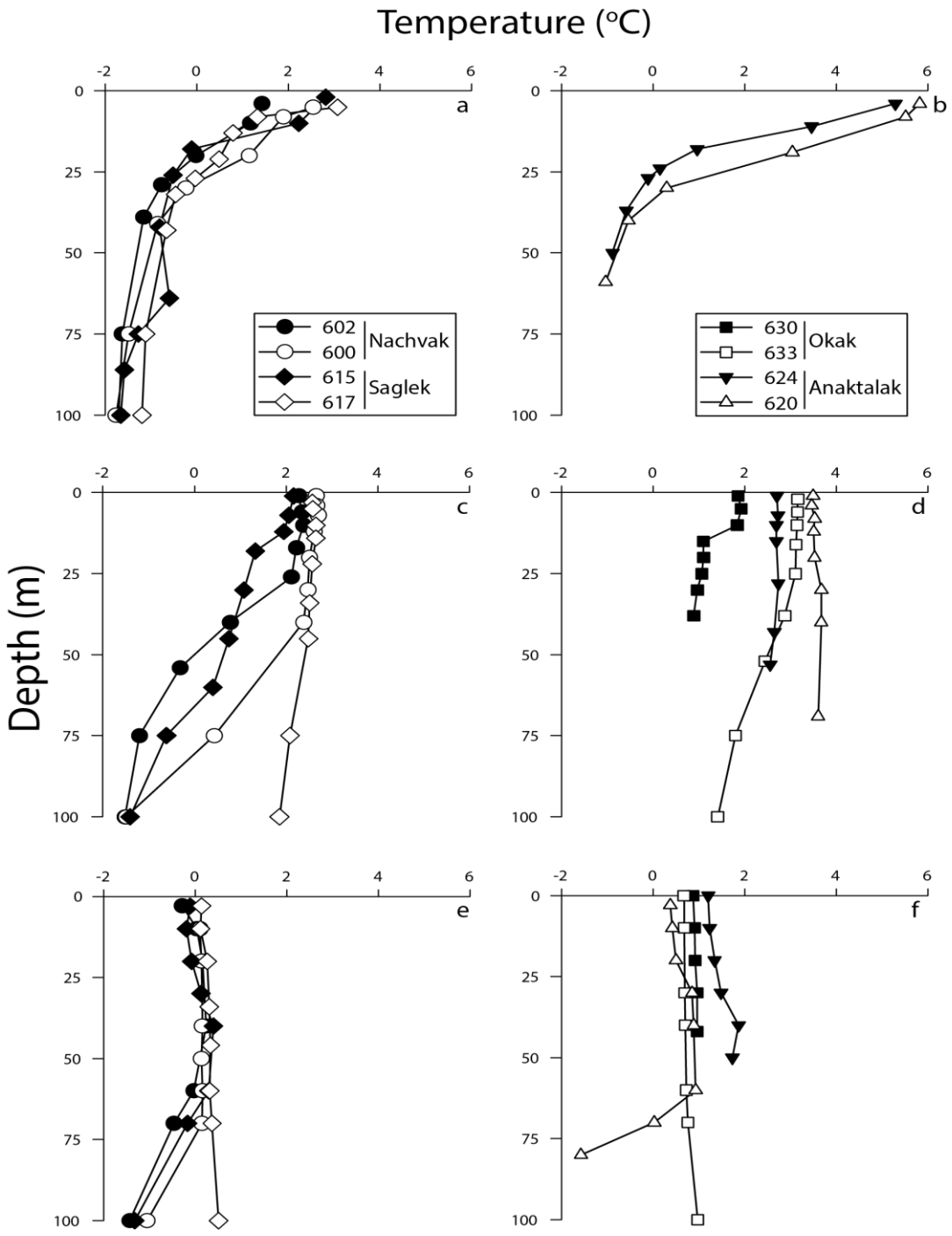

Fig. S1. Temperature profiles for Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during (a, b) summer, (c, d) early fall and (e, f) late fall. Black symbols represent the inner stations and white symbols the outer stations

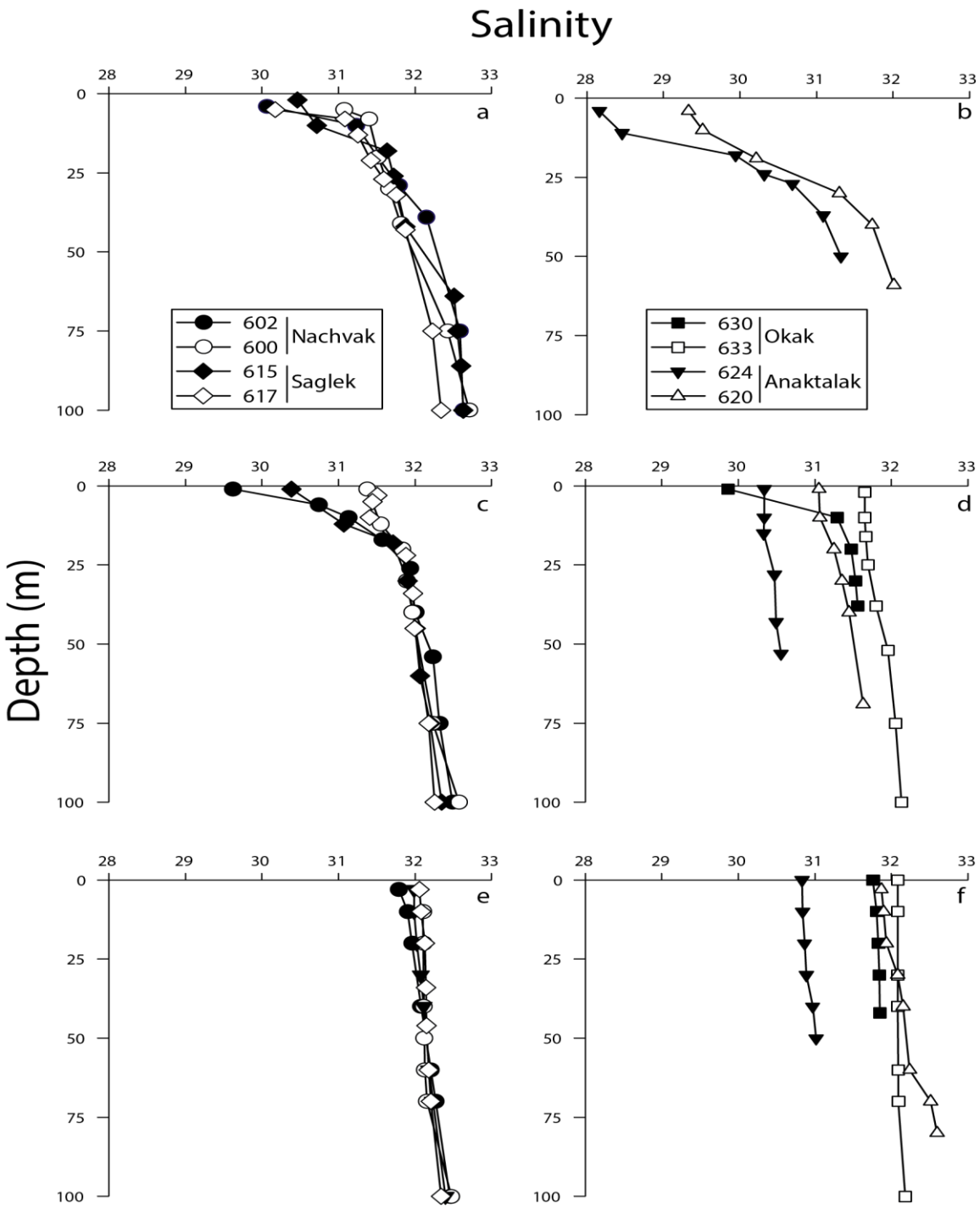

Fig. S2. Salinity profiles for Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during (a, b) summer, (c, d) early fall and (e, f) late fall. Black symbols represent the inner stations and white symbols the outer stations

CHAPITRE 2

RÉPARTITION DU PHYTOPLANCTON EN RELATION AVEC LES VARIABLES ENVIRONNEMENTALES PENDANT L'ÉTÉ ET L'AUTOMNE DANS LES FJORDS DU LABRADOR, NORD-EST DU CANADA, AVEC UNE PARENTHÈSE SUR *PHAEOCYSTIS POUCHETII*

Ce deuxième article scientifique, intitulé « Summer and fall distribution of phytoplankton in relation to environmental variables in Labrador fjords, northeastern Canada, with a wink to *Phaeocystis pouchetii* » a été corédigé par moi-même, le professeur Michel Gosselin, le chercheur Michel Poulin, le chercheur postdoctoral Mathieu Ardyna et la taxonomiste Sylvie Lessard. Il sera bientôt soumis à la revue *Marine Ecology Progress Series*.

En tant que premier auteur, j'ai effectué la description détaillée de la composition taxonomique des protistes, de même que la rédaction de l'article. J'ai également participé aux sorties en mer et au traitement statistique des résultats. Michel Gosselin et Michel Poulin ont fourni l'idée originale et grandement contribué à la révision de l'article. Mathieu Ardyna a apporté son aide pour les analyses statistiques et la révision de l'article.

Les résultats de cet article ont été présentés à plusieurs conférences nationales : l'assemblée annuelle de Québec-Océan en novembre 2013 à Rivière-du-Loup, le congrès annuel de la Société canadienne de météorologie et d'océanographie (SCMO) en juin 2014 à Rimouski et la réunion annuelle d'ArcticNet en décembre 2014 à Ottawa.

RÉSUMÉ

La composition taxonomique des protistes (>2 μm) a été analysée pour la toute première fois dans quatre fjords du Labrador (Nachvak, Saglek, Okak et Anaktalak) pendant les étés 2007 et 2013, le début de l'automne et la fin de l'automne. L'identification et le dénombrement des cellules ont été réalisés dans les couches de surface (50% de lumière de surface) et de fond (15% à 1% de lumière de surface) de la zone euphotique par microscopie inversée. L'analyse de redondance basée sur la distance et la procédure Bio-Env ont été utilisées pour analyser les relations entre la composition taxonomique et les variables environnementales. Le cadrage multidimensionnel non-métrique a révélé que la composition taxonomique des protistes était significativement différente d'une saison à l'autre. La composition des protistes a présenté des différences spatiales significatives uniquement à l'été 2013. Pendant l'été 2007, la communauté était caractérisée par les diatomées et un assemblage mixte de flagellés. Pendant l'été 2013, les flagellés ont largement dominé la communauté et un bloom intense de *Phaeocystis pouchetii* a été observé dans le fjord de Nachvak (jusqu'à 18×10^6 cellules l^{-1}). Dans les eaux automnales mélangées, peu éclairées et enrichies en nutriments, la communauté a été dominée par les flagellés non identifiés, les prymnesiophytes et les diatomées, en proportions variables du début de l'automne à la fin de l'automne. Les principales variables environnementales contrôlant les différences saisonnières dans la composition taxonomique des protistes étaient différentes de l'été à la fin de l'automne. La salinité était la plus récurrente des variables explicatrices de la communauté de protistes pendant toute la période d'étude, suivie par l'intensité de la stratification verticale. La lumière *in situ* et la température de l'eau ont eu une influence importante seulement pendant l'été 2013 et le début de l'automne, respectivement. La profondeur de la couche de mélange a été la seule variable expliquant la communauté à la fin de l'automne. En combinant nos observations à celles de la littérature, nous avons été capables de suggérer la succession annuelle suivante dans la communauté phytoplanctonique des fjords du Labrador : (hiver) dinoflagellés et autres flagellés ─ (printemps) *Fragilariopsis* spp., *Chaetoceros* spp., *Thalassiosira* spp. et *Phaeocystis pouchetii* ─ (été) *Chaetoceros* spp., *P. pouchetii* et *Chrysochromulina* spp. ─ (automne) flagellés, *Gymnodinium/Gyrodinium* spp. et *Chrysochromulina* spp. Nous avons également présenté la toute première liste de protistes planctoniques identifiés dans les fjords du Labrador. Dans l'ensemble, la richesse des protistes a été deux fois plus élevée à l'automne qu'à l'été, la richesse la plus forte étant observée au début de l'automne avec 201 taxons, 72 genres et 131 espèces identifiés.

Mots-clés : Composition taxonomique, protistes, phytoplancton, diatomées, *Phaeocystis*, variabilité saisonnière, Nord-Est du Canada, Labrador, fjords

SUMMER AND FALL DISTRIBUTION OF PHYTOPLANKTON IN RELATION TO ENVIRONMENTAL VARIABLES IN LABRADOR FJORDS, NORTHEASTERN CANADA, WITH A WINK TO *PHAEOCYSTIS POUCHETII*

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ABSTRACT

Protist (>2 μm) taxonomic composition was investigated for the very first time in four Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during summers 2007 and 2013, early fall and late fall. Cell identification and enumeration were conducted at the surface (50% of surface irradiance) and bottom (15% to 1% of surface irradiance) layers of the euphotic zone using inverted microscopy. Distance-based redundancy analysis and Bio-Env procedure were used to analyze relationships between community composition and environmental variables. Non-metric multidimensional scaling revealed that protist taxonomic 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 (up to 18×10^6 cells l^{-1}). In mixed, low-lit and nutrient-repleted autumn waters, the community was dominated by unidentified flagellates, prymnesiophytes and diatoms, in various proportions from early fall to late fall. 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. By combining our observations with those from the literature, we were able to suggest the following annual succession in Labrador fjord phytoplankton community: (winter) dinoflagellates and other flagellates ─ (spring) *Fragilariopsis* spp., *Chaetoceros* spp., *Thalassiosira* spp. and *Phaeocystis pouchetii* ─ (summer) *Chaetoceros* spp., *P. pouchetii* and *Chrysochromulina* spp. ─ (fall) flagellates, *Gymnodinium/Gyrodinium* spp. and *Chrysochromulina* spp. We also presented the very first list of planktonic protists identified in Labrador fjords. Overall, the protist richness was two 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.

Keywords: Taxonomic composition, protists, phytoplankton, diatoms, *Phaeocystis*, seasonal variability, northeastern Canada, Labrador, fjords

2.1 Introduction

Phytoplankton accounts for <1% of the photosynthetic biomass on Earth, but is nevertheless 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 these processes are critically dependent on phytoplankton taxonomic composition and any change at the base of the marine food web can have 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). Understanding the composition of phytoplankton community and the factors 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 winter darkness period 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 factors, such as water temperature, stratification, nutrient inputs 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 algal cells can be resumed as followed: in winter and early spring, polar night and sea-ice thickness prevent any photosynthetic activity and the community is dominated by nano-sized (<20 µm) heterotrophic protists (Sherr et al. 2003, Terrado et al. 2008). Under these unfavorable conditions, some diatoms and dinoflagellates produce resting spores or cysts (Różańska et al. 2008) or become dormant in darkness conditions (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 plenty of nutrients due to previous winter mixing (and regeneration), the algal community is not much 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 nitracline (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). In late summer and early fall, the decrease in water column stratification by surface cooling and wind mixing favors the supply of the surface waters in nutrients. 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* written 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 two 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's niches are 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 organic matter cycling, the diversity of these crucial microorganisms has never, to the best of our knowledge, been studied in the fjords along the Labrador coast, Canada. The objectives of our study were (1) to describe the detailed taxonomic composition of phytoplankton in four Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during the transition from summer to fall, and (2) to assess the influence of environmental factors on their variability. Understanding the factors that control species composition and dynamics is fundamentally important for a better prediction of the impact of environmental changes on marine ecosystems.

2.2 Materials and methods

2.2.1 Study area

The study region is located in Nunatsiavut (meaning "Our Beautiful Land") in northern Labrador (Fig. 1). This vast region is on the eastern seaboard of Canada and extends between 56°N and 60°N, along the Labrador Sea. Since 2007, several oceanographic campaigns have been conducted along the Labrador coast, especially in four

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 four successive basins separated by sills composed of bedrock or glacial deposits. The duration of the sea-ice cover is 6.6 months yr^{-1} in Nachvak and 6.3 to 6.4 months yr^{-1} in the other fjords (Brown et al. 2012), lasting from about mid-December to mid-July. Nachvak is a pristine fjord, considered as a reference site to assess natural climatic and environmental variability of Nunatsiavut fjord ecosystems.

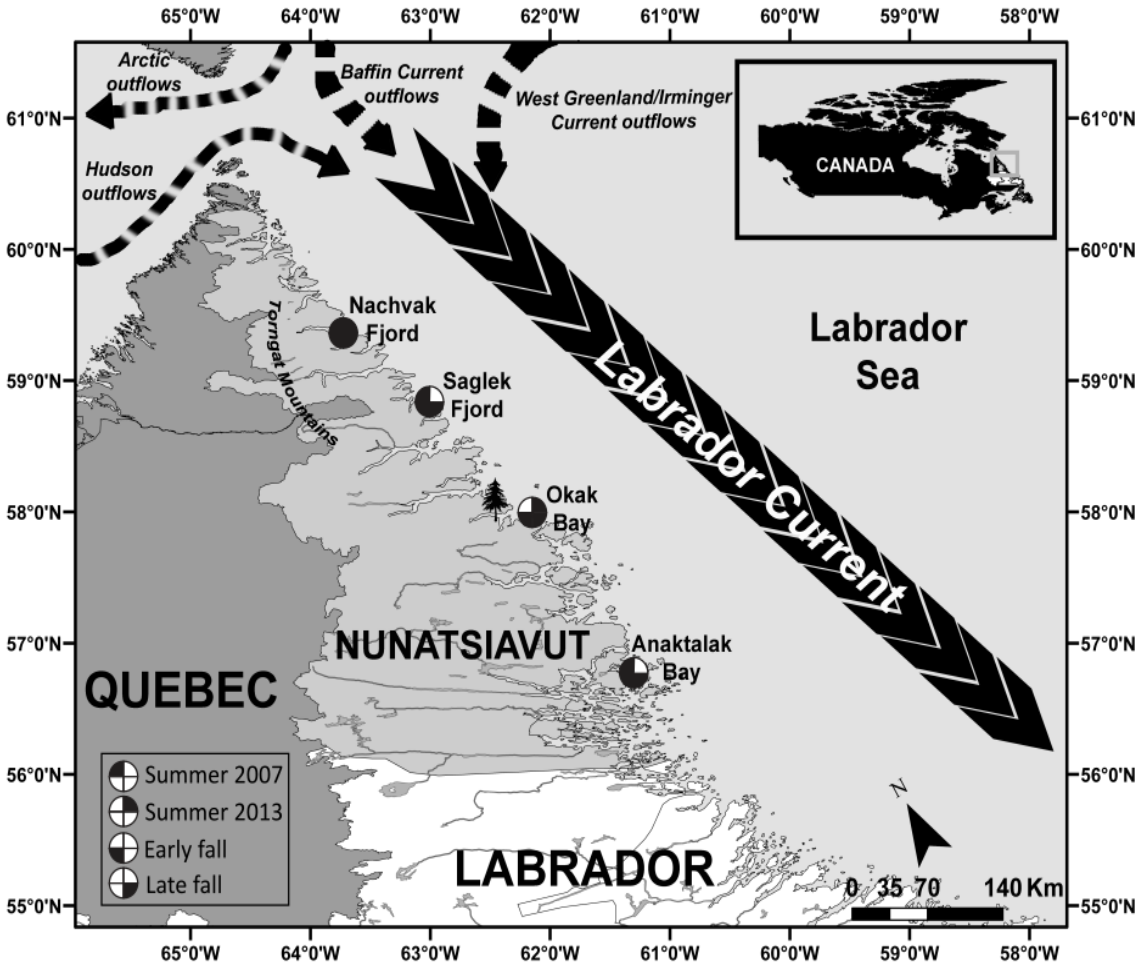


Fig. 1. Sampling periods and location of Nachvak Fjord, Saglek Fjord, Okak Bay and Anaktalak Bay in Nunatsiavut, northern Labrador (adapted from Richerol et al. 2012)

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

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. 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. Anaktalak Bay is the southernmost site of 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).

For the sake of simplicity, Okak and Anaktalak bays will be considered, from here on, as typical fjords, just as Nachvak and Saglek fjords. 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°N and 58°N, south of the tree line and within the Subarctic ecoregion. In contrast to Nachvak and Okak fjords, Saglek and Anaktalak fjords are directly influenced by industrial and modern-day human activities.

2.2.2 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*. Hereafter, these sampling periods are referred to as summer 2007, summer 2013, early fall and late fall, respectively; November 2009 being the period with the lowest water temperature and *in situ* irradiance (Tables 2 & 3). The monthly averaged precipitation measured at Nain Airport in Labrador in July 2013 (4.0 ± 5.7 mm) was three times higher than in July 2007 (1.3 ± 1.4 mm) (http://climat.meteo.gc.ca,

assessed on 31 May 2016). Table 1 presents the samples collected in the fjords during each season.

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° 4.5’	63° 25.5’	158	Surface	NIS
						Bottom	NIB
	600	Outer	59° 2.6’	63° 52.5’	207	Surface	NOS
						Bottom	NOB
Saglek	615	Inner	58° 16.4’	63° 31.5’	130	Surface	SIS
						Bottom	SIB
	617	Outer	58° 30’	62° 41.3’	139	Surface	SOS
						Bottom	SOB
Okak	630	Inner	57° 36’	61° 53.3’	51	Surface	OIS
						Bottom	OIB
	633	Outer	57° 28.1’	62° 27’	178	Surface	OOS
						Bottom	OOB
Anaktalak	624	Inner	56° 23.6’	61° 12.4’	71	Surface	AIS
						Bottom	AIB
	620	Outer	56° 24.4’	62° 4.1’	96	Surface	AOS
						Bottom	AOB

Sampling was carried out at two stations (inner and outer) in each fjord. At each station, downwelling photosynthetically active radiation (PAR, 400-700 nm) underwater profile was performed 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 two depths (50% and 15 to 1% of surface irradiance). For

simplicity, these two depths are hereafter respectively referred to as the surface and the bottom layers 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).

2.2.3 Laboratory analyses

Nutrients

Triplicate samples for dissolved inorganic nutrients were filtered through Whatman GF/F glass-fiber filters (nominal pore size of 0.7 μm) and the filtrate was collected in 15-ml acid-washed polyethylene tubes. Nutrient samples were directly analyzed or stored in a -80°C freezer for later analyses of nitrate plus nitrite (NO_3+NO_2), nitrite (NO_2), phosphate (PO_4) and silicic acid ($Si(OH)_4$) concentrations using a Bran-Luebbe 3 autoanalyzer (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).

Light microscopy analysis

Samples for the identification and enumeration of protist cells >2 μm were preserved in acidic Lugol's solution (Parsons et al. 1984) and 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 Lund et al. (1958). For each sample, a minimum of 400 cells (accuracy ± 10%) and three transects of 20 mm were counted 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).

2.2.4 Calculations

The strength of the vertical stratification was estimated using two different indices: (1) the difference in density (σ_t) between 80 m (or the last sampled depth in <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 analysis. The surface mixed layer (Z_m) was defined as the depth where the vertical gradient in density (σ_t) between two successive depths is >0.03 kg m^{-4} (threshold gradient method: Thomson & Fine 2003, Tremblay et al. 2009). The nitracline depth (Z_{nut}) was estimated to be where the vertical gradient of NO_3 concentration (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):

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

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

2.2.5 Statistical analyses

A four-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 mean (Tukey's honesty 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 two 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 non-metric 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 two 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 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 (one-way ANOSIM) was also performed on the Bray-Curtis similarity matrix to test whether the spatial and seasonal differences in taxonomic composition were significant or not. 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 two 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 five high correlations between environmental variables: between water temperature and salinity ($r = -0.86$) in summer 2007; between nitracline 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; 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 the Akaike's information criterion (AIC). The distance-based redundancy analysis plot (dbRDA, Anderson et al. 2008) from the DistLM analysis was used to visualize the final model. Four dbRDA 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 determine using multiple partial correlations (r_p). These ordinations were carried out using PRIMER v6 and PERMANOVA+ software (Clarke & Gorley 2006).

2.3 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 significantly different between fjords, stations, sampled depths and seasons. All other environmental variables were significantly different between the 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.

Table 2. Environmental conditions of the upper water column and 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}: nitracline 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 (mmol m^{-3})	$Si(OH)_4$ (mmol m^{-3})	PO_4 (mmol m^{-3})	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

Table 3. Environmental conditions 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. 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	T (°C)	S	E_z (mol quanta m^{-2} d^{-1})	NO_3+NO_2 (mmol m^{-3})	$Si(OH)_4$ (mmol m^{-3})	PO_4 (mmol m^{-3})	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

2.3.1 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 at the two southernmost fjords (i.e. Okak and Anaktalak, Table 2). The surface layer of the euphotic zone (Z_{eu}) was warmer and less salty than the bottom one (Fig. 2, Table 4). $\Delta\sigma_t$ was higher in both summers compared to early fall 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, six times higher in the surface layer than in the bottom layer of Z_{eu} (Fig. 2, Tables 2 & 3). Due to the seasonal day length differences in polar ecosystems, E_z was higher during summer than in early fall and late fall (Fig. 2, Tables 2 & 3). In the four 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 ($r = 0.46$, $p < 0.001$).

Table 4. Summary of the analysis of variance (ANOVA) and subsequent tests for environmental and biological variables measured at the inner and outer stations of 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. ns: not significant. For *a posteriori* multiple comparison Tukey's HSD test and Student's *t*-test: A > B > C

	Four-way ANOVA				Tukey test or Student test ($\alpha \leq 0.05$)											
	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 (^{o}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 (mmol m^{-3})	<0.001	ns	<0.05	<0.0001	A	B	B	B			B	A	C	C	B	A
$Si(OH)_4$ (mmol m^{-3})	ns	<0.05	ns	<0.0001					A	B			B	A	A	A
PO_4 (mmol m^{-3})	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

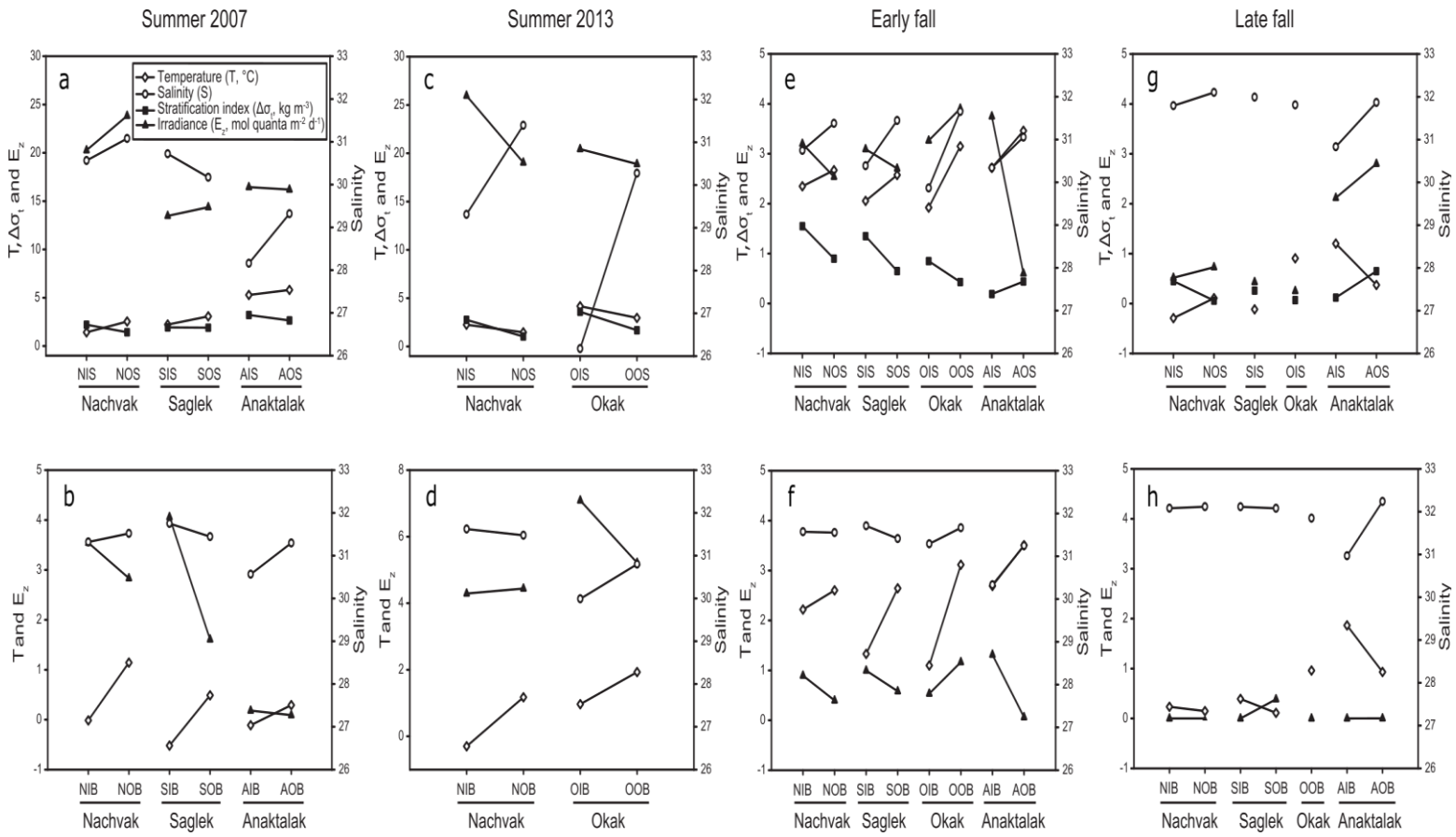


Fig. 2. Variations of water temperature (T), salinity (S) and *in situ* irradiance (E_z) at the surface (top row) and bottom (bottom row) layers of the euphotic zone in Nachvak, Saglek, Okak and Anaktalak fjords during (a, b) summer 2007, (c, d) summer 2013, (e, f) early fall and (g, h) late fall. Variations 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-axis

2.3.2 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 two 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 fjords. $Si(OH)_4$ and PO_4 concentrations showed similar variations to that of NO_3+NO_2. But in summer 2007, in contrast to NO_3+NO_2 and $Si(OH)_4$, PO_4 was never exhausted 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 mmol m^{-3} 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 was attributed to three 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, Tables 2 & 3). In the four fjords and for the whole sampling period, NO_3+NO_2 at both depths was positively correlated with Z_m ($r = 0.54$, $p < 0.0001$) and salinity ($r = 0.53$, $p < 0.0001$), and negatively correlated with $\Delta\sigma_t$ ($r = -0.63$, $p < 0.0001$), E_z ($r = -0.58$, $p < 0.0001$), water temperature ($r = -0.42$, $p < 0.01$) and Z_{eu} ($r = -0.33$, $p < 0.05$). $Si(OH)_4$ was correlated only with Z_{eu} ($r = -0.52$, $p < 0.0001$). PO_4 was significantly correlated with all physical variables, except Z_{eu} and Z_{nut}.

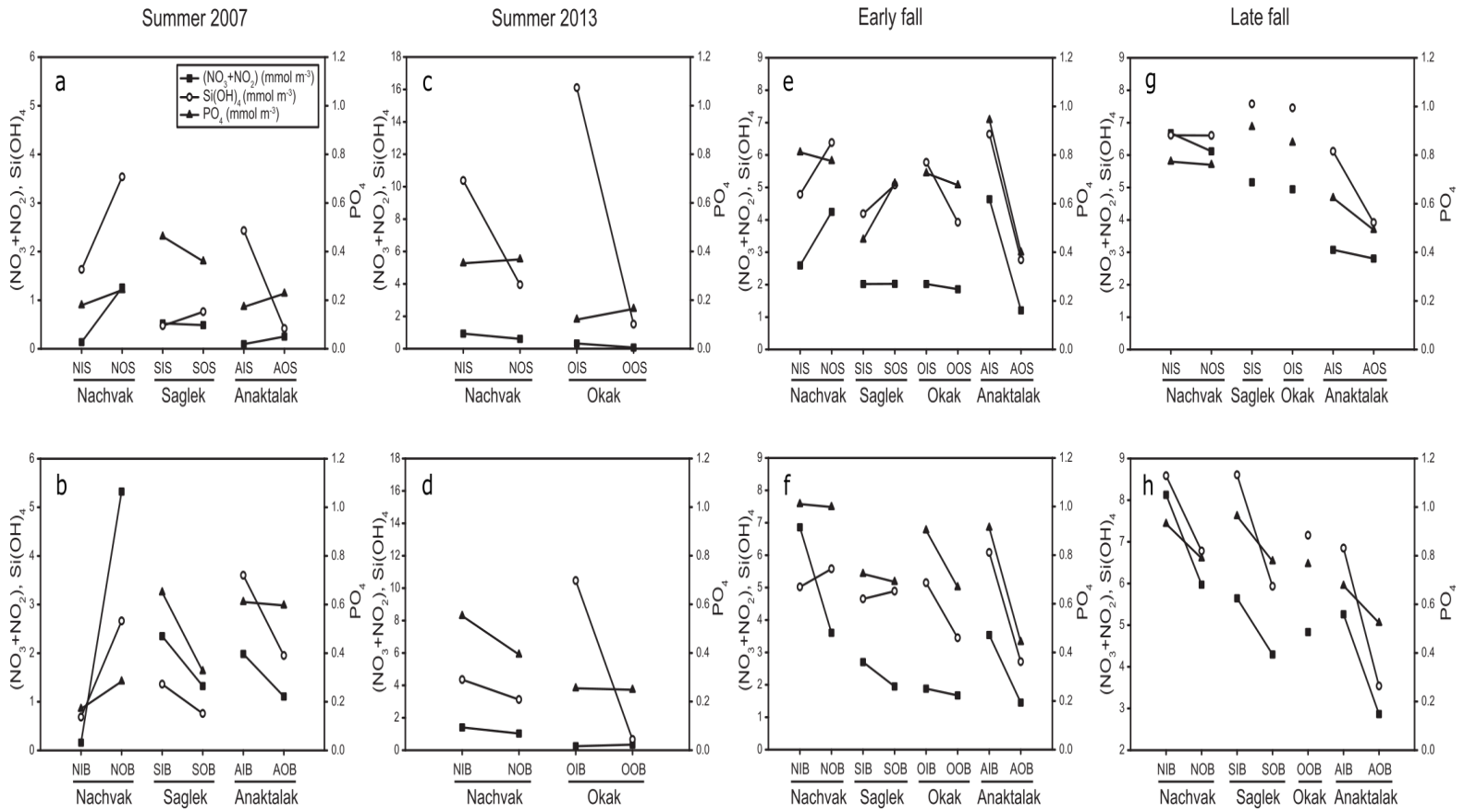


Fig. 3. Variations of nitrate plus nitrite (NO_3+NO_2), silicic acid ($Si(OH)_4$) and phosphate (PO_4) concentrations at the surface (top row) and bottom (bottom row) layers of the euphotic zone in Nachvak, Saglek, Okak and Anaktalak fjords during (a, b) summer 2007, (c, d) summer 2013, (e, f) early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

2.3.3 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 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 Appendix 1. Among the fjords, the highest (200) and lowest (163) number of taxonomic entries was recorded in Nachvak and Okak, respectively (Appendix 1). 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 was recorded during early fall and summer 2007, respectively (Appendix 1). A total number of 131 species were reported for the whole sampling period, whereas the number of species, genera and taxonomic entries was two times higher in fall than in summer.

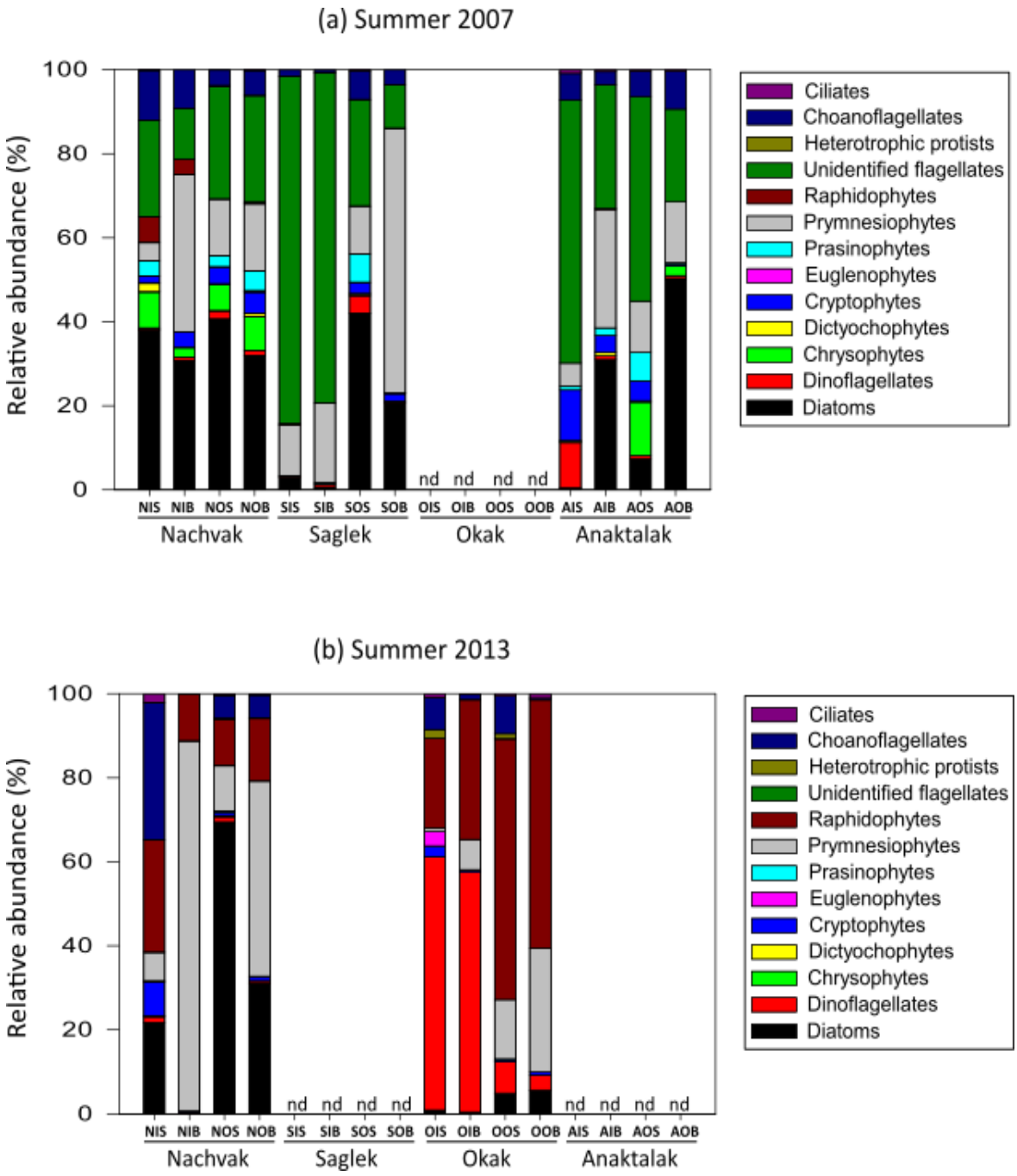
The taxonomic composition of the four fjord phytoplankton communities showed clear seasonal differences (Fig. 4). Spatial variations between fjords, stations and depths were less marked (Fig. 4). During summer 2007, the protist community was numerically dominated by diatoms and a mixed assemblage of flagellated cells (Fig. 4a). The numerically dominant taxa (and their mean abundances) were the centric diatoms *Chaetoceros socialis* Lauder (210×10^3 cells l^{-1}) and *C. tenuissimus* Meunier (93×10^3 cells l^{-1}), the prymnesiophytes *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 (Appendix 1). Maximum abundances of *C. socialis* (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 (Table 6, Figs. 4b & 5). An intense bloom of *P. pouchetii* (up to 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 inner Nachvak sample, *Chaetoceros* spp. (≤20 µm) was the most abundant diatom, but its abundance did not exceed 3000 cells l^{-1}. In the outer Nachvak sample, *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 fall 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 non significant) 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*, *Amphidinium* 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 μm) and *Amphidinium* 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).


(a) Summer 2007
Relative abundance (%)
100
80
60
40
20
0
nd nd nd nd
NIS NIB NOS NOB SIS SIB SOS SOB OIS OIB OOS OOB AIS AIB AOS AOB
Nachvak
Saglek
Okak
Anaktalak
Ciliates
Choanoflagellates
Heterotrophic protists
Unidentified flagellates
Raphidophytes
Prymnesiophytes
Prasinophytes
Euglenophytes
Cryptophytes
Dictyochophytes
Chrysophytes
Dinoflagellates
Diatoms
(b) Summer 2013
Relative abundance (%)
100
80
60
40
20
0
nd nd nd nd nd nd nd nd
NIS NIB NOS NOB SIS SIB SOS SOB OIS OIB OOS OOB AIS AIB AOS AOB
Nachvak
Saglek
Okak
Anaktalak
Ciliates
Choanoflagellates
Heterotrophic protists
Unidentified flagellates
Raphidophytes
Prymnesiophytes
Prasinophytes
Euglenophytes
Cryptophytes
Dictyochophytes
Chrysophytes
Dinoflagellates
Diatoms

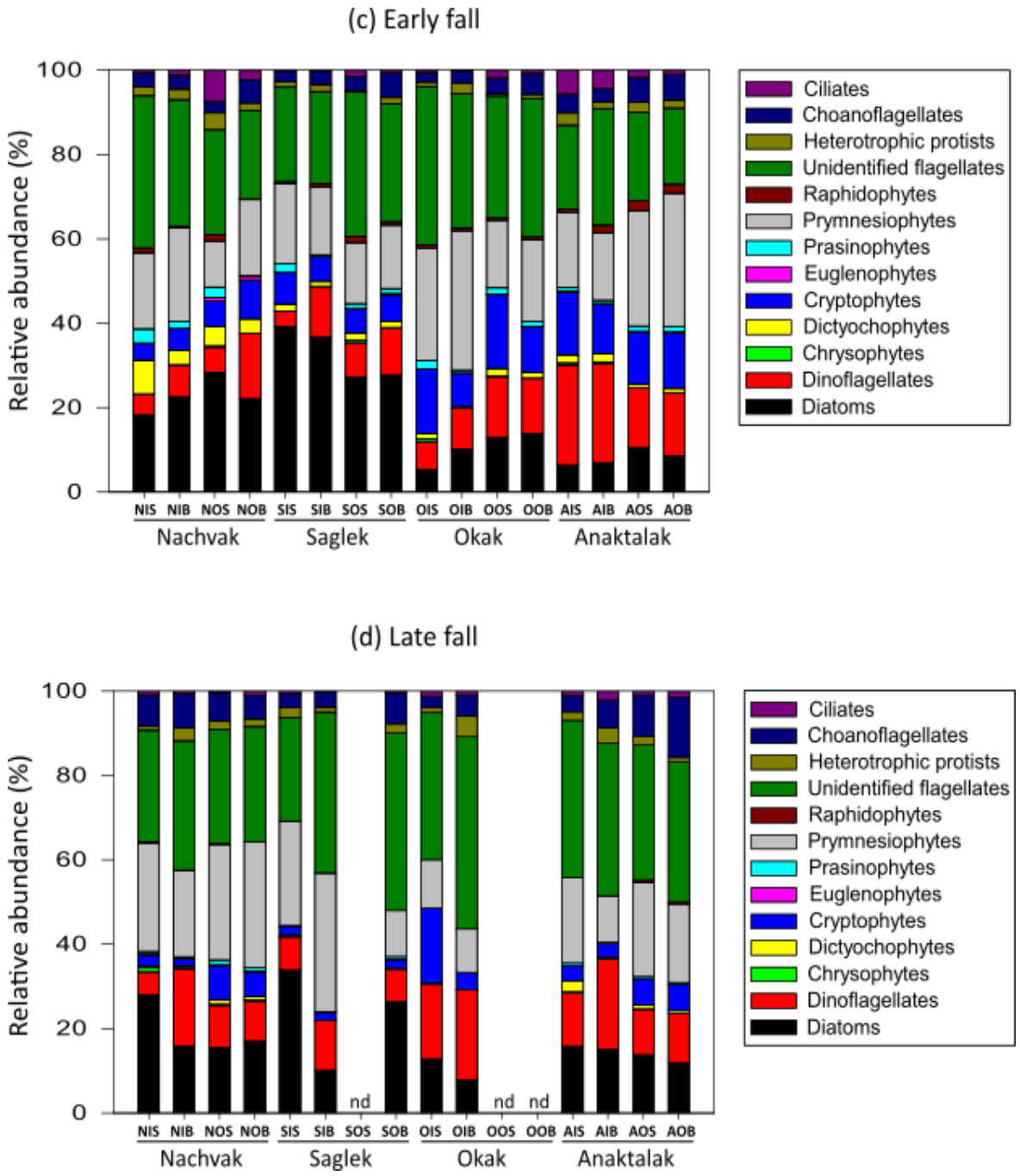


Fig. 4. Variations in the relative abundance of protist groups at the surface and bottom layers of the euphotic zone in Nachvak, Saglek, Okak and Anaktalak fjords during (a) summer 2007, (b) summer 2013, (c) early fall and (d) late fall. Codes for the samples are listed in Table 1. nd means no data available

Many protist taxonomic groups showed significant correlations with environmental variables (Table 5). During summer 2007, dinoflagellates and chrysophytes were negatively correlated with salinity and Z_{nut}, respectively (Table 5a). Cryptophytes were negatively linked to Z_{eu}, salinity and PO_4 while prymnesiophytes were related only to E_z. Unidentified flagellates and choanoflagellates were both correlated with Z_{eu} whereas ciliates were positively correlated with water temperature and E_z, and negatively with Z_{eu} and salinity (Table 5a). Of particular interest because of its numerical dominance in the bottom layer of Z_{eu} during both summers, particularly in 2013, the prymnesiophyte *P. pouchetii* showed significant correlations with abiotic factors only during summer 2007. It was positively correlated with Z_m ($r = 0.89$, $p < 0.05$), water temperature ($r = 0.87$, $p < 0.05$) and NO_3+NO_2 ($r = 0.86$, $p < 0.05$). No other significant correlation was found. During summer 2013, diatoms were significantly correlated with Z_m and $\Delta\sigma_t$ while dinoflagellates were related to $\Delta\sigma_t$, salinity and $Si(OH)_4$ (Table 5b). Chrysophytes and choanoflagellates were both positively linked to E_z. Euglenophytes were related to water temperature, salinity and $Si(OH)_4$. Prymnesiophytes and heterotrophic protists were correlated with water temperature, salinity and PO_4, the former also correlated with E_z. Unidentified flagellates were negatively linked to NO_3+NO_2 (Table 5b). During early fall, diatoms were significantly correlated with $\Delta\sigma_t$ (Table 5c). Dinoflagellates and cryptophytes were related to Z_m and $\Delta\sigma_t$. Chrysophytes were linked to salinity and E_z while choanoflagellates were related to water temperature and E_z. Euglenophytes, prasinophytes and unidentified flagellates were correlated with water temperature, E_z and Z_{nut}, respectively (Table 5c). During late fall, more significant correlations were obtained and only chrysophytes, cryptophytes and heterotrophic protists did not show significant links with environmental factors (Table 5d).

Table 5. Pearson's correlation coefficients between the abundance of protist taxonomic groups and environmental variables in Nachvak, Saglek, Okak and Anaktalak fjords during (a) summer 2007, (b) summer 2013, (c) early fall and (d) late fall. 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. Empty cells: correlation not significant. 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

(a) Summer 2007

	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*	

(b) 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*

(c) Early fall

	Z_m	Z_{nut}	$\Delta\sigma_t$	T	S	Ez
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*

(d) 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*

2.3.4 Variability in protist taxa

In the euphotic zone, five groups of samples with taxonomically similar protists were assessed with the group-average cluster analysis superposed to the MDS (Fig. 5). The global one-way ANOSIM test revealed significant differences between the four 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 prymnesiophyte *Chrysochromulina* spp. (≤5 µm), unidentified Choanoflagellidea (≤5 µm) and the centric diatom *C. socialis* (Table 6).

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 unidentified 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 6).

Group III was composed of all samples collected in Okak Fjord in summer 2013 and was dominated by raphidophytes (43.9%) and dinoflagellates (32.1%). The average similarity between the samples was of 46.4%, and unidentified flagellates (≤10 µm) and the dinoflagellate *H. rotundata* were the main taxa contributing to this group (Table 6).

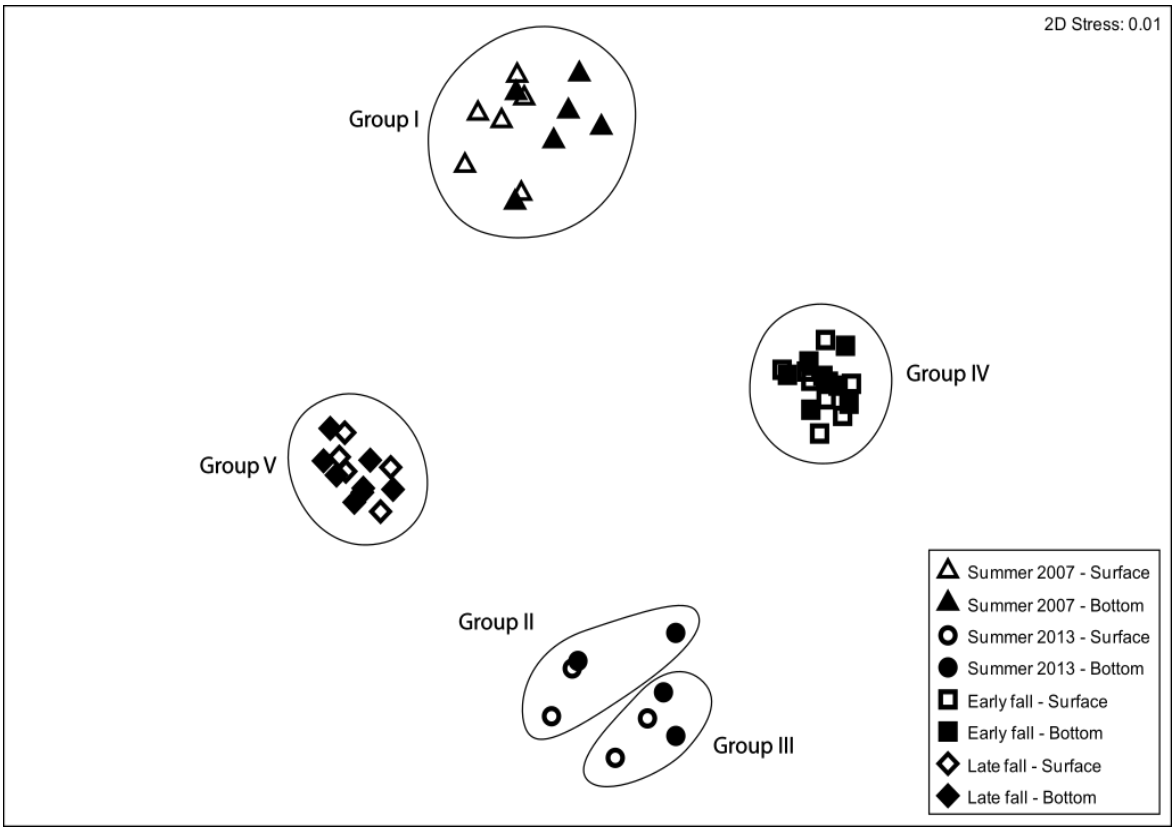


Fig. 5. Non-metric multidimensional scaling (MDS) of the 49 samples collected in Nachvak, Saglek, Okak and Anaktalak fjords during summer 2007 (triangles), summer 2013 (circles), early fall (squares) and late fall (diamonds). Open symbols and closed symbols represent samples taken at the surface and 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 superimposed on the MDS

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 of 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 6).

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 of 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 *Amphidinium* cf. *kesslitzii*, and the diatom *Chaetoceros* spp. (≤20 µm) were the main taxa explaining this group (Table 6).

Table 6. 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%

Group	Average similarity (%)	Main taxa	Contribution (%)
Group I (Summer 2007)	42.4	Unidentified flagellates (≤5 µm)	42.9
		Chrysochromulina spp. (≤5 µm)	10.9
		Unidentified flagellates (6-10 µm)	8.4
		Unidentified Choanoflagellidea (≤5 µm)	6.2
		Chaetoceros socialis	4.2
Group II (Nachvak, Summer 2013)	21.7	Unidentified flagellates (≤5 µm)	23.9
		Phaeocystis pouchetii	19.2
		Detonula confervacea	16.4
		Chaetoceros spp. (≤5 µm)	6.8
		Unidentified Choanoflagellidea (≤5 µm)	5.3
Group III (Okak, Summer 2013)	46.4	Unidentified flagellates (≤5 µm)	47.5
		Heterocapsa rotundata	17.9
		Unidentified flagellates (6-10 µm)	13.4
Group IV (Early fall)	52.1	Unidentified 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
		Unidentified flagellates (6-10 µm)	3.8
		Heterocapsa rotundata	3.3
		Unidentified Prymnesiophyceae (≤5 µm)	3.1
Group V (Late fall)	57.3	Unidentified flagellates (≤5 µm)	34.7
		Chrysochromulina spp. (≤5 µm)	10.9
		Gymnodinium/Gyrodinium spp. (≤20 µm)	8.5
		Unidentified flagellates (6-10 µm)	5.8
		Unidentified Prymnesiophyceae (≤5 µm)	4.9
		Amphidinium cf. *kesslitzii*	3.1
		Chaetoceros spp. (≤20 µm)	3.0

2.3.5 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 two axes of the dbRDA explained 82.0% of the fitted variation (Fig. 6a). The first axis (dbRDA1) explained 55.2% of this variation and it 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 shallow euphotic zone and nitracline whereas unidentified flagellates were more numerous in waters with 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 to less-salty, warm, stratified and well-lit waters. The other protist groups were linked to warm, well-lit, PO_4-depleted waters. The Bio-Env analysis identified salinity and euphotic zone depth, whose combined explain 70% of the variability in protist groups during summer 2007.

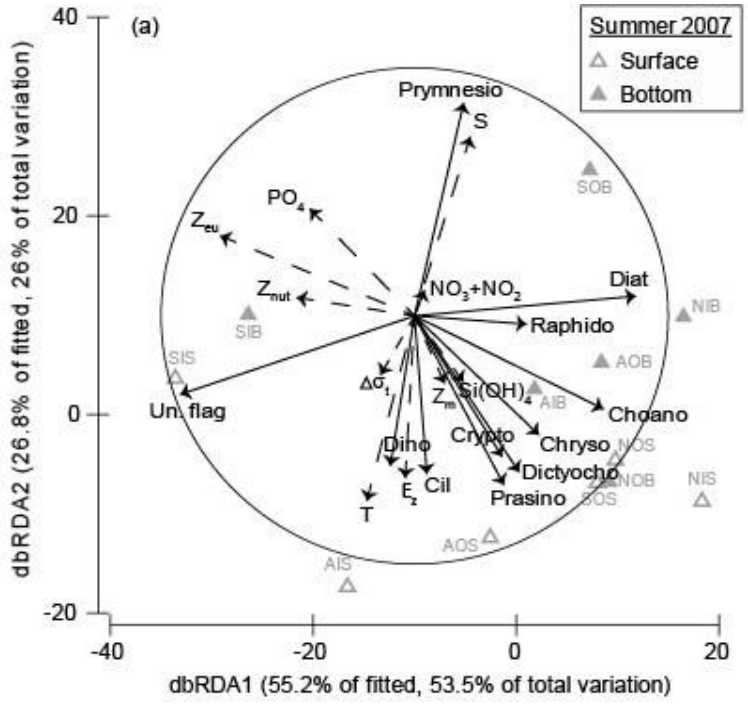
During summer 2013, the first two axes of the dbRDA explained 78.2% of the fitted variation (Fig. 6b). The first axis (dbRDA1) explained 48.7% of this variation and was strongly correlated with $Si(OH)_4$ (r_p = 0.52), PO_4 (r_p = -0.50) and NO_3+NO_2 (r_p = -0.50). The second axis (dbRDA2) explained 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; Nachvak having colder and saltier waters, deeper surface mixed layer and nitracline, 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

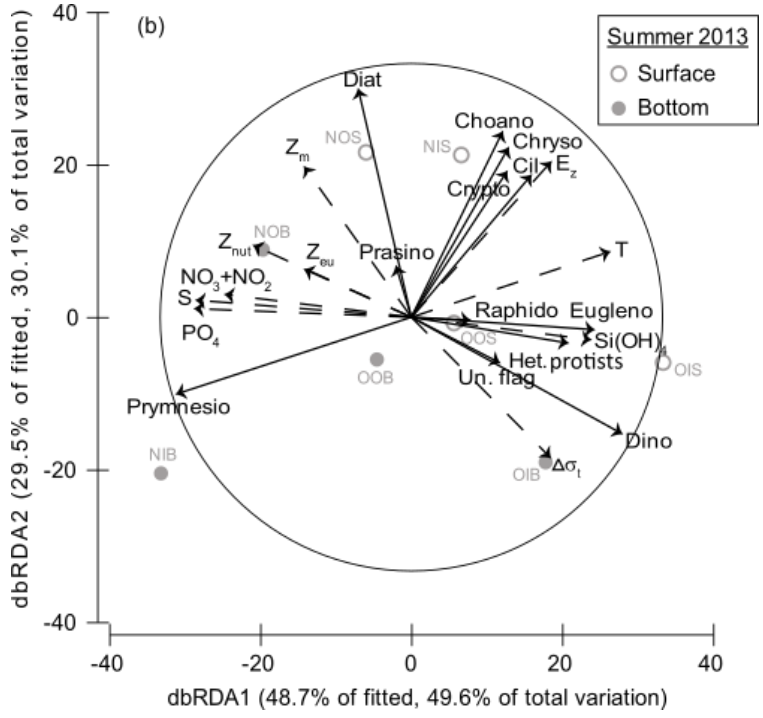
layer whereas prymnesiophytes were associated with colder, more saline and NO_3+NO_2- and PO_4-rich waters. In contrast, dinoflagellates and unidentified flagellates were more abundant in well-stratified waters with shallow nitracline and surface mixed layer. Euglenophytes and heterotrophic protists were associated with warm, $Si(OH)_4$-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 five environmental variables: salinity, stratification index, *in situ* irradiance, PO_4 and NO_3+NO_2 which, when combined, explain 80% of the summer 2013 community.

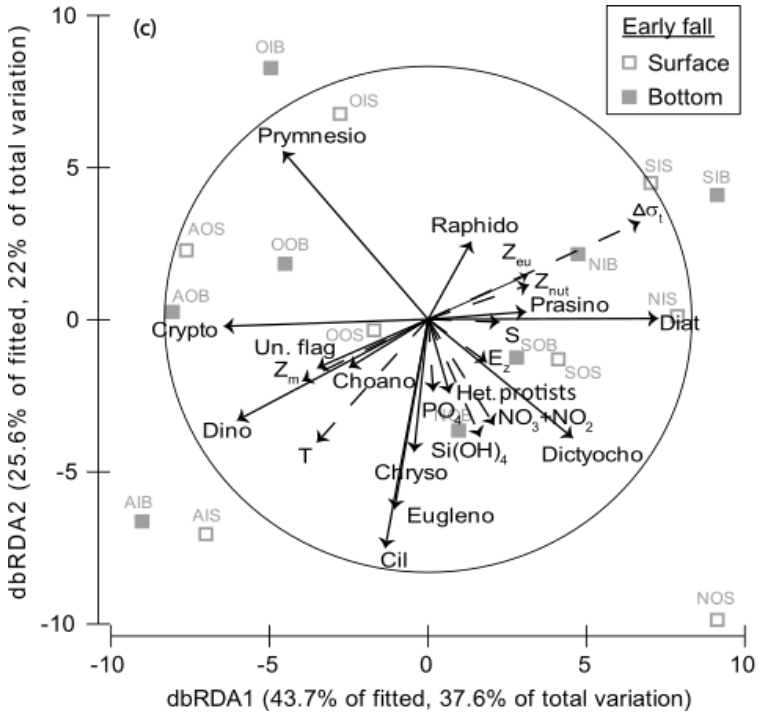
For early fall, the first two axes of the dbRDA explained 69.3% of the fitted variation (Fig. 6c). The first axis (dbRDA1) explained 43.7% of this variation and was highly correlated with the stratification index (r_p = 0.68). Water temperature (r_p = -0.64) and $Si(OH)_4$ (r_p = -0.61) were strongly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

In late fall, the first two 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 layer. The other protist groups (i.e., raphidophytes, choanoflagellates, cryptophytes, dictyochophytes and ciliates) were more abundant in well-stratified waters with deep nitracline 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 it was combined with other environmental variables, the percentage of variation explained decreased.


(a)
Summer 2007
Surface
Bottom
Prymnesio
S
PO4
Zeu
Znut
NO3+NO2
Diat
Raphido
Un. flag
Δσt
Zm
Si(OH)4
Choano
Crypto
Chryso
Dictyocho
Dino
Cil
Ez
Prasino
T
SOB
NIB
SIB
SIS
AOB
AIB
NOS
NOB
NIS
SOS
AOS
AIS
dbRDA2 (26.8% of fitted, 26% of total variation)
dbRDA1 (55.2% of fitted, 53.5% of total variation)


(b)
Summer 2013
Surface
Bottom
Diat
Choano
Chryso
Cil
Ez
Crypto
Zm
NOS
NIS
Znut
NOB
Zeu
Prasino
T
NO3+NO2
S
PO4
Raphido
Eugleno
Si(OH)4
OOS
OIS
Het. protists
Un. flag
OOB
Prymnesio
Dino
NIB
OIB
Δσt
dbRDA2 (29.5% of fitted, 30.1% of total variation)
dbRDA1 (48.7% of fitted, 49.6% of total variation)


(c)
Early fall
Surface
Bottom
OIB
OIS
Prymnesio
SIS
SIB
$\Delta\sigma_t$
Raphido
Z_{eu}
NIB
Z_{nut}
AOS
OOB
AOB
Prasino
NIS
Crypto
Diat
OOS
S
SOB
Un. flag
E_z
Z_m
Choano
SOS
Het. protists
PO_4
NO_3+NO_2
Dino
T
$Si(OH)_4$
Dictyocho
Chryso
AIB
AIS
Eugleno
Cil
NOS
dbRDA2 (25.6% of fitted, 22% of total variation)
dbRDA1 (43.7% of fitted, 37.6% of total variation)
10
5
0
-5
-10

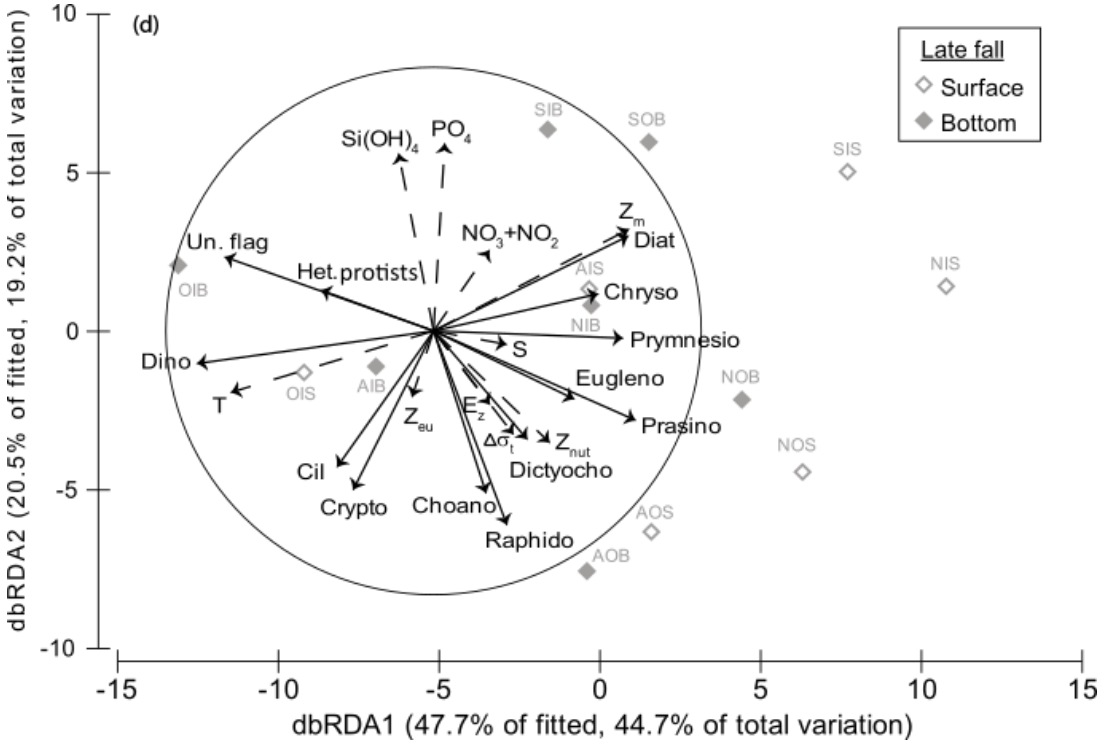

(d)
Late fall
Surface
Bottom
SIB
SOB
SIS
$Si(OH)_4$
PO_4
Z_m
Diat
NO_3+NO_2
Un. flag
NIS
Het. protists
AIS
OIB
Chryso
NIB
Prymnesio
S
Dino
Eugleno
NOB
T
OIS
AIB
E_z
Prasino
Z_{eu}
$\Delta\sigma_t$
Z_{nut}
NOS
Cil
Dictyocho
Crypto
Choano
AOS
Raphido
AOB
dbRDA2 (20.5% of fitted, 19.2% of total variation)
dbRDA1 (47.7% of fitted, 44.7% of total variation)
10
5
0
-5
-10
-15
15

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

2.4 Discussion

This study highlighted a strong seasonality in the environmental variables of the Labrador fjords allowing studying the succession of the phytoplankton communities. Surprisingly, the protist taxonomic composition was not significantly different between the four fjords even if a variability in the abiotic factors is perceptible. However, in summer 2013 characterized by heavy precipitation, Nachvak and Okak fjords showed large taxonomic differences. In addition, differences between fjords could have probably been better observed at the onset of the summer bloom, which has not been possible to achieve during this study.

2.4.1 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 *C. socialis* and *C. tenuissimus*, the prymnesiophytes *Chrysochromulina* spp. (≤5 µm) and *P. pouchetii* and the chrysophyte *D. 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 summer protist community was mainly dominated by unidentified flagellates (37.2%), diatoms (24.8%) and prymnesiophytes (19.8%) (Fig. 4a), indicating a post-bloom intermediate situation between a diatom-based and a flagellate-based system. 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 coming from the glacier melt in the surface waters of the inner part of Nachvak. 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* (up to 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 mmol m^{-3}). In addition, *P. pouchetii* was 15 times less abundant (1.21×10^6 cells l^{-1}) but still representing 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). They follow the retreat of ice caps 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 behavior 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 found to be variable (Throndsen & Heimdal 1976, Eilertsen et al. 1981, Lutter et al. 1989). 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 *C. socialis* were the two dominant taxa during the spring bloom in these fjords. Moreover, Degerlund & Eilertsen (2010) suggested the ability for *P. pouchetii* to grow under silicon-depleted conditions and thus to be abundant throughout the bloom. Although we did not find a significant correlation between *P. pouchetii* abundance and $Si(OH)_4$ concentration during summer, this assertion supports our summer 2007 results showing *P. pouchetii* co-dominating the community at inner Nachvak Fjord where silicic acid was nearly exhausted (0.68 mmol m^{-3}, Table 3).

A maximum of 101 taxonomic entries, 27 genera and 57 species were identified in Labrador fjords during both summers 2007 and 2013 (Appendix 1). 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 two-fold higher than in Kongsfjorden where a maximum of 51 taxa were 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 stations (Table 2), suggesting that phytoplankton uptake was greater than supply. According to Liebig's law of minimum (Liebig 1940) and the NO_3:PO_4 molar ratio (Redfield et al. 1963; ranging from 0.4 to 8.9 during both summers), nitrogen was the inorganic nutrient in lowest availability for phytoplankton growth. 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 why Nachvak and Saglek had higher diatom abundances whereas flagellates were more abundant in Okak and Anaktalak fjords. Although the ANOSIM analysis 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, Appendix 1) while the lowest record was noted in Okak Fjord (163 taxa, Appendix 1). This relation between

marine protist diversity and nutrient richness in the Arctic has been reported in previous studies (Bluhm et al. 2011, Michel et al. 2012).

2.4.2 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 overriding 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 indicating 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 (Appendix 1); it was two-fold higher than in summer. This supports the fact that both summer communities were mainly dominated by two groups (diatoms and prymnesiophytes) while in fall, we had a mixed community showing higher occurrence percentages of various flagellate (dictyochophytes, euglenophytes and prasinophytes) taxa (Appendix 1).

2.4.3. 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 protist

community. Irradiance largely influences the layer in which protists can be found within the water column. Owing to their freely swimming capabilities, flagellates can undergo diel migrations in the water column. This aptitude to motility allows them to settle in a layer according to its nutrient richness and to their photoacclimation capacities, while non-motile cells such as diatoms are being moved by water turbulence and local currents (Smayda & Reynolds 2003, Wasmund & Uhlig 2003). During summer, the high light intensities experienced by protists 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 is often higher in the bottom layer of the euphotic zone compared to the surface layer. This is the case in our study where the total cell abundance in the surface layer was 30.3×10^6 cells l^{-1} (total in Table 2) while it attained 51.6×10^6 cells l^{-1} (total in Table 3) in the bottom layer of the euphotic zone, where *in situ* irradiance was six times lower than in the surface layer. In addition to light avoidance, downward migration of phytoplankton is also related to nutrient limitation experienced in the surface layer of the water column.

Water temperature was a major variable controlling protist 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 favorable 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 control marine protist communities.

2.4.4 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 nanoflagellates (<20 µm). In Kobbefjord, the winter pelagic protist community was mainly composed of *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*-dominated community in April to a *Chaetoceros*-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*, 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 6), we suggest the following annual succession in the Labrador fjord protist community: dinoflagellates and other flagellates 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.

2.4.5 Distribution of *Phaeocystis 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 that there was 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 NE Atlantic and the Arctic, but 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). Based on the results of Schoemann et al. (2005) and Degerlund & Eilertsen (2010), we strongly argue that the positive relation we had between *P. pouchetii* abundance and water temperature ($r = 0.87$, $p < 0.05$) follows a Gaussian distribution and is valid up to a threshold temperature which remains to be determined.

2.4.6 Mechanisms behind *Phaeocystis* success

Several mechanisms could be responsible for *P. pouchetii* success: 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 *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 well consumed by microzooplankton including ciliates and heterotrophic dinoflagellates. 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 laboratory, the copepod *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 investigations. Having a diatom- or a *Phaeocystis*-dominated community entails many implications for the ecosystem. Diatom-dominated ecosystems are characterized by an 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).

2.5 Conclusion

This study was conducted in four Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during summers 2007 and 2013, early fall and late fall. Our results revealed that the phytoplankton taxonomic composition changed from summer to fall. 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 four Labrador fjords. During summer 2007, diatoms (mainly *C. socialis* and *C. tenuissimus*) and a mixed assemblage of flagellated cells dominated the community. In summer 2013, flagellates were dominant and an intense *P. pouchetii* bloom was observed in the bottom layer of the euphotic zone in Nachvak Fjord (up to 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 very first data on protist spatial and seasonal variations in northeastern Canada fjords. To date, published data on detailed protist distribution along the east coast of Canada are, to the best of our knowledge, non-existent. Such lack of knowledge is very regretful, and while this contribution tries to compensate this weakness, it is also intended to pave the way to future more in-depth investigations on protist dynamics. Whether or not our observations in Labrador fjords can be extrapolated to other fjords of Canada's east coast is yet to be confirmed by future studies. In order to determine

a more precise annual succession in protist community, a sampling expedition in Labrador fjords should be conducted in the first half of July, immediately after the sea ice break-up. Moreover, in future investigations, it will be interesting to determine 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. It is out of 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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Appendix 1. List of planktonic protists (>2 µm) identified in the euphotic zone of Nachvak, Saglek, Okak and Anaktalak fjords (northern Labrador) during summers 2007 and 2013, early fall and late fall. The total number of samples collected at the surface and bottom layers of the euphotic zone for each fjord and season is in parentheses. Mean relative abundance (A) and occurrence (O) are shown in percent (%).Values are rounded. Protist abundance ≥5% and occurrence ≥50% are in bold. nd: taxon not detected

Protist taxon	Fjord								Season							
	Nachvak (16)		Saglek (11)		Okak (10)		Anaktalak (12)		Summer 2007 (12)		Summer 2013 (8)		Early fall (16)		Late fall (13)	
	A	O	A	O	A	O	A	O	A	O	A	O	A	O	A	O
Bacillariophyta (diatoms)																
Centric diatoms																
Arcocellulus cornucervis Hasle, von Stosch & Syvertsen	3	**88**	**8**	**75**	2	**75**	1	**92**	<0.5	**58**	<0.5	**50**	**9**	**100**	2	**100**
Attheya longicornis Crawford & Gardner	<0.5	19	<0.5	8	nd	nd	<0.5	25	<0.5	**58**	nd	nd	nd	nd	nd	nd
A. septentrionalis (Østrup) Crawford	<0.5	**50**	<0.5	22	<0.5	17	<0.5	42	<0.5	33	<0.5	13	<0.5	13	<0.5	**69**
Chaetoceros concavicornis Mangin	nd	nd	nd	nd	<0.5	8	<0.5	8	nd	nd	nd	nd	<0.5	13	nd	nd
C. constrictus Gran	nd	nd	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd	<0.5	8
C. contortus Schütt	<0.5	19	<0.5	19	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	<0.5	31
C. convolutus f. *trisetosa* Brunel	<0.5	6	<0.5	25	<0.5	25	<0.5	17	<0.5	8	nd	nd	<0.5	31	<0.5	23
C. debilis Cleve	<0.5	38	<0.5	33	<0.5	8	<0.5	42	<0.5	8	<0.5	25	<0.5	13	1	**77**
C. decipiens Cleve	nd	nd	<0.5	11	<0.5	8	nd	nd	nd	nd	<0.5	13	nd	nd	<0.5	8
C. diadema (Ehrenberg) Gran	<0.5	6	<0.5	17	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	13	<0.5	8
C. fallax Proschkina-Lavrenko	<0.5	25	nd	nd	nd	nd	<0.5	25	<0.5	17	<0.5	25	nd	nd	<0.5	23
C. furcellatus Bailey	nd	nd	<0.5	8	<0.5	8	<0.5	8	<0.5	17	<0.5	13	nd	nd	nd	nd

Protist taxon	Fjord								Season							
	Nachvak (16)		Saglek (11)		Okak (10)		Anaktalak (12)		Summer 2007 (12)		Summer 2013 (8)		Early fall (16)		Late fall (13)	
	A	**O**	**A**	**O**	**A**	**O**	**A**	**O**	**A**	**O**	**A**	**O**	**A**	**O**	**A**	**O**
C. ingolfianus Ostenfeld	<0.5	13	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	15
C. cf. *minimus* (Levander) Marino, Giuffré, Montresor & Zingone	<0.5	6	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	13	nd	nd	nd	nd
C. neogracilis VanLandingham	<0.5	31	<0.5	44	nd	nd	<0.5	8	nd	nd	nd	nd	<0.5	**50**	<0.5	23
C. pseudobrevis Pavillard	nd	nd	<0.5	11	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd	<0.5	15
C. similis Cleve	<0.5	19	<0.5	31	<0.5	25	<0.5	25	<0.5	17	nd	nd	<0.5	44	<0.5	23
C. simplex Ostenfeld	<0.5	19	<0.5	8	<0.5	8	<0.5	8	nd	nd	<0.5	38	<0.5	19	nd	nd
C. socialis Lauder	2	44	<0.5	19	<0.5	8	**5**	25	**8**	**67**	<0.5	25	<0.5	6	<0.5	15
C. subtilis Cleve	nd	nd	<0.5	17	<0.5	8	<0.5	8	nd	nd	nd	nd	<0.5	19	<0.5	7
C. tenuissimus Meunier	1	**88**	4	**92**	<0.5	17	1	**92**	**5**	**92**	<0.5	25	<0.5	**81**	1	**85**
Chaetoceros sp. B *sensu* Bérard-Therriault et al. (1999)	<0.5	6	<0.5	33	<0.5	17	nd	nd	nd	nd	nd	nd	<0.5	44	nd	nd
Chaetoceros sp. 1	3	38	<0.5	17	nd	nd	<0.5	17	4	**58**	nd	nd	<0.5	19	nd	nd
Chaetoceros sp. 2	<0.5	6	nd	nd	nd	nd	nd	nd	<0.5	**75**	<0.5	13	nd	nd	nd	nd
Chaetoceros spp. (≤20 µm)	2	**69**	2	**74**	1	**66**	1	**64**	2	**61**	2	**71**	2	**69**	2	**87**
Chaetoceros spp. (21-50 µm)	<0.5	19	nd	nd	<0.5	8	<0.5	25	<0.5	**58**	<0.5	13	nd	nd	<0.5	46
Dactyliosolen fragilissimus (Bergon) Hasle	nd	nd	1	**67**	<0.5	17	<0.5	8	nd	nd	nd	nd	<0.5	38	<0.5	31
Detonula confervacea (Cleve) Gran	**5**	19	nd	nd	nd	nd	nd	nd	nd	nd	**10**	38	nd	nd	nd	nd
Eucampia groenlandica Cleve	<0.5	31	<0.5	11	nd	nd	<0.5	8	<0.5	8	nd	nd	<0.5	6	<0.5	38
Lennoxia faveolata Thomsen & Buck	<0.5	19	<0.5	8	<0.5	17	<0.5	8	<0.5	8	nd	nd	<0.5	38	nd	nd
Leptocylindrus danicus Cleve	<0.5	13	<0.5	22	nd	nd	<0.5	8	<0.5	8	nd	nd	nd	nd	<0.5	31
L. minimus Gran	<0.5	6	<0.5	25	nd	nd	<0.5	25	<0.5	8	nd	nd	<0.5	31	<0.5	8
Porosira glacialis (Grunow) Jørgensen	nd	nd	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd	nd	nd

Protist taxon	Fjord								Season							
	Nachvak (16)		Saglek (11)		Okak (10)		Anaktalak (12)		Summer 2007 (12)		Summer 2013 (8)		Early fall (16)		Late fall (13)	
	A	O	A	O	A	O	A	O	A	O	A	O	A	O	A	O
Rhizosolenia hebetata f. *semispina* (Hensen) Gran	<0.5	6	nd	nd	<0.5	8	<0.5	17	nd	nd	nd	nd	<0.5	19	<0.5	8
Skeletonema cf. *costatum* (Greville) Cleve	<0.5	25	<0.5	19	nd	nd	<0.5	8	<0.5	8	<0.5	13	<0.5	19	<0.5	15
Thalassiosira gravida Cleve / *T. antarctica* var. *borealis* Fryxell, Doucette & Hubbard	<0.5	6	<0.5	17	nd	nd	nd	nd	nd	nd	<0.5	13	<0.5	13	nd	nd
T. nordenskioeldii Cleve	<0.5	38	<0.5	28	<0.5	17	nd	nd	<0.5	33	<0.5	38	<0.5	13	<0.5	15
T. pacifica Gran & Angst	<0.5	19	nd	nd	1	33	<0.5	**58**	nd	nd	nd	nd	<0.5	19	1	**70**
T. poroseriata (Ramsfjell) Hasle	nd	nd	<0.5	8	<0.5	8	nd	nd	nd	nd	nd	nd	<0.5	13	nd	nd
Thalassiosira spp. (≤20 µm)	<0.5	35	<0.5	49	<0.5	25	<0.5	25	<0.5	4	<0.5	25	<0.5	41	<0.5	**50**
Thalassiosira spp. (21-50 µm)	<0.5	31	<0.5	25	<0.5	25	<0.5	33	<0.5	17	<0.5	38	<0.5	38	<0.5	31
Thalassiosira spp. (>50 µm)	<0.5	6	nd	nd	nd	nd	<0.5	8	nd	nd	<0.5	13	nd	nd	<0.5	8
Urosolenia eriensis (Smith) Round & Crawford	<0.5	25	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	25	nd	nd
Unidentified centric diatoms (≤10 µm)	<0.5	13	<0.5	11	nd	nd	<0.5	8	nd	nd	nd	nd	<0.5	6	<0.5	15
Pennate diatoms																
Cocconeis spp.	<0.5	6	nd	nd	<0.5	17	<0.5	8	nd	nd	nd	nd	<0.5	13	<0.5	15
Cylindrotheca closterium (Ehrenberg) Reimann & Lewin	<0.5	38	<0.5	33	<0.5	**67**	1	**67**	<0.5	17	<0.5	**75**	<0.5	**56**	<0.5	**54**
Entomoneis spp.	nd	nd	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	<0.5	7	nd	nd
Fragilariopsis cylindrus (Grunow ex Cleve) Frenguelli	<0.5	19	<0.5	22	<0.5	8	<0.5	8	<0.5	17	nd	nd	nd	nd	<0.5	23
Fragilariopsis spp. (≤20 µm)	<0.5	6	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	8
Fragilariopsis spp. (21-50 µm)	<0.5	6	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	8
Gyrosigma fasciola (Ehrenberg) Griffith & Henfrey	nd	nd	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd	<0.5	8
Licmophora spp.	<0.5	13	<0.5	8	<0.5	8	<0.5	17	nd	nd	<0.5	25	<0.5	19	<0.5	8

Protist taxon	Fjord								Season							
	Nachvak (16)		Saglek (11)		Okak (10)		Anaktalak (12)		Summer 2007 (12)		Summer 2013 (8)		Early fall (16)		Late fall (13)	
	A	O	A	O	A	O	A	O	A	O	A	O	A	O	A	O
Navicula directa (W. Smith) Ralfs	nd	nd	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd	<0.5	8
N. transitans Cleve	<0.5	6	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	8
N. transitans var. *derasa* f. *delicatula* Heimdal	<0.5	25	<0.5	33	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	**54**
Navicula sp. 1	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd
Navicula spp. (21-50 µm)	<0.5	6	<0.5	8	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	6	nd	nd
Navicula spp. (>50 µm)	nd	nd	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	<0.5	6	nd	nd
Nitzschia longissima (Brébisson) Ralfs	<0.5	31	nd	nd	nd	nd	<0.5	25	<0.5	50	nd	nd	nd	nd	<0.5	15
Nitzschia sp. 5	nd	nd	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd	<0.5	8
Nitzschia spp. (21-50 µm)	nd	nd	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd	<0.5	8
Nitzschia spp. (>50 µm)	<0.5	6	<0.5	8	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	13	nd	nd
Pseudo-nitzschia cf. *delicatissima* (Cleve) Heiden	nd	nd	<0.5	17	<0.5	17	<0.5	25	<0.5	8	nd	nd	<0.5	13	<0.5	23
P. cf. *pseudodelicatissima* (Hasle) Hasle	nd	nd	<0.5	22	<0.5	33	<0.5	33	nd	nd	nd	nd	nd	nd	<0.5	**62**
P. seriata (Cleve) H. Peragallo	<0.5	6	<0.5	19	<0.5	8	<0.5	17	nd	nd	nd	nd	<0.5	19	<0.5	23
P. obtusa (Hasle) Hasle & Lundholm	<0.5	6	nd	nd	<0.5	8	nd	nd	nd	nd	<0.5	25	nd	nd	nd	nd
Rhoicosphenia spp.	<0.5	13	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	6	nd	nd
Stenoneis wojtek-kowalskii Witkowski, Lange-Bertalot & Metzeltin	nd	nd	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd	<0.5	8
Tabularia investiens (W. Smith) Williams & Round	nd	nd	<0.5	11	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	8
Thalassionema nitzschioides (Grunow) Mereschkowsky	nd	nd	nd	nd	<0.5	17	<0.5	50	nd	nd	nd	nd	<0.5	13	<0.5	38
Unidentified pennates (≤20 µm)	1	**58**	1	**53**	<0.5	**56**	1	45	1	19	<0.5	**58**	2	**63**	1	**67**
Unidentified pennates (21-50 µm)	<0.5	31	<0.5	47	<0.5	50	<0.5	25	<0.5	17	<0.5	**50**	<0.5	25	<0.5	**54**
Unidentified pennates (>50 µm)	<0.5	13	nd	nd	<0.5	8	nd	nd	nd	nd	<0.5	13	<0.5	13	nd	nd

Protist taxon	Fjord								Season							
	Nachvak (16)		Saglek (11)		Okak (10)		Anaktalak (12)		Summer 2007 (12)		Summer 2013 (8)		Early fall (16)		Late fall (13)	
	A	O	A	O	A	O	A	O	A	O	A	O	A	O	A	O
Dinophyceae																
Amphidinium cf. *carterae* Hulburt	nd	nd	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd	<0.5	8
A. crassum Lohmann	nd	nd	nd	nd	<0.5	8	<0.5	8	nd	nd	nd	nd	<0.5	13	nd	nd
A. cf. *kesslitzii* Schiller	1	**75**	1	**67**	2	**100**	2	**67**	nd	nd	1	**100**	1	**100**	3	**100**
A. sphenoides Wülff	<0.5	31	<0.5	28	<0.5	17	<0.5	17	<0.5	17	<0.5	13	<0.5	31	nd	31
Amphidinium spp.	nd	nd	nd	nd	nd	nd	<0.5	17	nd	nd	nd	nd	<0.5	6	<0.5	8
Cochlodinium spp.	<0.5	6	<0.5	17	<0.5	8	nd	nd	nd	nd	<0.5	13	<0.5	19	nd	nd
Dicroerisma psilonereiella F.J.R. Taylor & Cattell	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	7	nd	nd
Gymnodinium elongatum Hope	<0.5	6	<0.5	28	nd	nd	<0.5	17	nd	nd	nd	nd	<0.5	19	<0.5	23
G. galeatum Larsen	<0.5	**56**	<0.5	47	<0.5	**100**	<0.5	**75**	<0.5	8	<0.5	**75**	<0.5	**88**	<0.5	**92**
G. cf. *gracilentum* Campbell	<0.5	6	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd	<0.5	15
G. ostenfeldii Schiller	nd	nd	nd	nd	<0.5	17	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	8
G. cf. *parvum* Larsen	<0.5	25	<0.5	**50**	<0.5	17	<0.5	33	nd	nd	nd	nd	<0.5	44	<0.5	**62**
G. simplex (Lohmann) Kofoid & Swezy	<0.5	19	nd	nd	<0.5	17	<0.5	17	nd	nd	nd	nd	<0.5	31	<0.5	15
G. cf. *subroseum* Campbell	<0.5	38	<0.5	**56**	<0.5	**58**	<0.5	33	nd	nd	<0.5	25	<0.5	**56**	<0.5	**85**
G. verruculosum Campbell	nd	nd	nd	nd	<0.5	17	<0.5	17	nd	nd	nd	nd	<0.5	25	nd	nd
G. vestifici Schütt	nd	nd	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd	<0.5	8
Gymnodinium sp. 1 *sensu* Bérard-Therriault et al. (1999)	<0.5	38	<0.5	**58**	<0.5	**50**	<0.5	50	<0.5	8	nd	nd	<0.5	**56**	<0.5	**92**
Gymnodinium sp. 6	<0.5	13	<0.5	11	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	23
Gymnodinium sp. 7	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	6	nd	nd
Gyrodinium cf. *aciculatum* Hansen & Larsen	nd	nd	<0.5	8	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd
G. flagellare Schiller	<0.5	**56**	<0.5	**56**	<0.5	**67**	1	**67**	nd	nd	<0.5	13	1	**100**	1	**92**
G. formosum Campbell	<0.5	6	<0.5	33	<0.5	17	<0.5	17	nd	nd	nd	nd	<0.5	**56**	nd	nd

Protist taxon	Fjord								Season							
	Nachvak (16)		Saglek (11)		Okak (10)		Anaktalak (12)		Summer 2007 (12)		Summer 2013 (8)		Early fall (16)		Late fall (13)	
	A	O	A	O	A	O	A	O	A	O	A	O	A	O	A	O
G. fusiforme Kofoid & Swezy	nd	nd	nd	nd	<0.5	8	<0.5	8	nd	nd	nd	nd	<0.5	6	<0.5	8
G. cf. *grave* (Meunier) Kofoid & Swezy	<0.5	6	nd	nd	nd	nd	<0.5	8	<0.5	17	nd	nd	nd	nd	nd	nd
G. cf. *guttula* Larsen	<0.5	**63**	<0.5	**58**	<0.5	**58**	<0.5	**58**	nd	nd	<0.5	**63**	<0.5	**75**	<0.5	92
G. cf. *katodiniascens* Campbell	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd	<0.5	6	nd	nd
G. cf. *resplendens* Hulburt	<0.5	6	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	8
G. spirale (Bergh) Kofoid & Swezy	<0.5	6	<0.5	17	<0.5	17	<0.5	25	<0.5	17	<0.5	25	<0.5	19	<0.5	8
Gyrodinium sp. 1 *sensu* Bérard-Therriault et al. (1999)	nd	nd	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	<0.5	6	nd	nd
Gyrodinium sp. 3 *sensu* Bérard-Therriault et al. (1999)	<0.5	6	<0.5	8	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	<0.5	8
Gyrodinium sp. 4 *sensu* Bérard-Therriault et al. (1999)	nd	nd	<0.5	8	nd	nd	<0.5	42	nd	nd	nd	nd	<0.5	19	<0.5	23
Gyrodinium sp. 5	<0.5	6	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	6	nd	nd
Gyrodinium sp. 6	<0.5	6	<0.5	19	nd	nd	<0.5	25	nd	nd	nd	nd	<0.5	13	<0.5	31
Gyrodinium spp. (21-50 µm)	<0.5	44	<0.5	47	<0.5	25	<0.5	25	nd	nd	<0.5	38	<0.5	**63**	<0.5	38
Gyrodinium spp. (>50 µm)	<0.5	13	nd	nd	<0.5	17	<0.5	17	nd	nd	<0.5	25	<0.5	19	<0.5	8
Gymnodinium/Gyrodinium spp. (≤20 µm)	1	47	2	**50**	3	**50**	2	**58**	<0.5	**59**	1	44	2	**50**	3	**50**
Gymnodinium/Gyrodinium spp. (21-50 µm)	<0.5	**50**	<0.5	**58**	<0.5	**50**	<0.5	**75**	<0.5	17	<0.5	**63**	<0.5	**75**	<0.5	**77**
Gymnodinium/Gyrodinium spp. (>50 µm)	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	<0.5	13	nd	nd	nd	nd
Katodinium glaucum (Lebour) Loeblich III	<0.5	13	<0.5	28	<0.5	**75**	<0.5	42	nd	nd	<0.5	**50**	<0.5	31	<0.5	**62**
Paulsenella chaetoceratis (Paulsen) Chatton	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd	<0.5	6	nd	nd
Protherythropsis vigilans Marshall	<0.5	19	<0.5	31	<0.5	17	<0.5	17	nd	nd	nd	nd	<0.5	31	<0.5	31
Torodinium robustum Kofoid & Swezy	<0.5	6	<0.5	11	<0.5	17	<0.5	33	nd	nd	nd	nd	<0.5	19	<0.5	31
Amphidoma acuminata Stein	<0.5	13	<0.5	22	<0.5	17	<0.5	17	nd	nd	nd	nd	<0.5	6	<0.5	46

Protist taxon	Fjord								Season							
	Nachvak (16)		Saglek (11)		Okak (10)		Anaktalak (12)		Summer 2007 (12)		Summer 2013 (8)		Early fall (16)		Late fall (13)	
	A	O	A	O	A	O	A	O	A	O	A	O	A	O	A	O
Dinophysis acuminata Claparède & Lachmann	<0.5	25	nd	nd	<0.5	17	<0.5	**50**	nd	nd	nd	nd	<0.5	**50**	<0.5	31
D. acuta Ehrenberg	<0.5	6	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	6	nd	nd
D. norvegica Claparède & Lachmann	<0.5	13	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	<0.5	19	nd	nd
D. rotundata Claparède & Lachmann	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd	<0.5	6	nd	nd
Gonyaulax gracilis Schiller	nd	nd	<0.5	8	<0.5	17	<0.5	8	nd	nd	nd	nd	<0.5	25	nd	nd
Heterocapsa cf. *niei* (Loeblich III) Morrill & Loeblich III	<0.5	6	<0.5	19	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd	<0.5	23
H. rotundata (Lohmann) Hansen	<0.5	**69**	1	**75**	**11**	**92**	3	**84**	1	50	**14**	**63**	3	**100**	1	**85**
Heterocapsa sp. A *sensu* Hansen & Larsen (1992)	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd	<0.5	6	nd	nd
Heterocapsa spp.	nd	nd	<0.5	8	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd
Micracanthodinium claytonii (Holmes) Dodge	<0.5	13	<0.5	11	<0.5	17	<0.5	25	nd	nd	nd	nd	<0.5	19	<0.5	31
Peridiniella danica (Paulsen) Okolodkov & Dodge	<0.5	13	<0.5	8	<0.5	**50**	<0.5	25	nd	nd	<0.5	38	<0.5	31	<0.5	23
Peridiniella spp.	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	6	nd	nd
Prorocentrum minimum (Pavillard) Schiller	<0.5	13	nd	nd	<0.5	8	<0.5	25	nd	nd	nd	nd	<0.5	25	<0.5	15
Protoperidinium americanum (Gran & Braarud) Balech	<0.5	6	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	8
P. bipes (Paulsen) Balech	<0.5	25	nd	nd	<0.5	25	<0.5	25	<0.5	17	<0.5	13	<0.5	38	<0.5	8
P. brevipes (Paulsen) Balech	<0.5	6	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	8
P. ovatum Pouchet	nd	nd	<0.5	19	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	6	<0.5	8
P. pellucidum Bergh	<0.5	13	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	13	nd	nd
Scrippsiella trochoidea (Stein) Balech ex Loeblich III	nd	nd	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd	<0.5	8
Scrippsiella spp.	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	6	nd	nd
Dinophyceae (≤20 µm)	<0.5	32	<0.5	18	<0.5	34	<0.5	33	<0.5	21	<0.5	38	<0.5	32	<0.5	31
Dinophyceae (21-50 µm)	<0.5	38	nd	nd	<0.5	33	<0.5	25	<0.5	33	<0.5	63	<0.5	25	<0.5	15

Protist taxon	Fjord								Season							
	Nachvak (16)		Saglek (11)		Okak (10)		Anaktalak (12)		Summer 2007 (12)		Summer 2013 (8)		Early fall (16)		Late fall (13)	
	A	O	A	O	A	O	A	O	A	O	A	O	A	O	A	O
Chrysophyceae																
Dinobryon balticum (Schütt) Lemmermann	2	38	nd	nd	<0.5	8	1	4	3	**58**	nd	nd	<0.5	19	<0.5	15
D. bavaricum Imhof	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	6	nd	nd
D. cylindricum Imhof	<0.5	6	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	13	nd	nd	nd	nd
D. faculiferum (Willén) Willén	<0.5	38	<0.5	19	<0.5	42	<0.5	17	<0.5	25	<0.5	25	<0.5	25	<0.5	38
Dinobryon spp.	<0.5	31	<0.5	47	<0.5	17	<0.5	8	nd	nd	<0.5	13	<0.5	38	<0.5	46
Chrysophyceae sp. 2 *sensu* Bérard-Therriault et al. (1999)	<0.5	6	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	8
Chrysophyceae (≤5 µm)	<0.5	6	<0.5	22	nd	nd	<0.5	25	nd	nd	nd	nd	<0.5	13	<0.5	31
Chrysophyceae (6-10 µm)	<0.5	6	<0.5	8	<0.5	17	<0.5	17	nd	nd	nd	nd	<0.5	19	<0.5	15
Cryptophyceae																
Hemiselmis virescens Droop	<0.5	13	<0.5	17	nd	nd	<0.5	17	<0.5	**50**	nd	nd	nd	nd	nd	nd
Hemiselmis spp.	<0.5	44	1	44	1	33	1	**58**	nd	nd	nd	nd	2	**100**	<0.5	**54**
Plagioselmis prolonga var. *nordica* Novarino, Lucas & Morrall	2	**94**	1	**83**	2	**92**	3	**100**	2	**83**	1	**75**	4	**100**	1	**100**
Plagioselmis / Teleaulax spp.	<0.5	6	nd	nd	nd	nd	<0.5	8	<0.5	17	nd	nd	nd	nd	nd	nd
Rhodomonas marina (Dangeard) Lemmermann	<0.5	25	<0.5	19	<0.5	17	<0.5	42	nd	nd	<0.5	13	<0.5	31	<0.5	46
Rhodomonas spp.	<0.5	6	nd	nd	nd	nd	<0.5	33	<0.5	17	nd	nd	<0.5	6	<0.5	15
Teleaulax acuta (Butcher) Hill	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd	<0.5	6	nd	nd
T. amphioxeia (Conrad) Hill	<0.5	6	<0.5	17	<0.5	**75**	<0.5	**58**	<0.5	33	<0.5	25	<0.5	44	<0.5	31
Teleaulax spp.	<0.5	19	<0.5	28	<0.5	33	<0.5	42	nd	nd	nd	nd	<0.5	**69**	<0.5	31
Cryptophyceae sp. 1	<0.5	6	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	13	nd	nd	nd	nd
Cryptophyceae (≤5 µm)	<0.5	**50**	<0.5	**61**	<0.5	17	<0.5	42	nd	nd	nd	nd	<0.5	**69**	<0.5	31
Cryptophyceae (6-10 µm)	2	**100**	1	**83**	1	**100**	1	**83**	nd	nd	1	**100**	2	**100**	1	**100**

Protist taxon	Fjord								Season							
	Nachvak (16)		Saglek (11)		Okak (10)		Anaktalak (12)		Summer 2007 (12)		Summer 2013 (8)		Early fall (16)		Late fall (13)	
	A	O	A	O	A	O	A	O	A	O	A	O	A	O	A	O
Cryptophyceae (11-20 µm)	<0.5	**69**	<0.5	**56**	2	**100**	1	**83**	nd	nd	<0.5	**88**	1	**94**	2	**92**
Dictyochophyceae																
Apedinella spinifera (Throndsen) Throndsen	<0.5	44	<0.5	11	<0.5	17	<0.5	33	<0.5	25	nd	nd	<0.5	**50**	<0.5	23
Dictyocha speculum Ehrenberg	1	44	<0.5	33	<0.5	8	<0.5	17	nd	nd	nd	nd	1	**69**	<0.5	23
Pseudopedinella pyriforme Carter	<0.5	31	<0.5	36	<0.5	25	<0.5	42	nd	nd	nd	nd	<0.5	**69**	<0.5	46
P. cf. *tricostata* (Roukhiyajnen) Thomsen	<0.5	13	nd	nd	nd	nd	<0.5	17	<0.5	33	nd	nd	nd	nd	nd	nd
Pseudopedinella spp. (≤5 µm)	<0.5	**50**	<0.5	**56**	<0.5	**67**	1	**67**	<0.5	25	<0.5	13	1	**100**	<0.5	**92**
Pseudopedinella spp. (6-10 µm)	<0.5	44	<0.5	28	<0.5	17	<0.5	**58**	nd	nd	nd	nd	<0.5	**69**	<0.5	**54**
Dictyochophyceae	<0.5	6	nd	nd	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd
Euglenophyceae																
Euglena spp. (21-50 µm)	<0.5	13	nd	nd	nd	nd	<0.5	17	nd	nd	nd	nd	<0.5	19	<0.5	8
Eutreptiella braarudii Throndsen	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	<0.5	13	nd	nd	nd	nd
E. gymnastica Throndsen	<0.5	25	<0.5	19	<0.5	25	<0.5	8	nd	nd	<0.5	13	<0.5	38	<0.5	23
Eutreptiella spp. (≤20 µm)	<0.5	6	nd	nd	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd
Eutreptiella spp. (21-50 µm)	nd	nd	nd	nd	<0.5	17	<0.5	8	nd	nd	<0.5	13	<0.5	13	nd	nd
Euglenophyceae (≤20 µm)	<0.5	19	nd	nd	<0.5	25	<0.5	8	nd	nd	<0.5	13	<0.5	19	<0.5	15
Euglenophyceae (21-50 µm)	<0.5	31	<0.5	19	<0.5	25	<0.5	17	<0.5	8	<0.5	38	<0.5	38	<0.5	23
Euglenophyceae (>50 µm)	<0.5	19	<0.5	8	<0.5	25	<0.5	25	nd	nd	<0.5	13	<0.5	44	<0.5	15
Prasinophyceae																
Dolichomastix nummulifera Manton	<0.5	6	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd	<0.5	13	nd	nd
D. cf. *tenuilepis* Throndsen & Zingone	nd	nd	nd	nd	nd	nd	<0.5	33	nd	nd	nd	nd	<0.5	19	nd	nd
Nephroselmis spp.	nd	nd	nd	nd	nd	nd	<0.5	17	nd	nd	nd	nd	nd	nd	<0.5	15
Pseudoscourfieldia marina (Throndsen) Manton	<0.5	31	<0.5	**64**	<0.5	33	<0.5	**83**	<0.5	25	nd	nd	<0.5	81	<0.5	**69**
Pyramimonas cf. *nansenii* Braarud	<0.5	6	<0.5	8	nd	nd	<0.5	8	<0.5	8	nd	nd	<0.5	6	<0.5	8

Protist taxon	Fjord								Season							
	Nachvak (16)		Saglek (11)		Okak (10)		Anaktalak (12)		Summer 2007 (12)		Summer 2013 (8)		Early fall (16)		Late fall (13)	
	A	O	A	O	A	O	A	O	A	O	A	O	A	O	A	O
P. cf. *orientalis* Butcher ex McFadden, Hill & Wetherbee	<0.5	31	<0.5	25	<0.5	8	<0.5	25	1	**58**	nd	nd	<0.5	25	<0.5	8
P. virginica Pennick	<0.5	25	<0.5	33	<0.5	8	<0.5	17	1	**58**	nd	nd	<0.5	25	nd	nd
Pyramimonas sp. 6	<0.5	19	<0.5	8	<0.5	17	<0.5	8	nd	nd	nd	nd	<0.5	31	<0.5	15
Pyramimonas spp. (≤5 µm)	<0.5	44	<0.5	36	<0.5	25	<0.5	8	<0.5	8	<0.5	25	<0.5	44	<0.5	38
Pyramimonas spp. (6-10 µm)	<0.5	**63**	<0.5	**56**	<0.5	33	<0.5	33	nd	nd	<0.5	25	1	**100**	<0.5	46
Pyramimonas spp. (11-20 µm)	<0.5	25	<0.5	8	<0.5	8	<0.5	8	nd	nd	<0.5	25	<0.5	19	<0.5	15
Prasinophyceae (≤5 µm)	nd	nd	<0.5	8	nd	nd	<0.5	8	<0.5	17	nd	nd	nd	nd	nd	nd
Prasinophyceae (6-10 µm)	<0.5	25	<0.5	22	<0.5	8	<0.5	8	<0.5	8	nd	nd	<0.5	25	<0.5	23
Prasinophyceae (11-20 µm)	<0.5	6	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	6	nd	nd
Prymnesiophyceae																
Chrysochromulina cf. *alifera* Parke & Manton	nd	nd	<0.5	28	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	13	<0.5	8
C. cf. *spinifera* (Fournier) Pienaar & Norris	2	38	1	**58**	<0.5	**50**	1	**58**	nd	nd	nd	nd	1	**75**	3	**92**
Chrysochromulina spp. (≤5 µm)	**7**	**94**	**10**	**100**	**5**	**100**	**11**	**100**	**8**	**100**	1	**88**	**13**	**100**	**11**	**100**
Chrysochromulina spp. (6-10 µm)	1	**63**	1	**67**	<0.5	**75**	1	**67**	nd	nd	<0.5	38	3	**100**	1	**100**
Chrysochromulina spp. (11-20 µm)	<0.5	19	<0.5	44	<0.5	25	1	42	nd	nd	nd	nd	<0.5	**63**	<0.5	38
Phaeocystis pouchetii (Hariot) Lagerheim	**6**	**63**	1	47	<0.5	33	1	42	3	**67**	**18**	**88**	<0.5	31	<0.5	31
Prymnesiophyceae sp. 1 *sensu* Bérard-Therriault et al. (1999)	<0.5	25	1	**50**	<0.5	33	<0.5	**67**	2	**92**	nd	nd	<0.5	**69**	nd	nd
Prymnesiophyceae sp. 2	<0.5	31	<0.5	33	<0.5	17	<0.5	33	nd	nd	<0.5	13	<0.5	19	<0.5	**69**
Prymnesiophyceae (≤5 µm)	2	**63**	4	**100**	3	**92**	3	**83**	1	**58**	3	**50**	3	**100**	**5**	**100**
Prymnesiophyceae (6-10 µm)	<0.5	**63**	<0.5	25	1	**83**	<0.5	**67**	<0.5	25	3	**100**	<0.5	**75**	<0.5	**54**
Raphidophyceae																
Heterosigma cf. *akashiwo* (Hada) Hada ex Hara & Chihara	1	**63**	<0.5	42	<0.5	**50**	1	**67**	1	42	<0.5	38	1	**100**	<0.5	38

Protist taxon	Fjord								Season							
	Nachvak (16)		Saglek (11)		Okak (10)		Anaktalak (12)		Summer 2007 (12)		Summer 2013 (8)		Early fall (16)		Late fall (13)	
	A	O	A	O	A	O	A	O	A	O	A	O	A	O	A	O
Unidentified flagellates																
Flagellates (≤5 µm)	2	42	**6**	49	**8**	36	**7**	**54**	**8**	**54**	**6**	25	**6**	**60**	**7**	**42**
Flagellates (6-10 µm)	1	30	1	36	1	30	1	45	1	35	1	20	1	39	1	34
Flagellates (11-20 µm)	<0.5	47	<0.5	46	<0.5	**50**	<0.5	38	<0.5	37	<0.5	38	<0.5	**50**	<0.5	**50**
Flagellates (>20 µm)	nd	nd	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd	<0.5	8
Choanoflagellidea																
Acanthocorbis unguiculata (Thomsen) Hara & Takahashi	nd	nd	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	<0.5	6	nd	nd
Bicosta antennigera Moestrup	<0.5	13	nd	nd	nd	nd	<0.5	8	nd	nd	<0.5	25	<0.5	6	nd	nd
B. minor (Reynolds) Leadbeater	nd	nd	<0.5	33	nd	nd	<0.5	17	<0.5	33	nd	nd	<0.5	13	nd	nd
B. spinifera (Throndsen) Leadbeater	<0.5	19	<0.5	8	<0.5	8	nd	nd	nd	nd	<0.5	**50**	<0.5	6	nd	nd
Bicosta spp.	<0.5	**50**	<0.5	25	<0.5	**50**	<0.5	25	nd	nd	<0.5	**88**	<0.5	**56**	<0.5	23
Calliacantha longicaudata (Leadbeater) Leadbeater	<0.5	**50**	<0.5	28	<0.5	**75**	<0.5	33	<0.5	8	<0.5	**88**	<0.5	63	<0.5	38
C. natans (Grøntved) Leadbeater	<0.5	**75**	<0.5	**67**	<0.5	**83**	<0.5	**67**	<0.5	17	1	**75**	<0.5	**94**	<0.5	**92**
C. simplex Manton & Oates	<0.5	19	<0.5	8	<0.5	17	<0.5	25	nd	nd	nd	nd	<0.5	44	<0.5	15
Calliacantha spp.	nd	nd	<0.5	8	nd	nd	<0.5	8	<0.5	17	nd	nd	nd	nd	nd	nd
Cosmoeca ventricosa Thomsen	<0.5	6	<0.5	8	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	13	nd	nd
Cosmoeca spp.	<0.5	6	<0.5	17	nd	nd	<0.5	17	nd	nd	nd	nd	<0.5	31	nd	nd
Diaphanoeca grandis Ellis	<0.5	38	<0.5	17	<0.5	17	<0.5	8	nd	nd	<0.5	**50**	<0.5	44	nd	nd
D. pedicellata Leadbeater	<0.5	31	<0.5	33	<0.5	33	<0.5	25	nd	nd	nd	nd	<0.5	**94**	<0.5	8
Diaphanoeca spp.	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	8
Monosiga marina Grøntved	<0.5	**50**	<0.5	**67**	<0.5	**50**	<0.5	**58**	<0.5	8	<0.5	**63**	<0.5	**69**	<0.5	85
Monosiga sp. *sensu* Bérard-Therriault et al. (1999)	<0.5	38	<0.5	**50**	<0.5	**58**	<0.5	**67**	<0.5	8	nd	nd	<0.5	**63**	1	**100**
Parvicorbicula quadricostata Throndsen	<0.5	**56**	<0.5	25	<0.5	42	<0.5	25	nd	nd	<0.5	25	<0.5	**75**	<0.5	38

Protist taxon	Fjord								Season							
	Nachvak (16)		Saglek (11)		Okak (10)		Anaktalak (12)		Summer 2007 (12)		Summer 2013 (8)		Early fall (16)		Late fall (13)	
	A	O	A	O	A	O	A	O	A	O	A	O	A	O	A	O
P. socialis (Meunier) Deflandre	<0.5	**81**	<0.5	**67**	<0.5	42	<0.5	**67**	1	33	<0.5	50	<0.5	**88**	<0.5	**85**
Pleurasiga minima Throndsen	<0.5	31	<0.5	8	<0.5	8	<0.5	33	nd	nd	<0.5	13	<0.5	31	<0.5	38
P. reynoldsii Throndsen	<0.5	31	<0.5	36	<0.5	8	<0.5	25	nd	nd	nd	nd	<0.5	**56**	<0.5	31
Pleurasiga spp.	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	6	nd	nd
Polyfibula sphyrelata (Thomsen) Manton	<0.5	19	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	19	nd	nd
P. stipitata Manton	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd	<0.5	6	nd	nd
Choanoflagellidea spp. (≤5 µm)	2	**88**	1	**100**	<0.5	**83**	2	**100**	**5**	**100**	2	**100**	<0.5	**88**	1	**92**
Choanoflagellidea spp. (6-10 µm)	1	**75**	<0.5	**67**	1	**92**	1	**67**	nd	nd	2	**100**	1	**94**	2	**100**
Choanoflagellidea spp. (11-20 µm)	1	**75**	1	**67**	1	**92**	1	**67**	nd	nd	1	**88**	1	**100**	3	**100**
Choanoflagellidea spp. (21-50 µm)	<0.5	**56**	<0.5	47	<0.5	**75**	<0.5	33	nd	nd	<0.5	**88**	<0.5	**56**	<0.5	**77**
Heterotrophic protists																
Cafeteria minuta (Ruinen) Larsen & Patterson	<0.5	13	<0.5	28	<0.5	**50**	<0.5	**50**	nd	nd	nd	nd	<0.5	**50**	<0.5	**54**
Commation cryoporinum Thomsen & Larsen	<0.5	13	<0.5	8	<0.5	17	<0.5	**58**	nd	nd	nd	nd	<0.5	38	<0.5	38
Cryothecomonas spp.	<0.5	25	<0.5	11	<0.5	17	<0.5	**58**	nd	nd	nd	nd	<0.5	31	<0.5	**62**
Enigma aculeata Daugbjerg & Vørs	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	6	nd	nd
Leucocryptos marina (Braarud) Butcher	<0.5	19	<0.5	39	<0.5	**50**	<0.5	**67**	<0.5	8	<0.5	25	<0.5	**56**	<0.5	**62**
Meringosphaera mediterranea Lohmann*	<0.5	38	<0.5	36	<0.5	33	<0.5	**58**	nd	nd	nd	nd	<0.5	**94**	<0.5	46
Notosolenus sp. *sensu* Bérard-Therriault et al. (1999)	nd	nd	<0.5	11	<0.5	33	<0.5	17	nd	nd	<0.5	25	<0.5	13	<0.5	15
Quadricilia rotundata (Skuja) Vørs	<0.5	25	<0.5	25	<0.5	25	nd	nd	nd	nd	nd	nd	<0.5	25	<0.5	38
Rhynchobodo taeniata (Skuja) Vørs	<0.5	6	nd	nd	<0.5	8	<0.5	8	nd	nd	nd	nd	<0.5	6	<0.5	15
Rhynchomonas nasuta (Stokes) Klebs	<0.5	6	<0.5	8	<0.5	17	<0.5	**50**	nd	nd	nd	nd	<0.5	19	<0.5	46
Telonema subtile Greissmann	<0.5	**50**	<0.5	36	<0.5	42	<0.5	**58**	<0.5	8	<0.5	25	<0.5	**88**	<0.5	**54**
Telonema sp. 1	1	**63**	1	**58**	<0.5	**75**	<0.5	**67**	nd	nd	<0.5	**50**	1	**88**	1	**100**

Protist taxon	Fjord									Season							
	Nachvak (16)		Saglek (11)		Okak (10)		Anaktalak (12)			Summer 2007 (12)		Summer 2013 (8)		Early fall (16)		Late fall (13)	
	A	O	A	O	A	O	A	O	A	O	A	O	A	O	A	O	
Thaumatomastix spp.	nd	nd	nd	nd	<0.5	17	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	8	
Vanella cf. simplex Wohlfarth-Bottermann	nd	nd	<0.5	11	nd	nd	<0.5	8	nd	nd	nd	nd	<0.5	6	<0.5	8	
Flagellate sp. B	<0.5	6	<0.5	8	<0.5	8	<0.5	8	nd	nd	nd	nd	<0.5	25	nd	nd	
Heterotrophic flagellates spp. (6-10 µm)	nd	nd	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd	<0.5	8	
Heterotrophic flagellates spp. (11-20 µm)	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd	<0.5	6	nd	nd	
Ciliates																	
Balanion comatum Wulff	nd	nd	nd	nd	<0.5	8	<0.5	17	nd	nd	<0.5	13	<0.5	13	nd	nd	
Laboea strobila Lohmann	<0.5	6	nd	nd	<0.5	25	nd	nd	nd	nd	<0.5	13	<0.5	6	<0.5	8	
Lohmanniella oviformis Leegaard	<0.5	38	<0.5	47	<0.5	**58**	<0.5	**58**	nd	nd	<0.5	25	<0.5	**75**	<0.5	**69**	
Myrionecta rubra (Lohmann) Jankowski	<0.5	**75**	<0.5	47	<0.5	**83**	1	**58**	<0.5	25	<0.5	**75**	1	**75**	<0.5	**85**	
Salpingella laminata Kofoid & Campbell	<0.5	19	<0.5	8	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	25	nd	nd	
Salpingella spp.	<0.5	6	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	8	
Strombidium acutum Leegaard	<0.5	6	nd	nd	nd	nd	<0.5	8	nd	nd	nd	nd	<0.5	6	<0.5	8	
S. conicum (Lohmann) Wulff	<0.5	19	<0.5	11	<0.5	17	<0.5	25	nd	nd	<0.5	**63**	<0.5	13	<0.5	15	
S. constrictum (Meunier) Wulff	<0.5	6	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	8	
S. delicatissimum (Leegaard) Bush	nd	nd	<0.5	11	nd	nd	<0.5	8	nd	nd	nd	nd	nd	nd	<0.5	15	
S. cf. *rhynchum* Lynn, Montagnes & Small	<0.5	6	nd	nd	<0.5	17	<0.5	17	nd	nd	nd	nd	<0.5	31	nd	nd	
Strombidium sp. 1 *sensu* Bérard-Therriault et al. (1999)	<0.5	19	<0.5	17	nd	nd	<0.5	25	<0.5	67	nd	nd	nd	nd	nd	nd	
Strombidium sp. 3 *sensu* Bérard-Therriault et al. (1999)	nd	nd	<0.5	8	<0.5	8	<0.5	8	nd	nd	nd	nd	<0.5	19	nd	nd	
Strombidium spp. (11-20 µm)	<0.5	6	nd	nd	<0.5	8	<0.5	17	<0.5	8	nd	nd	<0.5	19	nd	nd	
Strombidium spp. (21-50 µm)	<0.5	25	<0.5	47	<0.5	17	<0.5	33	<0.5	25	<0.5	38	<0.5	44	<0.5	15	
Strombidium spp. (>50 µm)	nd	nd	nd	nd	nd	nd	<0.5	17	<0.5	8	nd	nd	nd	nd	<0.5	8	
Tintinnopsis baltica Brandt	<0.5	6	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	8	
T. beroidea Stein	<0.5	6	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	8	

Protist taxon	Fjord								Season							
	Nachvak (16)		Saglek (11)		Okak (10)		Anaktalak (12)		Summer 2007 (12)		Summer 2013 (8)		Early fall (16)		Late fall (13)	
	A	O	A	O	A	O	A	O	A	O	A	O	A	O	A	O
Vorticella spp.	<0.5	6	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	<0.5	6	nd	nd
Ciliates spp. (11-20 µm)	<0.5	**69**	<0.5	**53**	<0.5	**100**	<0.5	**83**	<0.5	25	<0.5	**100**	<0.5	**100**	<0.5	**77**
Ciliates spp. (21-50 µm)	<0.5	**81**	<0.5	39	<0.5	**83**	<0.5	**67**	<0.5	25	<0.5	**100**	<0.5	**69**	<0.5	**85**
Ciliates spp. (>50 µm)	<0.5	13	<0.5	8	<0.5	42	<0.5	33	nd	nd	<0.5	**75**	<0.5	38	nd	nd
Number of species	131		115		107		128		57		57		131		121	
Number of genera	68		56		54		68		26		27		72		64	
Number of taxonomic entries	200		170		163		196		90		101		201		186	

*: This species is often considered photoautotroph (Leadbeater 1974)

CHAPITRE 3

VARIATIONS DE L'ABONDANCE ET DU CONTENU EN ACIDE NUCLÉIQUE DES BACTÉRIES HÉTÉROTROPHES ET DU BROUTAGE DU PHYTOPLANCTON PAR LE MICROZOOPLANCTON DANS LES FJORDS DU LABRADOR, NORD-EST DU CANADA

Ce troisième article scientifique, intitulé « Variations of the abundance and nucleic acid content of heterotrophic bacteria and of phytoplankton grazing by microzooplankton in Labrador fjords, northeastern Canada » a été corédigé par moi-même et le professeur Michel Gosselin. Il est en préparation et sera soumis à la revue *Aquatic Microbial Ecology*.

En tant que premier auteur, j'ai participé aux sorties en mer, au traitement statistique des données et j'ai rédigé cet article. Michel Gosselin a défini la problématique et a contribué à la révision de l'article.

RÉSUMÉ

Cette étude a été réalisée dans quatre fjords du Labrador (Nachvak, Saglek, Okak et Anaktalak) pendant les étés 2007 et 2013, le début de l'automne 2010 et la fin de l'automne 2009. Nous avons évalué l'influence de la température de l'eau et du carbone organique dissous (COD) labile sur l'abondance et l'activité potentielle des bactéries hétérotrophes, déterminé la relation entre l'abondance des nanoflagellés hétérotrophes (HNF) et celle des bactéries hétérotrophes, et estimé le taux de broutage du phytoplancton par le microzooplancton (MZP) en utilisant la méthode de dilution. À l'été 2013, les taux de broutage ont été mesurés à deux profondeurs : la couche de surface (50% de lumière incidente) et la couche de fond (15% à 1% de lumière incidente) de la zone euphotique. Nos résultats ont révélé une influence significative de la température de l'eau et de la biomasse chlorophyllienne sur l'abondance des bactéries hétérotrophes pendant l'été 2013, le début de l'automne et la fin de l'automne. Aucune relation significative n'a été trouvée avec le COD labile. Pour l'ensemble de la période d'étude, nous avons trouvé une relation positive et significative entre l'abondance des HNF et celle des bactéries hétérotrophes. Le taux de croissance intrinsèque du phytoplancton a varié entre <0 jr^{-1} et 0,64 jr^{-1}, avec une moyenne de 0,36 jr^{-1}. Le taux de broutage par le MZP a été très variable durant l'été 2013, allant de 0,01 à 0,86 jr^{-1}, avec un taux moyen de 0,31 jr^{-1}. La mortalité due au broutage a été jusqu'à six fois plus élevée que le taux de croissance du phytoplancton. Les taux moyens de broutage par le MZP dans les fjords du Labrador pendant l'été ont été comparables aux valeurs dans les mers de Barents et de Béring.

Mots-clés : Bactéries hétérotrophes, phytoplancton, microzooplancton, broutage, Arctique, Canada, Labrador, fjords

VARIATIONS OF THE ABUNDANCE AND NUCLEIC ACID CONTENT OF HETEROTROPHIC BACTERIA AND PHYTOPLANKTON GRAZING BY MICROZOOPLANKTON IN LABRADOR FJORDS, NORTHEASTERN CANADA

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ABSTRACT

This study was conducted in four Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during summers 2007 and 2013, early fall 2010 and late fall 2009. We assessed the influence of water temperature and labile dissolved organic carbon (DOC) on the abundance and potential activity of heterotrophic bacteria, determined the relation between heterotrophic nanoflagellates (HNF) and heterotrophic bacteria abundances, and estimated the grazing rate of phytoplankton by microzooplankton (MZP) using the dilution method. In summer 2013, grazing rates were measured at two depths: the surface (50% of surface irradiance) and the bottom (15% to 1% of surface irradiance) layers of the euphotic zone. Our results revealed significant influence of water temperature and phytoplankton chlorophyll *a* biomass on heterotrophic bacteria abundance during summer 2013, early fall and late fall. No significant relation was found with labile DOC. For the whole sampling period, we found a positive and significant relationship between HNF and heterotrophic bacteria abundances. Intrinsic phytoplankton growth rate varied between <0 d^{-1} and 0.64 d^{-1}, with a mean value of 0.36 d^{-1}. MZP grazing rate was highly variable during summer 2013, ranging from 0.01 to 0.86 d^{-1}, with a mean rate of 0.31 d^{-1}. Grazing mortality was up to six times higher than phytoplankton growth rate. Mean phytoplankton growth and MZP grazing rates in Labrador fjords during summer were comparable to values in the Barents and Bering seas.

Keywords: Heterotrophic bacteria, phytoplankton, microzooplankton, grazing, Arctic, Canada, Labrador, fjords

3.1 Introduction

Most abundant organisms on the planet, heterotrophic bacteria are key components of marine food webs and play crucial roles in controlling carbon fluxes in the oceans. In coastal waters, heterotrophic bacteria can consume up to 50% of the primary production (Robinson 2008), which is dissolved (dissolved organic carbon: DOC) by various mechanisms. This DOC becomes almost solely accessible to heterotrophic bacteria and archaea (Ducklow & Carlson 1992), and is called labile DOC, defined as the fraction of DOC which can be decomposed by bacteria within a week or two (Sondergaard & Middelboe 1995).

Many studies have pointed temperature, labile DOC (Amon & Benner 1996, Azam & Malfatti 2007, Kirchman et al. 2009b) and nutrient concentrations (Guildford & Hecky 2000, Sala et al. 2002, Matz & Jurgens 2003) as the main bottom-up factors influencing bacteria dynamics in marine environments. Based on their optimal growth temperature, bacteria found in polar environments are usually psychrophilic or psychrotolerant, the latter organisms being the most frequently found (Hoover & Pikuta 2010). Psychrophilic bacteria have an optimal temperature for growth below 15°C and maximal growth temperature at 20°C. Psychrotolerant bacteria have an optimal temperature between 20-40°C, although they are able to grow at lower temperatures (Hoover & Pikuta 2010). In pelagic marine systems, various organic matter sources contribute to satisfy bacterial DOC demand: phytoplankton exudation (Azam & Cho 1987, Kirchman et al. 1993), phytoplankton spontaneous autolysis (van Boekel et al. 1992), lysis resulting from viral attack (Bratbak et al. 1992), excretion by herbivores (Nagata & Kirchman 1991), sloppy feeding of large zooplankton (Roy et al. 1989), and degradation of fecal material and other detritus (Jumars et al. 1989). It is now well known that heterotrophic bacteria account for a large portion of total uptake of both phosphate and ammonium in marine systems (Kirchman 1994), and under limiting nutrient conditions, they may compete with phytoplankton for inorganic nutrients (phosphate, ammonium and nitrate; Joint et al. 2002). Microzooplankton grazing is also a significant factor influencing bacteria communities. Many studies have shown that

heterotrophic nanoflagellates (HNF), ubiquitous protozooplankton in the size range of 2 to 20 μm, are one of the most important bacterial consumers (Gasol & Vaqué 1993, Nakamura 1994, Lin et al. 2014).

When stained with a fluorescent nucleic acid stain, two different bacterial populations can be identified, according to their nucleic acid content: the low nucleic acid (LNA) bacteria and the high nucleic acid (HNA) bacteria. Due to their higher DNA and RNA content per cell, HNA bacteria display higher fluorescence intensities (Belzile et al. 2008). There is a controversy about the use of nucleic acid content as an indicator of bacterial activity. At one extreme, HNA cells have been shown to have a higher growth rate and be more active than LNA cells (Gasol & del Giorgio 2000, Lebaron et al. 2001, Seymour et al. 2004). At the other extreme, LNA bacteria sometimes considered inactive or dead (Gasol et al. 1999) were found to have an activity as equal as that of HNA bacteria (Zubkov et al. 2004, Longnecker et al. 2005) and even higher in some cases (Zubkov et al. 2001, Jochem et al. 2004).

Despite the key role played by heterotrophic bacteria in organic matter cycling, they have been little studied in the fjords along the Labrador coast, Canada. The objectives of our study were (1) to assess the influence of water temperature, labile dissolved organic carbon and nutrient (nitrate, phosphate and dissolved silicon) concentrations on the abundance and potential activity of heterotrophic bacteria in four Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during the transition from summer to fall, (2) to determine the relation between the abundance of heterotrophic nanoflagellates and that of heterotrophic bacteria, and (3) to estimate the grazing rate of phytoplankton by microzooplankton. This study gives us the opportunity to test the influence of the prymnesiophyte *Phaeocystis pouchetii* (Hariot) Lagerheim, which was abundant in Nachvak Fjord during summer 2013 (see Chapter 2), on the grazing rate of microzooplankton. Indeed, the mucilaginous matrix of this specie seems to be a mechanical hindrance to his consumption (Schoemann et al. 2005).

3.2 Materials and Methods

3.2.1 Study area

The study region is located in Nunatsiavut (meaning "Our Beautiful Land") in the northern part of Labrador (Fig. 1). This vast region is on the eastern seaboard of Canada and extends between 46°N and 60°N, along the Labrador Sea. Sampling was conducted in four fjords: Nachvak, Saglek, Okak and Anaktalak (Fig. 1), influenced by both Atlantic and Arctic water masses. Detailed description of the study area can be found in Simo-Matchim et al. (2016; Chapter 1). Located in the Torngat Mountains National Park, Nachvak is the northernmost fjord in this study and the only glaciated fjord. Saglek Fjord has been the site of a military radar station since 1953 as part of Distant Early Warning (DEW) Line. This leads to an extensive polychlorinated biphenyl (PCB) contamination in soil, sediments and marine environment (Kuzyk et al. 2005a). Okak Bay is occasionally used for travelling and harvesting by the Nain Inuit. Anaktalak Bay is the southernmost site of 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). The duration of the sea-ice cover is ca. 6.6 months yr^{-1} in Nachvak and ca. 6.3 to 6.4 months yr^{-1} in the other inlets (Brown et al. 2012). For the sake of simplicity, Okak and Anaktalak bays will be considered, from here on, as typical fjords, just as Nachvak and Saglek fjords.

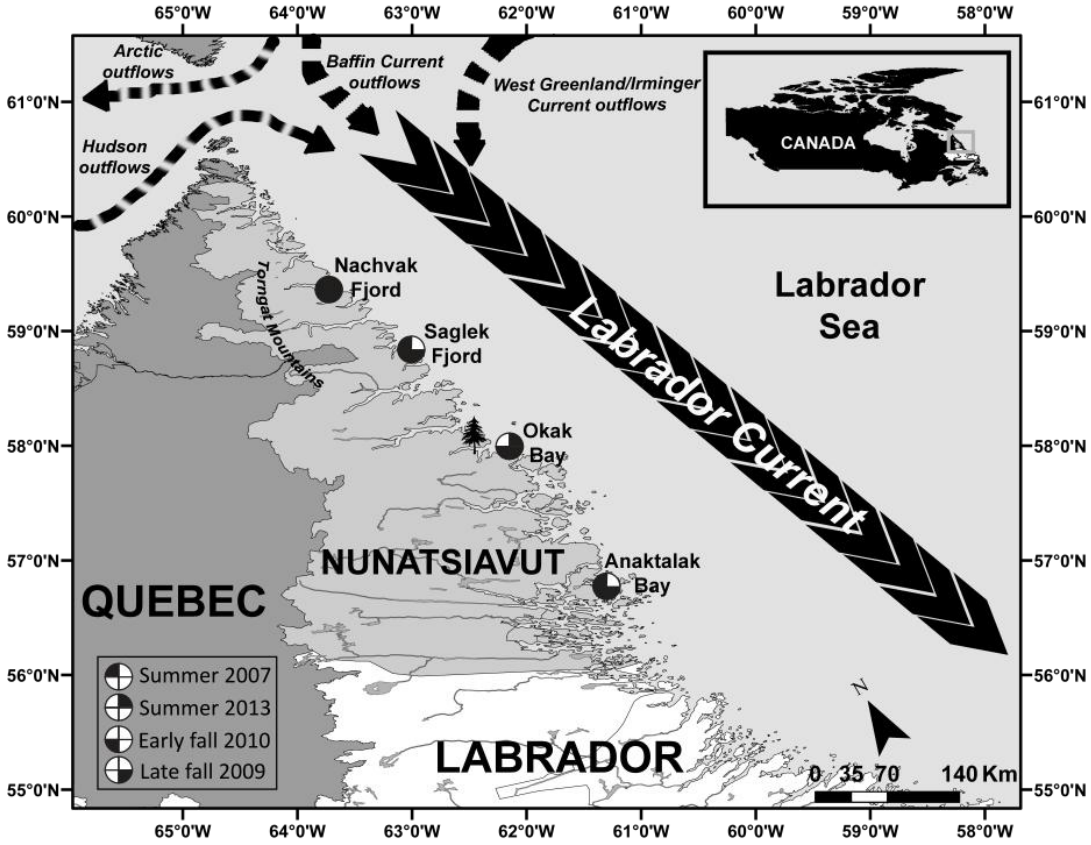

Fig. 1. Sampling periods and location of Nachvak Fjord, Saglek Fjord, Okak Bay and Anaktalak Bay in Nunatsiavut, northern Labrador (adapted from Richerol et al. 2012)

3.2.2 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*. Hereafter, these sampling periods are referred to as summer 2007, summer 2013, early fall and late fall, respectively. Sampling was carried out at the inner and the outer stations of each fjord. Table 1 presents the geographical position and sampling period for each station. At each station, downwelling photosynthetically active radiation (PAR, 400-700 nm) underwater profile was performed 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.

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 fjords during summer 2013

Fjord	Station	Position	Latitude (°N)	Longitude (°W)	Water depth (m)	Sampling period
Nachvak	602	Inner	59° 4.5’	63° 25.5’	158	Summer 2007 Summer 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	

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 measure water temperature, salinity and *in vivo* chlorophyll fluorescence from the surface to about 10 m from the bottom.

Water samples were collected at seven optical depths (95, 50, 30, 15, 5, 1 and 0.2% of surface irradiance), as well as at the subsurface fluorescence maximum (SCM) depth, and at 75 m and 100 m in the aphotic zone for the determination of nutrients, dissolved organic carbon (DOC), total dissolved nitrogen (TDN) chlorophyll (chl) *a*, primary production and bacterial abundances. Water samples for the dilution experiments in 2013 and the determination of protist abundances were taken at two depths (50% of surface irradiance and 15% to 1% of surface irradiance), one of which was the SCM depth. For the sake of simplicity, these two depths are hereafter respectively referred to as the surface and the bottom layers of the euphotic zone.

3.2.3 Laboratory analyses

Nutrients

Triplicate samples for dissolved inorganic nutrients were filtered through Whatman GF/F glass-fiber filters (nominal pore size of 0.7 μm) and the filtrate was collected in 15 ml acid-washed polyethylene tubes. Nutrient samples were directly analyzed or stored in a –80°C freezer for later analyses of nitrate plus nitrite (NO_3+NO_2), nitrite (NO_2), phosphate (PO_4) and silicic acid ($Si(OH)_4$) concentrations using a Bran-Luebbe 3 autoanalyzer (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).

Dissolved organic carbon (DOC) and total dissolved nitrogen (TDN)

In 2007 and 2009, seawater was filtered through a precombusted (450°C for 5 h) 25 mm Whatman GF/F filter and the filtrate was collected in 5 ml Kimble Brand borosilicate vials with Teflon-lined caps previously cleaned 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^oC until analysis. DOC was determined on a high-temperature combustion Shimadzu TOC-5000A analyzer using the analysis procedure given in 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 kept in the dark at 4^oC until analysis with a Shimadzu TOC-V_{CPN} analyzer with a total nitrogen measuring unit (TNM-1), following the precautions given in Benner & Strom (1993). Potassium hydrogen phthalate and potassium nitrate were used to standardize DOC and TDN measurements. In addition, samples were systematically checked against low carbon (1 µM) and nitrogen (0 µM) water and Florida Strait at 700 m reference water (41–44 µM C and 31-33 µM N) every seventh sample analysis. These seawater DOC reference standards were produced by the Hansell's certified reference materials (CRM) program (http://yyy.rsmas.miami.edu/groups/biogeochem/CRM.html). The mean DOC of three replicate injections of each water sample showed a typical coefficient of variation of 3%.

The fraction of labile DOC (DOC_L) was estimated using the equation of Sondergaard & Middelboe (1995):

$$\mathbf{DOC_L = 0.19 \times DOC_T} \qquad \mathbf{(1)}$$

where DOC_T is total dissolved organic carbon.

Dissolved organic nitrogen (DON) was estimated as follow:

$$\mathbf{DON = TDN - (NO_3 + NO_2)} \qquad \mathbf{(2)}$$

Bacteria abundance

Duplicate subsamples were fixed with 0.1% final concentration glutaraldehyde Grade I (Sigma), stored in liquid nitrogen onboard the ship, and kept frozen at -80°C until analysis by flow cytometry (Marie et al. 2005). Using a 488 nm laser (15 mW output; blue), planktonic cyanobacteria, which fluoresce at 570 nm (orange), were distinguished from eukaryotes, which fluoresce at 690 nm (red). In each subsample, microspheres (1 µm and 2 µm, Fluoresbrite plain YG, Polysciences) were added as an internal standard and allowed to verify there was no degradation of the side scatter signal despite the relatively high flow rate used (Tremblay et al. 2009). Heterotrophic bacteria were stained with SYBR Green I and measured at 525 nm to detect low and high nucleic acid content (Belzile et al. 2008). Analyses were performed on an Epics Altra flow cytometer (Beckman Coulter) using Expo32 v1.2b software (Beckman Coulter). Sampled volume was quantified by weighing a subsample before and after processing. Archaea could not be discriminated from bacteria using this protocol; therefore bacterial abundances include both archaea and bacteria.

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 stored in the dark at 4°C until analysis. Cells were identified to the lowest possible taxonomic rank using an inverted microscope (Zeiss Axiovert 10) according to Lund et al. (1958). For each sample, a minimum of 400 cells (accuracy ± 10%) and three transects were counted at a magnification of 200× and 400×. The main taxonomic references used to identify the protist cells were Tomas (1997) and Bérard-Therriault et al. (1999).

Phytoplankton biomass

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

Primary production

Primary production was estimated by the ^{14}C-assimilation method (Knap et al. 1996, Ferland et al. 2011) using *in situ* simulated incubations during summer 2013. Two light and one dark 500 ml Nalgene polycarbonate bottles were filled with seawater from each light level and then inoculated with 20 μCi of $NaH^{14}CO_3$. The dark bottle contained 250 μl of 0.02 M 3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU, Legendre et al. 1983). Bottles were incubated for 24 h, generally starting in the morning (Mingelbier et al. 1994), in a Plexiglas deck incubator, under simulated *in situ* conditions, with running surface seawater. At the end of the incubation period, 250 ml were 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 polycarbonate membrane filters (referred to as production of large phytoplankton 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 incorporated (Lean & Burnison 1979). Subsequently, 10 ml of Ecolume scintillation cocktail was added to each vial. The activity of each sample was determined using a Packard Tri-Carb 2900 TR liquid scintillation counter. Production rates of particulate organic carbon were calculated according to Parsons et al. (1984). Production of small phytoplankton (P_S, 0.7–5 μm) was obtained by subtracting P_L from P_T.

Dilution experiments

Dilution experiments were carried out in summer 2013 following the two-point dilution method adapted to shipboard use of Landry et al. (2011). We realized three different treatments at two depths (surface and bottom layers of the euphotic zone): (1) a mixture of 25 to 55% of whole seawater diluted with filtered seawater from the same depth to which nutrients were added, (2) unfiltered seawater (100%) with nutrient enrichment, and (3) unfiltered seawater (100%) without nutrient enrichment. Nutrients were added in two treatments because previous studies in Labrador fjords have indicated a potential limitation of phytoplankton by nutrients (Simo-Matchim et al. 2016, Chapter 1). 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.

Microzooplankton grazing rate (g; d^{-1}) and phytoplankton intrinsic growth rate (μ; d^{-1}) were calculated using the following equations (Sherr et al. 2013):

$$\mathbf{g = (k_d - k) / (1 - x)} \quad \mathbf{(3)}$$

$$\mathbf{\mu = k + g} \quad \mathbf{(4)}$$

where k_d is the chl *a*-based growth rate (d^{-1}) in the diluted treatment, k is the chl *a*-based growth rate (d^{-1}) in the 100% (unfiltered seawater) treatment and x is the fractional dilution used in the diluted treatment.

Whole seawater (WSW) was gently transferred from Niskin-type bottles into 20 l carboys through silicone tubing. A 350 μm net was attached at the end of the tube to exclude large grazers. Care was taken to avoid bubbles in the tubing as the carboys were filled. After sampling WSW, all other preparation steps were carried out under dim light. For dilutions, filtered seawater (FSW) was prepared by successive gravity filtration of WSW through a 5 μm cartridge and a 0.2 μm pore-size cartridge (Pall-Gelman Suporcap);

both cartridges were presoaked in 5% HCl for 8 h and thoroughly rinsed with deionized water. Five liters of WSW were passed through the cartridges before beginning the collection of FSW for the dilutions.

FSW was added to a carboy and WSW was gently added to yield the corresponding dilution. WSW was also collected in two other carboys for the two 100% treatments. Nutrients were added in the two enriched treatments and the carboys were then gently mixed. Triplicate 2 l acid-washed polycarbonate bottles were filled for each treatment using a silicone tube, starting from the unamended treatment. A 2 l bottle was also filled with the FSW. During this process, the end of the silicone tube was always submerged to avoid bubbles. Then, Parafilm was placed on top of each bottle before securing the cap, in order to minimize air bubbles in the bottles, as protist cells can lyse on contact with air (Gifford 1988). Prior to the treatments, the bottles were wrapped with black screen to mimic the approximate *in situ* light intensity of the sampled depth. Bottles were incubated for 24 h in a Plexiglas deck incubator with running surface seawater. Temperature in the incubator was continually monitored.

Initial samples were taken directly from the carboy of the corresponding treatment for the determination of nutrient and DOC concentrations, bacterial and protist cell (>2 μm) abundances and chl *a* concentration. Initial samples of the FSW were also taken. At the end of the incubation, final samples were collected from all the 2 l bottles for the determination of the variables listed previously. The FSW was analyzed to check if the cartridges have let go microorganisms and if they have multiplied during the incubation. Except for chl *a* concentration, data of the initial samples and the other data at the end of the incubation are not presented in this manuscript. In this study, the microzooplankton community includes heterotrophic protists (i.e., flagellates, ciliates and phagotrophic dinoflagellates) and metazoans <350 μm in size.

Prior to these manipulations, all carboys, bottles and silicone tubes were soaked overnight with 10% HCl and thoroughly rinsed with deionized water. The silicone tubing was further rinsed with FSW and WSW 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 WSW just before each experiment. Between experiments, all material was protected in plastic bags. Disposable polyethylene gloves were worn during experimental set-up. At all sampling stations, experiments were conducted immediately after collection of seawater, except at inner Nachvak (station 602), where WSW was kept at 4°C during 9 h before starting the treatment because the incubation of the previous station was still running and the 2 l bottles were thus occupied. During the storage at 4°C, no treatment (nutrient enrichment or dilution) was done on the WSW.

3.2.4 Calculations

At each station, temperature was averaged in the upper 100 m of the water column (or in the entire water column in <100 m water depth). Bacteria abundances, nutrient and labile DOC concentrations were integrated over the upper 100 m of the water column (or entire water column in <100 m water depth) using the trapezoidal method (Knap et al. 1996). Phytoplankton production and biomass were integrated over the Z_{eu} using the trapezoidal method. Phytoplankton intrinsic growth (μ) and microzooplankton grazing (g) rates in the incubated triplicate bottles were averaged to have one final value for each set of triplicates.

3.2.5 Statistical analyses

Pearson's correlation coefficient (r) and model II linear regression (reduced major axis) were used to evaluate the relationship between two variables (Sokal & Rohlf 1995). These tests were carried out using SigmaPlot version 12.5 software.

3.3 Results

3.3.1 Environmental and biological 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 while the minima were noted at inner Nachvak (-0.22°C) during late fall and inner Saglek (-0.17°C) during summer 2007 (Table 2). In the upper 100 m of the water column, mean labile DOC concentrations were relatively constant over the study period, with values ranging from 3.6 µM at inner Okak during late fall to 20.8 µM in 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 fjords (Okak and Anaktalak; Table 2).

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

3.3.2 Bacteria abundance

During the whole sampling period, cyanobacteria abundances were extremely low, making <0.01% to 0.08% of total (autotrophic plus heterotrophic) bacteria abundance. Therefore, only heterotrophic bacteria were considered in the present study. Overall, the profiles of heterotrophic bacteria abundances (Fig. 3) followed those of phytoplankton chlorophyll *a* biomass (Fig. 2). The distribution of bacteria was vertically uniform at inner Saglek during summer 2007 and at most stations during late fall (Fig. 3a, g, h), while it showed large variations in other cases (Fig. 3b-f). The lowest (0.11×10^9 cells l^{-1}) and highest (2.3×10^9 cells l^{-1}) heterotrophic bacteria abundances were registered during summer 2007 (Fig. 2a, b).

Areal heterotrophic bacteria abundances ranged from 7.5×10^{12} cells m^{-2} at inner Okak during summer 2013 to 115.9×10^{12} cells m^{-2} at outer Saglek during early fall (Table 2; Fig. 4b, c). During the whole study period, bacteria with high nucleic acid content (HNA) dominated the bacterial 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 (Table 2, Fig. 4b, d).

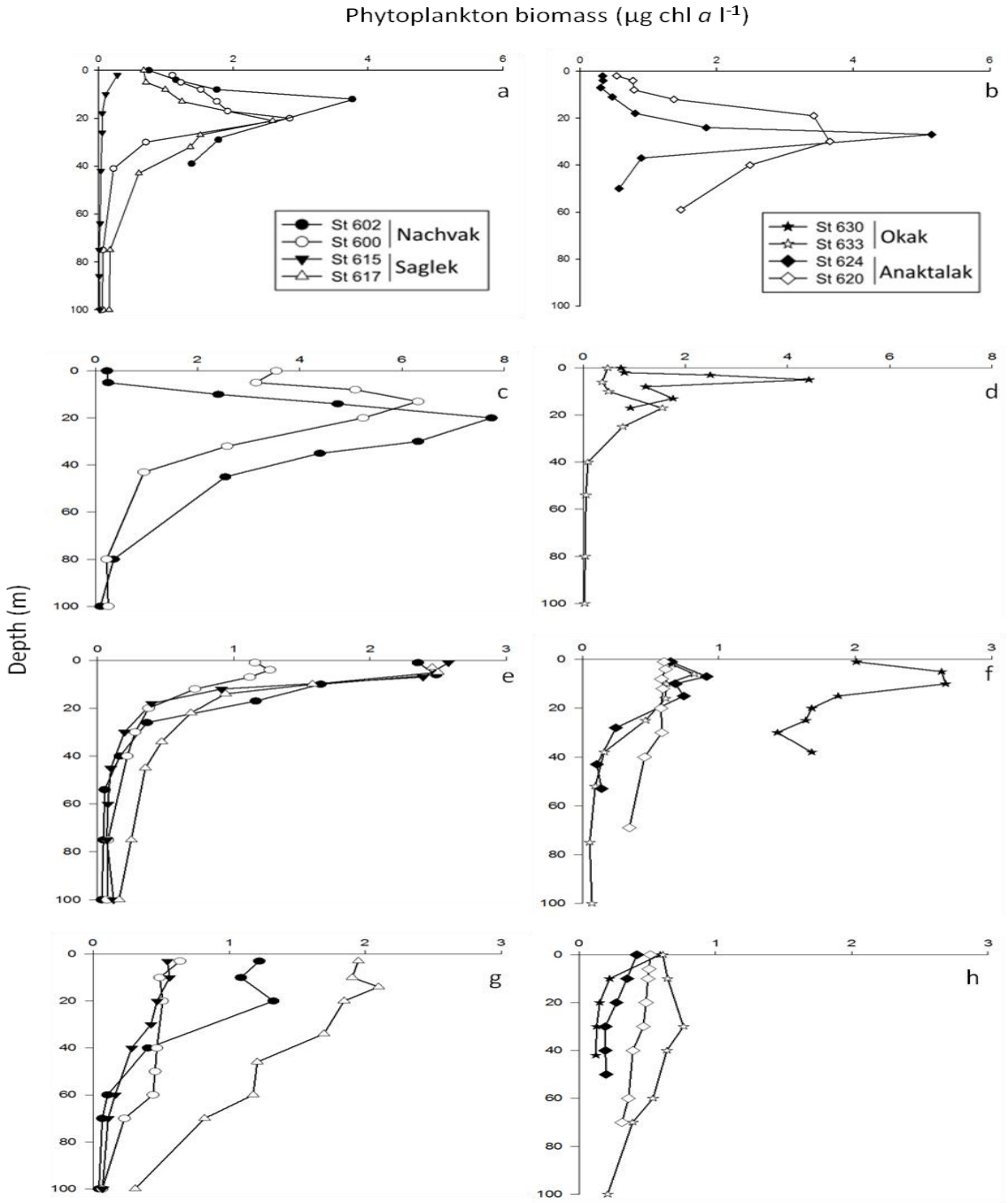

Fig. 2. Vertical profiles of the chlorophyll *a* concentration in Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during (a, b) summer 2007, (c, d) summer 2013, (e, f) early fall and (g, h) late fall. Black symbols represent the inner stations and white symbols the outer stations

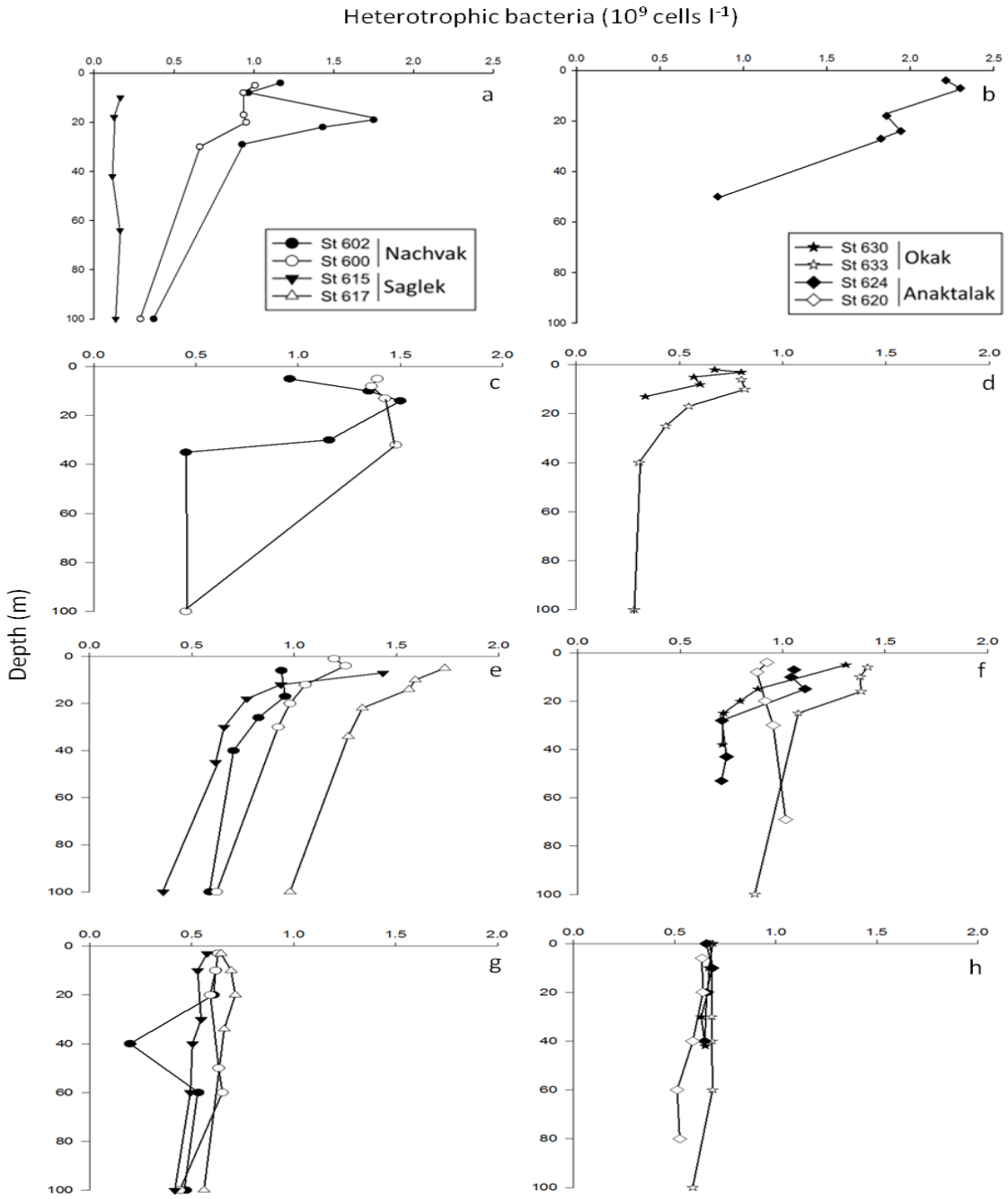

Fig. 3. Vertical profiles of the total abundance of heterotrophic bacteria in Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during (a, b) summer 2007, (c, d) summer 2013, (e, f) early fall and (g, h) late fall. Black symbols represent the inner stations and white symbols the outer stations

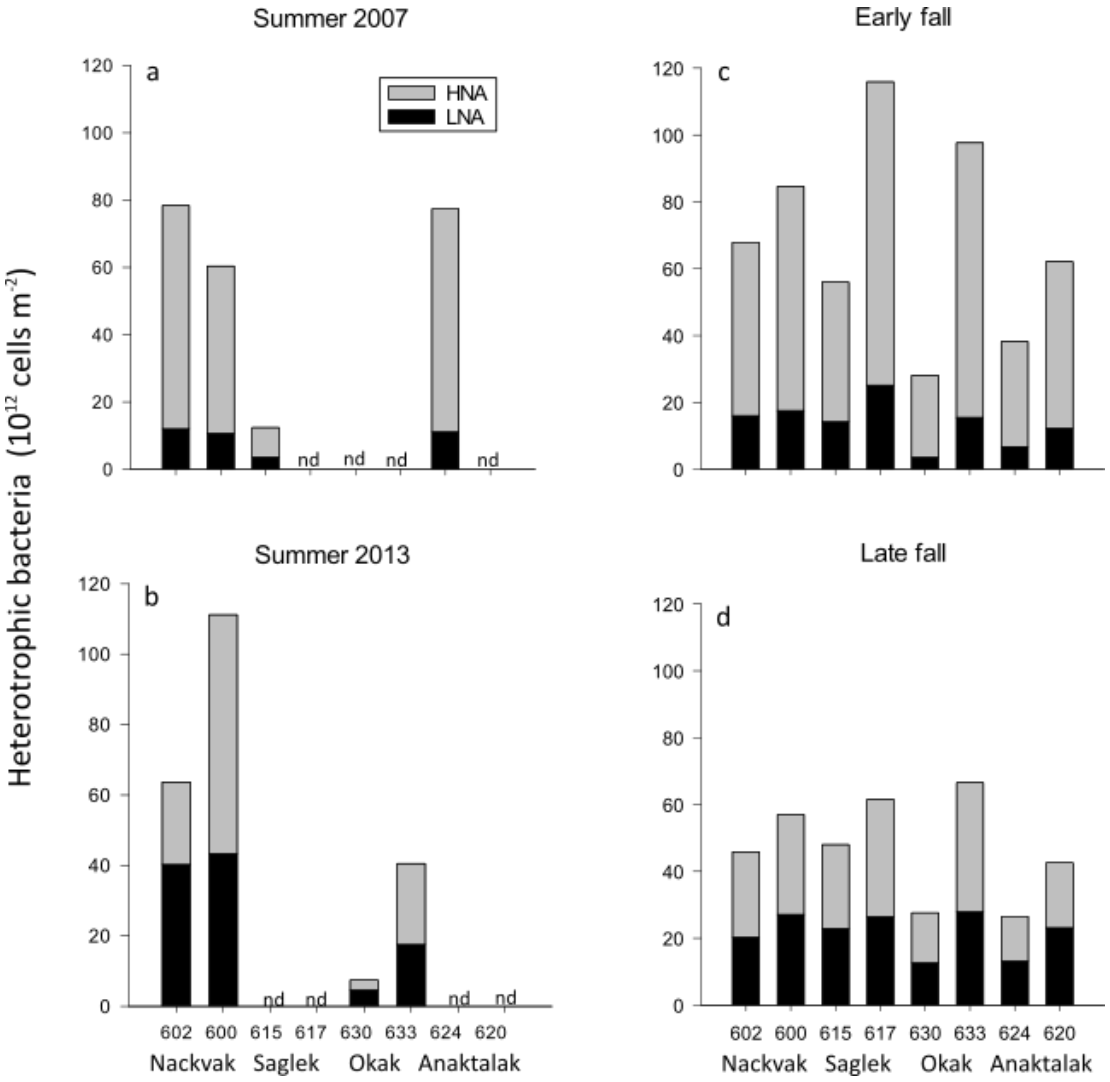

Fig. 4. Variations in total heterotrophic bacteria abundance in Nachvak, Saglek, Okak and Anaktalak fjords during (a) summer 2007, (b) summer 2013, (c) early fall and (d) late fall. Abundances of bacteria with high (HNA) and low nucleic acid (LNA) content were integrated over the upper 100 m of the water column (or the entire water column in <100 m water depth), except at stations 602 and 630 during summer 2013 where they were integrated over the euphotic zone. nd: data not available

Table 2. Environmental and biological conditions in Nachvak, Saglek, Okak and Anaktalak fjords during summer 2007, summer 2013, early fall and late fall. T: water temperature averaged over the upper 100 m of the water column (or entire water column in <100 m water depth); DOC_L: labile 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 bacteria abundance; HNA bacteria: percentage of high nucleic acid (HNA) bacteria. Values were integrated over the upper 100 m of the water column (or entire water column in <100 m water depth). Mean integrated concentrations are given for DOC_L and nutrients. *: values calculated for the euphotic zone

	Station	T (°C)	DOC_L (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	15.8	5.20	6.96	0.62	124.8	82.7	84.7
	600	0.47	20.8	4.96	6.38	0.52	61.7	60.4	82.4
	615	-0.17	11.3	4.77	5.85	0.82	4.7	13.9	71.4
	624	2.16	15.0	1.93	3.67	0.49	66.6	86.4	85.2
Summer 2013	**602**	0.02	13.3	5.82	8.23	0.88	340.8	63.7*	36.9*
	600	1.02	11.6	4.13	5.86	0.73	222.6	111.1	61.0
	630	2.05	12.4	2.38	6.16	0.53	43.2	7.5*	37.9*
	633	0.83	13.3	2.83	4.94	0.6	41.5	40.5	56.8
Early fall	**602**	1.19	13.5	7.23	8.23	1.36	46.5	67.8	76.4
	600	1.90	15.8	5.62	7.28	1.17	30.0	84.6	79.3
	615	0.96	12.3	4.80	7.08	1.0	40.0	56.0	74.7
	617	2.46	13.4	3.06	5.89	0.89	59.6	115.9	78.3
	630	1.21	13.5	2.71	6.52	1.01	73.5	28.1	87.2
	633	2.79	15.7	2.81	5.34	0.87	24.7	97.7	84.2
	624	2.67	13.8	3.58	6.33	0.92	21.6	38.2	82.2
	620	3.56	14.3	0.85	1.73	0.28	34.3	62.1	80.3
Late fall	**602**	-0.22	13.7	9.69	10.73	1.05	48.4	45.9	55.6
	600	-0.07	14.1	6.95	8.03	0.84	37.2	57.0	52.4
	615	-0.14	14.8	5.94	8.57	0.92	25.5	48.0	52.3
	617	0.26	14.1	4.33	5.87	0.75	124.9	61.5	57.1
	630	0.92	3.6	4.90	7.31	0.80	8.8	27.6	54.4
	633	0.74	15.1	3.35	4.76	0.74	53.0	66.5	58.1
	624	1.41	16.6	4.29	6.18	0.63	13.2	26.5	50.4
	620	0.20	7.4	2.75	3.61	0.49	35.5	42.6	45.7

3.3.3 Phytoplankton production and heterotrophic protist community during summer 2013

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. 5a). Total phytoplankton chl *a* biomass varied between 39 mg chl *a* m^{-2} and 217 mg chl *a* m^{-2} at outer Okak and inner Nachvak, respectively (Fig. 5b). 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. 5). The production:biomass ratio (P_T:B_T) ranged from 4.6 to 26.3 mg C mg chl *a* d^{-1} at the inner and outer stations of Nachvak Fjord, respectively.

Ciliates and heterotrophic dinoflagellates from ca. 12 µm to 200 µm in size are dominant herbivores in planktonic food webs, whereas heterotrophic nanoflagellates (HNF), including choanoflagellates, are key bacterial grazers (Calbet & Landry 2004, Sherr et al. 2013). During summer 2013, the heterotrophic protistan community in Nachvak and Okak fjords was composed of ciliates, heterotrophic dinoflagellates, choanoflagellates, unidentified flagellates (<20 µm) and other heterotrophic groups. Ciliates were dominated by the spirotrichs of the genera *Stombidium* Claparède & Lachmann, *Laboea* Lohmann and *Balanion* Wulff, and the choreotrichid *Lohmanniella oviformis* Leegaard. The main phagotrophic dinoflagellates were *Heterocapsa rotundata* (Lohmann) Hansen and *Gymnodinium*/*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.

Detailed information on phytoplankton dynamics and taxonomic composition of planktonic protists during summers 2007 and 2013, early fall and late fall are available in Simo-Matchim et al. (2016) and in Chapters 1 and 2 of this thesis.

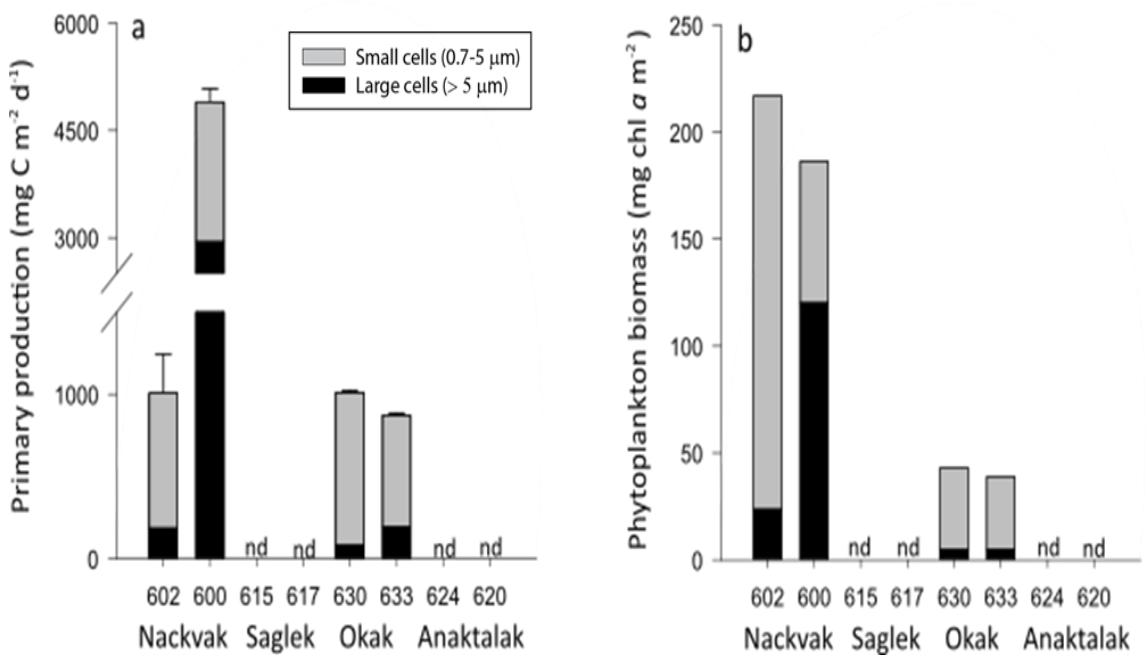

Fig. 5. Variations in (a) primary production and (b) phytoplankton chlorophyll *a* biomass in Nachvak and Okak fjords during the grazing experiments of summer 2013. Production and biomass of small (0.7-5 µm) and large cells (≥5 µm) were integrated from the surface down to 0.2% of surface irradiance. In (a), vertical lines represent the standard deviation of the estimated rates. nd: no data available

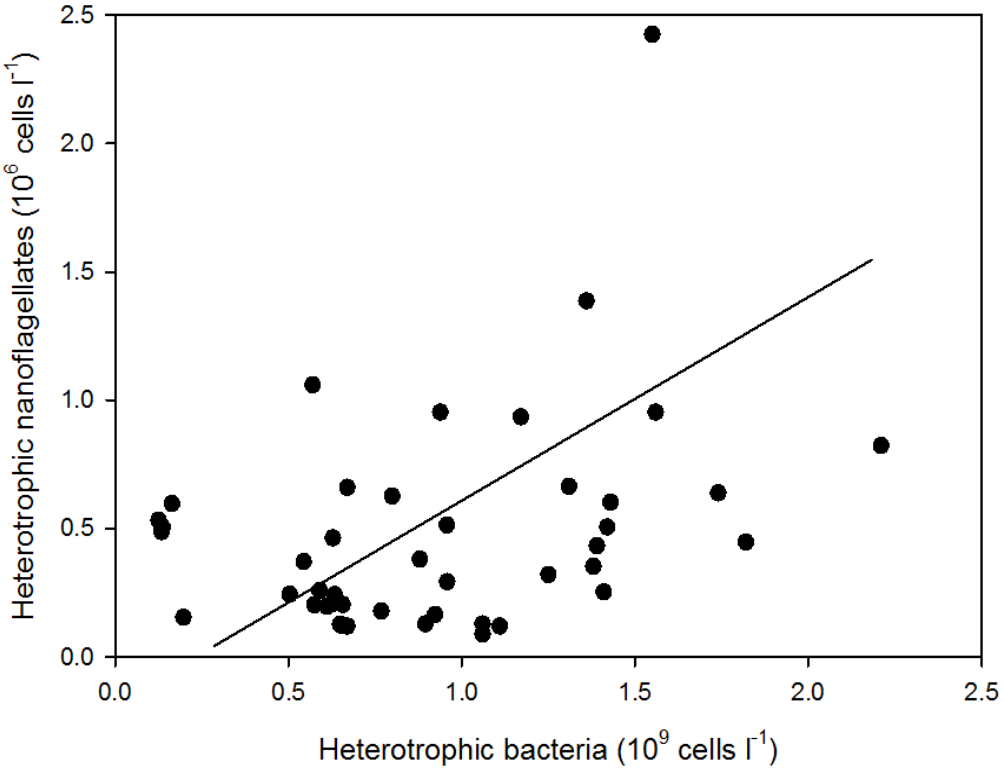

Fig. 6. Regression between heterotrophic nanoflagellate abundance and total heterotrophic bacteria abundance in Nachvak, Saglek, Okak and Anaktalak fjords during the whole study period (summers 2007 and 2013, early fall and late fall). Heterotrophic nanoflagellates include choanoflagellates, unidentified flagellates and the other heterotrophic cell group. The equation of the reduced major axis (model II) regression is: $x_2 = (0.87\ x_1 - 0.33) \times 10^{-3}$, $r^2 = 0.12$, $p < 0.05$

3.3.4 Relationships between phytoplankton biomass, heterotrophic bacteria and heterotrophic protists

A correlation analysis was performed using data from the surface and bottom layers of the euphotic zone. Total heterotrophic bacteria were significantly correlated with chl *a* during summer 2013 ($r = 0.24$, $p < 0.05$), with water temperature ($r = 0.33$, $p < 0.001$), primary production ($r = 0.34$, $p < 0.001$) and chl *a* ($r = 0.24$, $p < 0.001$) during early fall, and with water temperature ($r = 0.28$, $p < 0.001$) and chl *a* ($r = 0.14$, $p < 0.05$) during late fall. Choanoflagellate abundance was significantly correlated with chl *a* during early fall ($r = 0.43$, $p < 0.01$) and late fall ($r = 0.68$, $p < 0.001$), whereas ciliates and dinoflagellates were correlated to chl *a* during late fall ($r = 0.55$, $p < 0.01$; $r = 0.34$, $p < 0.05$, respectively).

For the whole study period, heterotrophic nanoflagellate (HNF) abundances varied between 0.08×10^6 cells l^{-1} and 2.4×10^6 cells l^{-1}, while total heterotrophic bacteria abundances ranged from 0.11×10^9 to 2.3×10^9 cells l^{-1}. HNF showed a significant positive linear regression with total heterotrophic bacteria (Fig. 6). However, this relationship was not significant when tested for each sampling period separately. A significant correlation between ciliate abundance and total heterotrophic bacteria was also found during summer 2007 ($r = 0.70$, $p < 0.01$).

During summer 2013, areal abundances of total heterotrophic bacteria and HNA bacteria were positively correlated with total dissolved nitrogen, NO_3+NO_2 and PO_4 ($r = 0.96$, $p < 0.05$ for each correlation). No significant correlation was found for LNA bacteria. During late fall 2009, areal abundances of total heterotrophic bacteria and HNA bacteria were positively correlated with phytoplankton chl *a* biomass ($r = 0.70$, $p < 0.05$; $r = 0.72$, $p < 0.05$; respectively). No other significant correlation was found.

3.3.5 Dilution assay results

A total of 8 dilution experiments were performed in Nachvak and Okak fjords during summer 2013 (Table 3). Water temperature and NO_3+NO_2 concentration at the sampling depth as well as chl *a* concentration at the beginning of the experiments are shown in Table 3. In the 100% (unfiltered seawater) treatments, the net rate of change of chl *a* was generally higher in the bottles with nutrient amendment (k_1) than in those without (k_2). Phytoplankton intrinsic growth rates (μ) varied between <0 d^{-1} and 0.64 d^{-1}, with a mean value of 0.36 d^{-1}. Microzooplankton grazing (g) 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 6. The highest phytoplankton intrinsic growth rate and lowest microzooplankton grazing rates were both observed in Nachvak Fjord (Table 3).

Table 3. Summary of dilution assay experiments conducted in Nachvak and Okak fjords during summer 2013. (T) water temperature and NO_3+NO_2 concentration at the sampling depth; chl *a*: initial phytoplankton chlorophyll *a* biomass in the whole (unfiltered) seawater; x: fractional dilution used in the diluted treatment; k_d: chl *a*-based growth rate in the diluted treatment with nutrient amendment; k_1 and k_2: chl *a*-based growth rate in the 100% (unfiltered seawater) treatment with and without nutrient amendment, respectively; μ: phytoplankton intrinsic growth rate; g: microzooplankton grazing mortality; g:μ: ratio of grazing to growth rate. μ and g were calculated using k_d and k_1. At each station, samples were collected at the surface (S) and bottom (B) layers of the euphotic zone.

Station	**Sampling depth (m)**	**T (°C)**	**NO_3+NO_2 (μM)**	**chl *a* ($\mu g\ l^{-1}$)**	x	**k_d (d^{-1})**	**k_1 (d^{-1})**	**k_2 (d^{-1})**	**μ (d^{-1})**	**g (d^{-1})**	**g:μ**
Nachvak											
602-S	2	2.3	0.93	1.05	0.34	-0.80	-1.26	-1.34	< 0	0.69	-
602-B	20	-0.3	1.41	0.24	-	-	-	-	-	-	-
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	-
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

3.4 Discussion

3.4.1 Control of bacteria abundance and potential activity

Temperature is an ever-present factor influencing bacterial abundance, production and specific growth rate in aquatic environments (White et al. 1991). Warm, productive and 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 good agreement with various studies indicating a positive relation between water temperature, substrate availability and bacteria abundances (Pomeroy et al. 1991, Pomeroy & Wiebe 2001). In addition, Kirchman et al. (2009a, 2009b) have shown that water temperature along with the supply of labile organic substrates and inorganic nutrients (e.g., phosphate) are the main factors controlling bacterial growth and activity in polar waters.

Although labile DOC did not show any significant relation with bacteria abundances, they were positively correlated with primary production and chl *a* concentration. Bird & Kalff (1984) showed that bacterial abundances are well correlated with chl *a* concentration in marine systems. These correlations indicate that a considerable fraction of the organic matter released via phytoplankton exudation, lysis and grazing, as labile DOC, is taken up by bacteria.

During this study, bacterial abundance was positively correlated with phosphate concentration. Due to the important freshwater influence, heterotrophic bacteria in estuarine systems and fjords may experience physiological phosphorus-deficiency (Thingstad et al. 1993). Phosphorus limitation may thus exert a tight control on bacterial DOC utilization in estuarine systems (Kritzberg et al. 2010).

Compared to summer 2007, *Phaeocystis pouchetii* were 10 times more abundant during summer 2013. However, the proportion of HNA bacteria in the total bacterial community was lower during summer 2013 (37%) than during summer 2007 (85%). This indicates a possible inhibitory effect of *P. pouchetii* on HNA bacteria, the bacterial group

potentially larger and more active than LNA bacteria. This inhibitor may be acrylic acid released by *P. pouchetii*. Indeed, when this species is grazed or stressed, its cellular dimethylsulfoniopropionate (DMSP) is converted by an extracellular membrane-bound DMSP-lyase into equimolar amounts of the volatile dimethylsulfide (DMS) and acrylic acid, this later compound being known for its ability to inhibit bacteria growth (Schoemann et al. 2005, Curson et al. 2014). However, since other studies have indicated that acrylic acid is an organic substrate that can be consumed by heterotrophic bacteria (Putt et al. 1994, Noordkamp et al. 1998, 2000), the link between bacterial dynamics and *Phaeocystis* colonies needs further investigations.

3.4.2 Relation between heterotrophic nanoflagellates and bacteria

The positive and significant relationship we found between heterotrophic nanoflagellates (HNF) and bacteria suggests a strong bottom-up control of the nanograzers by bacteria. This positive relation has been previously reported in many studies (Sherr et al. 1984, Sanders et al. 1992, Lin et al. 2014). However, the variance explained by this regression model is low ($r^2 = 0.12$). Gasol & Vaqué (1993) proposed three reasons to explain the lack of a strong correspondence between HNF and bacteria: (1) organisms other than HNF (e.g., small ciliates) are important predators of bacteria and other loss processes (e.g., viral mortality) could be more important than predation; (2) HNF may use carbon sources other than bacteria in aquatic systems, such as picophytoplankton and labile DOC which are abundant in the Labrador fjords, and (3) significant top-down control on HNF by large ciliates, phagotrophic dinoflagellates or small metazoans may limit their grazing pressure on bacteria.

3.4.3 Growth and grazing processes

The dilution technique is based on three fundamental assumptions: (1) the intrinsic growth of phytoplankton is the same in all treatments (i.e., it is independent of cell density); (2) MZP grazing rate is proportional to the encounter rate of grazers with prey cells (i.e., the more diluted the sample is, the more the grazing pressure is reduced); (3) change in phytoplankton density is assumed to be represented appropriately by the exponential equation given in Landry & Hassett (1982). It is important to distinguish the net growth rate (also called apparent growth rate, k) from the intrinsic growth rate (also called instantaneous growth rate, μ) calculated in this study. The intrinsic growth rate is obtained by adding the MZP grazing rate to the net growth rate of phytoplankton.

Mean phytoplankton intrinsic growth rate in Labrador fjords (0.36 d^{-1}) was very similar to the Barents Sea (0.32 d^{-1}; Verity et al. 2002) and the Bering Sea (0.35 d^{-1}; Strom & Fredrickson 2008) during summer. The mean rate of MZP grazing in Labrador fjords (0.31 d^{-1}) was also comparable to the Barents Sea (0.24 d^{-1}; Verity et al. 2002) and the Bering Sea (0.43 d^{-1}; Olson & Strom 2002) during summer. In addition, we consider our grazing rate similar to the mean value of 0.41 d^{-1} estimated by Calbet & Landry (2004) in subpolar oceanic regions. However, summer MZP grazing in Labrador fjords was high compared to the mean value of 0.09 d^{-1} calculated in the Arctic Ocean by Sherr et al. (2013).

Overall, phytoplankton growth rates responded positively to nutrient addition, as the chl *a*-based growth rates were generally higher in the treatments with added nutrients (k_1) than in those without (k_2). However, the increase in phytoplankton growth due to nutrient addition seemed to be insufficient to compensate the losses owed to grazing. During this study, we calculated two negative rates of phytoplankton growth during summer (see samples 602-S and 630-S in Table 3). Recently, Stoecker et al. (2015) showed that the preparation of filtered seawater from water containing high biomass of phytoplankton often results in the release of allelochemicals that inhibit phytoplankton growth. Under some conditions, dilution grazing experiments may underestimate phytoplankton growth

coefficients and microzooplankton grazing coefficients. According to these authors, polyunsaturated aldehydes (PUA) produced by *Phaeocystis pouchetii* notably during late stages of a bloom have a self-inhibitory effect. In addition, it has also been shown that grazing could stimulate the production of many inhibitory allelochemicals (Ribalet et al. 2009, 2014). PUA released by *P. pouchetii* are inhibitory not only for phytoplankton species (Pohnert 2000, Hansen & Eilertsen 2007) but also for zooplankton growth (Pohnert et al. 2002, Ianora & Miralto 2010). Inhibitory effects are most likely to occur during dense phytoplankton blooms. An intense bloom of *P. pouchetii* (up to 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 the euphotic zone at the inner and outer stations of Nachvak Fjord, respectively (Simo-Matchim et al. 2016, Chapters 1 & 2). We argue that such inhibition of phytoplankton growth or grazing rate by PUA may have occurred during summer 2013 in Nachvak Fjord where integrated chl *a* biomass was very high, reaching 217 mg m^{-2}.

One of the issues addressed in this study was the influence of *P. pouchetii* on MZP grazing rate. Indeed, various studies indicated low (Calbet et al. 2011) or negative (Stoecker et al. 2014) MZP grazing rates during summer blooms of *P. pouchetii*, supporting the suggestion of Schoemann et al. (2005) that the mucilaginous matrix of *P. pouchetii* seems to be a mechanical hindrance to his consumption. The relatively high MZP grazing rate (0.69 d^{-1}) estimated at inner Nachvak where the intense bloom of *P. pouchetii* was observed disagree with such conclusions. However, considering the novel data published by Stoecker et al. (2015), results of dilution experiments performed during late stages of *P. pouchetii* bloom need to be interpreted with caution.

During this study, we estimated the grazing activity of herbivorous microzooplankton. It should be remember that microzooplankton may also feed on non-algal preys. Indeed, several studies indicated that ciliates (Verity 1991) and heterotrophic dinoflagellates (Jeong et al. 2007) can consume choanoflagellates, which were, interestingly, also abundant at inner Nachvak (see Chapter 2).

3.5 Conclusion

In Labrador fjords, we found significant influence of water temperature and phytoplankton chl *a* biomass on the vertical distribution of heterotrophic bacteria. The abundances of heterotrophic nanoflagellates were positively related to those of heterotrophic bacteria, showing a bottom-up control of nanograzers by bacteria throughout the study period. During summer 2013, phytoplankton intrinsic growth and microzooplankton grazing rates were highly variable but comparable to values reported in other Arctic seas such as Barents and Bering seas. The elevated abundance of the prymnesiophyte *Phaeocystis pouchetii* may explain the low grazing rate of phytoplankton by microzooplankton in outer Nachvak during summer. Our study provides novel data on the function and structure of planktonic communities in Labrador fjords. In further investigations, it will be interesting to determine the impact of the presence or absence of *P. pouchetii* on the grazing rates of herbivorous and omnivorous mesozooplankton and to assess the grazing rate of bacteria by heterotrophic protists. This information is essential to improve modeling of the trophodynamics in coastal waters in general and in fjords in particular.

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during flow cytometric analysis; C. Jose and S. Lessard for cell identification and enumeration. This is a contribution to the research programs of ArcticNet, ISMER and Québec-Océan.

CONCLUSION GÉNÉRALE

Déjà observables à l'heure actuelle, les effets des changements climatiques sur des écosystèmes aussi fragiles que les fjords vont incontestablement s'amplifier au cours des prochaines décennies, entraînant des conséquences majeures sur la productivité de ces milieux et sur la dynamique des communautés planctoniques qu'ils abritent. Au vu du manque total de connaissances sur le plancton des fjords du Labrador (côte est du Canada), il était nécessaire d'acquérir des données sur le fonctionnement des maillons inférieurs du réseau alimentaire pélagique (Fig. 1), notamment sur la production et le devenir de la matière organique ainsi que sur la structure de taille et la composition taxonomique du phytoplancton. C'est dans ce contexte que cette thèse présente les toutes premières données sur la dynamique des communautés planctoniques des fjords du Labrador pendant l'été et l'automne. L'ensemble des objectifs de recherche développés dans les trois articles scientifiques issus de cette thèse ont été résumés sous forme d'un nuage de mots (Fig. 2).

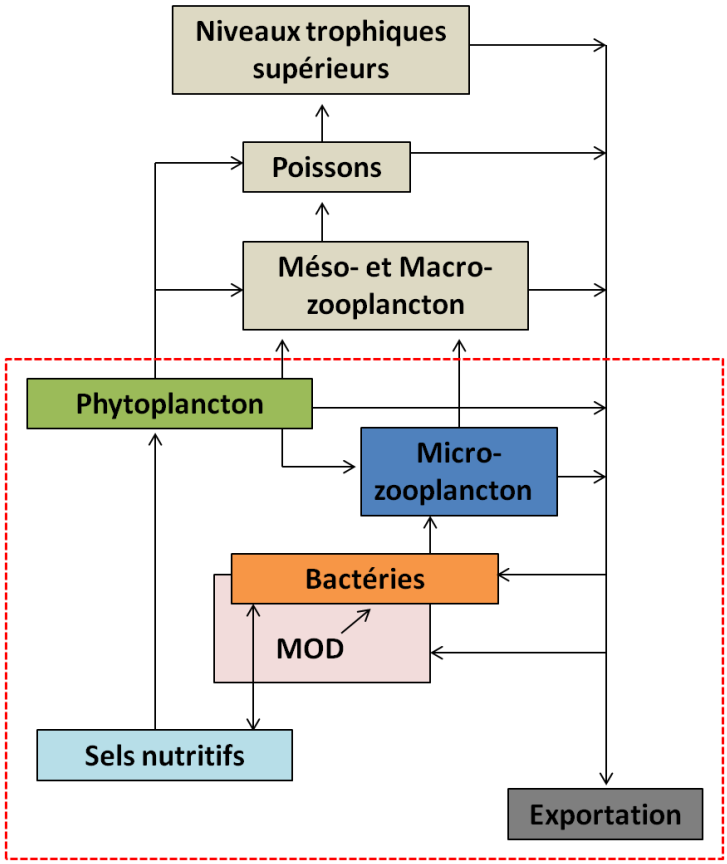

Fig. 1. Représentation schématique de la structure d'un réseau trophique pélagique. Le rectangle rouge encadre les maillons inférieurs du réseau trophique (bactéries, phytoplancton et microzooplancton) qui ont été étudiés dans le cadre de cette thèse. La taille des compartiments et des flèches n'est pas proportionnelle à leur importance au niveau de la biomasse ou du flux de matière. MOD : matière organique dissoute. Modifiée de Mostajir et al. (2012)

Fig. 2. Nuage des 62 mots- clés (ou groupes de mots) de cette thèse. La taille des mots est proportionnelle à leur importance dans les trois articles scientifiques présentés dans cette thèse

Le premier chapitre de cette thèse a tout d'abord permis de quantifier la production et la biomasse phytoplanctoniques, de même que l'exportation verticale du carbone biogène. Les résultats obtenus nous ont permis d'établir que les fjords du Labrador sont des écosystèmes hautement productifs et que la majeure partie de la matière organique produite *in situ* est broutée par le microzooplancton au lieu d'être exportée hors de la zone euphotique. Nous avons pu déterminer que la production primaire est principalement réalisée par le petit phytoplancton (0.7-5 μm) tandis que la biomasse chlorophyllienne est majoritairement dominée par le gros phytoplancton (≥5 μm). Ensuite, l'analyse de la structure de taille a montré que la communauté estivale était principalement composée de nanophytoplancton (2-20 μm) alors que la communauté automnale présentait de plus fortes abondances de picophytoplancton (<2 μm). Enfin, nous avons pu démontrer que la variabilité saisonnière marquée, observée dans la dynamique du phytoplancton des fjords du Labrador, est principalement due à l'intensité de la stratification verticale et au régime lumineux. Malgré de fortes différences spatiales dans les variables environnementales, la dynamique du phytoplancton n'a pas présenté de variations significatives le long du gradient latitudinal.

Les résultats de ce chapitre ont également permis de déterminer que le bloom pélagique a lieu pendant l'été dans les fjords du Labrador. Cette période de déclenchement du bloom est d'autant plus intéressante qu'elle diffère du bloom printanier si caractéristique des fjords du Groenland, de Norvège et de la côte ouest du Canada. Avec le réchauffement climatique qui entraînera un dégel précoce de la glace de mer, les fjords du Labrador pourraient être libres de glace beaucoup plus tôt dans la saison et il n'est pas exclu que le bloom pélagique puisse alors survenir au printemps. La productivité des écosystèmes marins étant largement dépendante de la nature des communautés planctoniques qu'ils abritent, ces résultats nous ont amené à nous intéresser de plus près à la composition taxonomique des protistes des fjords du Labrador.

Les résultats du second chapitre ont permis de caractériser les communautés estivale et automnale de protistes dans les fjords du Labrador. Dans les eaux de l'été 2007,

appauvries en nitrates et en silicium dissous, la communauté a été caractérisée par les diatomées et divers flagellés. Par contre, dans les eaux de l'été 2013, pauvres en nitrates et en phosphates mais riches en silicium dissous, les flagellés ont largement dominé la communauté à la profondeur du maximum de chlorophylle et un bloom intense du prymnésiophyte *Phaeocystis pouchetii* (jusqu'à 18×10^6 cellules l^{-1}) a même été observé dans le fjord de Nachvak. Diverses suggestions ont été avancées pour expliquer cette dominance de *P. pouchetii* à l'été 2013, malgré la forte concentration de silicium dissous (jusqu'à 16 mmol m^{-3}) qui aurait logiquement présagé une prépondérance des diatomées. Pendant l'automne, la communauté a été principalement dominée par les prymnésiophytes et les flagellés non identifiés. Ces différences saisonnières significatives dans la composition taxonomique des protistes ont été expliquées par différentes variables environnementales : la salinité, la stratification, l'éclairement *in situ*, la température de l'eau et la profondeur de la couche de mélange de surface. La composition taxonomique des protistes a présenté des différences spatiales significatives uniquement pendant l'été 2013.

Par la suite, en combinant nos observations à celles de la littérature, nous avons pu suggérer une possible succession annuelle de protistes dans les fjords du Labrador. Pour terminer, la liste exhaustive de l'ensemble des taxons identifiés pendant l'été et l'automne dans les fjords du Labrador a été présentée. Plus de 200 taxons ont été identifiés au début de l'automne, deux fois plus qu'en été. Ces résultats ont également permis de démontrer que contrairement à certaines études qui ont noté une diversité spécifique réduite dans les fjords (Becker 1994), les protistes des fjords du Labrador présentent une très grande diversité.

Composantes essentielles du plancton marin et capables de consommer jusqu'à 50% de la production primaire (Robinson 2008), nous n'aurions pu clôturer cette thèse sans aborder les bactéries hétérotrophes. Ainsi, le troisième chapitre a permis de confirmer l'influence significative de la température de l'eau et de la biomasse chlorophyllienne sur l'abondance des bactéries hétérotrophes pendant l'été et l'automne dans les fjords du Labrador. Aucune relation significative n'a été trouvée entre les bactéries et la concentration de carbone organique dissous labile. Pour l'ensemble de la période d'étude,

une relation positive et significative a été trouvée entre l'abondance des nanoflagellés hétérotrophes et celle des bactéries hétérotrophes. Les résultats du premier chapitre ayant fortement suggéré que la majeure partie de la production primaire était broutée, il était donc pertinent de nous intéresser au broutage par le microzooplancton. Nous avons estimé que le taux de croissance du phytoplancton varie de <0 à 0,64 jr^{-1}, tandis que le taux de broutage par le microzooplancton varie de 0,01 à 0,86 jr^{-1} pendant l'été dans les fjords du Labrador.

Contribution et portée de la thèse

À notre connaissance, aucune étude n'avait encore été conduite sur les communautés planctoniques des fjords du Nunatsiavut. Cette thèse de doctorat présente donc des données inédites sur la structure et le fonctionnement des échelons inférieurs du réseau alimentaire pélagique dans les fjords du Labrador. Elle met également en évidence l'influence des processus physiques et chimiques du milieu sur la production et le devenir de la matière organique (exportation hors de la zone euphotique, broutage par le microzooplancton et reminéralisation par les bactéries hétérotrophes) ainsi que sur la composition taxonomique des protistes. Nos résultats contribuent ainsi à pallier le déficit actuel de connaissances sur la dynamique des communautés planctoniques des fjords du Labrador et ils serviront de référence pour des études futures beaucoup plus approfondies.

Au-delà de cette quête de connaissances fondamentales, cette thèse tire son originalité du fait qu'elle s'intéresse non seulement à l'écologie microbienne des fjords du Nunatsiavut, mais aussi aux perturbations climatiques et celles induites par les activités anthropiques sur ces environnements vulnérables. En effet, étudier simultanément des fjords influencés par l'industrialisation (Saglek et Anaktalak) et d'autres plus naturels (Nachvak et Okak) nous a permis d'examiner le fonctionnement de ces environnements en présence et en absence des activités humaines. Considérant la rapidité des changements climatiques auxquels sont assujettis ces écosystèmes, il était plus qu'impératif d'acquérir ces connaissances nécessaires pour une meilleure compréhension de la dynamique des

communautés planctoniques qu'ils abritent mais aussi pour mieux prévoir leurs réponses aux perturbations environnementales.

Perspectives de recherche

Notre étude ayant été réalisée uniquement pendant l'été et l'automne, il est peu probable que nos résultats puissent être extrapolés au reste de la saison productive. En effet, les fjords du Labrador étant libres de glace à partir de la mi-juillet (jusqu'à la mi-décembre), notre échantillonnage commencé à la fin juillet, soit deux semaines environ après le dégel, n'a probablement pas couvert l'ensemble de la saison de production qui commence immédiatement après le dégel. Afin de remédier à cela et nous assurer de couvrir la période pendant laquelle la production phytoplanctonique est maximale, l'échantillonnage estival des fjords du Labrador devrait démarrer pendant la première quinzaine du mois de juillet et non à la fin juillet comme nous l'avons fait dans cette étude.

Il serait également très pertinent d'effectuer des mesures directes de l'exportation verticale du carbone à l'aide de pièges séquentiels à particules mouillés à des localisations précises et pour une période couvrant l'été et l'automne. Ces pièges pourraient être installés à la base de la zone euphotique et à 50 m environ du fond dans le fjord de Nachvak, le plus profond de nos quatre sites d'étude. Cela permettra de confirmer nos résultats qui suggèrent que la production primaire est principalement retenue dans la zone euphotique au lieu d'être exportée vers les profondeurs. En outre, il serait aussi intéressant de déterminer comment le broutage par le zooplancton influence la structure de taille et la composition taxonomique du phytoplancton. Une telle analyse fournira des résultats supplémentaires quant à l'influence de la communauté zooplanctonique sur la rétention ou l'exportation de la matière organique. Enfin, effectuer des mesures de production et de respiration bactériennes directement sur la matière organique collectée à l'aide de pièges à particules dérivants permettrait de quantifier l'action minéralisatrice des bactéries hétérotrophes dans les fjords du Labrador et d'élargir l'étude des processus microbiens.

ANNEXE

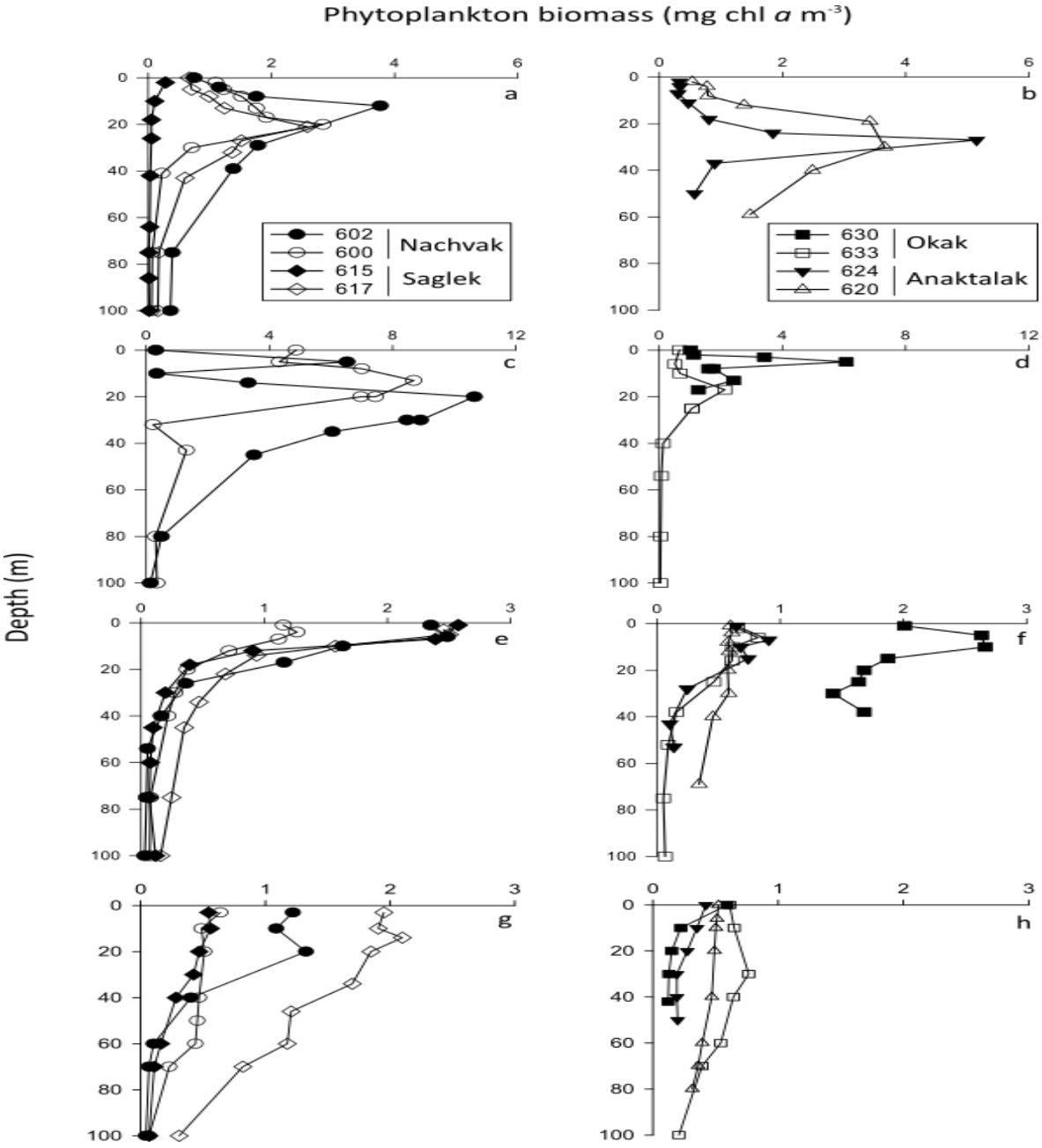

Fig. 1. Profiles of phytoplankton chlorophyll *a* biomass for Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during (a, b) summer 2007, (c, d) summer 2013, (e, f) early fall and (g, h) late fall. Black symbols represent the inner stations and white symbols the outer stations

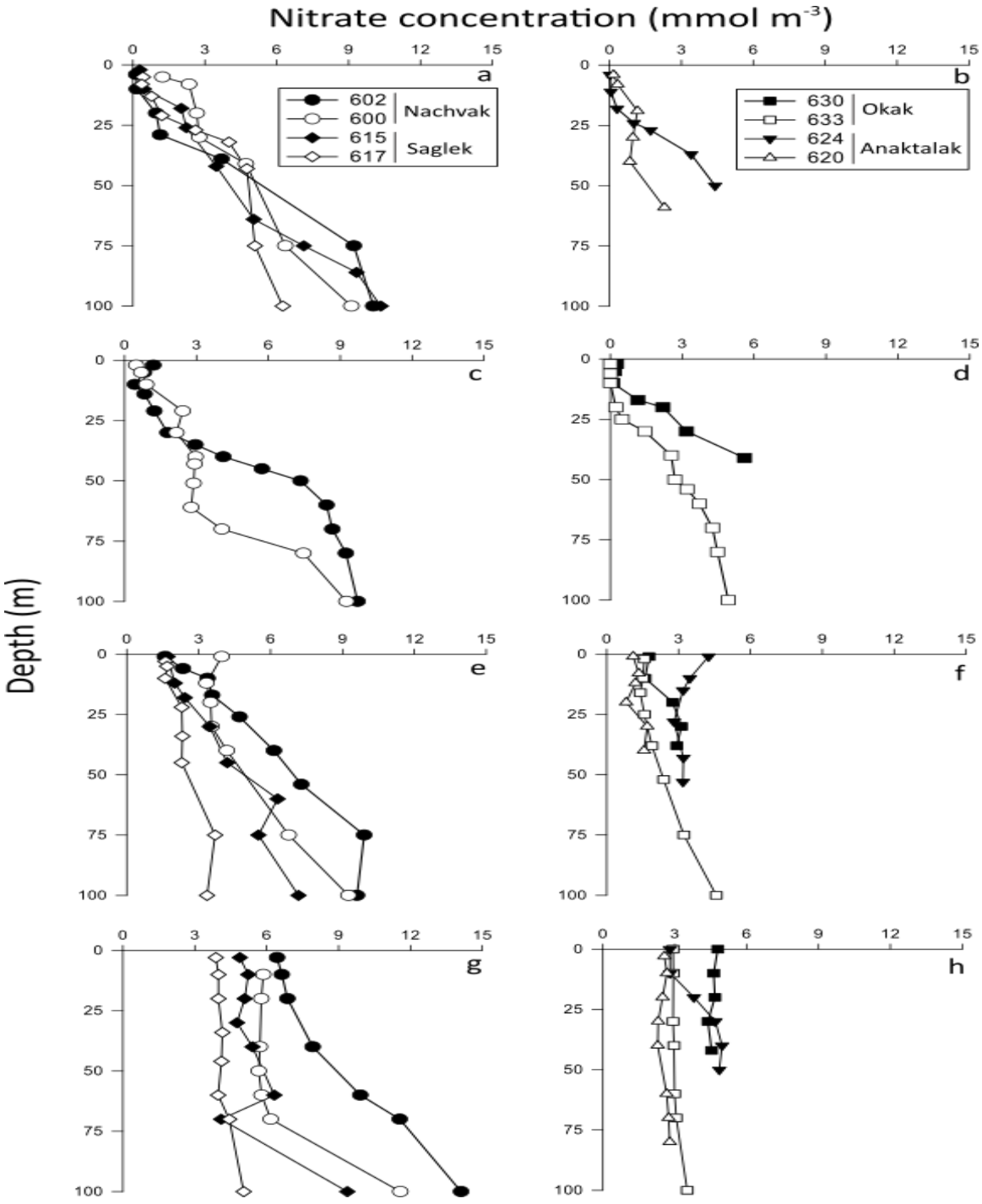

Fig. 2. Nitrate profiles for Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during (a, b) summer 2007, (c, d) summer 2013, (e, f) early fall and (g, h) late fall. Black symbols represent the inner stations and white symbols the outer stations

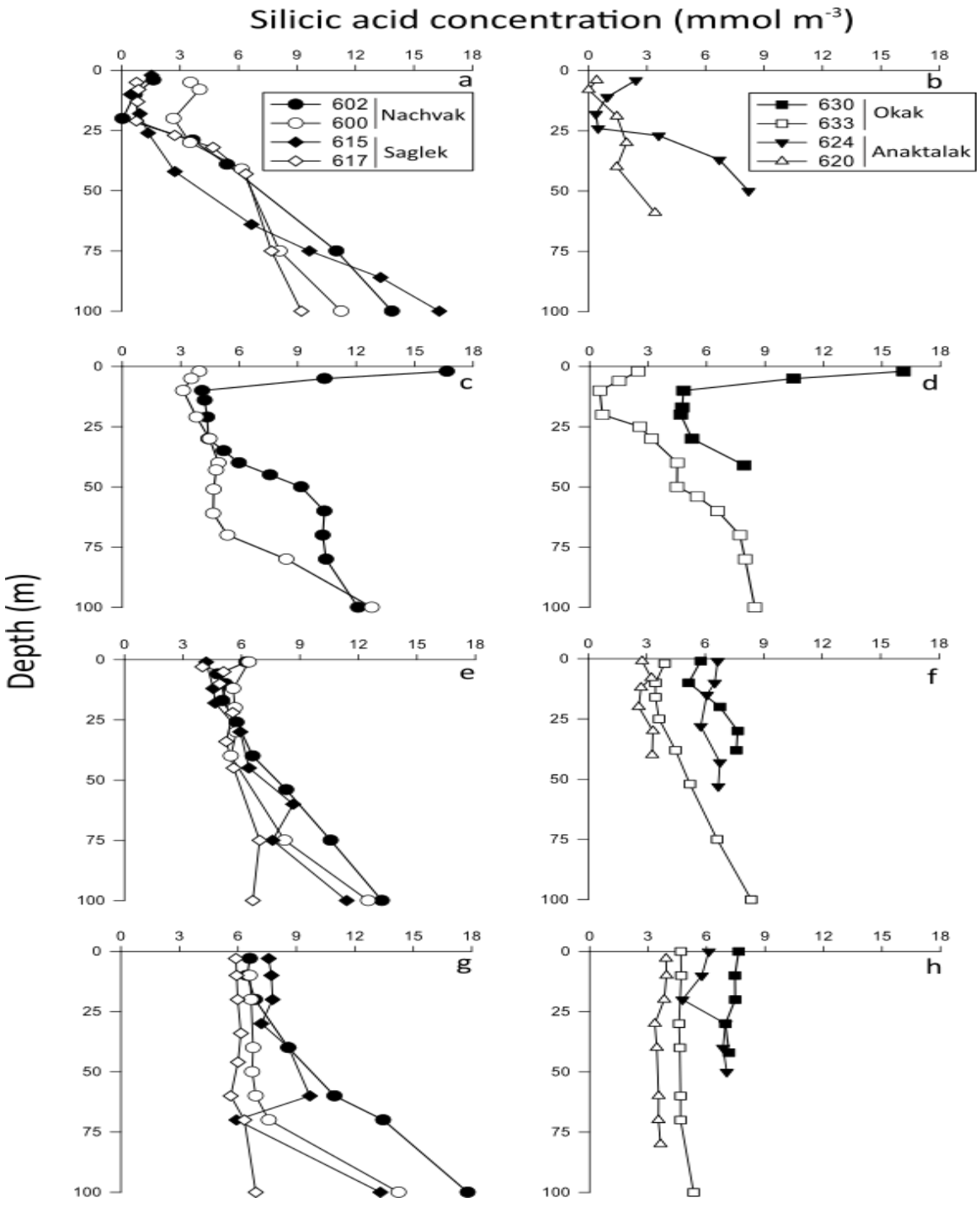

Fig. 3. Silicic acid profiles for Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during (a, b) summer 2007, (c, d) summer 2013, (e, f) early fall and (g, h) late fall. Black symbols represent the inner stations and white symbols the outer stations

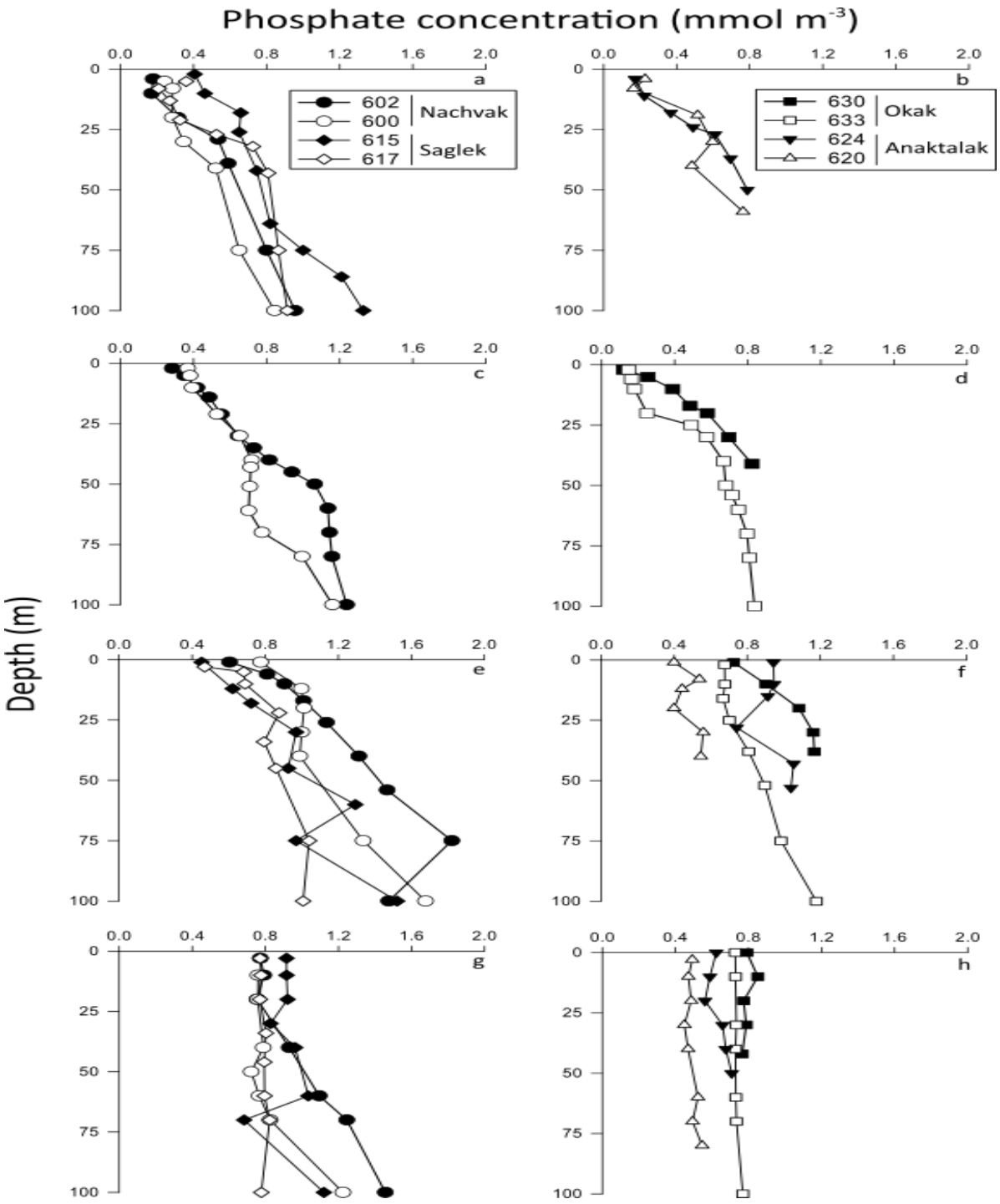

Fig. 4. Phosphate profiles for Labrador fjords (Nachvak, Saglek, Okak and Anaktalak) during (a, b) summer 2007, (c, d) summer 2013, (e, f) early fall and (g, h) late fall. Black symbols represent the inner stations and white symbols the outer stations

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