UNIVERSITÉ DU QUÉBEC À RIMOUSKI

ÉCOLOGIE ALIMENTAIRE DE LA BALEINE BORÉALE (*BALAENA MYSTICETUS*) DANS L'ARCTIQUE DE L'EST CANADIEN

Thèse présentée

dans le cadre du programme de doctorat en océanographie

en vue de l'obtention du grade de philosophiae doctor

PAR

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Novembre 2012

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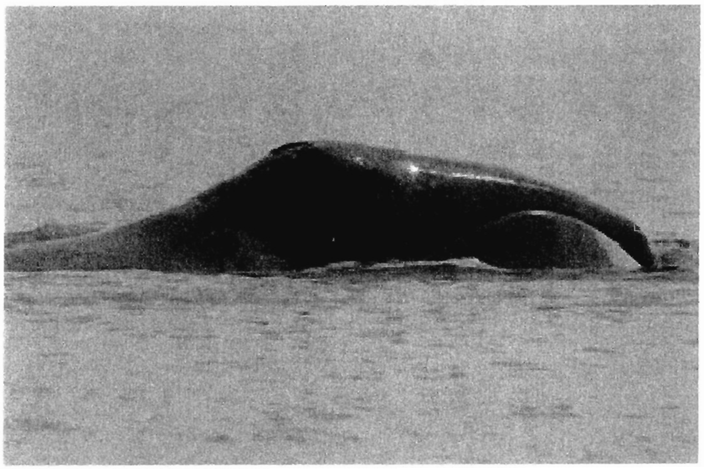
Dépôt initial le 15 août 2012 **Dépôt final le 7 novembre 2012**

Cette thèse de doctorat est dédiée aux
personnes importantes dans ma vie,
tout particulièrement mes parents,
Céline et Yvan.



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REMERCIEMENTS

Je tiens à remercier mon directeur de thèse, Steven Ferguson, pour son support inconditionnel et ses encouragements, et pour toutes les opportunités offertes durant mon programme. Merci Steve pour tout, et spécialement pour tes précieux conseils ! J'aimerais également remercier mes deux codirectrices de recherche, Véronique Lesage et Gesche Winkler. Merci énormément pour votre aide, votre grande disponibilité et votre soutien tout au long de ce processus, et ce même à distance. Votre application et votre grand talent pour l'écriture scientifique m'ont grandement aidée et inspirée !

Je remercie mon guide et mentor Eddy Carmack ainsi que mes collègues et amis du projet canadien de l'Année Polaire Internationale (API) *Les trois océans du Canada* (C3O) ; Bill Williams, John Nelson, Akash Sastri, Moira Galbraith, Svein Vagle et Jane Eert. Merci également à Gustavo Ferreyra, membre de mon comité de thèse, et un gros merci à Yves Morin pour son aide au laboratoire. Merci à Jeff Higdon, Cory Matthews, Jack Orr, Bernard Leblanc et Stephen Petersen pour leur aide sur le terrain.

Merci aux communautés inuit d'Arctic Bay, Igloolik, Hall Beach, Pangnirtung, Pelly Bay, Repulse Bay, Cape Dorset, Coral Harbour et Kangirsujuaq pour leur collaboration lors de la collecte d'échantillons de baleines boréales. Merci également aux officiers et membres d'équipage des brise-glaces NGCC Louis S St-Laurent, Sir-Wilfrid Laurier et DesGroseilliers qui furent d'une grande aide pour la collecte de mes échantillons.

Merci à nos organismes subventionnaires; le Réseau des Centres d'excellence du Canada ArcticNet, les programmes de l'Année Polaire Internationale (API) (*Canada Three Oceans*, *Circumpolar Flaw Lead Study* et *Global Warming and Marine Mammals*), le ministère des Affaires indiennes et du Nord via le Programme de Formation Scientifique dans le Nord (PFSN), l'Association universitaire canadienne d'études nordiques (AUCEN) (*The W. Garfield Weston Award for Northern Studies*), le Conseil de Recherche National en

Sciences Naturelles et en Génie du Canada (CRSNG), le ministère de Pêches et Oceans Canada et le Conseil de gestion des ressources fauniques du Nunavut (CGRFN).

J'aimerais également exprimer toute ma gratitude à ma famille, spécialement ma mère Céline, pour son soutien inconditionnel et ses encouragements perpétuels dans les moments de doute, mon père Yvan, ma sœur Geneviève. Merci à tous mes amis, proches et loin, tout spécialement à Samantha, Adriana et Benoit, et Amélie, et surtout merci à mon fiancé Steven.

AVANT-PROPOS

Cette thèse de doctorat a été réalisée dans le cadre d'un projet conjoint entre l'Institut des Sciences de la Mer (Université du Québec à Rimouski), *The Centre for Earth Observation Science* à l'Université du Manitoba, et le Ministère des Pêches et Océans Canada (Institut des Eaux Douces à Winnipeg, MB et l'Institut des Sciences de la Mer à Sidney, CB). Cette thèse porte sur l'écologie alimentaire de la baleine boréale dans l'Arctique de l'Est canadien. La thèse se compose d'une introduction générale rédigée en français, de cinq chapitres écrits en anglais sous forme d'articles scientifiques et d'une conclusion générale en français qui résume l'ensemble de la recherche. Les trois premiers chapitres de thèses sont publiés, le quatrième est accepté et sous presse et le cinquième est en révision. Voici les références pour chacun des cinq chapitres :

Chapitre 1.

Pomerleau C., Patterson T.A., Luque S., Lesage V., Heide-Jørgensen M.P., Dueck L., Ferguson S.H. (2011). Bowhead whale (*Balaena mysticetus*) diving and movement patterns in the Eastern Canadian Arctic: Implications for foraging ecology. Endangered Species Research 15(2):167-177

Chapitre 2.

Pomerleau C., Ferguson S.H., Walkusz, W. (2011). Stomach contents of bowhead whales (*Balaena mysticeus*) from four locations in the Canadian Arctic. Polar Biology 34:615-620

Chapitre 3.

Pomerleau C., Winkler G., Sastri A., Nelson R.J., Vagle S., Lesage V., Ferguson S.H. (2011). Spatial patterns in zooplankton communities across the Eastern Canadian subarctic and Arctic waters: Insights from stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios. Journal of Plankton Research 33(12):1779-1792 (Featured article)

Chapitre 4.

Pomerleau C., Lesage V., Ferguson S.H., Winkler G., Petersen S., Higdon J. (2012) Prey assemblage isotopic variability as a tool for assessing diet and the spatial distribution of bowhead whale (*Balaena mysticetus*) foraging in the Canadian eastern Arctic. Marine Ecology Progress Series 469 :161-174

Chapitre 5.

Pomerleau C., Lesage V., Winkler G., Rosenberg B., Ferguson S.H. Estimating diet of bowhead whales (*Balaena mysticetus*) from the Eastern Canadian Arctic using blubber fatty acid composition. *Arctic* (En revue – novembre 2012)

Certains résultats de cette thèse ont également été publiés dans deux articles où je suis co-auteure :

Darnis G., Robert D., Pomerleau C., Link H., Archambault P., Nelson R.J., Geoffroy M., Tremblay J-É., Lovejoy C., Ferguson S.H., Hunt B.P.V., Fortier L. (2012) Current state and trends in Canadian Arctic marine ecosystems: II. Heterotrophic food web, pelagic-benthic coupling, and biodiversity. Climatic Change. pp. 1-27, doi:10.1007/s10584-012-0483-8

Lesage V., Morin Y., Rioux E., Pomerleau C., Ferguson S.H., Pelletier E. (2010). Stable isotopes and trace metals as indicators of diet and habitat use in cetaceans: predicting errors related to preservation, lipid extraction and normalization. Marine Ecology Progress Series 419:249-265

Les résultats de cette thèse ont été présentés dans le cadre de plusieurs conférences nationales et internationales, sous forme de présentations orales et/ou d'affiches scientifiques:

Pomerleau C., Ferguson S.H., Lesage V., Winkler G. June 2012. Bowhead whale feeding ecology in the Eastern Canadian Arctic. Institute of Ocean Sciences, Sidney, BC, Canada (Invited lecture).

Pomerleau C., Ferguson S.H., Lesage V., Winkler G. Spatial patterns in zooplankton communities across the eastern Canadian sub-Arctic and Arctic waters. 2nd International Symposium on the Effects of Climate Change on the World's Oceans, Yeosu, South Korea, May 13-19 2012.

Pomerleau C., Ferguson S.H., Lesage V., Winkler G. Spatial clustering of bowhead whale foraging patterns based on prey availability in the Canadian Arctic. Society of Marine Mammalogist (SMM) Biennial Conference on the Biology of Marine Mammals, Tampa Bay, FL, USA, Nov. 28-Dec. 2 2011.

Pomerleau C., Ferguson S.H., Lesage V., Winkler G. June 2011. Bowhead whale feeding grounds and diet composition in the Arctic: Insights from a Bayesian stable isotope mixing model. Gulf of Maine Research Institute, Portland, Maine, USA (Invited Lecture).

Pomerleau C., Ferguson S.H., Lesage V., Winkler G. Foraging ecology of bowhead whales in the Canadian High Arctic: Insights from stable isotope and stomach content analyses. 79th ACFAS, Sherbrooke, QC, Canada, May 9-12 2011.

Pomerleau C., Ferguson S.H., Lesage V., Winkler G. Zooplankton prey species and foraging ecology of bowhead whales in the Canadian High Arctic: Insights from stable isotope and stomach content analyses. 5th International Zooplankton Symposium, Pucon, Chile, Mar. 14-18 2011.

Pomerleau C., Ferguson S.H., Luque S., Patterson T., Lesage V., Dueck L. Bowhead whale diving and movement patterns in the Eastern Canadian Arctic in relation to sea ice: Implications for foraging ecology. ArcticNet ASM, Ottawa, Canada, Dec. 14-17 2010.

Pomerleau C., Ferguson S.H., Luque S., Patterson T., Lesage V., Dueck L. Foraging ecology and habitat selection of bowhead whales in the Eastern Canadian Arctic. C3O – IPY final meeting, Gabriola Island, BC, Canada, Oct. 25-29 2010.

Pomerleau C., Ferguson S.H., Luque S., Patterson T., Lesage V., Dueck L. Bowhead whales habitat selection in the eastern Canadian Arctic during 2002-2006 using an Hidden Markov Model. IPY Oslo Science Conference, Oslo, Norway, June 8-12 2010.

Pomerleau C., Ferguson S.H., Lesage V., Winkler G. Spatial and inter-annual variation of bowhead whale feeding behaviour in the Eastern Canadian Arctic from stable isotopes of C, N and S. State of the Arctic Conference (SOA), Miami, FL, USA, Mar. 16-19 2010.

Pomerleau C., Ferguson S.H., Lesage V., Winkler G. Spatial variations of bowhead whale feeding behaviour in the Eastern Canadian Arctic. Society of Marine Mammalogist (SMM) Biennial Conference on the Biology of Marine Mammals, Québec, QC, Canada, Oct. 12-16 2009.

Pomerleau C., Ferguson S.H., Lesage V., Winkler G. Foraging ecology and habitat selection of bowhead whales in the Canadian High Arctic. Arctic Frontiers, Tromso, Norway, Jan. 19-23 2009.

Pomerleau C., Ferguson S.H., Lesage V., Winkler G. Foraging ecology of bowhead whales in the Arctic. Arctic Change, Québec, QC, Canada, Déc. 9-12 2008.

Je tiens à remercier le Réseau des Centres d'excellence du Canada ArcticNet, Québec-Océan, la Fondation de l'Université du Québec à Rimouski, *The Centre for Earth Observation Science* de l'Université du Manitoba, *North Pacific Marine Science Organization* (PICES), *International Arctic Science Committee* (IASC), *International Council for the Exploration of the Sea* (ICES), l'Année Polaire internationale (API-IPY), la *Society for Marine Mammalogy* ainsi que le gouvernement du Canada pour leurs contributions financières pour ma participation aux conférences énumérées ci-haut.

RÉSUMÉ

L'Arctique est l'endroit sur la planète où les effets du réchauffement climatique sont les plus rapides et plus fortement ressentis. La diminution soutenue de l'étendue et de l'épaisseur du couvert de glace en été transforme l'écosystème dans lequel évolue la baleine boréale (*Balaena mysticetus*), unique mysticète endémique à l'Arctique. Dans ce contexte, l'amélioration de nos connaissances quant à l'écologie alimentaire de cette espèce et ses aires probables d'alimentation permettrait de mieux évaluer les effets possibles de ces changements sur la baleine boréale. Cette thèse de doctorat porte sur l'écologie alimentaire de la baleine boréale de la population de l'est du Canada et de l'ouest du Groenland (EC-WG). Les principaux objectifs de ce doctorat visaient à déterminer la diète de cette espèce et à définir les aires probables d'alimentation estivale. Ce projet de recherche a fait appel à plusieurs approches, notamment la télémétrie satellite, l'analyse des contenus stomacaux et l'utilisation de traceurs écologiques (isotopes stables et acides gras) dans les tissus des baleines et leurs proies potentielles. L'hypothèse générale entourant ce projet de recherche propose que la baleine boréale s'alimente dans des régions caractérisées par des paramètres physiques et des processus océanographiques qui concentrent des proies riches en lipides, tout en lui fournissant une certaine protection (bathymétrie, couvert de glace) contre la prédation exercée par les épaulards (*Orcinus orca*).

L'étude des mouvements et des comportements de plongée a permis d'identifier les aires d'alimentation estivale plausibles de la baleine boréale. Sept baleines, dont quatre dans le bassin Foxe nord et trois dans le détroit de Cumberland, ont été suivies par télémétrie satellite et les patrons de mouvement de quatre individus furent analysés à l'aide d'un modèle de Markov caché (MMC) afin d'évaluer la probabilité des individus d'être dans l'un des deux modes comportementaux suivants: transit ou résident. La comparaison des caractéristiques de plongée durant ces deux modes suggère que le golfe de Boothia, avec un couvert de glace modéré (54-62 %), est utilisé comme site d'alimentation estival par les quatre individus, et ce, malgré le fait que ces baleines provenaient de régions différentes. Cette étude a démontré que les baleines passent la majorité de leur temps à de faibles profondeurs (8-16 m) lorsqu'elles sont en mode résident, et ce peu importe la période de la journée, un comportement qui peut être lié à une alimentation sur des densités de zooplancton situées près de la surface.

L'analyse des contenus stomacaux de quatre baleines chassées entre 1994 et 2008 dans l'Arctique canadien a fourni des informations de base au niveau des proies ingérées. Les quatre individus avaient de la nourriture dans leur estomac et leur diète variait d'exclusivement pélagique, *Limnocalanus macrurus* étant la proie principale, à épibenthique avec *Mysis oculata* comme proie dominante.

Une première caractérisation à grande échelle de la composition spécifique et des signatures isotopiques des communautés de mésozooplancton des régions subarctiques-atlantique jusqu'à la portion ouest de l'archipel arctique canadien a également été effectuée dans le cadre de ce projet et a permis de définir les domaines biogéographiques dans l'aire de répartition de la baleine boréale. Cinq types de masses d'eau furent identifiés ainsi que huit assemblages d'espèces de zooplancton, correspondant pour la vaste majorité à des régions distinctes. Les variations observées dans les communautés de mésozooplancton, de même que dans les ratios isotopiques, peuvent être attribuées en partie aux variations de la température et de la salinité des masses d'eau. Les analyses des signatures isotopiques du carbone ($\delta^{13}C$) et de l'azote ($\delta^{15}N$) ont révélé que les valeurs en $\delta^{15}N$ variaient spatialement chez les quatre espèces omniprésentes dans l'aire d'étude. La saisonnalité, la présence de fronts océaniques ou des variations spatiales dans la structure trophique des communautés planctoniques, pourraient expliquer cette variabilité dans le $\delta^{15}N$ du mesozooplancton.

La variabilité observée dans les signatures isotopiques des assemblages de proies potentielles fut utilisée pour étudier la diète de la baleine boréale. Les contributions des différentes proies (zooplancton) à la diète des baleines furent calculées en utilisant un modèle de mélange isotopique bayésien (SIAR). Cette étude a démontré l'existence de variabilité dans la composition isotopique des groupes d'individus, mais non spécifiquement entre les mâles et les femelles, ni entre les différentes classes d'âge. Les résultats des modèles de mélange isotopiques suggèrent que le détroit de Lancaster de même que le golfe de Boothia et la baie de Baffin, constituent des aires plausibles d'alimentation printanières et estivales. Les modèles ont également révélé que les mysidacés, les euphausiacés et les chaetognathes, de même que les ptéropodes et les amphipodes sympagiques étaient des proies importantes de certains groupes de baleines. Malgré l'existence d'une variabilité interindividuelle au niveau de la diète, les baleines boréales des quatre groupes identifiés s'alimentaient de copépodes arctiques (*C. hyperboreus, C. glacialis, M. longa* et *Paraeuchaeta* spp.). Finalement, la composition en acides gras du tissu adipeux sous-cutané de la baleine boréale suggère une contribution importante des copépodes calanoides à leur diète, ainsi que d'autres espèces de zooplancton omnivores et carnivores. En somme, les trois méthodes utilisées pour analyser la diète des baleines boréales ont conduit à des résultats similaires.

Les résultats obtenus dans le cadre de cette thèse de doctorat ont permis d'élargir les connaissances sur l'écologie alimentaire de la baleine boréale dans l'Arctique de l'Est canadien. La forte dépendance de la baleine boréale au zooplancton polaire peut rendre cette espèce endémique de l'Arctique vulnérable au déclin éventuel de la biomasse de copépodes calanoides que pourraient entraîner des changements climatiques soutenus.

Mots clés : Arctique, acides gras, baleine boréale, *Balaena mysticetus*, écologie alimentaire, isotope stables, répartition spatiale, mammifères marins, zooplancton

ABSTRACT

The ongoing warming in the Arctic is occurring more rapidly and severely than anywhere else on the planet. The thinning and decreasing trend of sea ice in summer months are transforming the habitat of the bowhead whale (*Balaena mysticetus*), the only mysticete endemic to the Arctic. This thesis main focus was on the feeding ecology of the Eastern Canada - West Greenland (EC-WG) bowhead whale population. The main objectives of this research project were to determine bowhead whale diet composition and to define the most probable summer feeding grounds. This thesis uses several analytical tools including satellite telemetry, stomach content analysis and biochemical tracers (stable isotopes and fatty acids) in the skin and blubber of bowhead whales and of their potential prey. The overall hypothesis surrounding this research project put forward that bowhead whales must have feeding grounds that are characterized by physical parameters and oceanographic features that concentrate lipid rich preys and provide shelter (bathymetry, ice cover) from predation by killer whales (*Orcinus orca*).

The study on the movements and dive behaviour of individual bowhead whales allowed to identify plausible summer feeding areas. Seven individuals from the northern Foxe Basin and Cumberland Sound were tracked by satellite telemetry and movement patterns from four whales were analyzed using a hidden Markov model (HMM) to inform the probability of whales being in one of two putative behavioural modes: transient or resident. The comparison of dive characteristics during transient and resident periods indicated that the Gulf of Boothia (GB) with moderate ice coverage (54–62 %) was probably used as a summer foraging area by all four whales even though they came from different regions. Whales spent most of their time at shallow depths (8–16 m) regardless of time of day when in resident mode, likely feeding on near-surface aggregations of zooplankton.

The analysis of the stomach contents of four bowhead whales harvested between 1994 and 2008 from the Canadian Arctic provided basic information on ingested preys. This study was the first diet analysis from this bowhead whale population. All four whales had food in their stomachs and their diet varied from exclusively pelagic, with *Limnocalanus macrurus* being the main prey, to epibenthic with *Mysis oculata* playing an important role.

Detailed study on spatial patterns of stable isotopes of carbon and nitrogen in mesozooplankton in relation to biophysical groupings allowed the definition of the status quo of biogeographic domains within the range of bowhead whales. This study represents the first broad-scale characterization of the composition and isotopic signatures for mesozooplankton communities ranging from the sub-Arctic Atlantic to the western Central Arctic Archipelago. Five broad water mass types corresponded to geographical regions and mesozooplankton community composition varied along the transect, revealing eight species assemblages. Nitrogen (δ^{15}N) and carbon (δ^{13}C) stable isotopes analysis have shown that δ^{15}N varied spatially in four ubiquitous species. Variation in mesozooplankton δ^{15}N could be attributed to regional baseline variation, seasonality or different trophic position occupied by the focal species in our study area.

The variability observed in isotopic signatures of prey assemblages across the eastern Arctic was used to examine variability in diet among bowhead whales and identify their potential foraging areas. The proportional contributions of various sources (zooplankton) to the diet of bowhead whales were calculated using a Bayesian stable isotope mixing model (SIAR). Results from this study indicated variability in isotopic composition among groups of individuals, but not specifically between males and females or age classes. The isotopic model discounted Davis Strait and Disko Bay as potential foraging areas for bowhead whales, at least in spring and summer. Lancaster Sound, Baffin Bay and the Gulf of Boothia were the three main areas likely used for summer feeding, where they fed primarily on large arctic calanoid copepods, mysids and euphausids. Finally, the analysis of the fatty acid composition of the outer blubber layer revealed the important contribution of large arctic calanoid copepods to the diet of bowhead whale. In this thesis, all three techniques used to analyse bowhead whale diet conducted to similar findings.

Results from this thesis contributed critical information on the feeding ecology of the bowhead whale in the eastern Canadian Arctic. Overall, findings highlighted the strong dependence of this endemic arctic species on arctic zooplankton which may leave them vulnerable to the predicted decline of Calanoid copepods biomasses in the Arctic as a result of the ongoing warming trend.

Keywords: Arctic, bowhead whales, *Balaena mysticetus*, fatty acids, feeding ecology, foraging habitat, marine mammals, movement, stable isotopes, zooplankton

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LISTE DES SYMBOLES ET DES ABRÉVIATIONS

ANOSIM	One-way analysis of similarity
BCB	Bering-Chukchi-Beaufort
BHT	Butylated hydroxytoluene
CS	Cumberland Sound
δ^{13}**C**	Delta Carbon-13
δ^{15}**N**	Delta Nitrogen-15
DAPC	Discriminant analysis of principal components
DS	Davis Strait
DVM	Diel vertical migration
EC-WG	Eastern Canada-West Greenland
FA	Fatty acid
FAME	Fatty acid methyl esters
FB	Foxe Basin
GB	Gulf of Boothia
GC	Gas chromatographic
HCl	Hydrogen chloride
HMM	Hidden markov model

MUFA	Monounsaturated fatty acid
nMDS	Non-metric multidimensional scaling
PCA	Principal component analysis
PL	Prosome length
POM	Particulate organic matter
PRI	Prince Regent Inlet
PRIMER	Plymouth Routines In Multivariate Ecological Research
PPT	Platform Transmitter Terminal
PUFA	Polyunsaturated fatty acid
SDR	Satellite-linked time-depth recorder
SFA	Saturated fatty acid
SI	Stable isotope
SIMPROF	Similarity profile test
SST	Sea-surface temperature
TAD	Time-at-Depth
TAG	Triacylglycerol
TL	Total length
TOD	Time of Day

INTRODUCTION GÉNÉRALE

1.1 Problématique de la thèse

Les régions situées en haute latitude sont les plus vulnérables au réchauffement global et c'est en Arctique que les changements climatiques se font sentir le plus rapidement et le plus fortement (Barber et al. 2012). Le déclin soutenu de l'étendue et de l'épaisseur de la glace de mer depuis 1979, et plus particulièrement depuis le début du 21^{e} siècle, constitue l'une des modifications de l'écosystème arctique les plus extrêmes (IPCC 2007, Overland et al. 2008). Ces changements dans la cryosphère marine ont de profondes répercussions au niveau du fonctionnement de l'écosystème, dont la dynamique des réseaux trophiques (Darnis et al. 2012, Stroeve et al. 2012). La productivité et la structure des chaînes alimentaires polaires pourraient passer de sympagique à un système plus pélagique, surtout en été, en conséquence de l'augmentation des zones d'eaux libres de glace (Vincent et al. 2011).

Tous les mammifères marins endémiques à l'Arctique dépendent de la glace, du moins à certains moments de l'année, de diverses manières. La glace peut servir de plate-forme de repos, de reproduction et soins parentaux ou pour la chasse, de barrière de protection contre les prédateurs, ou encore d'aire d'alimentation en y concentrant certains organismes (Bluhm et Gradinger 2008). Les changements climatiques en Arctique peuvent avoir divers impacts sur ces espèces spécialistes de la glace tant au niveau des aires de répartitions, des patrons de migrations saisonnières ou de la condition nutritionnelle, pour ne nommer que quelques exemples. En outre, l'abondance et la dynamique de ces populations pourraient être affectées par les modifications soutenues de leur habitat (Kovacs et al. 2010).

La baleine boréale (*Balaena mysticetus*) est un grand cétacé à fanons qui réside à l'année dans les eaux polaires (Figure 1). C'est d'ailleurs le seul mysticète endémique à l'Arctique et cette baleine est morphologiquement et physiologiquement adaptée aux conditions et aux variabilités extrêmes qui caractérisent l'environnement arctique (Moore et Huntington 2008, Harrington 2008). La chasse commerciale des baleines boréales dans l'est du Canada et l'ouest du Groenland, qui a débuté dans les années 1500 et s'est poursuivie jusqu'au début des années 1900, a gravement décimé cette population. Le nombre de baleines boréales a augmenté depuis la fin de la chasse commerciale, mais la population ne s'est pas encore rétablie de cette surexploitation et seule des estimations imprécises du nombre d'individus existent à ce jour. Les données provenant de relevés aériens suggèrent une population de quelques milliers d'individus (i.e., 6344 individus, 95% CI 3119 à 12 906) (COSEPAC 2009). En avril 2009, le Comité sur la situation des espèces en péril au Canada (COSEPAC) a désigné cette population de baleine boréale comme une espèce ayant un statut préoccupant et une étude est présentement en cours afin d'évaluer la possibilité de protéger légalement cette population en vertu de la Loi sur les espèces en péril (LEP) du gouvernement fédéral.

La baleine boréale demeure à risque de voir son statut s'aggraver par divers facteurs qui menacent son rétablissement et sa survie. Tout d'abord, le cycle biologique particulier de la baleine boréale, qui se caractérise par une longévité extrême (+ de 200 ans), un faible taux de croissance, une faible fécondité et une maturité sexuelle acquise tardivement (vers 25 ans), est l'un des facteurs qui explique la lenteur de la croissance de la population (George et al. 1999, Zeh et al. 1993). Le réchauffement global entraine des modifications rapides dans l'habitat de la baleine boréale, particulièrement au niveau de la glace de mer et des densités de proies. La glace de mer fournit un habitat critique pour la production des algues de glace qui sont à la base du réseau trophique sympagique très riche en lipides (Vincent et al. 2011). Cette production algale est critique à l'alimentation de plusieurs espèces de zooplancton, dont les larges copépodes herbivores (*Calanus* spp.), qui sont des proies clés des prédateurs arctiques spécialistes de la glace tels que la baleine boréale. Bref, les modifications en cours dans le régime de glace auront vraisemblablement d'importantes implications pour les mammifères marins arctiques (Tynan et DeMaster, 1997). Le réchauffement océanique peut entrainer des changements au niveau de la structure des masses d'eau ainsi que des modifications au niveau de la composition et de la biodiversité des espèces de zooplancton. Des changements au niveau de la biogéographie de certaines espèces de zooplancton, notamment les copépodes calanoides, ont été observés dans l'Atlantique. Certaines espèces planctoniques boréales ou tempérées (ex : *Calanus finmarchicus* et *Calanus helgolandicus*) se déplacent plus au nord (Beaugrand et al. 2002, Beaugrand et al. 2009, Edwards et al. 2008). Ces espèces de zooplancton sont de plus petites tailles et moins riches en lipides que les espèces arctiques. Les modifications dans la biogéographie des espèces devraient s'accentuer avec le réchauffement soutenu ce qui risque d'entrainer des changements profonds au niveau de la structure trophique des écosystèmes nordiques (ICES 2008).

Par ailleurs, l'accroissement anticipé de l'activité humaine dans le Grand Nord pose un stress additionnel. L'augmentation de la durée de la saison d'eau libre risque d'accroitre significativement le trafic maritime dans l'archipel arctique augmentant les risques de collision entre les animaux et les navires (Jensen et Silber 2003) de même que la pollution sonore (Richardson 2006). Les baleines boréales sont fidèles à certaines aires d'alimentation ou d'hivernage et à certaines routes de migrations qu'elles empruntent annuellement (Heide-Jorgensen et al. 2006). L'augmentation de la présence humaine, voire l'apparition de nouvelles activités industrielles (ex : explorations gazière et minière) pourraient être en conflit avec les routes de migrations et les habitats critiques de cette espèce (ex : aire d'alimentation ou de soins parentaux) et pourraient accroître les risques de collision en plus de détériorer l'environnement sonore et la qualité de l'habitat. C'est le cas notamment pour le Bassin de Foxe et le Détroit d'Hudson où les développements miniers à la terre de Baffin récemment approuvés (mine de fer de Mary River) entraîneront un trafic de brise-glace constant dans l'habitat d'hivernage de la baleine boréale.

D'autre part, la diminution de la glace de mer permet aux épaulards (*Orcinus orca*) d'étendre leur répartition géographique vers le nord (Higdon et Ferguson 2009). Le nombre d'épaulards observé dans l'Arctique canadien a augmenté depuis 2008, en comparaison aux observations faites précédemment (1850-2000) (Higdon et al. 2011). En Arctique, les épaulards voyagent en groupes de plusieurs individus et chassent principalement le narval (*Monocedon monoceros*), ainsi que les baleines boréales immatures et juvéniles. D'ailleurs, plusieurs baleines boréales portent des marques d'attaque sur leur corps, surtout au niveau de la nageoire caudale (Higdon 2009). L'épaulard pourrait devenir le nouveau prédateur au sommet de la chaîne alimentaire arctique, et remplacer l'ours polaire (*Ursus maritimus*), ce qui constitue une nouvelle menace pour la baleine boréale (Higdon et al. 2011). Le statut précaire de la population de baleine boréale de l'Arctique de l'est et de l'ouest du Groenland combiné aux différents facteurs et menaces découlant d'un Arctique en pleine mutation pose un risque au rétablissement, au maintien et à la survie de cette espèce, d'où l'importance d'augmenter les connaissances sur l'écologie de la baleine boréale.

1.2 La baleine boréale (*Balaena mysticetus*)

La baleine boréale est l'unique mysticète qui habite les eaux septentrionales à l'année (Nowak et Walker 2003). Cette espèce est présente dans les eaux de la Russie, de l'Alaska, du Canada, du Groenland et de la Norvège selon quatre stocks différents (Rugh et al. 2003). On retrouve deux populations de baleines boréales distinctes dans les eaux canadiennes; la population des mers Bering-Chukchi-Beaufort (BCB) dans l'arctique de l'ouest et la population de l'est du Canada et de l'ouest du Groenland (EC-WG) sur laquelle porte cette thèse de doctorat.

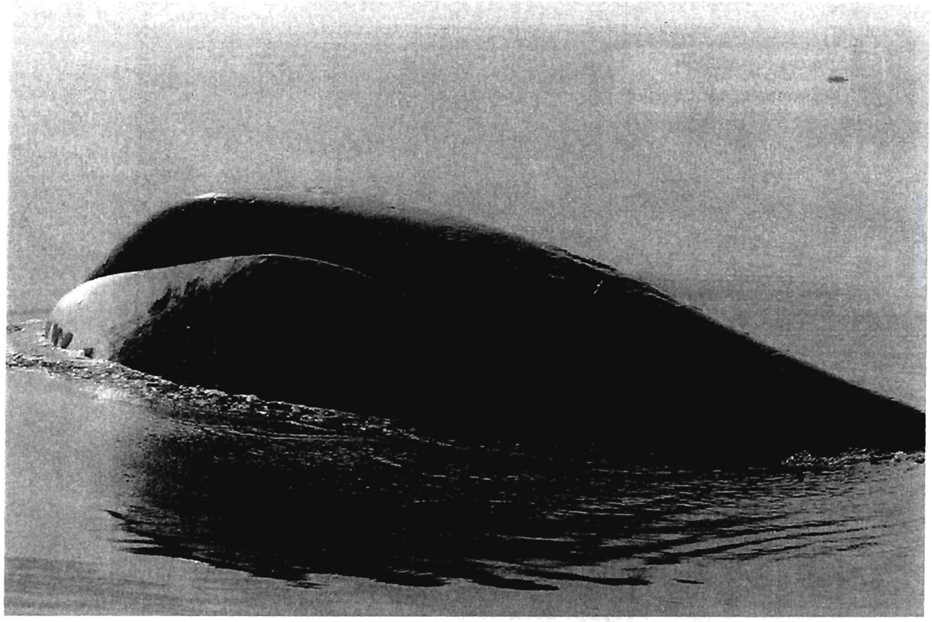

Figure 1. Baleine boréale (*Balaena mysticetus*). La taille moyenne d'une femelle adulte est de 16 à 18 m et d'un mâle adulte de 14 à 17 m (Photo par J.W. Higdon/MPO).

Des études portant sur l'analyse des mouvements des baleines boréales de la population EC-WG ont démontré que ces animaux effectuent de longues migrations saisonnières entre leurs aires d'hivernages et estivales (Heide-Jørgensen et al. 2003) (Figure 2). La zone d'occurrence des baleines boréales dans l'Arctique de l'est est d'environ 1 100 000 km^2 (COSEPAC 2009). La répartition saisonnière de même que les migrations effectuées par les baleines boréales sont intimement liées à la glace de mer et au développement du zooplancton (Moore et Reeves 1993, Finley et al. 2001, Ferguson et al. 2010). En hiver, une partie de la population s'agrège dans l'embouchure des baies de Cumberland et Frobisher situées sur la côte sud-est de l'ile de Baffin, tandis que d'autres individus restent dans le détroit d'Hudson (Heide-Jørgensen et al. 2006, Koski et al. 2006) ou encore traversent la mer de Baffin et hivernent le long de la côte ouest du Groenland (Heide-Jørgensen et al. 2007).

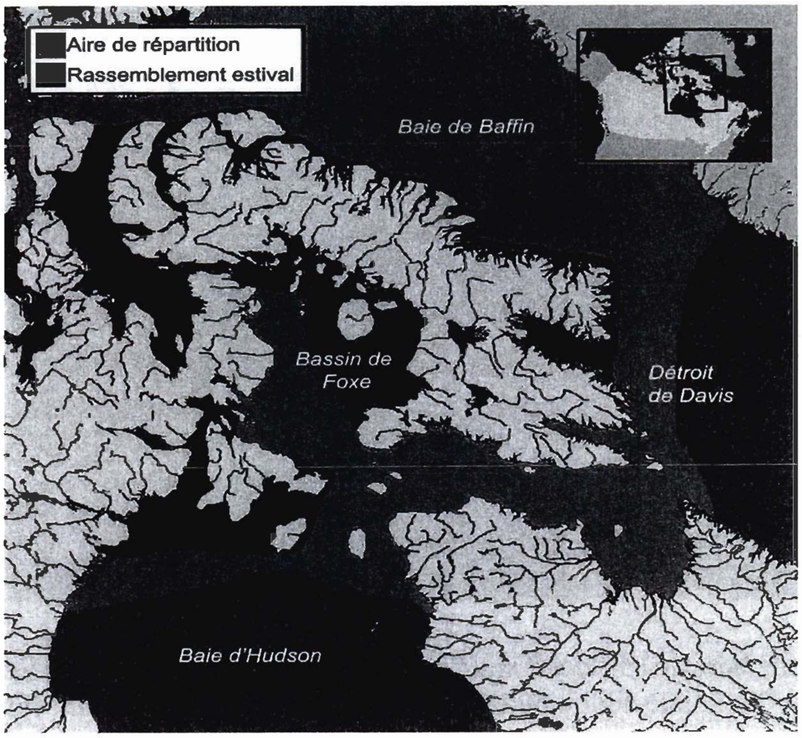

Figure 2. Répartition de la baleine boréale (Population de l'est du Canada et de l'ouest du Groenland) (Espèces aquatiques en péril, MPO).

Plusieurs baleines quittent les détroits d'Hudson et de Davis à la fin de l'hiver et se dirigent plus au nord le long de l'Île de Baffin et dans l'archipel arctique. D'autres convergent vers la baie de Disko sur la côte ouest du Groenland au début du printemps pour ensuite traverser de nouveau la mer de Baffin et passer l'été dans les eaux de l'arctique canadien, tandis que certains individus vont vers le nord-ouest de la baie d'Hudson et plus au nord dans le bassin Foxe (Reeves et al. 1983, Cosens et al. 1997, Cosens et Innes 2000).

Malgré les études effectuées sur les mouvements et les distributions saisonnières des baleines boréales dans l'Arctique de l'est, les sites d'alimentation, de même que la diète de cette espèce sont peu documentés (Higdon et Ferguson 2010 et Kovacs et al. 2010). L'Arctique est un milieu extrême caractérisé par de grands écarts saisonniers au niveau de la production primaire et secondaire, qui varie grandement dans le temps et l'espace (Vincent et al. 2011). Pendant l'été, la baleine boréale doit optimiser ses apports alimentaires afin de maintenir son métabolisme et maximiser ses réserves énergétiques en vue des périodes où les ressources alimentaires sont moins abondantes. Même si cette dernière est adaptée aux variabilités extrêmes qui caractérisent l'environnement polaire, les changements rapides qui surviennent dans le milieu peuvent modifier d'une part les processus océanographiques qui concentrent les proies et d'autre part les assemblages de proies (Neibauer et Schell 1993). Il est donc essentiel d'acquérir de l'information sur les facteurs qui affectent la distribution des baleines boréales pendant la saison productive et donc sur leur écologie alimentaire. Il est possible d'utiliser la télémétrie satellite afin d'étudier les mouvements et ainsi obtenir de l'information sur l'utilisation de l'habitat dans un contexte d'écologie alimentaire. Par exemple, le comportement d'un animal peut être analysé et inféré grâce à des enregistreurs/émetteurs à liaison satellite archivant les données et ainsi révéler l'importance relative d'un habitat particulier (Patterson et al 2009). Ce type d'étude est manquant pour la population EC-WG et c'est la raison pour laquelle cette composante de recherche est abordée dans cette thèse.

La majorité de l'information disponible sur l'écologie alimentaire de la baleine boréale provient d'études sur la population BCB. Dans l'Arctique de l'ouest, l'analyse de contenus stomacaux, d'isotope stables et d'acides gras ont révélés que les baleines boréales s'alimentent principalement de copépodes calanoides et d'euphausiacés, et d'autres espèces de zooplancton pélagiques et épi-benthiques dont des mysidacés, des isopodes et des amphipodes (Lowry et Frost 1984, Schell et al. 1987, Lowry 1993, Schell et Saupe 1993, Lowry et al. 2004, Budge et al. 2008). Les quelques études portant sur l'écologie alimentaire de cette espèce dans l'Arctique de l'est proviennent d'observations, d'inférences suite à un trait de filet de plancton, de données de plongée de courte durée ou encore d'une combinaison de ces techniques. Un segment de la population utilise la baie de Disko, au Groenland, comme site d'alimentation à la fin de l'hiver et au début du printemps, notamment pour s'alimenter sur des copépodes calanoides en fin de diapause (Laidre et al. 2007, Simon et al. 2009). Des observations antérieures suggèrent que certains individus se nourrissent de *Calanus hyperboreus* dans des fjords au Nunavut, dont la baie Isabella, au début de l'automne (Finley et al. 2001, Finley pers. comm.). Bref, des études utilisant des indices de diètes intégrées dans le temps (ex : isotopes stables, acides gras) permettraient d'approfondir les connaissances sur l'écologie alimentaire de la baleine boréale dans l'est du Canada.

1.3 L'écologie alimentaire

Les habitudes alimentaires des grandes baleines sont difficiles à étudier, compte tenu que celles-ci passent la plupart de leur temps sous l'eau et que les épisodes d'alimentation près de la surface sont rarement observés (Pauly et Trites 1998). L'une des techniques utilisée pour estimer la diète est l'analyse des contenus stomacaux, qui sont prélevés suite à un échouage ou lors de la chasse traditionnelle. Cette technique d'analyse du régime alimentaire est directe et permet d'identifier, selon la condition de l'échantillon, les proies ingérées par l'animal. Toutefois, cette méthode comporte des limitations, spécialement lorsque les échantillons proviennent d'animaux échoués. La vitesse de digestion des proies molles est beaucoup plus rapide que celles de proies contenant des parties chitineuses (ex. exosquelette) qui résistent à la digestion (Scholz et al. 1991, Sheffield et al. 2011). Le biais engendré par la digestion des différentes proies contraint grandement la portée des résultats, mais fournit des informations uniques sur l'identité des proies récemment ingérées par l'animal.

L'analyse des isotopes stables, particulièrement du carbone et de l'azote dans les tissus d'un organisme, est une technique alternative aux méthodes traditionnelles directes, qui est de plus en plus utilisée dans les études d'écologie trophique, d'utilisation de l'habitat et pour estimer la diète (Hobson 1999, Inger et Bearhop 2008, Newsome et al.

2010). Cette approche indirecte permet d'obtenir de l'information sur la diète selon différentes échelles de temps de même que sur les proies assimilées (Peterson et Fry 1987). Cette analyse consiste à mesurer l'abondance des isotopes stables de certains éléments, particulièrement du carbone et de l'azote, sous forme de ratio (‰) de la forme la plus rare (isotope le plus lourd) (^{13}C, ^{15}N) relativement à la forme la plus abondante de l'élément (isotope le plus léger) (^{12}C, ^{14}N). Les ratios isotopiques sont déterminés durant la synthèse d'un tissu (ex. plasma sanguin, peau, fanons, collagène des os) (Hobson et Welch 1992). Par exemple, un échantillon de peau représente la période de croissance de l'épiderme et reflète la diète au cours des deux derniers mois (Hicks et al. 1985, Ruiz-Cooley et al. 2004) La signature en δ^{15}N d'un animal est un indicateur de la position trophique, puisqu'un prédateur est typiquement enrichi de 3 à 4 ‰ par rapport à la signature en δ^{15}N de sa diète (Minagawa et Wada, 1984). Cet enrichissement découle du fait que l'isotope léger de l'azote (^{14}N) est préférentiellement excrété sous forme de déchets azotés, alors que l'isotope lourd (^{15}N) est assimilé par l'organisme (Fry 2006). Contrairement au δ^{15}N, le processus d'enrichissement en δ^{13}C, qui survient principalement lors de la respiration, est faible et peu variable entre les différents niveaux trophiques (< 1.0 ‰) (DeNiro et Epstein 1978, Fry et Sherr 1989). Le δ^{13}C sert principalement à déterminer l'origine des sources de carbone à la base de chaîne alimentaire qui sont liées aux processus de photosynthèse (Rau et al. 1983, Kelly 2000). En milieu marin, le δ^{13}C permet de faire la distinction entre les apports pélagiques et benthiques et entre les apports néritiques et océaniques (Hobson et al. 1994).

Les isotopes stables du carbone et de l'azote peuvent être employés dans des modèles de mélanges isotopiques (*stable isotope mixing model*) afin d'estimer les proportions de différentes proies à la diète d'un consommateur (Phillips et Greg 2003, Phillips 2012). Ces modèles de mélange isotopique utilisent les signatures en carbone et en azote de plusieurs proies potentielles d'un animal, ainsi que les signatures isotopiques de ce prédateur, et sont basés sur la prémisse « *you are what you eat* » (DeNiro et Epstein 1978).

Récemment, ces modèles de mélange isotopiques ont été développés dans un cadre statistique bayésien (*Stable Isotope Analysis in R*; Parnell et al. 2010 et *MixSIR in Matlab*; Moore et Semmens 2008) qui permet d'incorporer plusieurs sources (ex : proies), ainsi que des informations *a priori*, et permettant de prendre en considération les incertitudes associées aux paramètres inclus dans le modèle (Ward et al. 2010). Les résultats découlant de l'estimation bayésienne sont exprimés en probabilité de distribution postérieure et en intervalles de crédibilité (équivalemment bayésien de l'intervalle de confiance) calculés autour de la moyenne et/ou de la médiane. Depuis le développement des modèles de mélange isotopiques bayésiens, ceux-ci sont maintenant couramment utilisés dans plusieurs études portant sur la détermination de la diète, tant d'espèces marines (Cherry et al. 2011, Fernandez et al. 2011, Drago et al. 2010, Witteveen et al. 2011) que terrestres (Yeakel et al. 2009, Voigt et al. 2010, Killengreen et al. 2011, Pisanu et al. 2011, Ruffino et al. 2011).

Similairement aux isotopes stables, l'analyse de la composition en acides gras des lipides d'un organisme peut aussi servir de marqueurs trophiques. La couche de graisse située sous la peau des mammifères marins est un tissu dynamique qui sert à la thermorégulation ainsi que de réserve énergétique (Iverson et al. 1995). L'analyse des acides gras qui composent cette couche de graisse reflète celle de la diète intégrée sur une période de quelques semaines à quelques mois (Iverson 1995, Iverson et al. 2004, Nordstrom et al. 2008). Certains acides gras, dont les polyinsaturés à longue chaîne carbonée (PUFAs), sont biosynthétisés exclusivement par les producteurs primaires et sont transférés de façon quasi intacte le long de la chaîne alimentaire (Sargent et al. 1987). Par exemple, les acides gras 20:5n-3 et 22:6n-3 sont des marqueurs typiques de diatomées et de dinoflagellés, respectivement (Kates et Volcani 1966, Yin et al. 2000, Graeve 1993). Cette caractéristique permet de déterminer l'origine des groupes algaux à la base de la chaîne alimentaire dont dépend un consommateur (ex : diatomées – copépodes – baleine planctivores). Certains acides gras peuvent servir de marqueur de l'ingestion d'un taxon ou d'une proie spécifique. C'est suite à l'étude de la composition en acides gras de la couche de graisse du rorqual commun (*Balaenoptera physalus*), qu'Ackman et Eaton (1966) ont émis le concept des lipides comme marqueurs trophiques, puisqu'ils ont découvert que la composition en acides gras du rorqual commun était très semblable à celle de l'euphausiacé *Meganyctiphanes norvegica*. D'autre part, les acides gras monoinsaturés à longue chaîne carbonée (MUFAs), tel que 20:1 et 22:1, sont formés uniquement *de novo* par biosynthèse chez les copépodes calanoides (Kattner et Hagen 1995) et leur présence indique une consommation directe de copépodes ou encore leur ingestion via leur prédateur. Donc, la présence de même que l'abondance relative des différents acides gras à longues chaînes dans un prédateur peut fournir de l'information sur les relations trophiques et la structure du réseau alimentaire (Iverson et al. 1997, Dahl et al. 2000, Iverson et al. 2004, Thiemann et al. 2008). Ces trois méthodes d'analyse, soit les contenus stomacaux, les ratios d'isotopes stables ainsi que les acides gras, sont utilisées dans cette thèse, comme outil afin d'étudier l'écologie alimentaire de la baleine boréale.

1.4 Objectifs de la thèse de doctorat.

L'objectif central de cette thèse de doctorat était d'accroître les connaissances quant à l'écologie alimentaire de la baleine boréale de la population de l'est du Canada et de l'ouest du Groenland, plus particulièrement au niveau de la diète et des aires probables d'alimentation. Cette thèse de doctorat comporte cinq chapitres principaux. Le premier chapitre examine les mouvements et le comportement de plongée de sept baleines afin d'identifier les zones de transit et de résidence et ainsi identifier les zones probables d'alimentation des baleines boréales durant l'été.

Le deuxième chapitre porte sur le régime alimentaire des baleines boréales par l'analyse de contenus stomacaux de quatre individus, dont trois provenaient de l'Arctique de l'est. L'objectif de ce chapitre était d'identifier les espèces de proies ingérées et obtenir ainsi une idée générale sur la taxonomie et l'écologie de la baleine boréale.

Le troisième chapitre traite de la structure générale des grandes masses d'eau, et visait à caractériser la composition spécifique et les rapports d'isotopes stables du carbone et de l'azote des communautés de mésozooplancton dans l'aire de répartition géographique estivale de la baleine boréale. Les domaines biogéographiques identifiés dans ce chapitre sont utilisés dans le chapitre suivant.

Dans le quatrième chapitre, j'ai utilisé la variabilité des signatures isotopiques des assemblages de proies identifiés dans l'Arctique de l'est afin d'examiner la variabilité de la diète de la baleine boréale et d'identifier des aires d'alimentation potentielles. J'ai utilisé une approche bayésienne aux modèles de mélange isotopique afin d'estimer la diète des baleines boréales ainsi que la contribution des proies potentielles.

Dans le dernier chapitre, j'ai étudié la composition en acides gras de la couche supérieure de la graisse de baleines boréales. L'objectif de ce chapitre était d'obtenir des informations au niveau de la diète de cette espèce en complément à celle obtenue par l'application des autres techniques utilisées dans cette thèse (contenus stomacaux et isotopes stables).

Finalement, les résultats faisant l'objet de chacun des chapitres sont intégrés afin de mettre en lumière le niveau d'avancement concernant l'écologie alimentaire de la baleine boréale obtenu dans le cadre de cette étude, et sont discutés dans le contexte des changements climatiques particulièrement soutenus et rapides en Arctique.

CHAPITRE 1

MOUVEMENTS ET PROFILS DE PLONGÉE DE LA BALEINE BORÉALE (*BALAENA MYSTICETUS*) DANS L'ARCTIQUE DE L'EST CANADIEN : IMPLICATION AU NIVEAU DE L'ÉCOLOGIE ALIMENTAIRE

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Paru en 2011 dans *Endangered Species Research*, vol. 15, p. 167-177

1.1 RÉSUMÉ

La baleine boréale (*Balaena mysticetus*) est la seule espèce de mysticète endémique à l'Arctique. La population de l'est du Canada et de l'ouest du Groenland (EC-WG) est considérée comme ayant un statut préoccupant au Canada et son statut pourrait s'aggraver puisque cette population demeure à risque de devenir menacée ou en voie de disparition de par sa biologie particulière (ex : taux de croissance très lent, faible fécondité) et les changements environnementaux rapides qui surviennent en Arctique. Dans ce contexte, nous avons utilisé des émetteurs satellites et de plongée (SDR-16) pour étudier les mouvements et les comportements de plongées de la baleine boréale afin d'identifier les aires d'alimentation estivale plausibles. Sept baleines, dont quatre dans le bassin Foxe nord (Juillet 2003) et trois dans le détroit de Cumberland (Juillet 2006), ont été suivies par télémétrie satellite. Les patrons de mouvement de quatre individus furent analysés à l'aide d'un Modèle de Markov Caché (MMC) afin d'évaluer la probabilité des individus d'être dans l'un des deux modes comportementaux suivants: transit ou résident. En comparant les caractéristiques de plongée durant ces deux modes, nous avons observé que le golfe de Boothia (GB), avec un couvert de glace modéré (54-62 %), est utilisé comme site d'alimentation estival par les quatre individus, et ce, malgré le fait que ces baleines provenaient de régions différentes. Tous les animaux ont transité rapidement par le détroit de Fury et Hecla, caractérisé par un couvert de glace important (80-98 %). Les baleines passent la majorité de leur temps à de faibles profondeurs (8-16 m) lorsqu'elles sont en mode « résident » et ce peu importe la période de la journée. Un comportement qui suggère une alimentation sur des densités de zooplancton située près de la surface. Etant donné l'importance apparente du golfe de Boothia comme aire d'alimentation estivale pour cette population, tous les efforts devraient s'orienter à maintenir l'intégrité de cet écosystème.

Mots clés : baleine boréale ; *Balaena mysticetus* ; mouvement ; comportement de plongée ; modèle de Markov caché ; aire d'alimentation ; glace de mer

Ce premier article, intitulé « *Bowhead whale Balaena mysticetus diving and movement patterns in the eastern Canadian Arctic: implications for foraging ecology* », fut corédigé par moi-même ainsi que par les chercheurs Toby A Patterson, Sebastian Luque, Véronique Lesage, Mads-Peter Heide-Jorgensen, Larry L. Dueck et Steven H. Ferguson. Il fut accepté pour publication dans sa version finale en 2011 par les éditeurs de la revue *Endangered Species Research*. En tant que premier auteur, ma contribution à ce travail fut principalement la rédaction de l'article et l'interprétation des résultats. Le chercheur Toby Patterson, second auteur, a créé le programme statistique pour l'analyse des mouvements des animaux (MMC) et le chercheur Sebastian Luque m'a aidé dans l'analyse des données de plongée. Véronique Lesage, troisième auteure, a contribué à l'écriture de l'article. Mads-Peter Heide-Jorgensen, cinquième auteur est l'inventeur de la méthode de déploiement des balises satellites. Le sixième auteur, Larry Dueck à participer à la campagne d'échantillonnage sur le terrain et le dernier auteur, Steven Ferguson, a dirigé le projet de recherche. Une version abrégée de cet article a été présentée à la conférence *International Polar Year Science Conference* à Oslo en Norvège, à l'été 2010 et à la conférence *ArcticNet* à Ottawa, en Ontario, à l'automne 2010.

1.2 ABSTRACT

The bowhead whale (*Balaena mysticetus*) is the only mysticete species endemic to the Arctic. The Eastern Canada-West Greenland (EC-WG) population is considered of special concern in Canada as these whales remain at risk of becoming threatened or endangered due to their slow rate of growth and low fecundity, and ongoing environmental changes in the Arctic. In this context, we used satellite-linked time-depth recorders (SDR-T16) to investigate their movements and dive behaviour and identify plausible summer feeding areas in the Canadian Arctic. Seven individuals from the northern Foxe Basin (FB) (n = 4 in July 2003) and Cumberland Sound (CS) (n = 3 in July 2006) were tracked by satellite for 17 to 293 d. Movement patterns from 4 whales were analyzed using a hidden Markov model (HMM) to inform the probability of whales being in one of 2 behavioural modes: transient or resident. Comparing dive characteristics during transient and resident periods, we observed that the Gulf of Boothia (GB) with moderate ice coverage (54–62%) was used as a summer foraging area by all 4 whales even though they came from different regions. All animals transited rapidly through Fury and Hecla Strait, an area of heavy ice coverage (80–98%). Whales spent most of their time at shallow depths (8–16 m) regardless of time of day when in resident mode, likely feeding on near-surface aggregations of zooplankton. Considering the apparent importance of the GB as a feeding area for this population, every effort should be made to maintain the integrity of this ecosystem.

KEYWORDS: Bowhead whale · *Balaena mysticetus* · Movement · Diving behaviour · Hidden Markov model · Foraging habitat · Sea ice

1.3 INTRODUCTION

The bowhead whale (*Balaena mysticetus*) is the only mysticete whale endemic to the Arctic (Nowak & Walker 2003). The species occurs in Canadian waters as 2 separate populations: the Bering-Chukchi-Beaufort (BCB) and the Eastern Canada-West Greenland (EC-WG) populations. Although commercial whaling severely depleted both populations during the 15th to 19th centuries (Woodby & Botkin 1993), recent abundance estimates show evidence of increase for these populations (Koski et al. 2006, Dueck et al. 2007, Heide-Jørgensen et al. 2007, IWC 2009).

Both populations are considered of "Special Concern" in Canada, as they are still considered at risk of becoming threatened or endangered (COSEWIC 2009). However, factors affecting their abundance, distribution and foraging ecology are only beginning to be understood. This long-lived species (>200 yr) is sexually mature at around 25 yr of age, and has a low fecundity combined with long inter-birth interval (George et al. 1999). These particular biological characteristics make this species more vulnerable to the effects of climate change, to increasing killer whale predation and to the impacts of human activities (e.g. shipping, mining, oil and gas field exploitation), especially those occurring near or within their feeding or nursery areas (IPCC 2007, Higdon & Ferguson 2009).

Previous studies on movements of EC-WG bowhead whales have shown that these animals are widely distributed throughout the Canadian eastern Arctic and West Greenland where they perform long seasonal migrations (Heide-Jørgensen et al. 2003). Their winter distribution includes Hudson Strait, northern Hudson Bay, east Baffin Island and the ice edge along West Greenland (Reeves & Heide-Jørgensen 1996, Koski et al. 2006), while in spring they are usually found along the west coast of Greenland, in Cumberland Sound (CS), Foxe Basin (FB) and Lancaster Sound (Fig. 1). Their summer range includes the fjords and bays of the Canadian High Arctic, Hudson Bay and FB (Cosens et al. 1997, Cosens & Innes 2000, Higdon & Ferguson 2010).

Bowhead whales are assumed to feed on pelagic and epibenthic zooplankton in late summer and fall (Finley 2001, Lowry et al. 2004, Pomerleau et al. 2011), and on pre-ascending diapausing calanoid copepods in late winter and early spring, at least in Disko Bay, Greenland (Laidre et al. 2007). Although bowhead whale movement patterns and diet have been studied previously, where and when they feed across the vast eastern Arctic remains poorly understood (Higdon & Ferguson 2010, Kovacs et al. 2010). Most studies on foraging behaviour of bowhead whales from the Eastern Canada-West Greenland (EC-WG) population have been based on observations of feeding, inferences from plankton net tow, short duration dive data or a combination of these approaches (Finley 2001, Lowry et al. 2004, Lee et al. 2005, Laidre et al. 2007). The Arctic climate leads to large-scale seasonal shifts in both primary and secondary production, which are highly patchy in space and time. Although Arctic species are adapted to this variability, for instance by rapid accumulation of large blubber stores in the case of whales, the adaptability of species, such as bowhead whales, living exclusively at high latitude may be impaired by the ongoing warming climate (Neibauer & Schell 1993). Thus, it is pressing to gain a better understanding of the factors affecting their abundance, distribution and foraging ecology.

Sea ice strongly influences the seasonal distribution of bowhead whales (Moore & Reeves 1993, Dyke et al. 1996, Ferguson et al. 2010a). Whales appear to select areas of lower ice concentration and thickness during winter, likely to reduce risks of ice entrapment. The reverse is observed during summer, possibly to reduce exposure to predators such as killer whales, and increase feeding opportunities near the productive marginal sea ice zone (Gosselin et al. 1997, Ferguson et al. 2010a). The decreasing trend in Arctic sea ice extent and quality (Gagnon & Gough 2005) is expected to have profound effects on habitat use and movement patterns of bowhead whales, as well as other Arctic species. Warming ocean temperatures affect plankton abundance and distribution (Greene & Pershing 2007).

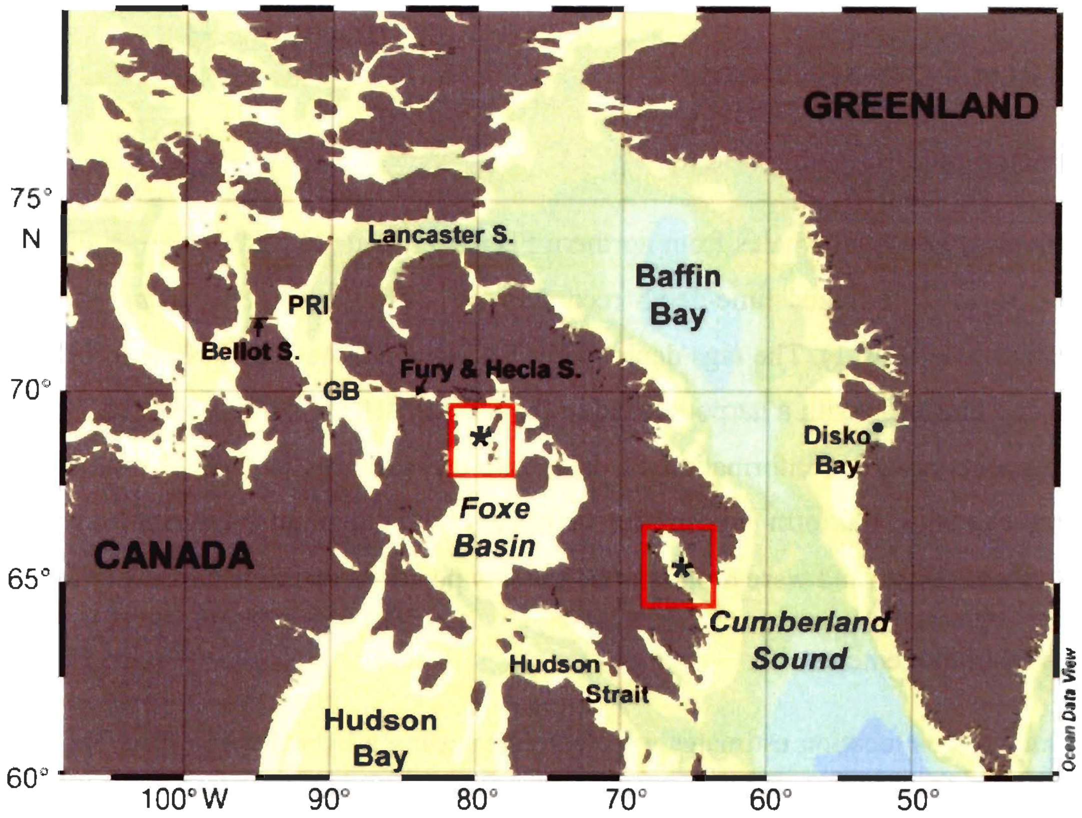

Figure 1. Bowhead whale tagging locations in the eastern Canadian High Arctic (red rectangles), in Foxe Basin in 2003 and Cumberland Sound in 2006. GB = Gulf of Boothia; PRI = Prince Regent Inlet

The dependence of bowhead whales on zooplankton as a food resource (Pomerleau et al. 2011) may leave them vulnerable to changes in plankton availability (Pershing et al. 2009). Here, we use a recently developed technique, a 2-state hidden Markov model (HMM), to gain insights into the location and characteristics of summer feeding areas of EC-WG bowhead whales. By combining dive and movement data in this analysis for 4 individual whales tracked remotely via satellite, we identified resident and transit modes and determined whether diving behaviour differed between resident and transit periods. Bowhead whales in resident mode are expected to be associated with sea ice. Diving depths during that mode should reflect feeding, although other behaviours cannot be excluded. Since time of day influences the vertical distribution of planktivorous marine mammal prey species in most of the world's oceans (Benoit-Bird et al. 2009), we also examined diel variation in dive behaviour of bowhead whales.

1.4 MATERIALS AND METHODS

1.4.1 Telemetry

Individual bowhead whales from northern FB (2003) and CS (2006) were equipped with SDR-T16 satellite-linked time-depth recorders (Wildlife Computers), using an 8 m long fiberglass pole (Fig. 1). The tags deployed in FB were float tags tethered 1 m behind the whales and anchored with a harpoon head in the blubber (Heide-Jørgensen et al. 2003). These instruments provided information on date, time and location, as well as a summary of dive characteristics. Platform Transmitter Terminals (PTTs) had an estimated longevity of 20 000 transmissions, and were programmed to relay positions and dive data every day.

1.4.2 Analysis of movements

The raw Argos location estimates were corrected using a hybrid speed filter/Kalman filter approach (Patterson et al. 2010). This method corrects for Argos error and produces a set of locations at regular intervals, which were chosen to be every 4 hours. The resulting positions were used to construct time series of speed of travel and turning angle between successive observations. These were analyzed using a 2-state HMM (Patterson et al. 2009) to classify the bowhead whale movements into 2 putative movement modes, which we labeled 'transit' and 'resident'. Step lengths between locations and turning angles, conditioned on the hidden behavioural state, were modeled by a Weibull and a wrapped Cauchy distribution, respectively. The HMMs were used to produce posterior probability distributions of state and the most likely state. The HMM output was then used in the diving analyses in order to contrast dive characteristics during transit and resident periods. To test the influence of habitat on behaviour, we used a second model where the probability of switching between states was assumed to be a linear function of ice concentration. Mean ice concentration from 2 degree boxes centered on each location point was obtained from the Weekly NOAA Optimum Interpolation (OI) SST V2 product (Reynolds 1988) that uses in situ and satellite sea-surface temperatures (SST) as well as simulated SST to estimate sea ice cover.

1.4.3 Analysis of diving behaviour

The raw pressure sensor data were summarized onboard the tag into 6-h blocks (03:00–09:00, 09:00–15:00, 15:00–21:00 and 21:00–03:00 h local time; set at the release location), and included information on dive depth, dive duration, and time-at depth (TAD) (Table 1). The average diving depth and duration for each period were calculated by multiplying the mid-range depth or duration of each bin by the number of dives in that bin, adding the products across all bins, and dividing the result by the total number of dives in that period. Maximum diving depth and duration for each period were defined as the mid-range value of the rightmost histogram bin (deepest or longest dive) with at least 1 dive. We investigated whether there were diurnal cycles and inter-individual differences in diving depth, and relationships with behavioural state as estimated from HMM by first decomposing time into sine and cosine angular coordinates for time of day (Bell 2008).

Table 1. Summary information of bowhead whales tagged in Foxe Basin (FB) and Cumberland Sound (CS), showing data available and not available (na) for the analyses. PTT = Platform transmitter terminal, HMM = Hidden markov model analysis.

PPT no.	Tagging date	Total no. of transmissions	Location	Sex	Length (m)	Dive depth	Dive duration	Time-at depth	HMM	Diurnal pattern
20160	5 July 2003	71	FB	F	15	✓	✓	✓	na	na
20167	8 July 2003	602	FB	M	13	✓	✓	✓	✓	✓
21802	11 July 2003	673	FB	F	13	✓	✓	✓	✓	✓
26712	18 July 2003	140	FB	F	12	✓	✓	✓	✓	✓
66352	11 July 2006	716	CS	F	11	✓	✓	na	na	na
66353	11 July 2006	1208	CS	M	12	✓	✓	✓	✓	na
66356	5 August 2006	568	CS	M	12	✓	na	na	na	na

A series of linear models with additive effects for these components were fitted to test for the existence of these cycles in average and maximum diving depth, considering the following full model:

$$Y = \beta_1 + \beta_2 \sin_{TOD} + \beta_3 \cos_{TOD} + \beta_4 I + \beta_5 M + \varepsilon \qquad (1)$$

where Y represents maximum or mean diving depth of an individual whale, $\sin_{TOD}$ and $\cos_{TOD}$ are the angular coordinates of time of day (TOD) in a 24 h cycle, and I is an indicator for the effect of individual, and M is the behavioural state from HMM. β_i are model coefficients to be estimated, and ε is residual error. The subset of candidate models consisted of all combinations of fixed effects from the full model where the angular coordinates, i.e. sine and cosine, were both included or excluded, as both are required to properly interpret cycles (Bell 2008). Thus, a total of 8 models for each response variable, average and maximum diving depth, were considered candidates (Table A1 in the Appendix). Dive duration was not included in analyses because it is strongly correlated with dive depth (Kooyman & Ponganis 1998). The second-order Akaike Information Criterion (AICc) was calculated for each model, and the AICc differences (ΔAICc) were used to select the best model from the candidate set (Burnham & Anderson 2002). Models were fit using the generalized least squares method implemented in the nonlinear mixed effects GNU R package (Pinheiro et al. 2011), where the observations for each individual were assumed to have a first-order autocorrelation structure.

1.5 RESULTS

1.5.1 Movement patterns

Seven bowhead whales were tagged in 2003 and 2006: 4 females (2 with calves), and 3 males. Three females and 1 male were tagged in FB near the community of Igloolik, and the other 3 individuals were tagged in CS in south-eastern Baffin Island. Each whale was identified by an individual PTT number (Table 2, Fig. 1). Only 4 whales, including 3 from FB and one from CS (66353), were used in the 2-state HMM for analysis of their movements. Reasons for short duration transmissions may be diverse, and include tag position on the whale and animal surface behaviour, i.e. height above water and pattern of immergence, PTT transmission versus satellite pass programming. Despite sample size limitations, broad-scale movement patterns were similar in all 4 whales even though tagging regions were separated by several hundreds of kilometres (Fig. 2). All whales traveled through Fury and Hecla strait and spent time, most probably foraging, in the Gulf of Boothia (GB) (Fig. 1).

There was little difference (2 to 3%) in the state prediction between the model implemented with and without sea ice. As a result, we provide the more parsimonious results from the simple model in the next section, with the qualitative effect of sea ice on behaviour. For 4 whales, residency was displayed mainly in the northern part of GB and lasted from 2 weeks to 2 months. Mean sea ice cover in this presumed foraging area ranged from 54 to 62% between the end of July and mid-August and from 24 to 83% from September to mid-November. Residency also occurred in the northern part of FB but lasted for shorter periods, i.e. from 1 to 10 days, and mean sea ice cover ranged from 40 to 45% in July. The whale with the longest track (66353) also displayed residency in CS both in July (mean sea ice cover: 12 to 36%) and between early January and the end of April (mean sea ice cover: 64 to 93%) (Fig. 2). Animals departed from their tagging region (FB or CS) 1 to 7 d after tagging, arriving in the vicinity of GB between mid-July and early September.

Maximum travel speeds ranged from 5 to 8 km h^{-1} depending on whale (Fig. 2a). Most tags failed in early August. The longest track available was from a CS individual, which spent time in CS areas of much lower ice cover (Table 2) before moving into FB for a period of residency during August, then to GB for September to November. This whale departed from GB via Prince Regent Inlet (PRI) in the first week of November when the ice cover was about 80% both in PRI and the other possible exit, the Fury and Hecla Strait. The whale circumnavigated Baffin Island via Lancaster Sound and Baffin Bay, and travelled into extensive ice-covered areas (up to 95% coverage) at speeds up to 12 km h^{-1} (Fig. 2a, Table 2). The whale returned to CS in early January and stayed within CS all winter until the last day of transmission (1 May 2007) (Fig. 2c). The average ice cover in CS during this second period of residency was 78%.

Table 2. Mean percent sea-ice cover (±SD) during resident and transient modes for the 4 whales included in the hidden Markov model. PTT = Platform transmitter terminal, n = number of 4 h time steps analyzed for the periods in resident and transient mode, respectively; FB = Foxe Basin; CS = Cumberland Sound; GB = Gulf of Boothia; DS = Davis Strait.

PTT	Resident mode				Transient mode		
	n	Dates	Location	Mean ice cover (%)	n	Dates	Mean ice cover (%)
20167	14	8–11 Jul	FB	39.6 (±9.9)	35	12–16 Jul	80.1 (±24.3)
	146	16 Jul –10 Aug	GB		6	10–11 Aug	53.9 (±5.5)
21802	58	12–22 Jul	FB	44.3 (±9.5)	5	13 Jul	54.7 (±4.9)
	69	26 Jul –7 Aug	GB	57.1 (±6.1)	25	22–26 Jul	75.9 (±12.8)
26712	18	22–25 Jul	GB	65.4 (±4.5)	18	19–22 Jul	73.7 (±11.5)
	44	28 Jul – 4 Aug	GB	54.8 (±4.4)	14	25–28 Jul	61.3 (±2.7)
66353[a]	31	22–27 Jul	CS	8.6 (±5.2)	62	12–22 Jul	17.8 (±5.1)
	13	9–11 Aug	FB	12.3 (±3.3)	76	28 Jul –9 Aug	0.1 (±0.9)
	39	15–25 Aug	FB	43.3 (±5.2)	27	11–15 Aug	49.5 (±21.4)
	250	8 Sep–11 Nov	GB	44.4 (±19.7)	80	26 Aug –9 Sep	35.2 (±13.7)
	24	28 Nov –4 Dec	DS	90.7 (±4.7)	90	17 Sep –5 Nov	45.9 (±16.7)
	14	21–24 Dec	DS	91.6 (±2.3)	209	12 Nov –30 Dec	86.8 (±11.2)

[a] Not all the data are presented due to a mix of resident and transient behaviour within CS from 1 January to May 2007

1.5.2 Dive profiles

Diving depth was generally shallow in the 7 tagged individuals. Over 90% of dives were at depths of 50 m or less, including 70 to 80% within 20 m from the surface. The 4 whales tagged in FB concentrated their diving activity above 16 m, while the 3 CS whales tended to make more use of the 16 to 20 m depth stratum. The immature female (26712) tagged in FB made the deepest dives (>350 m) and was the individual diving the most regularly at depths below 16 m. These occasional deep dives occurred in the northern part of GB where the bathymetry is generally deep (500 m) for the Canadian Arctic Archipelago (AMSA 2009). The intense use of near-surface depths by bowhead whales was reflected in dive duration, as dives of 6 min or less comprised 74 to 100% of the dive record in 6 of the 7 individuals. This tendency was particularly striking in CS individuals, which had over 60% of their dives lasting 1 min or less. The one exception to this general pattern was the immature female (26712) tagged in FB, nearly 50% of whose dives lasted longer than 6 min, including 6% of dives >15 min.

1.5.3 Diving behaviour during resident and transient modes

Of the 4 whales whose movement patterns were classified into resident versus transient modes, only 3 provided dive data for both modes (Table 1). In general, these 3 whales dived deeper during transit than during residency (Fig. 3a). Indeed, behavioural state was a significant term in the 4 most parsimonious models for average and maximum diving depth (average diving depth: $F_{1,282} = 5.77$; maximum diving depth: $F_{1,280} = 19.72$; $p < 0.05$ both cases). Inter-individual effects were included in the 2 best-ranking models for maximum dive depth ($F_{2,280} = 5.67$, $p < 0.001$), but only in the second best-ranked model for average dive depth. Time of day was not a significant factor in the best-ranking models for average or maximum diving depth, nor was it a significant predictor of behaviour in any of the candidate models ($p > 0.05$, for all candidate models). Mean diving depth was usually between 20 and 50 m while in transit, whereas it was often shallower during residency mode (especially within GB) for the 3 whales (Fig. 3b).

1.6 DISCUSSION

We were able to determine the location and characteristics of what appears to be a summer feeding area in the Canadian eastern Arctic for 4 whales from the EC-WG bowhead whale population. During summer, and regardless of tagging region, resident behaviour occurred mostly in the GB, and while in this mode and area, whales spent most of their time close to the surface. Bowhead whales were associated with sea ice during both transit and residency modes, although ice coverage was generally less extensive in areas where residency occurred compared to areas used for transit.

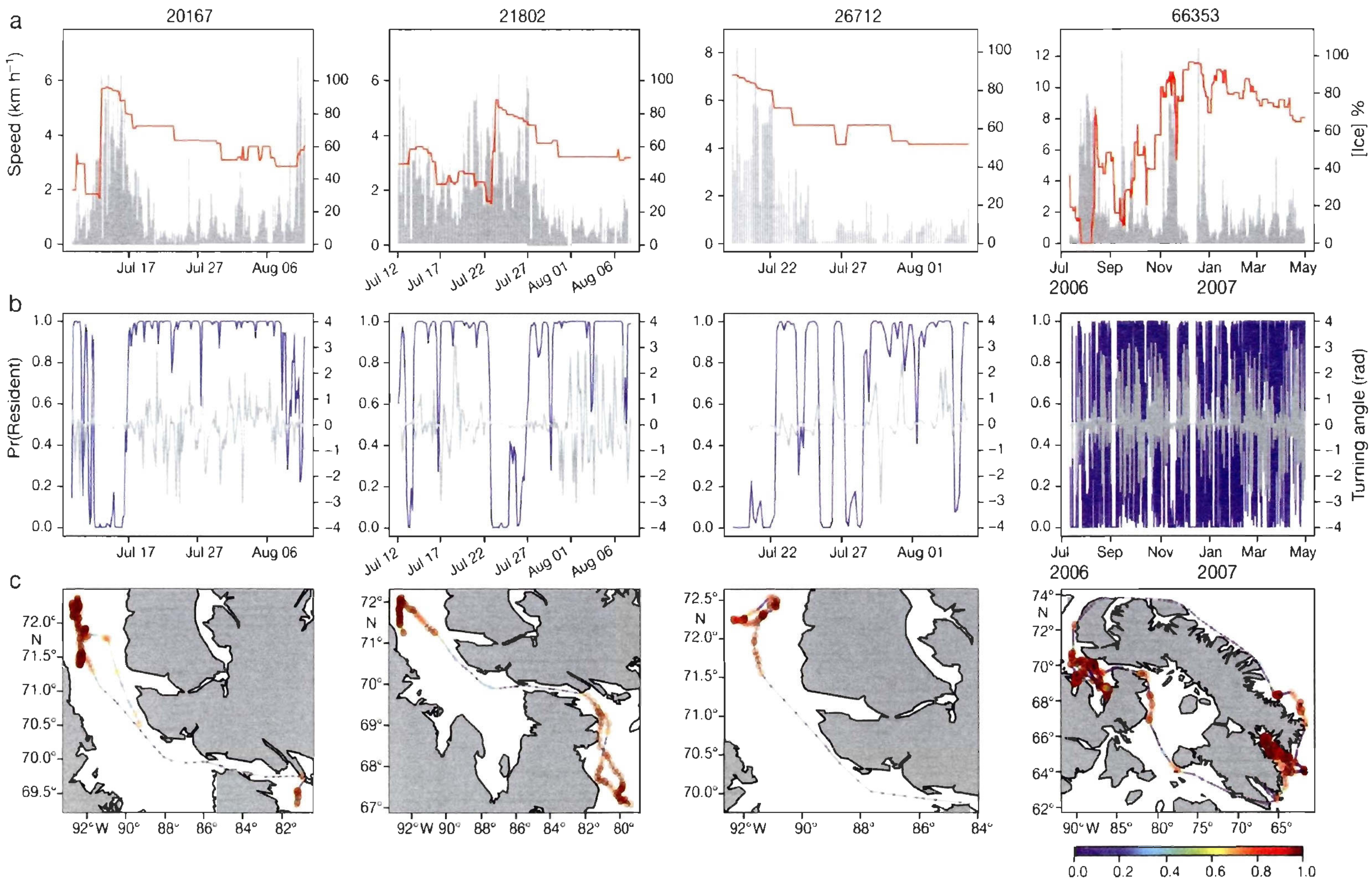

Fig. 2. Input data and state predictions from the hidden Markov model (HMM) used to classify the bowhead whale movements into transient and resident states. Each column shows the result for an individual bowhead whale identified by its Platform Transmitter Terminal (PTT) number. (a) Speed between inferred locations (every 4 h; red solid line) and percent sea ice cover (grey bars). (b) Turning angle (rad = radius) between subsequent locations and probability (Pr) of whales being in resident state along their tracked movements. Grey lines: turning angle between subsequent locations; blue lines: probability of most likely state of 4 whales along their tracked movements. (c) Probability of state mapped onto the movement paths where red indicates higher probability of resident (foraging) mode relative to blue that indicates transient (searching) mode. July and August dates are for 2003 where not otherwise given

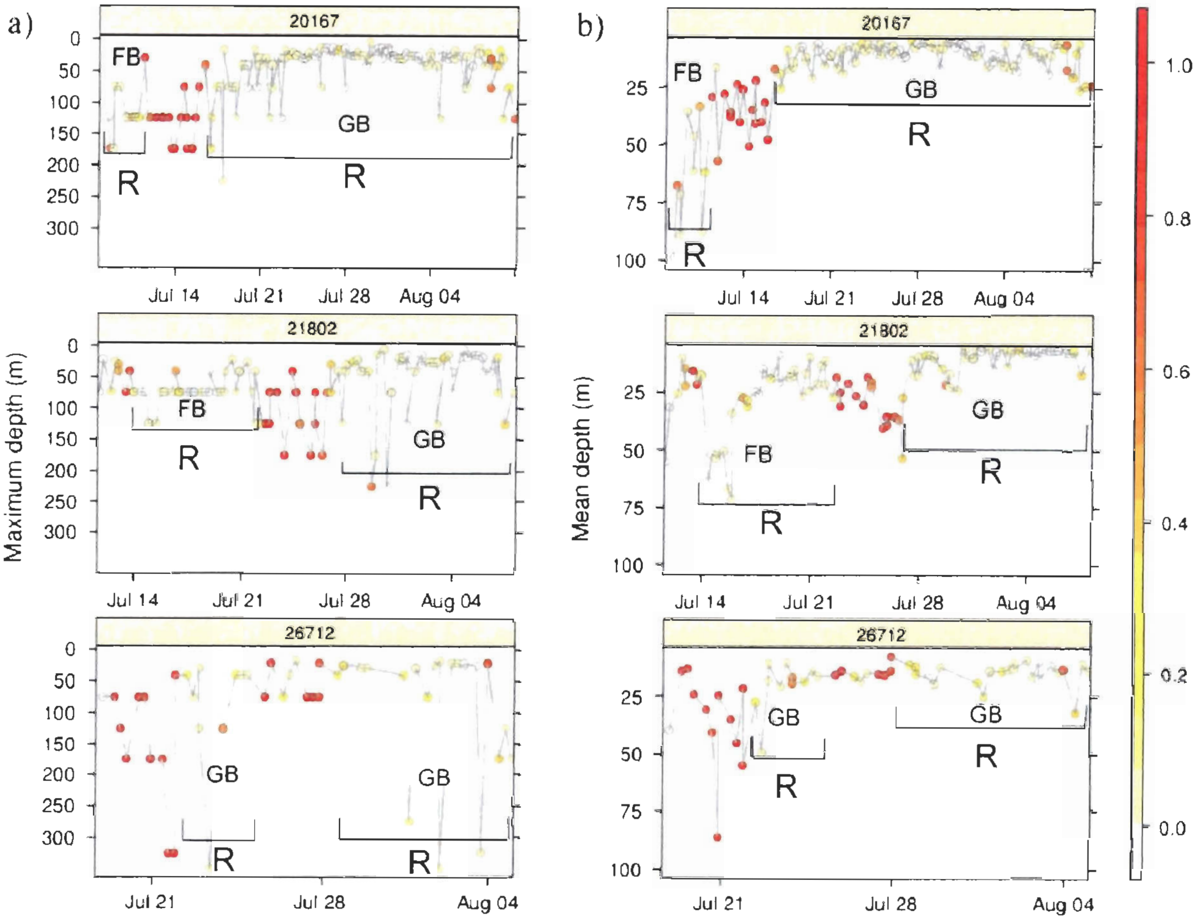

Fig. 3. Temporal changes in (a) maximum and (b) mean dive depth as a function of behavioural mode according to the probability of state. Values in the right-hand colour bar are probability, from 0 to 1, of being in transient state; red represents transit mode and yellow/white resident mode. R = resident mode; FB = Foxe Basin; GB = Gulf of Boothia. Dates are for 2003

The similarity in state prediction between models with and without ice probably reflects our limited ability to model effects of ice on movement patterns with current sample size rather than a lack of influence of ice on bowhead whale behavior. A much larger sample size will be needed to properly quantify the effect of environmental factors such as sea ice density on their behavior.

Residency mode is assumed to include foraging, as predators, especially those like bowhead whales, will typically decrease travel speed and increase turning angles when they come across an aggregation of prey (Jonsen et al. 2005, Bailey et al. 2009, Patterson et al.

2009). We presume that the major proportion of residency is linked to feeding, given the suspected importance of this behaviour during summer (Burns et al. 1992). However, we acknowledge that not all residency may be associated with active foraging, as it may include other behaviours such as nursing in cow-calf pairs or social activities.

In this study, we have used the output of the HMM for the analysis of dive data. This reflects a limitation of current state-space and other methods which tend to analyze the horizontal components of movement in isolation. This highlights a need to build behavioural analysis approaches which can use horizontal and vertical movement data simultaneously. Because of the small number of individuals included in the analysis, we deliberately chose to keep the models simple. However, we note that, with a more extensive data set, covariates such as water depth and ice concentration could be included directly in the HMMs rather than as a linear correlate to behavioural switching as done here for ice concentration (Patterson et al. 2009). For the present study the intent of using the HMMs was exploratory rather than inferential. Nonetheless, the results suggest that with more extensive data, these methods could be used successfully to explore the links between habitat variables and movement and foraging behaviour of bowhead whales.

GB was a common summer feeding area for all 4 whales, regardless of tagging region, indicating that there must be adequate food resources, e.g. dense aggregations of zooplankton prey at that time of the year in this particular area. Data from a biogeochemical mooring deployed in eastern Bellot Strait, between Boothia Peninsula and Somerset Island, from October 2007 to September 2009 suggest substantial primary production from strong water column mixing and enhanced availability of nutrients induced by strong tidal movements in the strait (S. Vagle pers. comm.). This could partly explain the aggregation of marine life in the eastern Bellot Strait region including sea birds, seals and walruses (Stirling 1997), although local productivity is currently unknown.

Predator avoidance is possibly a reason why bowhead whales remained within GB in association with sea ice during summer. Killer whale *Orcinus orca* sightings in the Arctic have become more frequent with warmer Arctic summers and increased open water areas (Ferguson et al. 2010b), including the northern portion of GB (Matthews et al. 2011). Calves and immature whales are likely more vulnerable to killer whale predation, as most documented cases in FB involved bowhead whale calves (DFO 2008). Diving patterns were not related to time of day, which suggests that deep dives were unrelated to vertical movements of zooplankton prey. Our ability to detect such an effect may be limited by the constraints imposed by the instruments, which allowed the collection of only histogram summary data during 4 periods of equal duration during the day. Continuous data, or a subsample thereof, might be a better test for the existence of a cyclical pattern in diving behaviour. In southern latitudes, the vast majority of zooplankton taxa perform diel vertical migration (DVM) (Longhurst 1976). As a result, several planktivorous whale species adjust their foraging behaviour accordingly and track the vertical migrations of their prey (Croll et al. 2005, Doniol-Valcroze et al. 2011). However, summer months at higher latitudes are characterized by up to 24 h of daylight and zooplankton do not perform DVM (Blachowiak-Samolyk et al. 2006), their vertical distribution probably being mostly influenced by sea ice cover and hydrodynamic factors (Buchanan & Haney 1980).

Several studies of the vertical distribution of Arctic zooplankton species revealed that maximum densities of key herbivorous calanoid copepods (i.e. *Calanus hyperboreus* and *C. glacialis*) were usually within 0 to 50 m from the surface during summer (Tande & Bamstedt 1985, Hassel 1986, Blachowiak-Samolyk et al. 2006). These 2 pelagic and herbivorous copepod species, along with *C. finmarchicus* (in areas where there is an influence of Atlantic waters, such as in Baffin Bay), are believed to be important prey of the EC-WG bowhead whale population (Finley 2001, Laidre et al. 2007). The strong preference of bowhead whales for depths between 8 and 20 m is consistent with intense filter-feeding on shallow zooplankton prey such as calanoid copepods.

In the marine environment, the seasonal variability and patchiness of food is a problem that predators need to overcome in order to fulfill their energetic requirements (Bluhm & Gradiger 2008). Baumgartner et al. (2003) found a strong correlation between the average diving depth of North Atlantic right whales *Eubalaena glacialis* and peak abundance of its preferred prey (*C. finmarchicus*). The same pattern was observed for bowhead whales in springtime in Disko Bay, Greenland, where all foraging dives were to the bottom where diapausing *C. finmarchicus* densities were the highest (Laidre et al. 2007).

Laidre et al. (2007) studied the dives of 14 individuals in Disko Bay, Greenland, and their findings describe deeper (400 m) maximum dives, and much deeper mean and maximum dive depths of 53 ± 35 to 109 ± 41 m, respectively. Similar findings were obtained from bowhead whales tagged elsewhere in Greenland (Simon et al. 2009). These differences could be due to the age of the study animals, as we uniquely observed deep diving in an immature female, the study duration, as the Greenland records tended to be short (a few hours to a few days), or seasonal differences. Feeding behaviour may vary seasonally and geographically depending on prey species availability and concentration. Both Greenland studies took place in the spring, when potential zooplankton prey species distribution is usually much more vertically expanded than in summer months (Hansen et al. 1996).

1.7 CONCLUSION

Our findings are limited to a small number of individuals from the EC-WG bowhead whale population, but provide meaningful information for the conservation of this population. Despite our small sample size, we were able to demonstrate that bowhead whales originating from regions separated by several hundreds of kilometers converged into an area in the northern part of the GB, likely to forage intensively during summer on near-surface zooplankton aggregations. In the context of the upcoming industrial development of the Arctic, every effort should therefore be made to maintain the integrity of this ecosystem.

1.8 ACKNOWLEDGEMENTS

We thank the communities of Igloolik and Pangnirtung for their assistance with tagging efforts. We express special thanks to Bill Williams and Svein Vagle for their information about the mooring experiment in Bellot Strait. Tagging procedures were approved by the DFO Freshwater Institute Animal Care Committee (AUP# FWIACC-2002,3, 4, 5,6-007) and permitted under DFO License to Fish for Scientific Purposes #S-02/03to05/06-1019-NU. This study was funded by Fisheries and Oceans Canada, the Nunavut Wildlife Management Board, the Nunavut Implementation Fund, and a NSERC Discovery Grant to S.H.F.

1.9 APPENDIX

Table A1. Summary of ranking of 8 fitted models for average diving depth. Model parameters follow the description of the full model in 'Materials and methods: Analysis of diving behaviour'. AICc = second-order Akaike Information Criterion

Parameters in model	AICc	ΔAICc
β_1, β_5	2073	0
$\beta_1, \beta_2, \beta_3, \beta_5$	2076	2,889
β_1	2076	3,213
$\beta_1, \beta_4, \beta_5$	2077	3,908
$\beta_1, \beta_2, \beta_3$	2079	5,765
$\beta_1, \beta_2, \beta_3, \beta_4, \beta_5$	2080	6,859
β_1, β_4	2080	7,190
$\beta_1, \beta_2, \beta_3, \beta_4$	2083	9,803

Table A2. Summary of ranking of 8 fitted models for maximum diving depth. Model parameters follow the description of the full model in 'Materials and methods: Analysis of diving behaviour'. AICc = second-order Akaike Information Criterion

Parameters in model	AICc	ΔAICc
$\beta_1, \beta_4, \beta_5$	3098	0
$\beta_1, \beta_2, \beta_3, \beta_4, \beta_5$	3098	0,1183
$\beta_1, \beta_2, \beta_3, \beta_5$	3100	2,028
β_1, β_5	3100	2,2730
$\beta_1, \beta_2, \beta_3, \beta_4$	3109	11,0000
β_1, β_4	3110	12,6600
$\beta_1, \beta_2, \beta_3$	3112	13,8500
β_1	3114	16,0000

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CHAPITRE 2

LES CONTENUS STOMACAUX DE BALEINES BORÉALES (*BALAENA MYSTICETUS*) DANS QUATRE RÉGIONS DE L'ARCTIQUE CANADIEN

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Paru en 2011 dans Polar Biology, vol. 34, p. 615-620

2.1 RÉSUMÉ

Les contenus stomacaux de quatre baleines boréales (*Balaena mysticetus*) chassées entre 1994 et 2008 dans l'Arctique canadien ont été examinés afin de déterminer la composition de la diète. Trois échantillons proviennent d'individus de la population de baleines boréales de l'est du Canada et de l'ouest du Groenland (EC-WG), et représentent la première analyse de la diète pour cette population. Nous avons également analysé le contenu stomacal d'une baleine boréale de la population des mers Bering-Chukchi-Beaufort (BCB) chassée en 1996. Les quatre individus avaient de la nourriture dans leurs estomacs et leurs diètes variaient d'exclusivement pélagique (BCB), *Limnocalanus macrurus* étant la proie principale, à épi-benthique (EC-WG) avec *Mysis oculata* comme proie dominante. Ces résultats indiquent que la baleine boréale possède un large spectre alimentaire et viennent s'ajouter aux connaissances de base de la diète de cette espèce.

Mots clés : alimentation ; Arctique; *Balaena mysticetus* ; baleine boréale ; contenus stomacaux ; diète; *Limnocalanus macrurus* ; *Mysis oculata*

Ce deuxième article, intitulé « *Stomach contents of bowhead whales (Balaena mysticetus) from four locations in the Canadian Arctic*», fut corédigé par moi-même ainsi que par mon directeur de recherche Steven H. Ferguson et le chercheur Wojciech Walkusz. Il fut accepté pour publication dans sa version finale en 2010 par les éditeurs de la revue *Polar Biology*. En tant que premier auteur, ma contribution à ce travail fut l'essentiel de la recherche, incluant l'analyse des trois échantillons de l'Arctique de l'est et la rédaction de l'article. Steven Ferguson, second auteur, a dirigé le projet de recherche et Wojciech Walkusz a analysé l'échantillon de l'Arctique de l'ouest.

2.2 ABSTRACT

The stomach contents of four bowhead whales (*Balaena mysticetus*) harvested between 1994 and 2008 from the Canadian Arctic were examined to assess diet composition. Three samples were collected from bowhead whales of the Eastern Canada–West Greenland (EC–WG) population and represent, according to our knowledge, the first diet analysis from this bowhead whale stock. We also examined the stomach content of one bowhead whale from the Bering-Chukchi-Beaufort (BCB) population hunted in 1996. All four whales had food in their stomachs and their diet varied from exclusively pelagic (BCB whale), with *Limnocalanus macrurus* being the main prey, to epibenthic and benthic (EC–WG) with *Mysis oculata* playing an important role. These results indicate broad foraging spectrum of the bowhead whales and add to a basic knowledge of their diet.

KEYWORDS: Arctic; *Balaena mysticetus*; Bowhead whale; Diet; Feeding; *Limnocalanus macrurus*; *Mysis oculata*; Stomach content

2.3 INTRODUCTION

The bowhead whale (*Balaena mysticetus*) has a nearly circumpolar distribution in the northern hemisphere and inhabits polar waters year-round. There are two recognized populations of bowhead whale in the Canadian Arctic, one in the western Arctic known as the Bering-Chukchi-Beaufort population (BCB) and one in the eastern Arctic known as the Eastern Canada and West Greenland population (EC–WG). These two populations undertake extensive seasonal migration throughout their geographic range (Moore and Reeves 1993; Heide-Jørgensen et al. 2006; Ferguson et al. 2010). Stomach content analysis (Lowry et al. 2004) and seasonal differences in blubber fatty acids composition of BCB bowhead whales (Budge et al. 2008) suggested that the Eastern Beaufort Sea and the region around Point Barrow are important foraging areas in summer and early fall. In the eastern Beaufort Sea, copepods were the major food source for bowhead whales, while euphausids were the main prey in the western Beaufort Sea (Lowry and Frost 1984; Lowry 1993; Lowry et al. 2004).

There is little information in the scientific literature on bowhead whale diet for the EC–WG population. A small number of studies conducted in west Greenland and Baffin Bay suggested that bowhead whales feed mostly on copepods, euphausids and mysids (Bradstreet et al. 1987; Griffiths et al. 1987; Finley 2001). In Disko Bay Greenland, bowhead whales in spring foraged at the ocean bottom during the majority of their dives likely to feed on high densities of diapausing *Calanus finmarchicus* (Laidre et al. 2007; Simon et al. 2009). None of these studies have provided a more extensive spatial and temporal assessment of the EC–WG bowhead whale diet. Therefore, it is presently unknown if the bowhead whale is preferentially feeding pelagically or epibenthically in the Eastern Canadian Arctic as both feeding modes have been observed for the BCB bowhead whale population (Lowry and Burns 1980; Hazard and Lowry 1984).

Here, we provide information on bowhead whale diet from stomach content analysis of four subsistence harvested specimens from the Canadian Arctic between 1994 and 2009. We present the first data on stomach content analysis from the EC–WG population including harvested whales from Igloolik in 1994, Kugaaruk (Pelly Bay) in 2008 and Kangiqsujuaq (Wakeham Bay) in 2009. We also describe the stomach content of one bowhead whale from the BCB stock harvested near Shingle Point, Beaufort Sea, in 1996.

2.4 MATERIAL AND METHODS

2.4.1 Sample collection

Stomach contents were collected as part of bowhead whale subsistence hunting by Inuit in Canada (Fig. 1). Fisheries and Oceans Canada collected stomach content samples and data on morphological measurements from each harvested whale (Table 1). The first whale was taken by Inuit near the community of Igloolik, Nunavut in northern Foxe Basin on 14 September 1994. The second specimen was hunted by the Inuit of the

Inuvialuit Settlement Region from the eastern Beaufort Sea, near the community of Shingle Point, on 24 July 1996. The third specimen was harvested near the community of Kugaaruk (Pelly Bay), Nunavut in the Gulf of Boothia on 4 September 2008. Inuit from Nunavik (Northern Quebec) harvested a bowhead whale on 21 August 2009 about 20 km southeast of Kangiqsujuaq (Wakeham Bay).

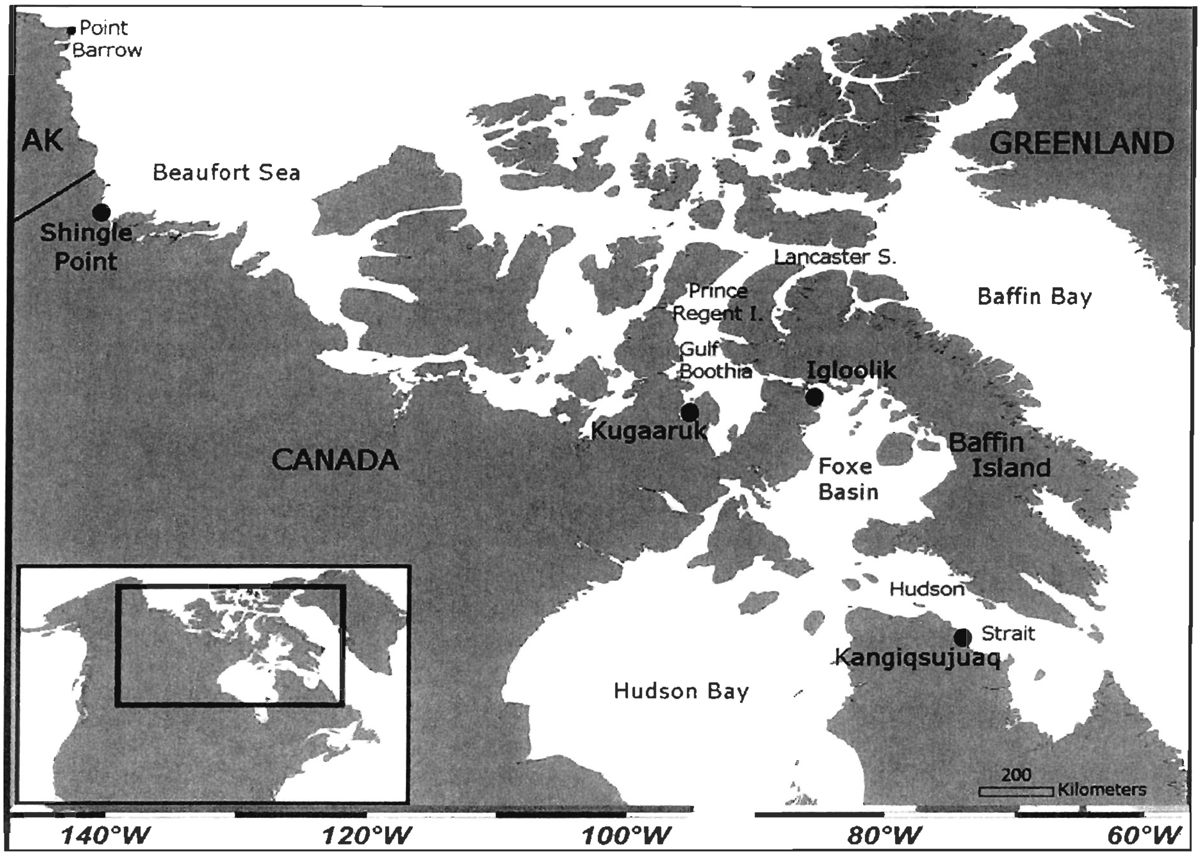

Figure 1. Bowhead whale stomach content sampling locations in the Canadian Arctic and communities where subsistence hunts occurred.

2.4.2 Stomach contents analysis

Stomach contents were kept frozen at -20°C prior to analysis in the laboratory. Stomach sample volume ranged from 0.2 to 1.0 L. Each sample was thawed, drained, and gently rinsed using a 250-µm mesh sieve. The prey items from each stomach sample were sorted, counted (Copepods were enumerated from split subsamples, while the other taxa were counted from the entire sample) and identified to the lowest taxonomic level, if possible to species (Harris et al. 2000). Contents of the bowhead stomach from Shingle Point were enumerated from subsamples. The number of individuals from each taxon and/or species was determined. Due to logistical constraints while in the field, the stomach samples analyzed represented a subsample from an unknown total stomach volume. Thus, we were only able to present the numerical abundance of prey items in the analyzed subsample for each whale.

Table 1. List of prey items identified in the stomach contents of four bowhead whales

Sample ID	Gender & maturity status*	V(L)	Food type	Species	N	Estimate ww (g)	% ww	Reference for ww
Igloolik (1994)	Female Subadult	0.5	Isopod	*Saduria entomon*	1	1.4	33.1	Own
			Gammarid amphipod	NA	8	0.4	9.5	2
			Bivalve	NA	7	1.75	41.4	2
			Gasteropod	NA	3	0.0	0.1	2
			Mysid	NA	1	0.12	2.8	1
			Decapod caridae	*Sabinea septemcarinata*	1	0.25	5.9	2
			Polychaete (tube)	NA	1	0.06	1.4	1
			Fish	NA	1	0.25	5.9	1
Shingle Point (1996)	Male Subadult	0.2	Calanoid copepod	*Calanus* spp.	200	1.41	2.7	2
			Calanoid copepod	*Limnocalanus macrurus*	34,400	39.05	73.4	3
			Hyperiid amphipod	*Themisto* spp.	100	0.80	1.5	2
			Mysid	*Mysis oculata*	100	12.00	22.6	1
Kugaaruk (2008)	Male Subadult	1.0	Mysid	*Mysis oculata*	6,815	817.80	99.7	1
			Calanoid copepod	*Metridia longa*	1,304	2.20	0.3	4
			Calanoid copepod	*Calanus* spp.	25	0.03	0.0	2
			Hyperiid amphipod	*Themisto* spp.	5	0.04	0.0	2
			Gammarid amphipod	NA	5	0.06	0.0	2
			Gammarid amphipod	*Onisimus* spp.	1	0.01	0.0	2
			Marine algae	*Fucus* sp.	1			
Kangiqsujuaq (2009)	Female adult	1.0	Mysida	*Mysis oculata*	6,495	779.40	99.9	1
			Hyperiid amphipod	*Themisto* spp.	10	0.08	0.0	2
			Gammarid amphipod	NA	40	0.45	0.1	2
			Polychaeta (tube)	NA	1	0.06	0.0	2

* Maturity status: Subadults 6–13 m, Adults >13 m

V Volume analyzed (L), *N* Number of individuals identified in the sample, *ww* Wet weight

References (1) Weslawski et al. (1994) (2) Weslawski et al. (2006) (3) Hirche (2003) (4) Hanssen (1997)

2.5 RESULTS

All bowhead whales had been feeding to some extent prior to harvest as indicated by the summary of prey items present in each sample of whale stomach contents (Table 1). The state of digestion of the stomach content samples varied. The stomach content of the female whale from Igloolik was comprised of only epibenthic and benthic organisms. Although the sample was heavily digested, a well-preserved benthic isopod, *Saduria entomon* (TL = 61 mm) as well as one benthic decapod, *Sabinea septemcarinata*, was found. Some gammarid amphipods and bivalves were also reported along with gastropods and some parts of fish. Finally, one telson of a mysid and traces of polychete tube were also identified. The stomach content from the male bowhead whale harvested in Kugaaruk was little digested. Mysid shrimps, *Mysis oculata*, largely dominated the sample along with the copepod *Metridia longa* (mostly females). Female calanoid copepods (*Calanus* spp.), hyperiid amphipods (*Themisto* spp.) and gammarid amphipods (*Onisimus* spp.) were also found in trace amounts. The diet of the female bowhead whale harvested from Kangiqsujuaq was dominated by *M. oculata*, but the sample was more deteriorated than the Kugaaruk sample. Gammarid amphipods and Themisto spp. were also found in negligible numbers. The stomach content of the male bowhead whale from the BCB population in the Western Arctic was highly digested. It consisted almost entirely of the copepod *Limnocalanus macrurus*. Small amounts of *Calanus* spp., *Themisto* spp. and mysids (*M. oculata*) were also recorded.

2.6 DISCUSSION

Stomach content analysis has some limitations, especially when performed on stranded animals. Prey with hard body parts may bias the results because of their slower rate of digestion compared to soft body preys (Scholz et al. 1991; Sheffield et al. 2001). Therefore, stomach samples collected from harvested animals may have the advantages of providing information on fresher contents that represent a less biased sample of the population.

Little information is available in the literature on the bowhead whale diet and foraging behavior of the EC–WG population. Finley et al. (1993) proposed that bowhead whales forage extensively on *Calanus* copepods during summer and particularly in fall when mature stages occurred in high densities. Finley (2001) put forward the hypothesis that the bowhead whale would target *Calanus* copepod similar to what has been described for the northern right whale (*Eubalaena glacialis*) in the Bay of Fundy (Baumartner and Mate 2003). Laidre et al. (2007) examined diving behavior profiles of fourteen bowhead whales in Disko Bay (Greenland) and identified most dives as being benthic in nature. In Disko Bay, available prey for bowhead whales consisted mostly of *C. hyperboreus, C. glacialis* and *C. finmarchicus* in the surface layer (up to 50 m depth) and large concentrations of the copepod *C. finmarchicus* close to the ocean bottom. However, our results reported only one whale from the Eastern Canadian Arctic contained the pelagic *Calanus* spp. and represented less than 1% of the abundance of the stomach content analyzed.

The results from the stomach content analysis of the whale harvested near Igloolik, in Northern Foxe Basin, suggested that the whale had fed at least partly near the bottom. *Saduria entomon*, that was found in the stomach, is a marine/estuarine isopod with a circumpolar distribution and is mostly found in shallow estuarine regions on different types of soft bottom (i.e., sand, clay, gravel and mud) (McCrimmon and Bray 1962; Haahtela 1990). The bowhead stomach content also consisted of the benthic crangonid decapod *Sabinea septemcarinata*. This predator shrimp is found throughout the Arctic and in a variety of benthic habitat but mostly in the upper subtidal and benthic environments (Christiansen 1972; Bluhm et al. 2001; Berge et al. 2009). The stomach content of the Igloolik whale also contained gammarid amphipods, fish vertebrae, rocks, bivalve shells and polychete tube remains. The presence of these items supports the assumption of near bottom feeding for this juvenile bowhead whale.

The stomach content of the bowhead whale from Kugaaruk revealed that the animal had fed prior to being harvested. Since this stomach content was well preserved, it was possible to identify all the items in the sample including fragile copepods. The mysid, *Mysis oculata*, accounted for the majority of the sample. This mysid is an arctic and subarctic epibenthic species and occurs generally in coastal shallow water (Mauchline 1980; Astthorsson 1990). *M. oculata* is known to be a food source for fish such as the arctic cod (*Boreogadus saida*) (Craig et al. 1982) and marine birds (Hobson and Welch 1992) as well as ringed and harp seals (Sergeant 1973; Lowry et al. 1978). *M. oculata* is a species known to dominate some macrobenthic communities in Arctic Seas and it often forms dense aggregations in shallow zones (Hobson et al. 2002; Steffens et al. 2006). Mysids aggregate in swarms, schools and shoals (Clutter 1969; Mauchline 1971; Ritz 1994). The overall dominance of *M. oculata* in this sample indicates that the whale likely fed on a large concentration of mysids.

Another abundant species found in the Kugaaruk sample was the copepod *Metridia longa*. *M. longa* is a predator/suspension-feeding pelagic copepod that is usually found in deeper water (Blachowiak-Samolyk et al. 2006). In Lancaster Sound, the greatest abundance of M. longa was typically located between 50 and 250 m depth (Sekerak et al. 1976). The bathymetry in the area where the whale was taken is not well known; however, marine charts indicate an irregular sea bottom and depth ranging between 20 and 200 m. Bowhead whales particularly juveniles and nursing females use this region during the peak open-water season possibly due to the regular occurrence of sea ice during summer (Ferguson et al. 2010). Other than these two prey species, the Kugaaruk bowhead whale sample also contained female calanoid copepods (*Calanus* spp.) along with hyperiid amphipod *Themisto* spp. and gammarid amphipods (including *Onisimus* sp.). The presence of pelagic prey such as *M. longa* and *Calanus* spp. in this sample suggests that the animal fed at least partly within the water column. However, the large dominance of *M. oculata* strongly indicates that the animal foraged mostly closer to the ocean bottom.

The results from the stomach content analysis of the Kangiqsujuaq bowhead whale are somewhat similar to the findings of the Gulf of Boothia whale. The predominance of *M. oculata* in the sample likely indicates feeding near shore or in coastal areas on the concentrations of mysids. The Northern Quebec location where the bowhead whale was hunted is characterized by a steep shoreline reaching depths of 400 m within 5 km off the coast (Kingsley et al. 2001), while the average depth of Hudson

Strait is between 200 and 400 m (Metz et al. 2008). This implies that the whale was foraging close to shore. The juvenile BCB population whale harvested on its summer feeding grounds near Shingle Point in the Beaufort Sea fed nearly exclusively on the copepod *Limnocalanus macrurus*. The stomach content also included *Calanus* copepods, *Themisto* spp. and *Mysis oculata*, *L. macrurus* is an estuarine-brackish-water species and is part of zooplankton community in marine waters strongly influenced by river inputs (Lischka et al. 2001; Hirche et al. 2003). The high lipid content of *L. macrurus* (Hirche et al. 2003) appears advantageous for the bowhead whales feeding on this copepod species. In the southeastern Beaufort Sea, *L. macrurus* is a known prey of bowhead whales along with *C. hyperboreus* and *C. glacialis* (Bradstreet and Fissel 1986, 1987; Carroll et al. 1987). Walkusz et al. (2010) determined *L. macrurus* to be a dominant species of the zooplankton community characteristic of the Mackenzie River plume water with the highest abundance in the more concentrated portion of the plume. Therefore, the clear dominance of *L. macrurus* in this sample strongly suggests that this bowhead whale fed to a degree on this brackish water copepod species within the Mackenzie River plume area prior to being harvested. However, Lowry et al. (2004) reported *L. macrurus* in stomachs of three bowhead whales harvested at Kaktovik, Alaska, approximately 200 km west of Shingle Point and the Mackenzie River plume.

2.7 CONCLUSION

This study provides the first evidence of prey consumption by three bowhead whales, two juveniles (one male and one female) and one large pregnant adult female, from the EC–WG population representing the first stomach content data for this population. Although previous studies suggested that juvenile whales are more likely to forage on epibenthic prey (Lowry 1993) as opposed to adult whales, here we demonstrated that one adult female taken near Kangiqsujuaq also fed almost exclusively on epibenthic *M. oculata*. Our results indicate the need for future research to test whether bowhead whales of the Canadian Arctic are generalist and what is the relative importance of pelagic versus epibenthic food in their seasonal diet.

2.8 ACKNOWLEDGEMENTS

This work would not have been possible without the help of the Inuit hunters and Fisheries and Oceans Canada (DFO) staff, in particular Blair Dunn, working in Igloolik, Kugaaruk, Kangiqsujuaq and Shingle Point who provided stomach samples from harvested bowhead whales. Funding was provided by the Nunavut Implementation Fund (DFO), Species At Risk Coordination des espèces en peril (SARCEP), Natural Sciences and Engineering Research Council (NSERC to SHF) and the International Polar Year (IPY) Canadian Federal Program Office.

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CHAPITRE 3

RÉPARTITIONS SPATIALES DES COMMUNAUTÉS DE ZOOPLANCTON DANS LES RÉGIONS SUB-ARCTIQUES ET ARCTIQUES CANADIENNES : UN APERCU SELON LES RATIOS D'ISOTOPES STABLES DU CARBONE ($\delta^{13}C$) ET DE L'AZOTE ($\delta^{15}N$)

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Paru en 2011 dans *Journal of Plankton Research*, vol. 33(12), p. 1779-1792

(Featured Article)

3.1 RÉSUMÉ

Cette étude définie le statut quo des domaines biogéographiques et examine les variations spatiales des ratios d'isotopes stables de carbone et d'azote en relation avec les groupes biophysiques afin de mieux comprendre comment les changements climatiques soutenus affecteront le mésozooplancton dans les régions arctiques et subarctiques canadiennes. Les communautés mésozooplanctoniques ont été échantillonnées à l'été 2007 le long d'un transect allant du détroit de Belle-Isle, TNL à Kugluktuk, NU (Canada) et à l'automne 2009 sur un transect reliant Pelly Bay à Hall Beach, NU. Cinq types de masses d'eau furent identifiés correspondant à cinq aires géographiques distinctes. En général, les masses d'eau et les compositions spécifiques d'espèces de zooplancton étaient corrélées, toutefois ces relations n'étaient pas toujours directes. La composition des communautés de mésozooplancton le long du transect a révélé huit assemblages spécifiques d'espèces. *Calanus finmarchicus* était abondant dans les eaux chaudes et salées atlantiques de la mer du Labrador, tandis que *Calanus hyperboreus, Calanus glacialis* et *Metridia longa* étaient plus abondants dans les eaux froides arctiques au centre de la baie de Baffin et dans la portion est de l'archipel Arctique canadien. Les analyses des ratios des isotopes stables de carbone et d'azote ont révélé que $\delta^{15}N$ (mais pas $\delta^{13}C$) variaient spatialement chez *C. glacialis, C. hyperboreus, Paraeuchaeta* spp. et *Themisto libellula*. Les valeurs de $\delta^{15}N$ étaient moins enrichies dans le détroit de Davis mais plus enrichies dans le golfe de Boothia. La saisonnalité, les fronts océaniques et les changements au niveau de la structure trophique à la base de la chaîne alimentaire peuvent expliquer les variabilités observés. Cette étude représente la première caractérisation à grande échelle de la composition spécifique et des signatures isotopiques des communautés de mésozooplancton des régions subarctiques atlantique jusqu'à la partie ouest de l'archipel Arctique canadien. Notre étude fournit une base sur les structures de communautés de zooplancton pour les études futures visant à suivre les changements possibles de répartition spatiale de certaines espèces.

Mots clés: Arctique; subarctique; *Calanus*; *Themisto*; mesozooplancton; isotopes stables; structure des communautés; masses d'eau

Ce troisième article, intitulé « *Spatial patterns in zooplankton communities across the eastern Canadian sub-Arctic and Arctic waters: insights from stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios*», fut corédigé par moi-même ainsi que par Gesche Winkler, Akash Sastri, John Nelson, Svein Vagle, Véronique Lesage et Steven Ferguson. Il fut accepté pour publication dans sa version finale en 2011 par les éditeurs de la revue *Journal of Plankton Research*. En tant que premier auteur, ma contribution à ce travail fut l'essentiel de la recherche, incluant la collecte des données et l'analyse taxonomique et isotopique de tous les échantillons de zooplancton, les analyses statistiques et l'écriture du manuscrit. Gesche Winkler, second auteur, m'a aidé dans le choix des analyses statistiques et l'écriture de l'article. Akash Sastri, troisième auteur, m'a aidé dans les pistes d'interprétation des résultats, Svein Vagle, quatrième auteur a fourni les données physico-chimiques brutes, John Nelson, Véronique Lesage et Steven Ferguson ont contribué à la rédaction.

Une version abrégée de cet article a été présentée à la conférence <<*2nd International Symposium on the Effects of Climate Change on the World's Oceans*>>, à Yeosu, en Corée du Sud, en mai 2012.

3.2 ABSTRACT

This study defined the status quo of biogeographic domains and examined spatial patterns of stable isotopes (SIs) of carbon and nitrogen in relation to biophysical groupings to gain greater insight into how mesozooplankton may respond to continuous environmental change in the Canadian Arctic and sub-Arctic regions. Mesozooplankton communities were sampled during the summer of 2007 along a transect from Belle-Isle Strait, NFL, to Kugluktuk, NU (Canada), and during the early autumn of 2009 along a transect extending from Pelly Bay to Hall Beach, NU. Five broad water mass types corresponded to geographical regions. In general, we found relationships between water mass and species composition; however, this relationship was not always straightforward. Mesozooplankton community composition varied along the transect, revealing eight species assemblages. *Calanus finmarchicus* was abundant in the warmer and saltier Atlantic waters of the Labrador Sea, whereas *Calanus hyperboreus, Calanus glacialis* and *Metridia longa* were most abundant in the cold Arctic waters of Central Baffin Bay and in the eastern portion of the Canadian Arctic Archipelago. Nitrogen and carbon SI analysis revealed that $\delta^{15}N$ (but not $\delta^{13}C$) varied spatially for *C. glacialis, C. hyperboreus, Paraeuchaeta* spp. and *Themisto libellula*. $\delta^{15}N$ values were less enriched in Davis Strait and more enriched in the Gulf of Boothia. Seasonality, oceanic fronts and changes in the trophic structure at the base of each regional food web may explain some of the observed variability. This study represents the first broad-scale characterization of the composition and isotopic signatures for mesozooplankton communities ranging from the sub-Arctic Atlantic to the western Central Arctic Archipelago. Our study provides a baseline of the zooplankton community for monitoring species biogeographical range.

KEYWORDS: Arctic; sub-Arctic; *Calanus*; *Themisto*; mesozooplankton; stable isotopes; community structure; water masses

3.3 INTRODUCTION

Biogeographic studies of mesozooplankton distribution patterns demonstrate that community composition is typically water mass-specific (Mackas 1984; Froneman and Pakhomov, 1998; Coyle and Mackas, 2005). However, tolerance to salinity and temperature varies between species, and might result in more cosmopolitan patterns of spatial distribution in certain species (Reynolds, 1993; Hughes, 2000). Thus, several studies have linked changes in mesozooplankton species composition to long-term variation of cyclical climate and oceanic patterns (Beaugrand et al., 2002; Mackas et al., 2007).

Air and ocean temperatures in the eastern Canadian sub-Arctic and Arctic regions are currently warming at a rate of two to three times that of the global average (International Panel on Climate Change, 2007). An increased volume of northward-flowing Atlantic water into the eastern Arctic is also causing a major heat advection within this marine system (Spielhagen et al., 2011). It is anticipated that these rapid and pronounced hydrological changes will: (i) trigger dramatic shifts in the biogeography of arctic zooplankton communities (Beaugrand, 2009; Wassmann et al., 2011); (ii) influence key lower trophic level interactions (i.e. transfer efficiency; Carmack and Wassmann, 2006); and (iii) affect the productivity of higher trophic levels (i.e. fisheries; Reid and Edwards, 2001; Edwards et al., 2002; Beaugrand et al., 2003; Heath, 2005).

To gain greater insight into how high-latitude marine ecosystems will respond to continued environmental change, we must identify the specificity of mesozooplankton species assemblages to water masses in ways that go beyond taxonomic characterization. The stable isotope (SI) ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) as trophic markers (Post, 2002) represent a useful tool to complement taxonomic composition studies. Group-specific isotopic signatures allow tracking of energy sources (Hobson, 1999) and provide important information about the flux of energy through food webs (Post, 2002). The very few studies that have examined large-scale spatial patterns of isotope ratios for Arctic zooplankton species have focused on single species and/or single taxa in specific areas, which include: (i) northern Baffin Bay (NOW polynya; Tidmarsh, 1973; Sameoto, 1984); (ii) Lancaster Sound/Barrow Strait area (Sekerak et al., 1976; Buchanan and Sekerak, 1982; Longhurst, 1984; Sameoto, 1986); and (iii) along the western side of Greenland and the Labrador Sea (Head et al., 2003). To our knowledge, no study has investigated how mesozooplankton community composition varies among the different regions of the eastern Arctic (i.e. boreal to sub-Arctic and Arctic areas). Here, we present data on mesozooplankton species assemblages and isotopic characteristics by sampling along a large transect extending from the southern Labrador Sea to the Central Canadian Arctic Archipelago. The aim of this study was 2-fold: (i) to define biogeographic domains in terms of physical parameters (water temperature and salinity) and zooplankton species composition; and (ii) to examine how spatial patterns of carbon and nitrogen isotope ratios vary with biophysical groupings. This spatial characterization is part of the larger suite of biological, chemical and physical measurements made during the IPY—Canada's Three Oceans project 2007–2008.

3.4 MATERIAL AND METHODS

3.4.1 Zooplankton collection and identification

Biophysical measurements (zooplankton and temperature–salinity) were carried out along two transects extending from: (i) Halifax, NS, to Kugluktuk, NU (21 stations; CCGS Louis S. St-Laurent); and (ii) Kugaaruk, NU, to Saluit, Nunavik (11 stations; CCGS DesGroseilliers; Fig. 1). The first research campaign took place in July 2007 and included stations in the southern and northern Labrador Sea, Davis Strait, Baffin Bay, Lancaster Sound and the Arctic Archipelago. The second campaign took place in September 2009 and targeted stations in the southern part of Prince Regent Inlet, the Gulf of Boothia, the entrance and exit of Fury and Hecla Strait and the northern part of Foxe Basin. The mesozooplankton communities were sampled during daytime using: (i) Bongo nets (50 cm mouth diameter and 236 mm mesh size) in 2007 and; (ii) an SCOR net (50 cm mouth diameter; 236 mm mesh) in 2009. Both nets were fitted with a TSK flowmeter. Nets were hauled (1 m s^{-1}) vertically (once with Bongo nets and twice with the SCOR net) from 100 m to the surface or from 10 m above the bottom where bottom depths were

100 m. At each station, one sample was preserved in 10% buffered formalin in seawater for taxonomic identification and enumeration and the contents of the other net were frozen (-20°C) until analysed for SIs. Back in the lab, a Folsom splitter was used to split the contents of each sample to a subsample consisting of a minimum of 400 individuals. Individuals were counted and identified to species and developmental stage using a dissecting microscope (10x or 20x oculars).

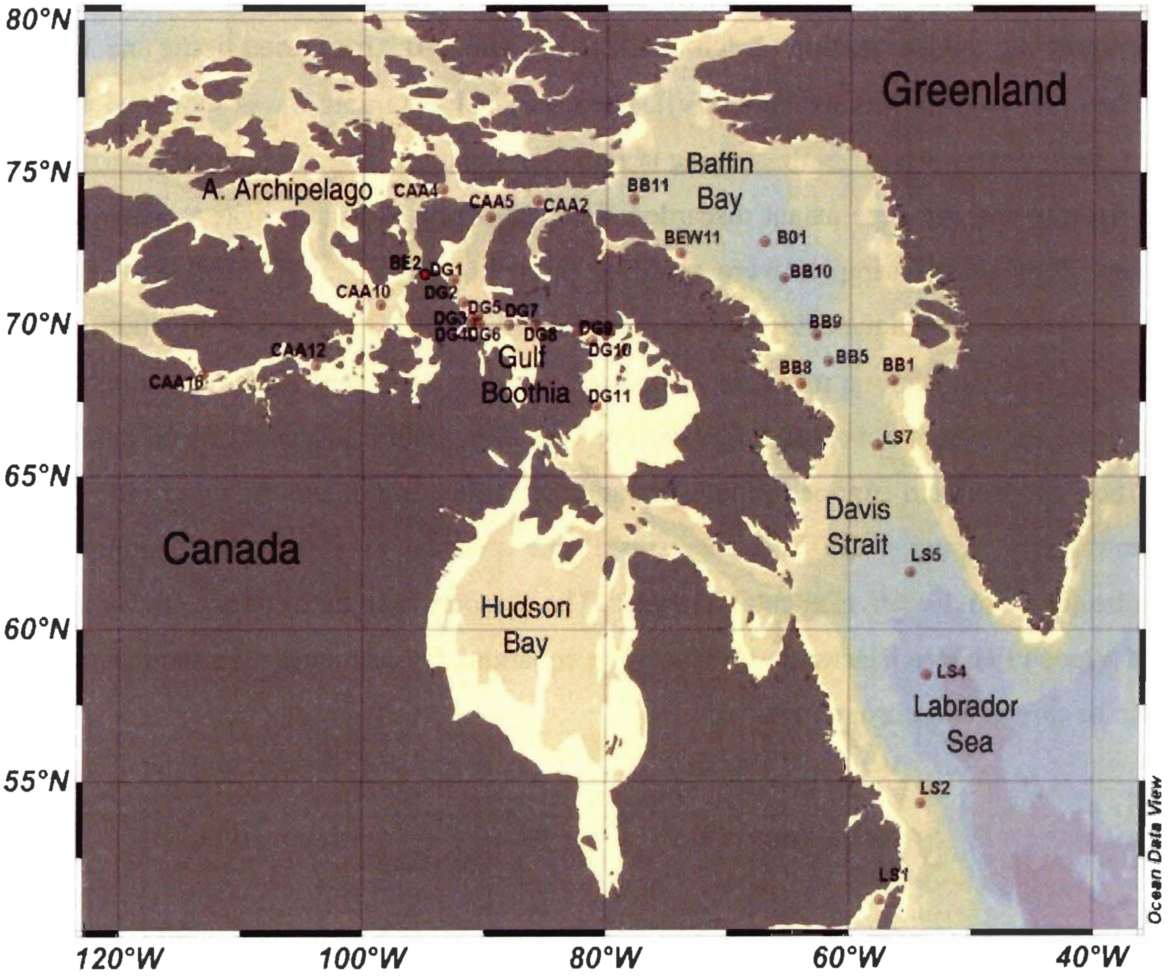


Figure 1. Sampling location for water column (n = 31) and zooplankton (n = 27) measurements conducted in July 2007 and September 2009 across the subarctic Atlantic Ocean and Eastern Canadian Arctic waters.

3.4.2 SI analysis

Mesozooplankton used for isotopic analysis were sorted by species when possible, freeze dried and then ground to a fine powder using a mortar and pestle. SI analyses were based on two replicate samples (each consisting of 1–12 whole individuals depending on the size of the organisms). Carbon and nitrogen isotope ratios were determined on separate aliquots because lipid extraction (required for $\delta^{13}C$ analysis; Post et al., 2007) alters $\delta^{15}N$ values (Sotiropoulos et al., 2004). Nitrogen isotope ratios were measured using dried homogenized samples, whereas carbon isotope ratios were carried out following lipid extraction (Folch et al., 1957) using ~0.2 g of dried tissue and 10 ml solvent [2:1 chloroform:methanol (v/v)]. The tissue–solvent mixture was sonicated for 15 min, followed by 4 h of gentle shaking at room temperature. The sample was centrifuged for 10 min and the supernatant discarded. This extraction procedure was repeated three times. Zooplankton samples were acidified prior to carbon isotope analysis with the "drop by drop" technique using concentrated HCl (0.1 M) (Mintenbeck et al., 2008), then dried at 60°C to remove moisture. Processed samples were sent to the Environmental Isotope Laboratory (University of Waterloo, Waterloo, Ontario, Canada) for SI analyses. Carbon and nitrogen isotope ratios were measured using continuous flow ion ratio mass spectrometry, using a GV-Instruments IsoPrime attached to a peripheral temperature controlled Euro Vector elemental analyzer. The standard was atmospheric N_2 for $\delta^{15}N$, and Vienna Pee Dee Belemnite for $\delta^{13}C$. The equations for calculating the stable isotopic ratio of carbon and nitrogen are:

$$\delta^{13}\mathrm{C\ sample}(‰) = \left(\frac{{}^{13}\mathrm{C}/{}^{12}\mathrm{C\ sample}}{{}^{13}\mathrm{C}/{}^{12}\mathrm{C\ standard}} - 1\right) \times 1000,$$

and

$$\delta^{15}\mathrm{N\ sample}(‰) = \left(\frac{{}^{15}\mathrm{N}/{}^{14}\mathrm{N\ sample}}{{}^{15}\mathrm{N}/{}^{14}\mathrm{N\ standard}} - 1\right) \times 1000.$$

3.4.3 Statistical analyses

The multivariate statistical software PRIMER (Plymouth Routines in Multivariate Ecological Research) version 6 (Clarke and Gorley, 2006) was used to address similarities among stations. Statistical analyses of zooplankton SI ratios were performed using R version 2.12.1 (R Development Core Team year 2010). In terms of environmental data, the average temperature and salinity corresponding to the depth range of each plankton tow were used to characterize environmental similarity. All data were normalized to a mean of zero and standard deviation of 1. A similarity profile based on permutation was tested using the SIMPROF routine to group stations with similar (i.e. branch with $P < 0.05$) normalized temperature and salinity data.

Groupings generated using the SIMPROF procedure were validated with a dissimilarity matrix based on Euclidean distance that was used in a hierarchical cluster analysis (routine CLUSTER). Patterns within and among groups of environmental data were also entered into a non-metric multidimensional scaling (nMDS) analysis using the SIMPROF group identifier.

Spatial patterns of zooplankton community composition were assessed separately using a Bray–Curtis similarity index (Bray and Curtis, 1957) on the square-root transformed (sqrt) average abundance of species per station to reduce bias from highly abundant species. The SIMPROF similarity profile permutation test was used as a prerequisite for defining the significance of species assemblages (SIMPROF, $P < 0.01$). A hierarchical cluster analysis using group average linkage (CLUSTER) and nMDS were applied to the resemblance matrix in order to examine and visualize groupings among stations based on species composition. The SIMPER exploratory analysis routine was used to determine which species contributed most to specific group definition or group separation identified by the CLUSTER and SIMPROF analyses. Possible correlations between the biotic similarity matrix and the abiotic variables were explored using the Bio-Env (BEST) function and Spearman's rank correlation coefficient. The BIOENV routine was used to examine linkage between species composition and water column properties. A one-way analysis of similarity (ANOSIM) was used to test for zooplankton community differences between the groups.

Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic signatures were examined for 24 mesozooplankton species sampled at 21 stations (Tables 5 and 6). Group differences in $\delta^{15}N$ and $\delta^{13}C$ values were tested for four ubiquitous species sampled across the study area (i.e. the herbivorous and/or omnivorous calanoid copepods *Calanus* hyperboreus and *Calanus* glacialis, the carnivorous copepod genus *Paraeuchaeta* spp., which consisted mostly of P. glacialis but also some *P. norvegica*, and the omnivorous hyperiid amphipod *Themisto libellula*) using two-way analysis of variances (ANOVAs) and the Tukey–Kramer HSD test for post hoc comparisons among station groups. Normality of isotopic data was determined using the Shapiro–Wilk's test.

3.5 RESULTS

3.5.1 Oceanography

The similarity test based on SIMPROF analysis of mean temperature and salinity (Table 1) revealed five distinct groupings, which were confirmed via hierarchical cluster analysis. The number of stations within a group varied between 2 and 15 (Fig. 2A). Group 1 (stations LS4 and LS5) was located in the Labrador Sea and defined by warmer and saltier Atlantic water (Table 1; Fig. 1). The stations in Group 2 (CAA12 and CAA16; Fig. 1) were located in Queen Maud Gulf and Coronation Gulf and were defined by cold water temperature and low salinity indicative of substantial freshwater input (Table 1). Group 3 was characterized by high salinity and a slightly higher water temperature. Although the three stations making up Group 3 were relatively distant, i.e. BB1 along the Greenland coast, DG11 in Foxe Basin and LS1 at the entrance of Belle-Isle Strait, their temperature and salinity characteristics were consistent with Arctic waters flowing west to east into the North Atlantic Ocean. Group 4 stations had cold water temperatures and somewhat fresher waters relative to Group 3. With the exception of the two northernmost stations (DG1 and DG2), Group 4 was composed entirely of stations sampled between Prince Regent Inlet and the northern part of Foxe Basin. The mean temperature and salinity of that grouping are indicative of sea-ice melt water. Lastly, Group 5 consisted of

15 stations characterized by cold and high salinity waters. Most of these stations were located in Northern Baffin Bay and Lancaster Sound. Similar grouping results were obtained when using the average temperature and salinity between the surface and 50 m (not shown). Results from a one-way ANOVA indicated that both temperature (F= 71.205, P < 0.001) and salinity (F = 55.301, P < 0.001) significantly differed among groups.

Table 1. CTD and zooplankton stations along the cruise transect

Station name	Date (d/m/y)	Latitude (N)	Longitude (W)	Bottom depth (m)	Sampled depth (m)	Temperature ± SD (°C)	Salinity ± SD (psu)
LS1	7/6/2007	54.254	−54.100	70	60	1.31 ± 3.00	31.95 ± 0.41
LS2	7/7/2007	54.254	−54.100	220	100	−0.99 ± 1.17	32.61 ± 0.72
LS4	7/8/2007	58.484	−53.662	3382	100	5.21 ± 1.35	34.75 ± 0.04
LS5	7/9/2007	61.864	−54.957	2640	100	4.56 ± 0.63	34.41 ± 0.41
LS7	7/10/2007	66.000	−57.673	577	100	−0.64 ± 1.09	33.16 ± 0.59
BB1	7/11/2007	68.195	−56.421	245	100	0.89 ± 0.85	33.55 ± 0.41
BB5	7/12/2007	68.830	−61.756	1849	100	−1.57 ± 0.37	32.89 ± 0.56
BB8	7/13/2007	68.089	−63.999	150	100	−1.23 ± 0.49	32.50 ± 0.54
BB9	7/13/2007	69.676	−62.746	2002	100	−1.56 ± 0.48	33.11 ± 0.45
BB10	7/14/2007	71.554	−65.416	2282	100	−1.63 ± 0.43	33.08 ± 0.39
B01	7/15/2007	72.757	−67.014	2401	100	−1.36 ± 0.94	33.29 ± 0.51
BEW11	7/16/2007	72.385	−73.898	150	100	−1.35 ± 0.61	32.36 ± 1.11
BB11	7/17/2007	74.124	−77.751	839	100	−0.128 ± 0.95	33.24 ± 0.54
CAA2	7/17/2007	74.051	−85.650	532	100	−0.52 ± 1.41	32.24 ± 0.59
CAA4	7/18/2007	74.094	−93.485	160	100	−0.84 ± 0.85	32.01 ± 1.29
CAA5	7/20/2007	73.023	−89.530	436	100	−0.77 ± 1.05	32.88 ± 0.63
BE2	7/21/2007	72.006	−94.586	100	90	−1.12 ± 0.02	32.43 ± 0.70
CAA10	7/23/2007	70.151	−98.585	190	100	−1.13 ± 0.31	32.21 ± 2.55
CAA12	7/24/2007	68.014	−103.918	100	90	−1.29 ± 0.51	28.46 ± 2.94
CAA16	7/25/2007	68.049	−113.121	210	100	−0.33 ± 0.47	27.95 ± 0.57
DG1	9/18/2009	71.480	−92.573	212	100	−0.91 ± 0.25	32.15 ± 0.21
DG2	9/18/2009	70.715	−91.781	160	100	−0.90 ± 0.67	31.86 ± 0.50
DG3	9/18/2009	70.194	−91.078	87	77	−0.36 ± 0.21	30.58 ± 0.41
DG4	9/18/2009	70.008	−91.080	88	78	−0.57 ± 0.41	30.08 ± 0.35
DG5	9/19/2009	70.017	−90.490	135	100	0.10 ± 0.52	30.59 ± 0.70
DG6	9/19/2009	70.269	−90.584	139	100	−0.29 ± 0.11	30.89 ± 0.35
DG7	9/19/2009	69.990	−88.018	155	100	−1.41 ± 0.05	31.34 ± 0.54
DG8	9/20/2009	69.965	−85.873	122	100	−1.31 ± 0.12	30.74 ± 1.09
DG9	9/21/2009	69.713	−82.218	100	90	−0.75 ± 0.01	30.60 ± 0.13
DG10	9/21/2009	69.455	−81.156	85	75	0.08 ± 0.11	30.66 ± 0.07
DG11	9/24/2009	67.332	−80.847	95	85	0.96 ± 0.05	32.04 ± 0.04

Sampled depth corresponds to the maximum sampling depth range. Temperature and salinity are the average value for the sampled depth range

Table 2. ANOSIM and SIMPER analyses showing differences in zooplankton assemblages between the groups (R, P) (in grey), intragroup similarity (middle of matrix) and average dissimilarity (%) between pair of groups (in white)

GROUP	A	B	C	D	E	F	G	H
A	—	1.00 (0.125)	1.00 (0.333)	—	—	1.00 (0.111)	1.00 (0.333)	1.00 (0.167)
B	69.62	57.47	1.00 (0.028)	0.986 (0.125)	0.932 (0.125)	0.897 (0.002)	0.994 (0.028)	0.991 (0.001)
C	93.21	80.52	68.00	1.00 (0.333)	1.00 (0.333)	1.00 (0.022)	1.00 (0.333)	1.00 (0.048)
D	93.6	73.88	60.16	—	—	1.00 (0.111)	1.00 (0.333)	1.00 (0.167)
E	86.09	63.36	67.02	65.32	—	0.625 (0.111)	1.00 (0.333)	0.96 (0.167)
F	88.17	59.39	66.67	51.89	40.04	67.94	0.909 (0.022)	0.867 (0.001)
G	90.59	71.61	47.39	51.05	52.59	48.19	72.57	0.93 (0.048)
H	87.49	70.04	67.04	63.54	46.4	44.71	44.57	67.26

A, DG1; B, Gulf Boothia; C, Labrador Sea; D, LS1; E, CAA16; F, Arctic Archipelago; G, Davis Strait; H, Baffin Bay.

3.5.2 Zooplankton

In 2007, 93 zooplankton species were identified at the 19 stations sampled, whereas 43 species were identified at the eight stations sampled in 2009. The similarity test based on permutations (SIMPROF) identified eight significantly different groups ($P < 0.01$) among the 27 sampled stations according to species abundance data (Fig. 2B). The number of stations within groups varied between 1 and 8 (Fig. 2B). Stations within each group were very similar (67–73%) in all cases except in the Gulf of Boothia (58%; Table 4). Stations were also generally close to one another geographically. As a result, species assemblages were named, and will be hereafter referred to on the basis of their general geographical location: (B) Gulf Boothia; (C) Labrador Sea; (F) Arctic Archipelago; (G) Davis Strait and (H) Baffin Bay.

Groups of stations differed markedly in species composition and relative abundance (ANOSIM: $R = 0.87$, $P < 0.001$), with the majority being distinct (R values close to 1) from any other groups considered (Tables 2 and 3). The P-values for groups A (DG1), D (LS1) and E (CAA16) were high, despite R values of 1 or close to 1, because they were composed of single stations. The largest cluster, the Arctic Archipelago group (F), was composed of eight stations. The copepods *Oithona similis*, Copepoda nauplii, *Calanus* spp. and *Pseudocalanus minutus* were numerically dominant in this region. The seven stations from the Gulf of Boothia were characterized by *P. minutus, Pseudocalanus* spp., Copepoda nauplii and *Oikopleura* sp., whereas the two stations from the Labrador Sea were characterized by *Calanus finmarchicus, Oithona atlantica* and *O. similis.* The Davis Strait group also consisted of two stations where *Calanus* spp., *O. similis, C. finmarchicus* and *C. hyperboreus* were the numerically dominant species. Finally, the Baffin Bay group was composed of five stations where *O. similis, Metridia longa, C. hyperboreus* and *P. minutus* were the dominant mesozooplankton species.

Table 3. ANOSIM and SIMPER analyses showing differences in species assemblage among groups (GR) of zooplankton (in grey), species contributing to the dissimilarities between pair of groups (middle of matrix) and species (with % contribution) contributing to similarity within groups (white).

GR	A	B	C	D	E	F	G	H
A	-	1.00 (0.33)	1.00 (0.17)	1.00 (0.33)	-	-	1.00 (0.11)	1.00 (0.33)
B	*Pseudocalanus sp.(17.6)* *P. minutus(10.3)* *Copepoda nauplii (9.8)* *Calanus sp. (8.8)*	*P. minutus* (15.8) Pseudocalanus sp. (13.6) *Copepoda nauplii* (13.0) *Oikopleura sp. (9.5)*	0.95 (0.05)	1.00 (0.33)	1.00 (0.33)	1.00 (0.33)	1.00 (0.02)	1.00 (0.33)
C	*C. finmarchicus(20.5)* *O. atlantica(14.5)* *O. similiis(13.3)* *Euphausiavea sp. (5.3)*	*C. finmarchicus(19.1)* *O. atlantica(13.4)* *O. similis(11.7)* *Euphausiacea sp. (5.0)*	*C. finmarchicus* (22.9) *O. atlantica* (18.7) *O. similis* (17.9) *Copepoda nauplii (6.6)*	1.00 (0.05)	1.00 (0.17)	1.00 (0.17)	0.99 (0.001)	1.00 (0.048)
D	*C. finmarchicus(15.6)* *Calanus sp.(11.3)* *O. similis(10.0)* *Oikopleura sp. (8.9)*	*C. finmarchicus (17.2)* *Calanus sp.(10.8)* *O. similis(10.5)* *P. newmani (8.8)*	*O. atlantica (8.9)* *P. newmani (8.1)* *Oikopleura sp.(8.1)* *Pseudocalanus sp.(7.2)*		1.00 (0.33)	1.00 (0.33)	1.00 (0.02)	1.00 (0.33)
E	*O. similis(14.5)* *O. borealis(9.3)* *M. pygmeus(8.9)* *Pseudocalanus sp.(5.9)*	*O. similis(14.4)* *O. borealis(9.8)* *M.pygmeus(9.5)* *M. pusillus (7.3)*	*C. finmarchicus(16.6)* *O. atlantica(11.5)* *O. borealis(6.5)* *M. pygmeus (5.8)*	*C. finmarchicus(15.4)* *Calanus sp.(10.1)* *Oikopleura sp.(8.7)* *P. newmani (6.2)*	-	-	1.00 (0.11)	1.00 (0.33)
F	*O. similis (9.9)* *Copepoda nauplii (8.6)* *Pseudocalanus sp.(7.1)* *Calanus sp. (7.0)*	*O. similis(11.1)* *Copepoda nauplii (7.1)* *O. borealis(6.2)* *M. longa(5.8)*	*C. finmarchicus(14.0)* *O. atlantica(10.0)* *Pseudocalanus sp.(5.1)* *O. borealis(4.3)*	*C. finmarchicus (16.9)* *P. newmani (8.9)* *Oikopleura sp.(7.9)* *Calanus sp. (7.9)*	*Copepoda nauplii(7.8)* *Calanus sp.(6.9)* *Evadne sp. (5.5)* *M. pygmeus (5.0)*	*O. similis (13.2)* *Copepoda nauplii (10.6)* *Calanus sp. (8.4)* *P. minutus (7.5)*	0.63 (0.11)	1.00 (0.33)
G	*Calanus sp.(17.5)* *C. finmarchicus(9.3)* *O. similis(8.9)* *C. glacialis (6.3)*	*Calanus sp.(15.9)* *C. finmarchicus(9.6)* *O. similiis(8.6)* *C. glacialis (6.0)*	*O. atlantica(12.0)* *Calanus sp.(11.2)* *C. finmarchicus(10.6)* *C. glacialis (7.2)*	*C. finmarchicus(10.8)* *P. newmani (9.1)* *Oikopleura sp.(8.4)* *P. minutus (7.8)*	*Calanus sp.(16.6)* *C. finmachicus(9.6)* *O. borealis(6.7)* *C. hyperboreus(4.9)*	*Calanus sp.(11.2)* *C. finmarchicus(8.3)* *Pseudocalanus sp.(5.2)* *Copepoda nauplii (4.9)*	*Calanus sp.(20.2)* *O. similis* (13.3) *C. finmarchicus(* 11.9) *C. hyperboreus (7.6)*	0.91 (0.002)
H	*O. similis(10.5)* *M. longa(9.2)* *C. hyperboreus(7.7)* *Calanus sp. (6.3)*	*O. similis(9.4)* *M. longa(8.2)* *C. hyperboreus(7.1)* *M. pygmeus (6.0)*	*C. finmarchicus(15.1)* *O. atlantica (10.9)* *C. hyperoreus(5.3)* *M. longa (5.3)*	*C. finmarchicus(14.6)* *Calanus sp.(8.0)* *Oikopleura sp.(7.8)* *P. newmani (7.8)*	*C. hyperboreus(6.2)* *O. borealis(5.4)* *Evadne sp. (5.2)* *C. hyperboreus (4.8)*	*Copepoda nauplii (9.8)* *Pseudocalanus sp.(6.7)* *Fritillaria sp.(4.8)* *L. helicina (4.8)*	*Calanus sp.(15.2)* *C. finmarchicus(9.4)* *M. l onga(4.3)* *Copepoda nauplii (4.0)*	*O.similis (15.0)* *M. longa (11.8)* *C. hyperboreus (8.9)* *P. minutus (8.1)*

3.5.3 Influence of environmental variables on species assemblages.

The best correlation between biological and environmental data occurred when both water temperature and salinity were considered [Bio-Env (BEST) analysis, $ps = 0.48$]. When considered as a single variable, salinity accounted almost for as much variance ($ps = 0.46$) as when combined with temperature. Results from the ANOSIM using the environmental groups as a factor revealed a significant difference in zooplankton community composition between each of the five water mass groups ($R = 0.65$, $P < 0.001$). The eight discrete zooplankton assemblages generally corresponded to the limits defined by water mass groupings (Fig. 2B). Neighbouring stations generally had similar species composition and were grouped together, even though this was usually not the case when considering physico-chemical parameters alone. Exceptions were the two Labrador Sea stations (LS4 and LS5), which were singled out based both on water mass type and zooplankton composition. The two neighbouring stations in Davis Strait (LS7 and BB1) had similar zooplankton composition, even though physico-chemical properties of LS7 were more similar to the neighbouring Baffin Bay stations than the more coastal BB1 station. The latter station was grouped with the one station in Foxe Basin and the southernmost station of Belle-Isle Strait. All stations in Baffin Bay were homogenous in terms of species composition, but had salinities and temperatures similar to most stations from the high Arctic (CAA series), and thus were grouped together based on water mass characteristics.

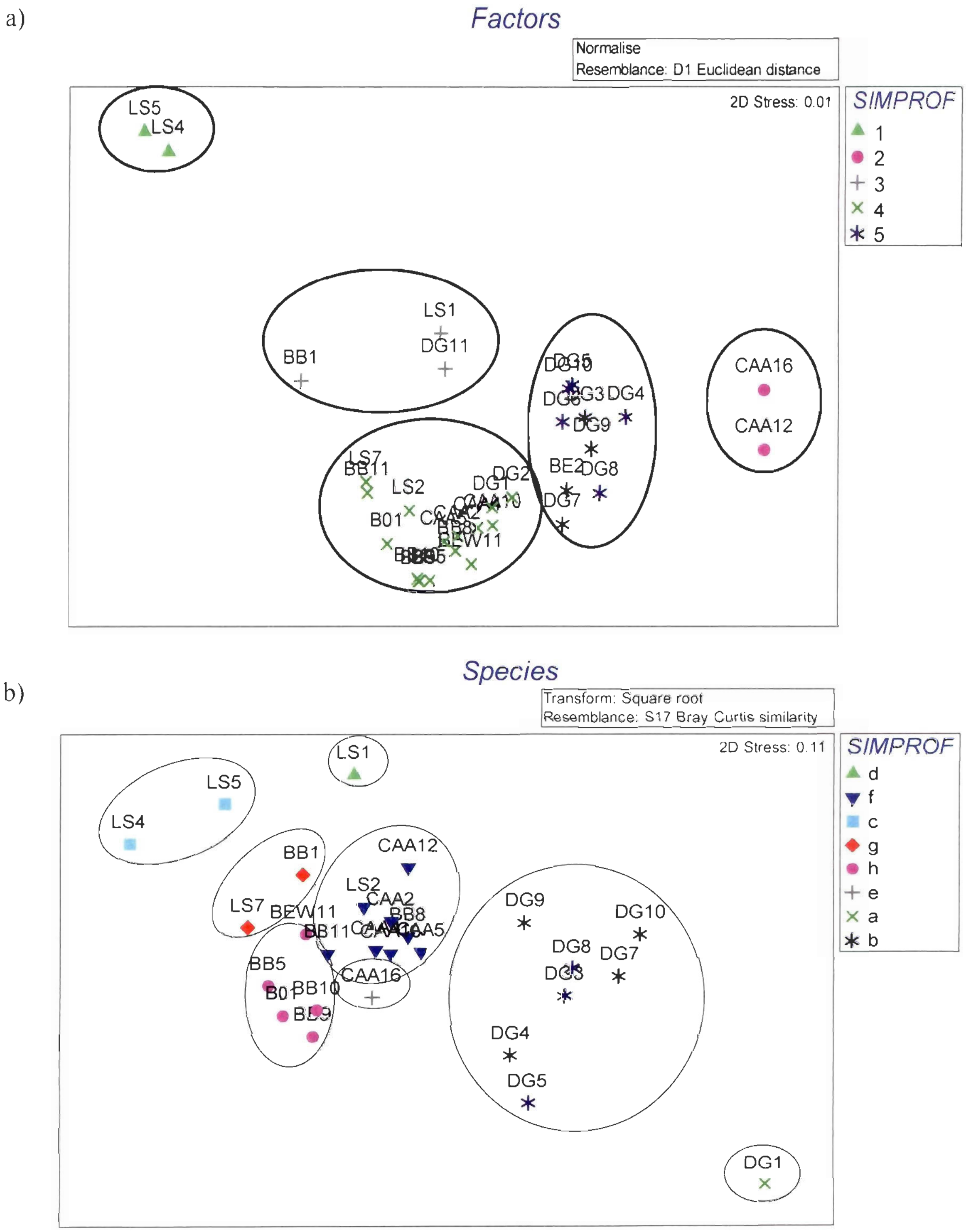


Figure 2. Multidimensional scaling ordination plots illustrating similarities among stations in terms of (A) average temperature and salinity between 0 and 100 m and (B) zooplankton composition.

Table 4. Mean abundance (ind m^{-3}) of copepod and non-copepod mesozooplankton in five biotic groupings.

Mesozooplankton	Groups and/or species	Labrador Sea (*n* = 2)	Davis Strait (*n* = 2)	Baffin Bay (*n* = 5)	Archipelago (*n* = 7)	Gulf of Boothia (*n* = 7)
Copepod	*Calanus finmarchicus*	206.1	44.5	1.6	0.5	0.0
Copepod	*Calanus hyperboreus*	0.1	21.1	24.3	14.4	0.7
Copepod	*Calanus glacialis*	0.0	23.3	10.1	9.5	0.6
Copepod	*Oithona similis*	101.1	54.1	48.7	67.4	2.4
Copepod	*Pseudocalanus* spp.	3.3	10.1	22.6	54.6	29.3
Copepod	*Microcalanus* spp.	3.1	10.1	12.4	17.4	0.0
Copepod	*Metridia longa*	1.4	8.8	29.1	26.8	0.8
Copepod	*Paraeuchaeta* spp.	3.1	3.6	1.9	0.5	0.02
Non-copepod	Chaetognaths	2.3	2.8	5.0	1.6	0.2
	Eukrohnia hamata	1.0	2.1	2.5	0.6	0.05
	Parasagitta elegans	0.6	0.3	1.6	1.0	0.1
	Pseudosagitta maxima	0.7	0.01	0.0	0.0	0.0
Non-copepod	Euphausids	12.4	2.9	1.1	0.4	0.0
	Euphausiacea sp.	12.4	2.3	1.1	0.4	0.0
	Thysanoessa inermis	0.0	0.1	0.0	0.0	0.0
	Thysanoessa longicaudata	0.05	0.5	0.0	0.004	0.0
Non-copepod	Amphipods	1.3	0.4	2.4	0.3	0.1
	Apherusa glacialis	0.0	0.01	0.0	0.0	0.002
	Hyperia galba	0.0	0.0	0.0	0.01	0.0
	Onisimus glacialis	0.0	0.0	0.0	0.01	0.01
	Themisto abyssorum	0.0	0.0	0.0	0.0	0.001
	Themisto compressa	1.3	0.2	0.0	0.0	0.0
	Themisto libellula	0.0	0.2	2.4	0.3	0.002
Non-copepod	Larvaceans	2.0	5.1	1.8	15.8	4.8
	Fritillaria borealis	0.0	0.0	0.1	9.5	2.1
	Oikopleura sp.	2.0	2.7	1.8	5.8	2.5
	Oikopleura vanhoeffeni	0.0	2.4	0.0	0.6	0.2
Non-copepod	Pteropods	1.4	1.2	1.8	22.5	0.8
	Clione limacina	0.0	0.0	0.1	1.9	0.1
	Limacina helicina	1.4	1.2	1.7	20.6	0.7
Non-copepod	Ostracods	3.1	5.9	4.6	0.3	0.0
	Boroecia maxima	0.0	0.0	0.2	0.1	0.0
	Conchoecia magna	0.0	0.4	0.0	0.0	0.0
	Conchoecia obtusata	0.7	0.0	0.0	0.0	0.0
	Conchoecinae sp.	1.1	5.5	3.4	0.2	0.0
	Discoconchoecia elegans	0.0	0.0	1.0	0.0	0.0
	Metaconchoecia sp.	1.4	0.0	0.0	0.0	0.0

The "*n*" represents the number of stations constituting a group

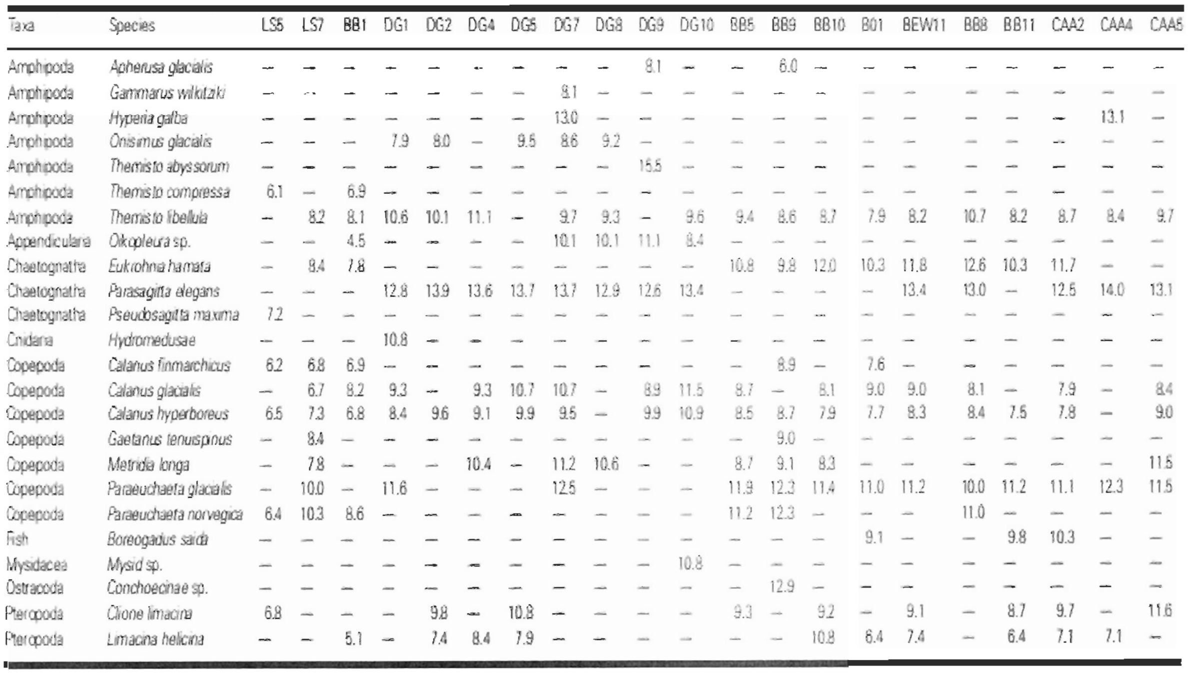
Exceptions were the two most westerly stations (CAA16 and CAA12), which were singled out on the basis of water mass characteristics. Although these two stations were deemed to be statistically dissimilar in terms of zooplankton composition, their proximity in the nMDS representation does indicate some degree of relatedness (Fig. 2B). Stations from the Gulf of Boothia were similar in water mass characteristics and species composition, with the exception of DG1, which was singled out on the basis of species composition.

Species composition and relative abundance followed a latitudinal pattern. This pattern was particularly prominent in the Labrador Sea to Baffin Bay area. For instance, the abundance of *C. finmarchicus* decreased progressively from the Labrador Sea north into Davis Strait, Baffin Bay and the Arctic Archipelago (Table 4). Conversely, species such as *C. hyperboreus*, *C. glacialis*, *Pseudocalanus spp.*, *Microcalanus* spp. and *M.*

longa increased in importance when moving north. *Oithona similis* was virtually absent in the Gulf of Boothia but otherwise abundant at all other stations and particularly numerous in the Labrador Sea region (Table 4).

The southernmost station, LS1 (Group D), was dominated by *C. finmarchicus* and *O. similis* and was singled out on the basis of zooplankton composition. This station shared the characteristics of high salinity and somewhat elevated temperature with the West Greenland and Foxe Basin stations, BB1 and DG11 (Group 3; Fig. 2; Table 3). Zooplankton was not sampled at station DG11. Station LS2 was placed in water mass Group 5 (Table 1), characterized as cold and salty and located on the Labrador Sea. The numerically dominant groups at this station were Copepoda nauplii, *Calanus* spp. and *Pseudocalanus* spp. and the taxonomic composition placed LS2 in the Arctic Archipelago biotic group (Fig. 2).

Table 5. Average nitrogen ($\delta^{15}N$) isotope ratios for zooplankton species at each station.



Taxa	Species	LS5	LS7	BB1	DG1	DG2	DG4	DG5	DG7	DG8	DG9	DG10	BB5	BB9	BB10	B01	BEW11	BB8	BB11	CAA2	CAA4	CAA5
Amphipoda	*Apherusa glacialis*	—	—	—	—	—	—	—	—	—	8.1	—	—	6.0	—	—	—	—	—	—	—	—
Amphipoda	*Gammarus wilkitzki*	—	—	—	—	—	—	—	8.1	—	—	—	—	—	—	—	—	—	—	—	—	—
Amphipoda	*Hyperia galba*	—	—	—	—	—	—	—	13.0	—	—	—	—	—	—	—	—	—	—	—	13.1	—
Amphipoda	*Onisimus glacialis*	—	—	—	7.9	8.0	—	9.5	8.6	9.2	—	—	—	—	—	—	—	—	—	—	—	—
Amphipoda	*Themisto abyssorum*	—	—	—	—	—	—	—	—	—	15.5	—	—	—	—	—	—	—	—	—	—	—
Amphipoda	*Themisto compressa*	6.1	—	6.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Amphipoda	*Themisto libellula*	—	8.2	8.1	10.6	10.1	11.1	—	9.7	9.3	—	9.6	9.4	8.6	8.7	7.9	8.2	10.7	8.2	8.7	8.4	9.7
Appendicularia	*Oikopleura sp.*	—	—	4.5	—	—	—	—	10.1	10.1	11.1	8.4	—	—	—	—	—	—	—	—	—	—
Chaetognatha	*Eukrohnia hamata*	—	8.4	7.8	—	—	—	—	—	—	—	—	10.8	9.8	12.0	10.3	11.8	12.6	10.3	11.7	—	—
Chaetognatha	*Parasagitta elegans*	—	—	—	12.8	13.9	13.6	13.7	13.7	12.9	12.6	13.4	—	—	—	—	13.4	13.0	—	12.5	14.0	13.1
Chaetognatha	*Pseudosagitta maxima*	7.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cnidaria	*Hydromedusae*	—	—	—	10.8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Copepoda	*Calanus finmarchicus*	6.2	6.8	6.9	—	—	—	—	—	—	—	—	—	8.9	—	7.6	—	—	—	—	—	—
Copepoda	*Calanus glacialis*	—	6.7	8.2	9.3	—	9.3	10.7	10.7	—	8.9	11.5	8.7	—	8.1	9.0	9.0	8.1	—	7.9	—	8.4
Copepoda	*Calanus hyperboreus*	6.5	7.3	6.8	8.4	9.6	9.1	9.9	9.5	—	9.9	10.9	8.5	8.7	7.9	7.7	8.3	8.4	7.5	7.8	—	9.0
Copepoda	*Gaetanus tenuispinus*	—	8.4	—	—	—	—	—	—	—	—	—	—	9.0	—	—	—	—	—	—	—	—
Copepoda	*Metridia longa*	—	7.8	—	—	—	10.4	—	11.2	10.6	—	—	8.7	9.1	8.3	—	—	—	—	—	—	11.5
Copepoda	*Paraeuchaeta glacialis*	—	10.0	—	11.6	—	—	—	12.5	—	—	—	11.9	12.3	11.4	11.0	11.2	10.0	11.2	11.1	12.3	11.5
Copepoda	*Paraeuchaeta norvegica*	6.4	10.3	8.6	—	—	—	—	—	—	—	—	11.2	12.3	—	—	—	11.0	—	—	—	—
Fish	*Boreogadus saida*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9.1	—	—	9.8	10.3	—	—
Mysidacea	*Mysid sp.*	—	—	—	—	—	—	—	—	—	—	10.8	—	—	—	—	—	—	—	—	—	—
Ostracoda	*Conchoecinae sp.*	—	—	—	—	—	—	—	—	—	—	—	—	12.9	—	—	—	—	—	—	—	—
Pteropoda	*Clione limacina*	6.8	—	—	—	9.8	—	10.8	—	—	—	—	9.3	—	9.2	—	9.1	—	8.7	9.7	—	11.6
Pteropoda	*Limacina helicina*	—	—	5.1	—	7.4	8.4	7.9	—	—	—	—	—	—	10.8	6.4	7.4	—	6.4	7.1	7.1	—

Table 6. Average carbon ($\delta^{13}C$) isotope ratios for zooplankton species at each station.

Taxa	Species	LS5	LS7	BB1	DG1	DG2	DG4	DG5	DG7	DG8	DG9	DG10	BB5	BB9	BB10	B01	BEW11	BB8	BB11	CAA2	CAA4	CAA5
Amphipoda	*Apherusa glacialis*	–	–	–	–	–	–	–	–	–	−17.7	–	–	−19.1	–	–	–	–	–	–	–	–
Amphipoda	*Gammarus wilkitzkii*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Amphipoda	*Hyperia galba*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	−19.6	–
Amphipoda	*Onisimus glacialis*	–	–	–	–	−15.5	–	−18.1	–	−12.5	–	–	–	–	–	–	–	–	–	–	–	–
Amphipoda	*Themisto abyssorum*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Amphipoda	*Themisto compressa*	−19.0	–	−20.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Amphipoda	*Themisto libellula*	–	−20.0	−19.2	−21.1	−19.6	−21.1	–	−20.7	−19.7	–	−20.5	−19.2	−20.1	−20.0	−20.6	−20.2	−19.9	−20.7	−19.9	−19.8	−19.4
Appendicularia	*Oikopleura* sp.	–	–	−22.4	–	–	–	–	−22.7	−21.1	−23.8	−22.8	–	–	–	–	–	–	–	–	–	–
Chaetognatha	*Eukrohnia hamata*	–	−19.7	−20.8	–	–	–	–	–	–	–	–	−19.3	−19.9	−19.2	−19.8	−19.2	−19.8	−20.3	−20.0	–	–
Chaetognatha	*Parasagitta elegans*	–	–	–	–	−19.2	−19.2	−19.6	−19.9	−19.6	−19.4	−18.9	–	–	–	–	−18.6	−19.0	–	−19.3	−18.8	−19.3
Chaetognatha	*Pseudosagitta maxima*	−20.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cnidaria	*Hydromedusae*	–	–	–	−20.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Copepoda	*Calanus finmarchicus*	−20.6	−21.2	−19.6	–	–	–	–	–	–	–	–	–	−20.3	–	−21.2	–	−20.5	–	–	–	–
Copepoda	*Calanus glacialis*	–	−21.6	−19.2	–	–	−22.0	−21.7	–	–	−19.7	–	−21.3	–	−21.1	−20.8	−20.8	–	–	−21.2	–	−21.1
Copepoda	*Calanus hyperboreus*	−21.1	−21.9	−20.5	−21.1	−20.2	–	−21.4	−21.8	–	−20.6	–	−21.6	−21.6	−21.8	−21.0	−21.5	−21.1	−21.5	−21.4	–	−20.8
Copepoda	*Gaetanus tenuispinus*	–	−20.7	–	–	–	–	–	–	–	–	–	–	−21.4	–	–	–	–	–	–	–	–
Copepoda	*Metridia longa*	–	−21.4	–	–	–	–	–	–	−21.7	–	–	–	−21.4	−22.3	–	–	–	–	–	–	–
Copepoda	*Paraeuchaeta glacialis*	–	−20.8	–	–	−20.8	–	–	−21.4	–	–	–	−21.0	−21.1	−20.9	−21.8	−21.5	−21.4	−21.5	−21.5	−22.1	−20.6
Copepoda	*Paraeuchaeta norvegica*	−20.5	−21.0	−20.7	–	–	–	–	–	–	–	–	−21.3	−21.1	–	–	–	−21.3	–	–	–	–
Fish	*Boreogadus saida*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	−20.0	–	–	−21.6	−19.9	–	–
Mysidacea	*Mysid* sp.	–	–	–	–	–	–	–	–	–	–	−20.1	–	–	–	–	–	–	–	–	–	–
Ostracoda	*Conchoecinae* sp.	–	–	–	–	–	–	–	–	–	–	–	–	−20.6	–	–	–	–	–	–	–	–
Pteropoda	*Clione limacina*	−18.2	–	–	–	−21.8	–	−20.9	–	–	–	–	−21.2	–	−19.9	–	−21.6	–	−22.0	−20.4	–	−20.1
Pteropoda	*Limacina helicina*	–	–	−20.8	–	−22.1	−20.5	–	–	–	–	–	–	–	−21.2	−21.1	−21.1	–	−21.4	−20.9	−20.7	–

The two deepest Labrador Sea stations, LS4 and LS5, were similar in species composition (Labrador Sea) and water mass (Group 1). These stations had warm water temperature and high salinity (Table 1; Fig. 2A). The most abundant species in this group were *C. finmarchicus, O. similis* and *O. atlantica.* This group also had the highest abundance of *Euphausiacea* spp. (Table 4).

Moving north to Davis Strait and along the coast of Greenland, we found that stations LS7 and BB1 were similar in species composition (Group Davis Strait) but not water mass characteristics. Stations LS7 and BB1 were very similar in salinity (Table 1), but LS7 was characterized by colder temperature (Group 5) than BB1 (Group 3). The most abundant members of Davis Strait group were *O. similis* and *C. finmarchicus*. The four stations located in central Baffin Bay, BB5, BB9, BB10, B01 and station BEW11 located off the coast of northeast Baffin Island were grouped together based on species composition (Baffin Bay) and were characterized by cold and saline waters (Group 5). The most abundant species for this group of stations were O. *similis, M. longa, C.*

hyperboreus and *Pseudocalanus* spp. The highest abundance of chaetognaths and amphipods were also found in Baffin Bay (Table 4).

The remaining stations BB8, BB11, CAA2, CAA4, CAA5 and CAA10 were singled out based on both water mass (Group 5) and species composition (Group Arctic Archipelago). The two westernmost stations in this region (CAA12 and CAA16) were combined with the other stations because of their similar species composition, although they had fresher water (Group 2) and the lowest salinity values measured in this study (Table 1). *Oithona similis, Pseudocalanus* spp. and Copepoda nauplii dominated the Arctic Archipelago group. The highest abundances of larvaceans, pteropods and *Microcalanus* spp. were measured in this group (Table 4).

Table 7. Mean (+SD) SI ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) in four ubiquitous species of zooplankton and for four biotic groups

Species	**Biotic group (geographical area)**	**$\delta^{13}C$ (‰) ± SD**	**$\delta^{15}N$ (‰) ± SD**
Calanus glacialis	Davis Strait	-20.4 ± 1.7	7.4 ± 1.1
	Gulf Boothia	-21.1 ± 1.2	10.1 ± 1.0
	Baffin Bay	-21.0 ± 0.3	8.7 ± 0.4
	Arctic Archipelago	-21.2 ± 0.1	8.1 ± 0.3
Calanus hyperboreus	Davis Strait	-21.2 ± 0.6	6.9 ± 0.4
	Gulf Boothia	-21.0 ± 0.6	9.6 ± 0.7
	Baffin Bay	-21.5 ± 0.3	8.2 ± 0.4
	Arctic Archipelago	-21.5 ± 0.7	8.6 ± 1.0
Paraeuchaeta sp.	Davis Strait	-20.7 ± 0.2	8.8 ± 1.8
	Gulf Boothia	-21.1 ± 0.4	12.0 ± 0.6
	Baffin Bay	-21.3 ± 0.3	11.5 ± 0.5
	Arctic Archipelago	-21.7 ± 0.8	11.3 ± 0.6
Themisto libellula	Davis Strait	-19.6 ± 0.6	8.2 ± 0.1
	Gulf Boothia	-20.5 ± 0.6	10.1 ± 0.7
	Baffin Bay	-20.0 ± 0.5	8.9 ± 0.8
	Arctic Archipelago	-20.0 ± 0.6	8.8 ± 0.7

3.5.4 Stable isotopes

All four species had $\delta^{13}C$ values that were consistent among regions (one-way ANOVAs, all $P > 0.05$). However, the $\delta^{15}N$ values varied significantly between regions (one-way ANOVAs, all $P > 0.05$), with the Gulf of Boothia appearing especially distinct from other regions. In the case of *C. glacialis* and *C. hyperboreus*, the Gulf of Boothia was significantly different from both Davis Strait and the Arctic Archipelago (post hoc pairwise Tukey's HDS tests, all $P < 0.05$), although the $\delta^{15}N$ values of *C. hyperboreus* also varied between Davis Strait and the Arctic Archipelago ($P < 0.05$). In the case of *Paraeuchaeta* spp., the $\delta^{15}N$ of the Davis Strait animals was significantly different from each of the other three regions, i.e. Gulf of Boothia ($P < 0.001$), the Arctic Archipelago ($P < 0.001$) and Baffin Bay ($P < 0.001$). Lastly, in the case of *T. libellula*, the Gulf of Boothia was also significantly different from both Davis Strait ($P < 0.05$) and Baffin Bay ($P < 0.05$) (Table 7).

3.6 DISCUSSION

Here we present spatial patterns of mesozooplankton community composition and the SI signatures ($\delta^{15}N$ and $\delta^{13}C$) of selected zooplankton taxa sampled over an area extending from sub-Arctic Atlantic to the Arctic Archipelago. We identified eight specific mesozooplankton assemblages that could be defined on the basis of temperature and salinity patterns. These biogeographic patterns in mesozooplankton assemblages were also characterized by differences in $\delta^{15}N$ (but not $\delta^{13}C$) values for the four most common zooplankton species.

Geographical regions defined on the basis of water mass corresponded to the: (i) Labrador Sea; (ii) Davis Strait; (iii) Baffin Bay; (iv) Arctic Archipelago and (v) the Gulf of Boothia. In general, the composition of mesozooplankton communities in our study area varied with water mass characteristics. Although only a few stations within the Labrador Sea and Davis Strait were sampled, we found three distinct biogeographic domains: (i) the Labrador Shelf; (ii) the deep basin of the Labrador Sea and (iii) the northernmost section of Labrador Sea and Davis Strait. *Calanus finmarchicus* was the species largely responsible for several of the community divisions. This calanoid copepod is a cold-temperate species that dominates the North Atlantic zooplankton biomass (Conover, 1988; Head et al., 2003) and has been used as a tracer of Atlantic waters in sub-Arctic and Arctic areas (Planque et al., 1997; Head et al., 2003). However, with the exception of the Barents Sea and the European side of the Arctic, *C. finmarchicus* has a limited distribution in true polar waters and we found no representatives of this species in our samples from the Arctic Archipelago.

As expected, the distribution of the three important Arctic copepod species, *M. longa, C. glacialis and C. hyperboreus*, was associated with cold Arctic waters (Smith and Schnack-Schiel, 1990; Falk-Petersen et al., 2009) and particularly, the cold-core water mass of central Baffin Bay and the polar waters of Lancaster Sound. Curiously, we found a low abundance of these large (Carmack and McLaughlin, 2011) Arctic copepods in the fresher water of the western section of the Archipelago, suggesting that these species are more abundant in cold waters (<0 °C). It is unlikely that these differences can be attributed to a vertical migration behaviour of *Calanus* spp. or differences in depth ranges sampled by our nets because zooplankton do not perform diel vertical migration during the midnight sun at high latitudes (Blachowiak-Samolyk et al., 2006). It is more likely that the low abundances were the result of the hydrodynamic and/or biophysical setting during our sampling. Within the Gulf of Boothia and Fury and Hecla Strait, we found communities dominated by very few large species and advanced developmental stages (adults and pre-overwintering stages). It is likely that the seasonal downward migration had already started at the time of sampling in this area (late summer/early autumn).

The $\delta^{13}C$ and $\delta^{15}N$ values of zooplankton in our study were within ranges reported for eastern Canadian (Hobson and Welch, 1992; Hobson et al., 2002; C. Pomerleau unpublished data) and European (Soreide et al., 2006) Arctic zooplankton. We found $\delta^{15}N$ to vary spatially in *C. glacialis, C. hyperboreus, Paraeuchaeta* spp. and *T. libellula.* Shifts in the $\delta^{15}N$ of particulate nitrogen at the base of the food web, food web structure and seasonal changes during or after the spring/summer bloom may modify and be responsible for the spatial variation of marine zooplankton $\delta^{15}N$ values observed in this study (Goering et al., 1990; Montoya, 1994; Richoux and Froneman, 2011). In the absence of a $\delta^{15}N$ baseline, it appears that seasonality is likely responsible for the enriched $\delta^{15}N$ values measured in Gulf Boothia animals. Elevated $\delta^{15}N$ values in zooplankton later in summer may result from efficient regeneration via grazing and excretion of nitrogenous nutrients and rapid uptake (Schell et al., 1998). Changes in $\delta^{15}N$ values in zooplankton may also arise from changes in water mass structure, frontal systems and nutrient sources between the different regions associated with the groupings for which we tested spatial differences.

Previous microzooplankton community studies within the northern Atlantic Ocean, Baffin Bay and Lancaster Sound highlight rather variable biomass distribution patterns (Paranjape, 1988; Burkill et al., 1993). Thus, it is conceivable that variation in mesozooplankton $\delta^{15}N$ values could be attributed to trophic position, but without direct measurements, we cannot rule out regional baseline variation and/or seasonality as in the Gulf of Boothia. Our results suggest that our focal species occupied either different trophic position within our study area, or that $\delta^{15}N$ of producers (e.g. phytoplankton and POM) changed throughout the study area. As no measurement of SIs for the lower trophic levels was available, we are not able to disentangle these confounding factors. These results highlight the need to measure isotopic variability in primary producers or else take advantage of compound-specific isotopic measurements (e.g. Hannides et al., 2009) in order to confidently relate differences in zooplankton isotopic signatures to actual differences in trophic structure and food-web efficiency (Sommer et al., 2002).

We found no significant patterns or changes in $\delta^{13}C$ between regions, which suggests that spatial variation in those factors (i.e. the contribution of ice versus pelagic POM to zooplankton diets, temperature, and phytoplankton productivity) that could have influenced $\delta^{13}C$ were not sufficiently pronounced to cause regional-scale differences in the species we studied. The lack of any spatial and group-specific differences in $\delta^{13}C$ is remarkable, given the measured differences in $\delta^{15}N$. In the Southern Ocean, Richoux and Froneman (Richoux and Froneman, 2009) found $\delta^{15}N$ in zooplankton to vary with latitude and found no patterns of enrichment or depletion in $\delta^{13}C$ across their large study area. Saupe et al. (1989) observed a west-to-east decrease in zooplankton $\delta^{13}C$ from the Chukchi/Western Beaufort Sea to the eastern Beaufort Sea/Amundsen Gulf. France et al. (1998) extended this transect into the CAA and through the Northwest Passage and found no evidence of a longitudinal $\delta^{13}C$ gradient as the values in zooplankton remained mostly constant.

3.7 CONCLUSION

We found a general correspondence in the spatial patterns of water mass characteristics, species composition and stable nitrogen isotope signatures. The mesozooplankton community composition varied across our study area, which covered Canadian Arctic and sub-Arctic waters, and some of the observed variations in species composition and SI ratios could be in part attributed to variation in temperature and salinity of the associated water masses. Our study suggests that trophic structure of the mesozooplankton community may vary spatially, and these results highlight the need for more detailed work on community-level trophic structure in sub-Arctic and Arctic seas. The predicted continuous warming trend of the ocean surface temperature is expected to favour the growth of smaller phytoplankton cells (picophytoplankton replacing large diatoms) that in turn would also favor small-sized zooplankton species (Li et al., 2009). Our study presents a baseline for monitoring a potential shift in species biogeographical range in the Canadian eastern Arctic and sub-Arctic regions including the potential increase in boreal species at higher latitudes.

3.8 ACKNOWLEDGEMENTS

We thank the officers and crew of the CCGS Louis S, St-Laurent and CCGS DesGroseilliers for all of their support during the cruises. We also thank Ed Hendricks and Marie-Claude Lamarche for assistance with net sampling and Moira Galbraith for her help with zooplankton identification.

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CHAPITRE 4

LA VARIABILITÉ ISOTOPIQUE DES ASSEMBLAGES DE PROIES COMME OUTIL AFIN D'ÉVALUER LA DIETE ET DE DÉTERMINER LES AIRES D'ALIMENTATION DE LA BALEINE BORÉALE (*BALAENA MYSTICETUS*) DANS L'ARCTIQUE DE L'EST CANADIEN

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Accepté le 8 août 2012 dans *Marine Ecological Progress Series,* vol. 469, p. 161-174

4.1 RÉSUMÉ

La population de baleine boréale (*Balaena mysticetus*) de l'est du Canada et de l'ouest du Groenland se remet lentement de la chasse commerciale intensive qui s'est déroulée du 18^{e} au 20^{e} siècle. Toutefois, les nombreux effets des changements climatiques sur les conditions de glace de mer et sur la disponibilité des proies s'ajoutent aux autres menaces existantes pouvant affecter le rétablissement de la baleine boréale. Dans la présente étude, nous exploitons la variabilité observée dans les signatures isotopiques des assemblages de proies potentielles dans l'Arctique de l'est afin d'étudier la diète de la baleine boréale et d'identifier ses aires d'alimentation probables. Nous avons comparé les ratios d'isotopes stables de carbone ($\delta^{13}C$) et d'azote ($\delta^{15}N$) dans les échantillons de peau de baleine (n=190) avec ceux des proies potentielles échantillonnées a plusieurs stations dans l'Arctique de l'est canadien en 2007-2009 et nous avons calculé les contributions des différentes sources (zooplancton) a la diète de la baleine boréale en utilisant un modèle de mélange isotopique bayésien. Une analyse de classification hiérarchique a déterminé de la variabilité dans la composition isotopique des groupes d'individus, mais non entre les mâles et les femelles, ni entre les différentes classe d'âge. Le modèle isotopique a indiqué que le détroit de Davis et la baie de Disko n'étaient pas des aires d'alimentation probables, du moins au printemps et en été. Le détroit de Lancaster, la mer de Baffin et le golfe de Boothia sont trois régions probablement utilisées par la baleine boréale pour s'alimenter notamment de larges copépodes calanoides arctique (*Calanus hyperboreus, Calanus glacialis, Metridia longa* et *Paraeuchaeta* spp.), de mysidacés et d'euphausiacés. La forte dépendance de la baleine boréale sur le zooplancton polaire peut rendre cette espèce endémique de l'Arctique vulnérable au déplacement latitudinal prévu des espèces vers le Nord en conséquence des changements climatiques soutenus.

Mots clés : Arctique canadien ; baleine boréale ; diète ; écologie alimentaire ; écologie trophique ; isotopes stables ; mammifères marins ; modèle de mélange isotopique bayésien ; siar; zooplancton

Ce quatrième article, intitulé « *Prey assemblage isotopic variability as a tool for assessing diet and the spatial distribution of bowhead whale (Balaena mysticetus) foraging in the Canadian eastern Arctic*», fut rédigé par moi-même ainsi que par Véronique Lesage, Steven Ferguson, Gesche Winkler, Stephen Petersen and Jeffrey Higdon. Il fut soumis à la revue *Marine Ecological Progress Series* en février 2012 et est présentement en révision finale depuis juin 2012. En tant que premier auteur, ma contribution à ce travail fut l'essentiel de la recherche, incluant une partie de la collecte des échantillons de baleines en août 2009 et l'analyse taxonomique et isotopique de tous les échantillons de zooplancton, les analyses statistiques et l'écriture du manuscrit. Véronique Lesage, second auteur, fut d'une grande aide dans l'interprétation des données du modèle de mélange isotopique SIAR et dans l'écriture du manuscrit. Steven Ferguson a contribué à la rédaction et m'a soutenu financièrement pour ma participation à un atelier de formation SIAR à l'Université de Fairbanks en Alaska. Gesche Winkler m'a aidé dans l'interprétation des résultats et a fournit plusieurs commentaires sur le manuscrit. Stephen Petersen a généré les données génétiques mâles/femelles et Jeffrey Higdon à participer aux collectes de données sur le terrain.

Une version abrégée de cet article a été présentée à plusieurs occasions notamment a la conférence << *Society of Marine Mammalogist (SMM) Biennial Conference on the Biology of Marine Mammals*, à Tampa Bay en novembre 2011 et à la conférence <<*5th International Zooplankton Symposium*>> à Pucon, au Chili, en mars 2011.

4.2 ABSTRACT

The Eastern Canada - West Greenland (EC-WG) bowhead whale (Balaena mysticetus) population is slowly recovering from the intensive commercial whaling of the 18th and 20th centuries. However, climate change, through effects on ice conditions and prey availability are among threats that might affect bowhead whale recovery. In this study, we exploited the variability observed in isotopic signatures of prey assemblages across the eastern Arctic to examine variability in diet among bowhead whales (n = 190) and identify their potential foraging areas. We compared $\delta^{13}C$ and $\delta^{15}N$ isotopes ratios of biopsied skin sample with those of potential zooplankton prey species collected across the Canadian Eastern Arctic and calculated the proportional contributions of various sources (zooplankton) to the diet of bowhead whales using a Bayesian stable isotope mixing model. A cluster analysis indicated some variability in isotopic composition among groups of individuals but not between males and females or age classes. The isotopic model discounted Davis Strait and Disko Bay as potential foraging areas for bowhead whales, at least in spring and summer. Lancaster Sound, Baffin Bay and the Gulf of Boothia were the three main areas likely used for summer feeding, where bowhead whales fed primarily on large arctic calanoid copepods (*Calanus hyperboreus, Calanus glacialis, Metridia longa*, *Paraeuchaeta* spp.), mysids and euphausids. While some inter-individual variability in diet was observed, the strong dependence of this endemic arctic species on arctic zooplankton may make them vulnerable to the predicted latitudinal shift in prey species composition as a result of the ongoing warming trend.

Keywords: Canadian Arctic; Bayesian mixing model; Bowhead whale; Diet; Foraging behaviour; Marine mammal; Zooplankton; Stables isotopes; SIAR; Trophic ecology

4.3 INTRODUCTION

Environmental conditions and prey abundance are the primary factors influencing the geographic distributions of most species (MacLeod 2009). However, other ecological, demographic or evolutionary attributes may also shape habitat use and resource partitioning within species (Peterson 2006). For instance, it is expected that for species with wide distribution ranges or with strong social structures, some partitioning of resources may exist among sex- or age-classes, or among social groups. Intraspecific differences in feeding location or diet composition are known in a wide array of species and are more frequent in species living in environments where little interspecific competition and strong intraspecific competition exist (Estes et al. 2003).

The bowhead whale is endemic to the Arctic, and occurs in Canadian waters as two genetically distinct populations: the Bering-Chukchi-Beaufort (BCB) and the Eastern Canada–West Greenland (EC-WG) population (Rugh et al. 2003, Nowak 2003). Satellite telemetry data indicate that EC-WG bowhead whales are widely distributed throughout the Canadian eastern Arctic and West Greenland where they perform extensive seasonal migrations (NWMB 2000, Heide-Jørgensen et al. 2003). Their winter distribution includes Hudson Strait, northern Hudson Bay, east Baffin Island and the ice edge along West Greenland (Reeves & Heide-Jørgensen 1996, Koski et al. 2006), while in spring they are usually found along the west coast of Greenland (e.g., Disko Bay), in Cumberland Sound, Foxe Basin and Lancaster Sound (Figure 1). Their summer range includes the fjords and bays of the Canadian High Arctic, Hudson Bay and Foxe Basin (Cosens et al. 1997, Cosens & Innes 2000, Higdon & Ferguson 2010).

Genetic and satellite telemetry studies indicate significant gender- and age-class segregation within the EC-WG population, at least at times other than winter (Ferguson et al. 2010a, Heide-Jørgensen 2003, 2006, Postma et al. 2006) (See Figure 1). For instance, Disko Bay is an important feeding area for adult bowhead whales and the vast majority of whales aggregating there in the spring are large adult females (> 14 m) (Laidre et al. 2008). In summer, Foxe Basin is used mainly by juvenile whales and females with their calves (Cosens & Blouw 2003), whereas the Gulf of Boothia appears to be used by all age or sex classes (Dueck & Ferguson 2009). Hudson Strait is the main wintering ground for this population (Koski et al. 2006) and mating is thought to occur during late winter within that area (Heide-Jørgensen et al. 2006) as well as in Disco Bay (Heide-Jørgensen et al. 2010). The seasonal distribution of bowhead whales is largely driven by sea ice (Moore & Reeves 1993, Dyke et al. 1996, Ferguson et al. 2010a). Whales select areas of lower ice concentration and thickness during winter, likely to reduce risks of ice entrapment (Ferguson et al. 2010a). The reverse is observed during summer, possibly to reduce exposure to predators such as killer whales, and to increase feeding opportunities near the productive marginal sea ice zone (Gosselin et al. 1997, Ferguson et al. 2010b, Pomerleau et al. 2011a).

Over the last several decades, the rapid decline of sea ice extent and thickness at higher latitudes as a result of the continuous warming of both the Earth atmosphere and ocean surface temperature (ACIA 2004) has affected plankton abundance and distribution (Greene & Pershing 2007). Although bowhead whales are adapted to the extreme seasonal variability in sea ice cover and associated productivity, they may be impaired by ongoing climate warming (Neibauer & Schell 1993). Bowhead whales feed exclusively on zooplankton species, but their degree of specialization on this resource at the population and individual levels, and thus vulnerability to changes in species composition, remains uncertain. Their diet varies among regions, and may include pelagic, sympagic and epibenthic species (Finley 2001, Lowry et al. 2004, Laidre et al. 2007, Pomerleau et al. 2011b). For the EC-WG population, diet has been inferred from short-term, indirect or qualitative approaches such as observation of surface feeding, stomach content analysis, plankton net sampling, dive data or a combination of these approaches (Finley 2001, Lowry et al. 2004, Lee et al. 2005, Laidre et al. 2007, Pomerleau et al. 2011a). Time-integrated studies of diet are lacking for this bowhead whale population.

Stable isotope analysis (SIA) has been used in a wide range of studies to investigate trophic ecology and habitat use of wild species (Hobson 1999), including marine mammals (Newsome et al. 2010). This approach provides time-integrated information on assimilated, not just ingested prey (Peterson & Fry 1987, Dalerum &

Angerbjorn 2005) and over periods that vary from a few hours to a lifetime depending on the tissue used (Tieszen et al. 1983, Hobson 1993). For instance, skin represents the period of epidermal growth, and was demonstrated to reflect in beluga whales and dolphins the diet over a period of 2 to 3 months prior to skin collection (Hicks et al. 1985, St. Aubin et al. 1990, Hobson et al. 1996, Ruiz-Cooley et al. 2004). The turnover rate is possibly longer than this in balaenids such as bowhead whales, as their epidermis is thicker (15–24 mm) than in beluga (5–12 mm) (Bonin & Vladykov 1940, Haldiman et al. 1985, Jones & Pfeiffer 1994). The stable isotope approach applied to bowhead whale skin could provide insights into their foraging ecology, and the relative importance of various feeding areas, especially considering the variability observed in prey assemblage isotopic signatures across the bowhead whale distribution range in the eastern Arctic (Pomerleau et al. 2011c). While consumer diets can be determined using mass-balance models, they are often limited by the number of isotopes as they are deterministic, and thus restricted to a small number of possible food sources (Phillips & Gregg 2003). More recently, a robust stable isotope mixing model has been developed in a Bayesian framework (Moore & Semmens 2008, Parnell et al. 2010). These models are less limited by the number of dietary sources. They incorporate uncertainty for each parameter and prior information on diet when available, and offer solutions in the form of probability estimates of source contributions to a consumer diet (Parnell et al. 2010).

In this study, we examined the degree of variability in diet among bowhead whales to identify possible patterns among age and sex classes, and regions most likely exploited as feeding grounds. While individual specialization cannot be specifically addressed in our study given the lack of repeated sampling of individuals over time, some insights into the degree of generalism or specialization at the population level can be gained from the inter-individual variability in diet composition (Bearhop et al. 2004). This was accomplished by first examining patterns in stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic signatures of skin among bowhead whales, and then by comparing them to those of potential zooplankton prey from various regions of the eastern Arctic using a Bayesian dietary mixing model.

4.4 MATERIAL AND METHODS

4.4.1 Study area and sample collection.

Bowhead whale skin samples (n = 202) were collected between June and September of 1988–2009 at several locations of the Canadian eastern Arctic including Foxe Basin, Admiralty Inlet, Cumberland Sound and Hudson Strait (Figure 1, Table 1). However, the vast majority of the whales included in this study were sampled in July–August (>94 %) and in Foxe Basin (84 %) (Table 1). Samples were obtained using a crossbow darting system (Brown et al. 1991), and were preserved frozen at -20 °C until isotopic analyses. Information on age class was collated directly in the field, and was available only from northern Foxe Basin whales and for 43 individuals, including 10 adults (> 13 m) and 33 sub-adults (6–13 m) (Higdon & Ferguson 2010). Gender was determined genetically (Shaw et al. 2003; Petersen et al. 2011), and was available for 153 of the 202 whales (Table 1).

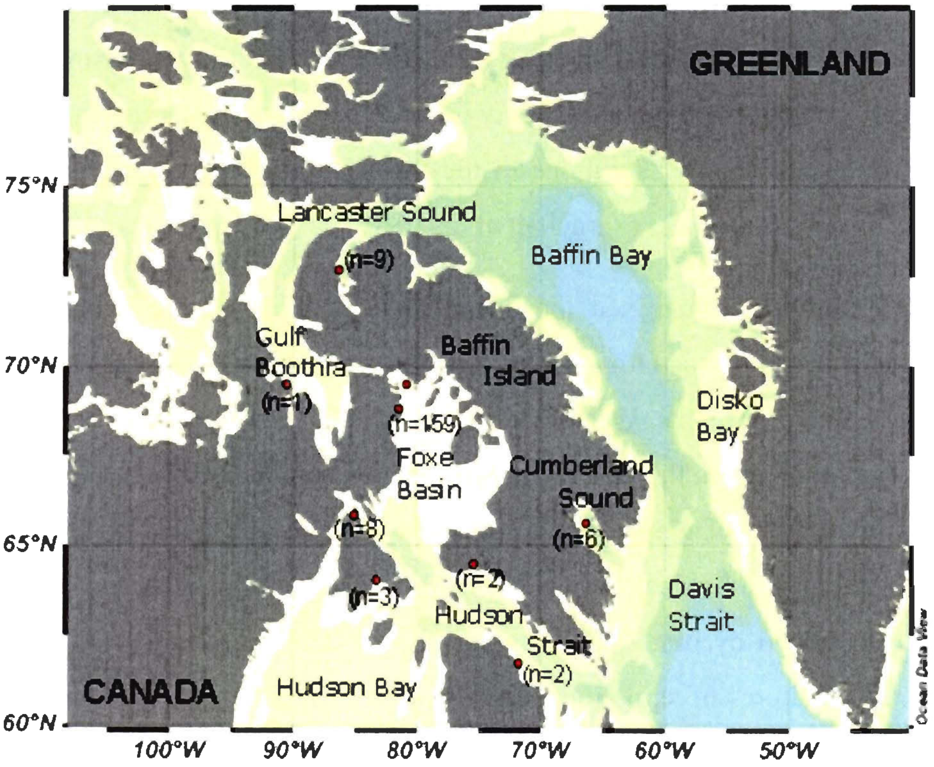


Figure 1. Sampling locations for bowhead whale skin samples without outliers in the Eastern Canadian Arctic

Zooplankton samples were collected in July 2007 and September 2009 on board Canadian Coast Guard icebreakers at 21 locations of the Canadian eastern Arctic, including the Labrador Sea, Davis Strait, Baffin Bay and the Canadian Arctic Archipelago (Figure 1). A complete description of the sampling protocol is presented in Pomerleau et al. (2011c). Briefly, samples were collected with a Bongo net, a set of two adjacent 1 m^2 framed nets, towed vertically from 100 m (or near the bottom if sampling was done in a shallower area) to the surface (mesh size 2 X 236 μm) at a speed of 1 $m s^{-1}$. Each zooplankton item was identified to genus or species, and was placed into 4 ml glass vials and kept frozen at -20 °C until analysis.

Table 1. Sample size (N), number of known bowhead whale females and males, range of sampling years and months of collection for each of the 6 sampling regions in the Canadian Arctic.

Region	Year range	Sample size (N)	Sampling month					Sex		
			June	July	August	September	Unknown	Male	Female	Unknown
N. Foxe Basin	1994-1999	19	0	5	1	1	12	3	7	9
	2001-2003	13	0	11	0	0	2	3	3	7
	2007	43	6	37	0	0	0	17	15	11
	2008	7	0	7	0	0	0	2	4	1
	2009	88	0	88	0	0	0	41	37	10
		170	6	154	1	1	8	66	66	38
S. Foxe Basin	1999-2001	5	0	0	0	0	5	1	2	2
	2008-2009	7	0	0	3	2	2	2	1	4
		12	0	0	3	2	7	3	3	6
Gulf Boothia	2008	1	0	0	0	1	0	1	0	0
Lancaster S.	2008-2009	9	0	0	9	0	0	2	6	1
Hudson Strait	2001-2009	4	0	0	2	1	1	2	1	1
Cumberland S.	1988-1997	3	0	0	0	0	3	1	0	2
	2003-2006	3	0	3	0	0	0	2	0	1
		6	0	3	0	0	3	3	0	3
Summary		202	6	157	15	5	19	77	76	49

Pomerleau et al. (2011c) defined four biogeographic domains within the EC-WG bowhead whale distribution range, which were characterized by specific prey assemblages and water mass characteristics. These regions included Davis Strait (DS), Baffin Bay (BB), Lancaster Sound (LS) and the Gulf of Boothia (GB) (Figure 1). Marine zooplankton stable isotope data from this study were used as sources in a mixing model along with additional data from the literature (Hobson 1993, Hobson et al. 2002). Since bowhead whales may also be found in Disko Bay (DB), West Greenland, during late winter and spring time (Laidre et al. 2007), we also incorporated stable isotope data from zooplankton species collected from this area in the spring (Møller 2006).

4.4.2 Sample preparation.

Bowhead whale skin samples were freeze-dried to remove moisture, and ground to a fine powder. Nitrogen isotope ratios were determined from dried homogenized sub-samples of bowhead skin, and composite samples of several whole individuals in the case of zooplankton. Carbon isotope ratios were determined from lipid-extracted samples of skin and zooplankton. Lipid extraction was performed following the Folch method (Folch et al. 1957) and using approximately 0.2 g of dried material and a solvent consisting of 2:1 chloroform:methanol (v/v). The tissue was placed in a glass tube with 10 ml of the solvent mixture, sonicated for 15 min and gently shaken for 4 h at room temperature. The sample was then centrifuged (2500 rpm) for 10 min prior to removing the supernatant. This extraction procedure was repeated three times. Once lipid were extracted, zooplankton samples were acidified with the "drop by drop" technique, using a weak acid solution (1 M HCl) (Mintenbeck et al. 2008), placed in an oven at 60 °C to remove moisture, and then analyzed for their carbon isotope ratios.

4.4.3 Stable isotope analysis.

Samples were analyzed for carbon and nitrogen isotope ratios at the University of Waterloo Environmental Isotope Laboratory, Ontario, Canada, by continuous flow ion ratio mass spectrometry (CF-IRMS), using a GV-Instruments IsoPrime coupled to a peripheral temperature-controlled Euro Vector elemental analyzer. Stable isotope ratios are expressed as delta (δ) notations, the normalized ratio of an unknown sample to an internationally accepted standard. Standards were atmospheric N_2 for $\delta^{15}N$, and Vienna-Pee Dee Belemnite (V-PDB) for $\delta^{13}C$. Analytical error based on replicate analyses of samples and laboratory standards was 0.1‰ for both $\delta^{13}C$ and $\delta^{15}N$.

4.4.4 Statistical analysis.

Statistical analyses were performed using R version 2.13.1 (R Development Core team 2010). Normality of isotopic data distribution was assessed using Shapiro-Wilk normality tests. A dissimilarity matrix based on Euclidean distances was constructed from the isotopic signatures of all 202 bowhead whales, and used in a single linkage non-hierarchical cluster analysis (nearest neighbor) to remove outliers as the latter are known to bias hierarchical cluster analysis results (Hair et al. 1995). A second dissimilarity matrix was then constructed while excluding outliers (n = 12), and used in a hierarchical cluster analysis to identify groupings among bowhead whales. We used three statistical indicators to assist with objective determination of the appropriate number of clusters: cubic-clustering criterion (CCC: Sarle 1983), pseudo F statistic (Calinski & Harabasz 1974), and pseudo t^2 statistic (similar to Hoteling's T^2: Duda & Hart 1973).

Statistical analyses testing for various effects were conducted exclusively on the 110 bowheads of known sex obtained from northern Foxe Basin during 2007 and 2009 given this site and years dominated our sample, and because whales were all biopsied during the same month (July). Gender and year effects were tested on this sample using a two-way analysis of variance (ANOVA), whereas comparisons among age classes were made using a Student's *t*-test or a Wilcoxon rank sum test (when data were not normally distributed). As a result of the small sample size for other seasons and sites (Table 1), no attempts were made to statistically assess seasonal or site effects. Nevertheless, results from the cluster analysis were scrutinized to insure particular clusters of bowhead whales were not biased towards specific seasons, sampling sites, sex or age classes.

4.4.5 Stable isotope mixing model.

Diet composition was quantitatively assessed for each bowhead group identified through the cluster analysis, using a Bayesian dietary multi-source SI mixing models (SIAR Stable Isotope Analysis in R, Parnell et al. 2010). Each bowhead group was evaluated against prey from each of the five biogeographical regions (Davis Strait, Disko Bay, Baffin Bay, Lancaster Sound and the Gulf of Boothia) to identify plausible feeding areas and diet composition associated with each set of prey. Input parameters to Bayesian models may include prior knowledge about diet composition, but none was available for bowhead whales. Therefore input parameters included isotopic signatures of each of the consumers, each potential prey (entered as mean ± SD), and the discrimination factors (DF) between the consumer tissue and that of the prey, with a measure of uncertainty (SD). To our knowledge, the only study on DFs for skin of cetaceans was conducted using a captive female killer whale, and resulted in a discrimination factor of +2.4 ‰ for δ^{13}C (after delipidation) and of +3.05 ‰ for δ^{15}N between the whale skin and whole fish prey (Caut et al. 2011). These results need to be interpreted with caution since the whale was sick for the three months prior to death from a bacterial infection. We used a DF (± SD) between bowhead whale skin and their zooplankton prey of +2.5 ± 0.2 ‰ for δ^{15}N and of +1.0 ± 0.1 ‰ for δ^{13}C. This value corresponds to the DF predicted based on prey isotopic value for mammals, i.e., ca. 2.5 ‰ (Caut et al. 2009), and is close to the value obtained for the captivity study on killer whales (Caut et al. 2011), and the estimated +2.3 ‰ obtained for skin of seals maintained in captivity under controlled conditions (Hobson et al. 1996). We used a value of 1.0 ‰ for δ^{13}C, the average enrichment predicted for mammals based on isotopic prey value (Caut et al. 2009), as we suspected the value obtained from captive seal skin (+2.7 ‰) to be likely overestimated by lipid extraction of prey but not the skin. Error terms for discrimination factors were determined arbitrarily, but were set to a higher value for δ^{15}N than δ^{13}C given the larger discrimination associated with the former isotopes. SIAR mixing models include diagnostic matrix plots for exploring the covariance structure between each pair of sources (Parnell et al. 2010). For instance, a strong negative correlation between two prey sources implies that for a given iteration, the contribution of one source affects negatively the contribution of the other, a phenomenon which inflates the uncertainty around the proportional contribution of each source to the diet. Sources that were strongly negatively correlated were combined to reduce uncertainty. Contributions of dietary sources are reported as mean and 95% Credibility Interval (CI).

4.5 RESULTS

Isotopic signatures of bowhead whales sampled in Foxe Basin during the same month (July) were consistent across the two years of sampling (2007 and 2009), as well as among age and sex classes. Carbon isotopic signatures were similar among sex classes in both years (sex: F (1,106) = 0.0065, p = 0.936; year: F = 3.0287, p = 0.085), and the same was obtained for δ^{15}N values (sex: F (1,106) = 0.0078, p = 0.929; year: F = 0.0471, p = 0.829). Isotope ratios of these two elements were also similar among adult and sub-adult whales (δ^{13}C: t = -0.47, p = 0.644; δ^{15}N: W = 204, p = 0.273). Assuming a similar trend for sites, years or seasons with insufficient sample size, all whales were pooled together in the cluster analysis to investigate individual isotopic variability further.

The hierarchical cluster analysis of bowhead whale isotopic signatures segregated bowhead whales into four groups, all of which were approximately composed of an equal number of males and females among the sexed individuals (Figure 2, Table 2). Examination of the outliers removed prior to this analysis did not reveal any bias towards particular site, year, sex or age class (not shown). There was also no clear pattern in the distribution of individuals from specific sites, years or age classes among the clusters, indicating that none of the groups was dominated by individuals from a particular site, year or age class. Group 1 was the largest, and encompassed 103 individuals, the majority (n=92) of which were biopsied in northern Foxe Basin. Group 2 comprised 44 whales,

Table 2. Sample size (N), number of known females and males and mean δ^{13}C ± SD and mean δ^{15}N ± SD of males and females for each of the four resulting groups from the hierarchical cluster analysis.

Group	N	Females	Males	δ^{13}C (‰)	δ^{15}N (‰)
1	103	37	44	-19.4 ± 0.3	13.2 ± 0.2
2	44	18	15	-19.4 ± 0.3	12.4 ± 0.3
3	28	11	9	-19.7 ± 0.3	14.1 ± 0.2
4	15	7	5	-20.4 ± 0.2	12.9 ± 0.4

with about half (n = 26) being biopsied in areas other than Foxe Basin. This group had $\delta^{13}C$ values similar to Group 1, but was less enriched in $\delta^{15}N$. The only calf included in this study was part of Group 2. Group 3 included 28 individuals, all from northern Foxe Basin, and was the most enriched in $\delta^{15}N$. Group 4 was comprised of 15 individuals, including 12 from northern Foxe Basin, and had the most depleted average $\delta^{13}C$.

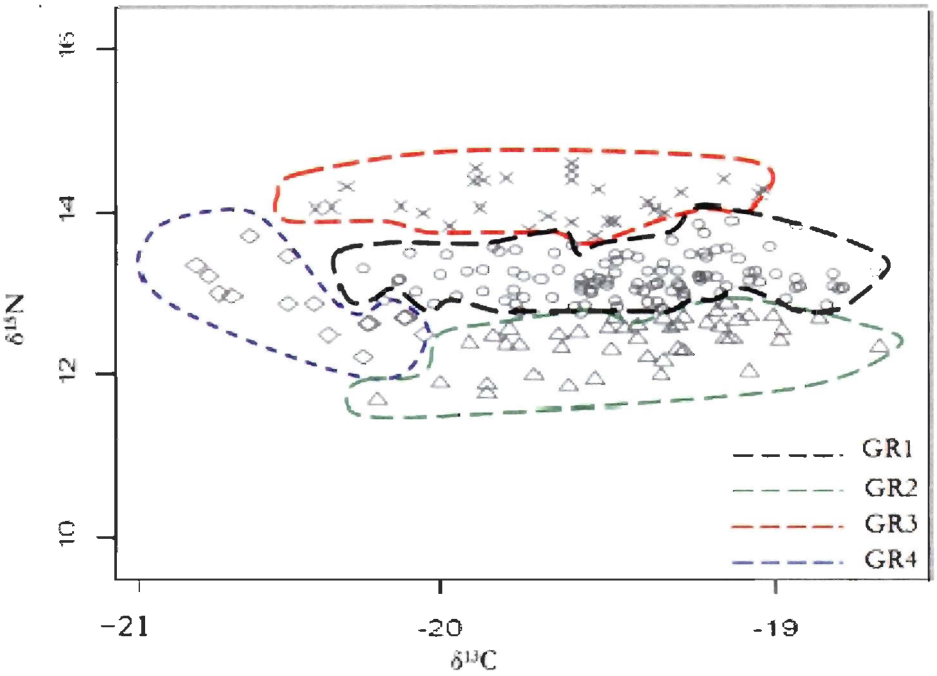
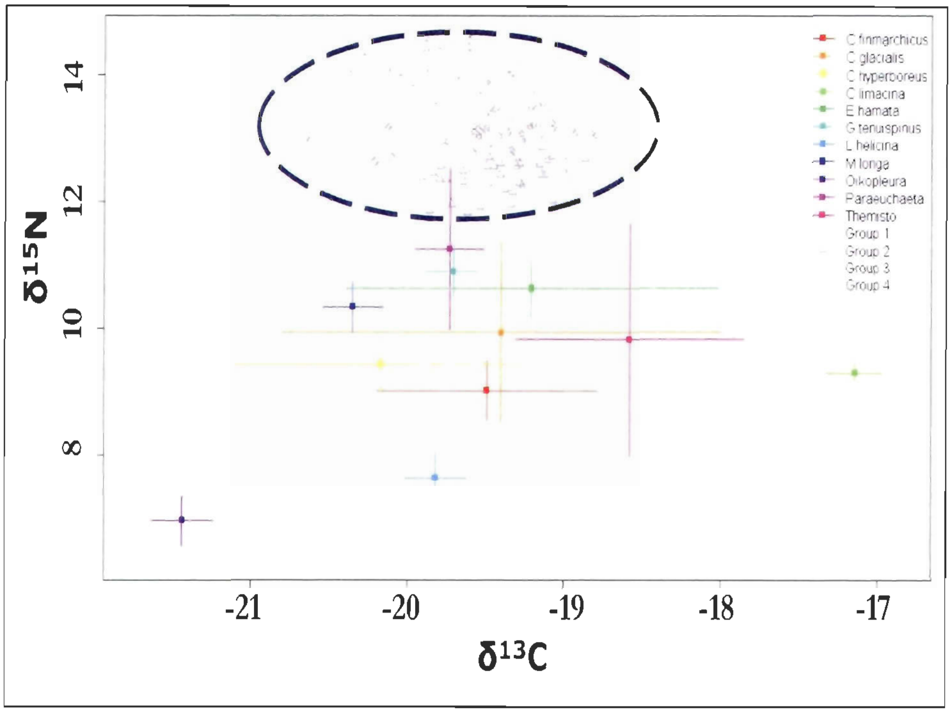


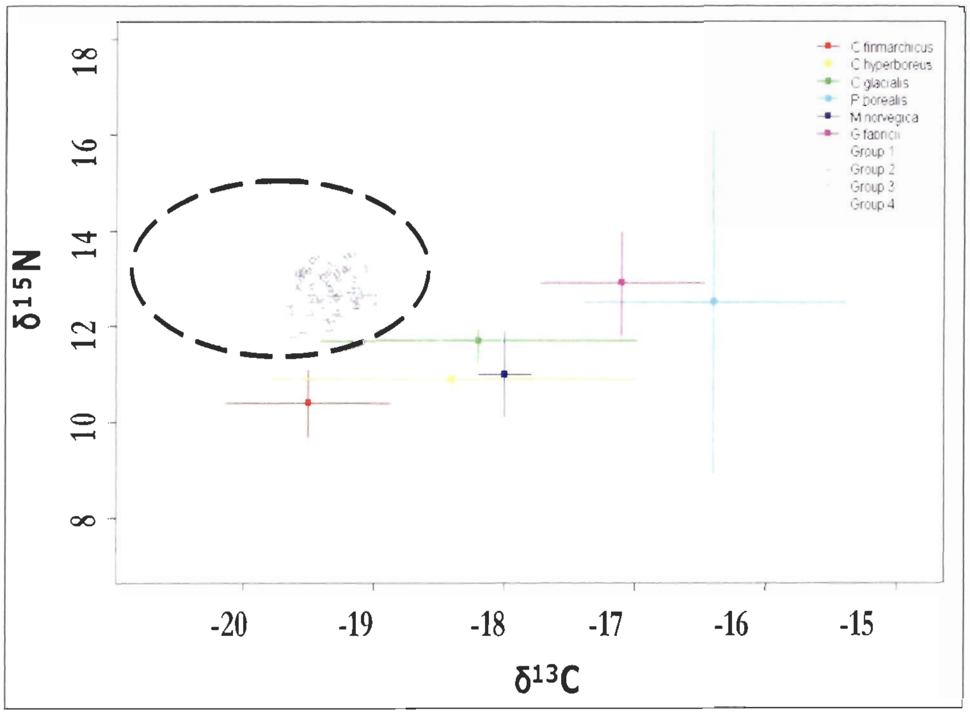
Figure 2. Stable isotopes ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) of bowhead whales (4 groups) determined by a hierarchical cluster analysis

Two-dimensional plots of mean isotopic signatures of the four bowhead groups relative to potential prey from the five biogeographic regions indicate that Baffin Bay, Lancaster Sound and Gulf Boothia represent plausible feeding areas for bowhead whales sampled in our study (Figure 3 c-e). In contrast, Davis Strait and Disko Bay are unlikely to be important feeding area (Figure 3 a-b). As a result, diet composition using Bayesian mixing models was evaluated for each of the four bowhead whale groups, but against only three of the five regional prey assemblages: Baffin Bay (BB), Lancaster Sound (LS) and Gulf Boothia (GB) (Figure 3 c-e). Potential prey base varied among regions from 9 to 12 species (Figure 3 c-e).

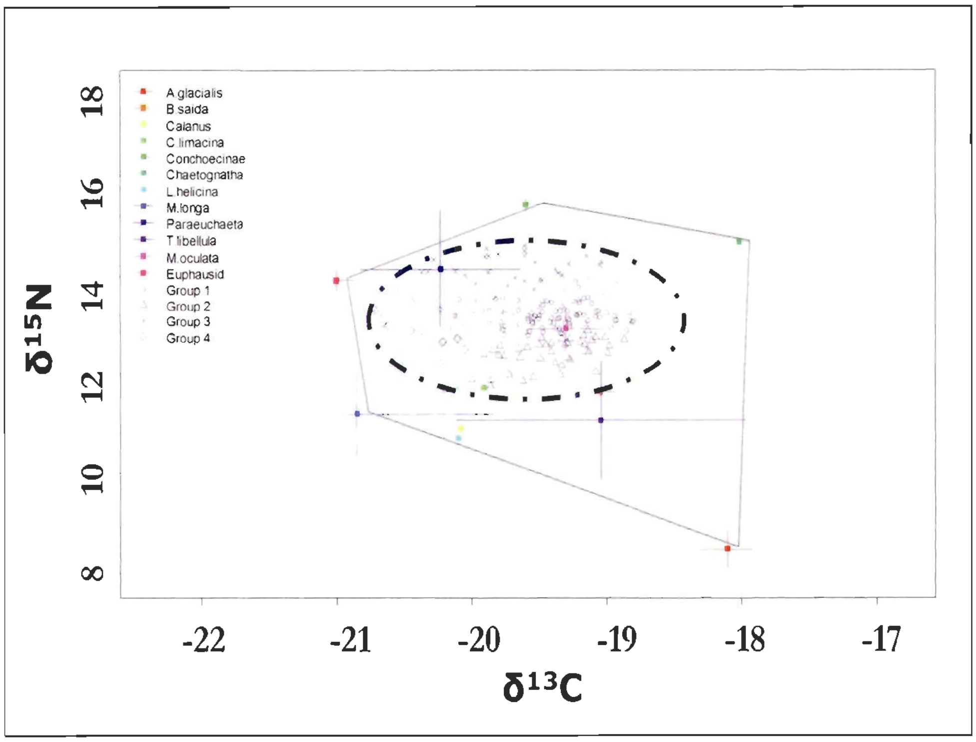
a)


C finmarchicus
C glacialis
C hyperboreus
C limacina
E hamata
G tenuispinus
L helicina
M longa
Oikopleura
Paraeuchaeta
Themisto
Group 1
Group 2
Group 3
Group 4
14
12
10
8
δ15N
-21
-20
-19
-18
-17
δ13C

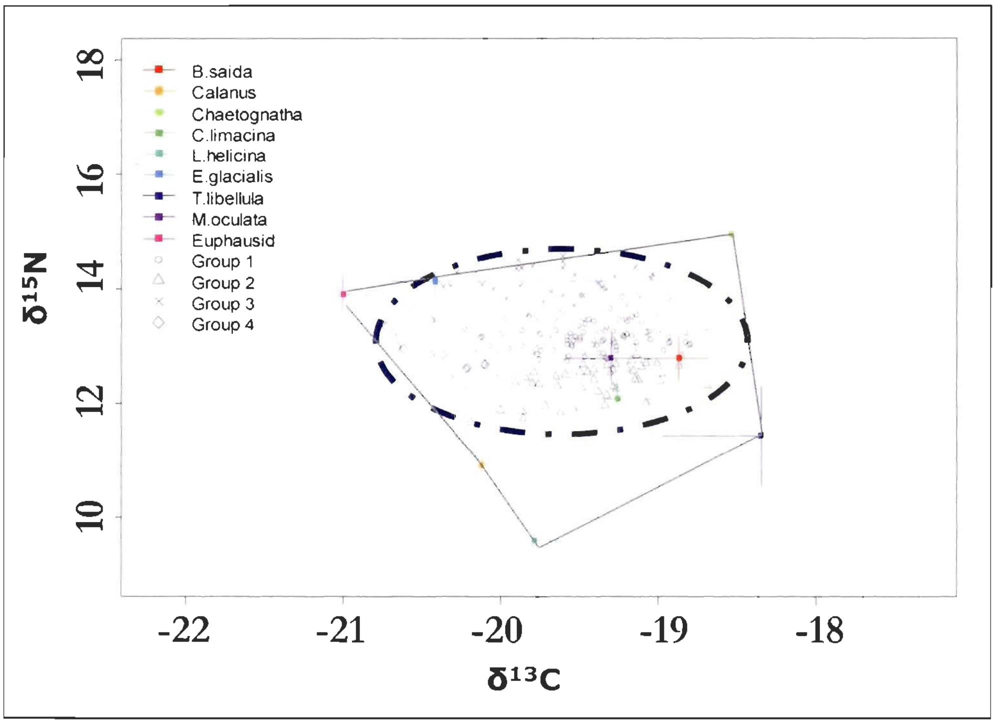
b)


C finmarchicus
C hyperboreus
C glacialis
P borealis
M norvegica
G fabricii
Group 1
Group 2
Group 3
Group 4
18
16
14
12
10
8
δ15N
-20
-19
-18
-17
-16
-15
δ13C

c)


A.glacialis
B.saida
Calanus
C.limacina
Conchoecinae
Chaetognatha
L.helicina
M.longa
Paraeuchaeta
T.libellula
M.oculata
Euphausid
Group 1
Group 2
Group 3
Group 4
18
16
14
12
10
8
δ15N
-22
-21
-20
-19
-18
-17
δ13C

d)


B.saida
Calanus
Chaetognatha
C.limacina
L.helicina
E.glacialis
T.libellula
M.oculata
Euphausid
Group 1
Group 2
Group 3
Group 4
18
16
14
12
10
δ15N
-22
-21
-20
-19
-18
δ13C

e)

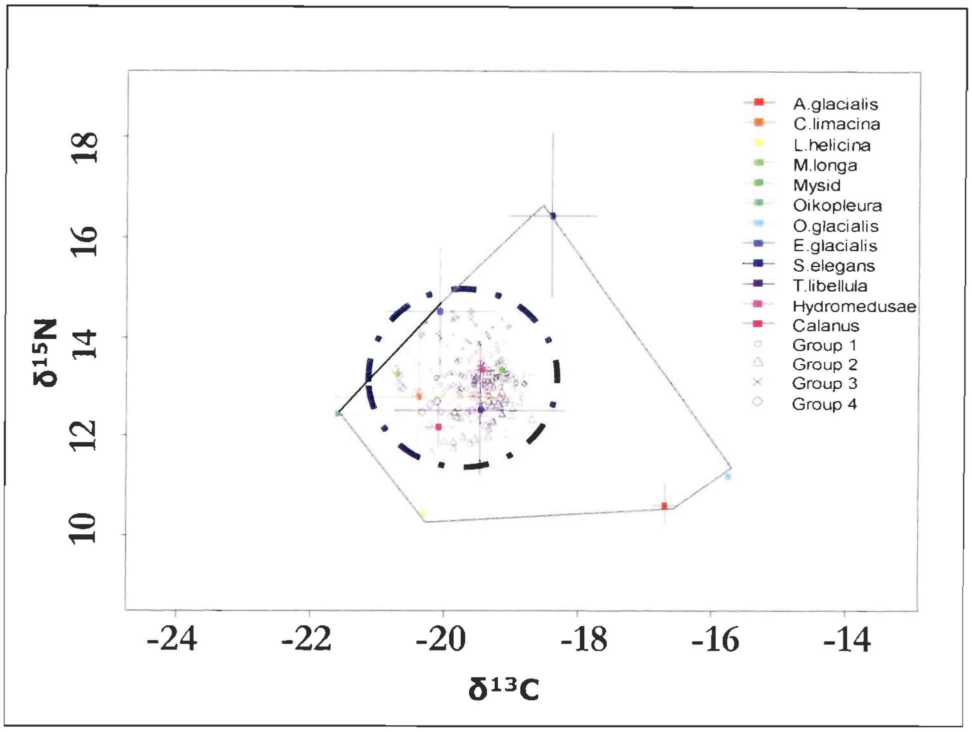


Figure 3. Stable isotope input data of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) of bowhead whales (within black circle). The source means (circles) and standard deviations (lines) are shown for each source (prey), corrected for diet-tissue discrimination. a) Davis Strait, b) Disko Bay, c) Baffin Bay, d) Gulf Boothia and e) Lancaster Sound.

Using potential prey as sources in mixing models, we found similarities and differences between the diets of the four groups of bowhead whales. Groups 1 and 3 consumed primarily a mixture of euphausids, mysids, *Paraeuchaeta* sp. and chaetognaths but the contribution of the different species was different between the two groups. Bowhead whales from groups 2 and 4 consumed a large amount of calanoid copepods (*Calanus* spp. and *Metridia longa*), but individuals from group 2 also consumed various amounts of amphipods, pteropods and chaetognaths. Bowhead whales in group 4 consumed the largest amount of euphausids. The contributions of a given species also varied depending on the biogeographic region being considered. For group 1, euphausids and *Paraeuchaeta* sp. contributed 27% (CI 20–35%) in LS and 18% (6–31%) in BB. *Mysis oculata* contributed the same amount in GB and BB (16%, CI 2–30%) but was more important in the diet if taken from LS (26%, CI 9–43%). Larvaceans and pteropods

(17%, CI 4–29%) were also contributing species to bowhead whale diets in GB (17%, CI 4 – 29%) (Figure 4). For group two, the most important dietary sources were *A. glacialis, Calanus* spp. *L. helicina* and chaetognaths (Figure 5). The ice amphipods *A. glacialis* and *O. glacialis* contributed 19% (CI 13–25%) in GB, and a similar amount (18%, CI 7–28%) in BB. *Calanus* spp. and *L. helicina* were important dietary sources in both LS (24%, CI 12–36%) and BB (14%, CI 2–27%). For group 3, euphausids comprised half of the diet in LS (51%, CI 42–60%) and about one quarter of it if consumed in BB (27%, CI 11–41%). Chaetognaths and *Paraeuchaeta* sp. contributed to nearly half of the diet (47%, CI 37–57%) of this group in GB (Figure 6), and possibly also substantially in LS an BB, although the similarity of their isotopic signature with other species precluded firm conclusions about their relative contributions. *Metridia longa* was also an important prey item (20%, CI 8–33%) in GB, followed by *M. oculata* (13%, CI 2–25%). Finally, *M. longa, Calanus* spp. and euphausids were the most important prey items to Group 4 (Figure 7). Most of the species attributed to the diet of whales feeding within LS and BB were euphausids (>50%) followed by M. longa in GB (41%, CI 26–57%) and BB (27%, CI 15–40%).

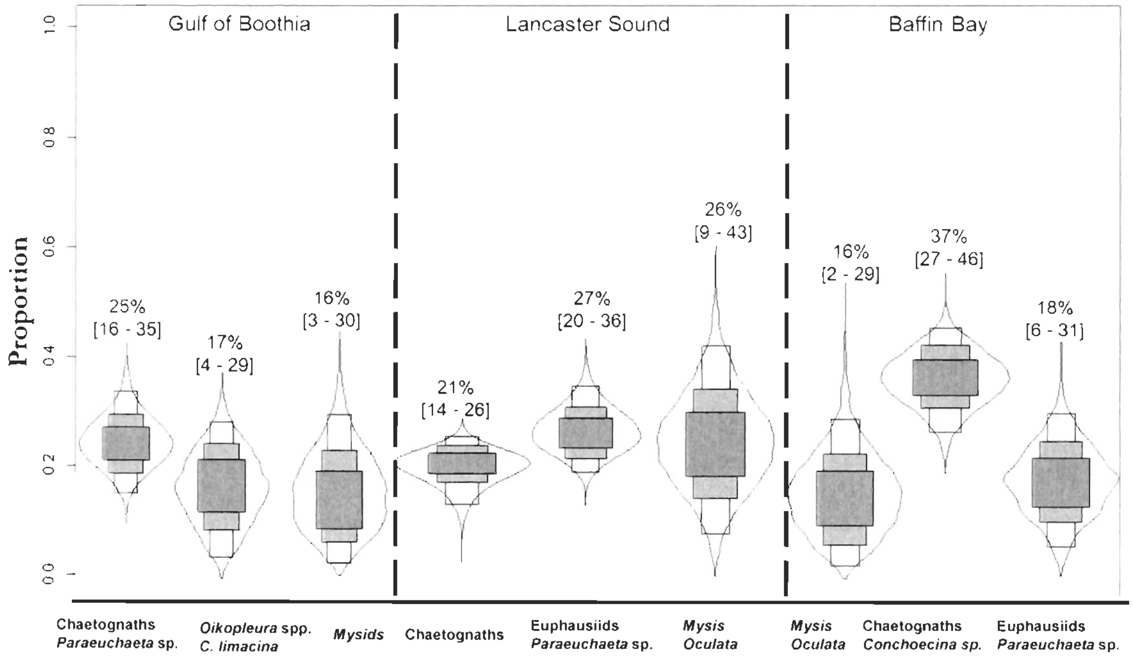


Figure 4. Important prey items (CI 50-75-95%) of bowhead whale group cluster 1

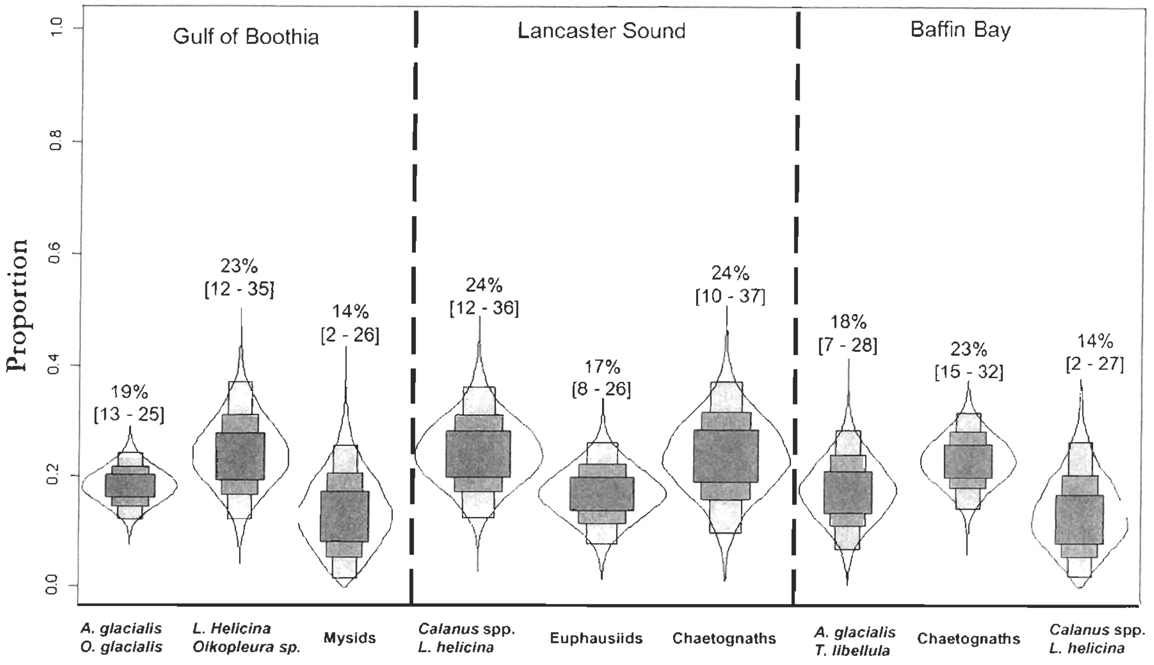


Figure 5. Important prey items (CI 50-75-95%) of bowhead whale cluster group 2

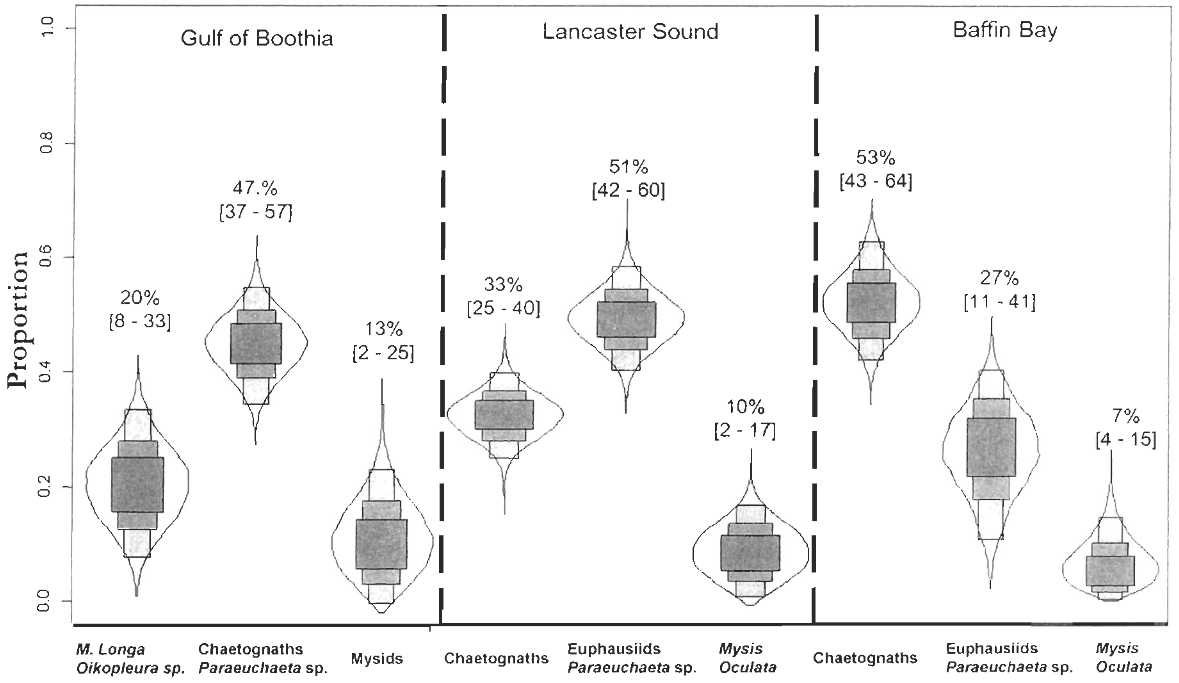


Figure 6. Important prey items (CI 50-75-95%) of bowhead whale cluster group 3

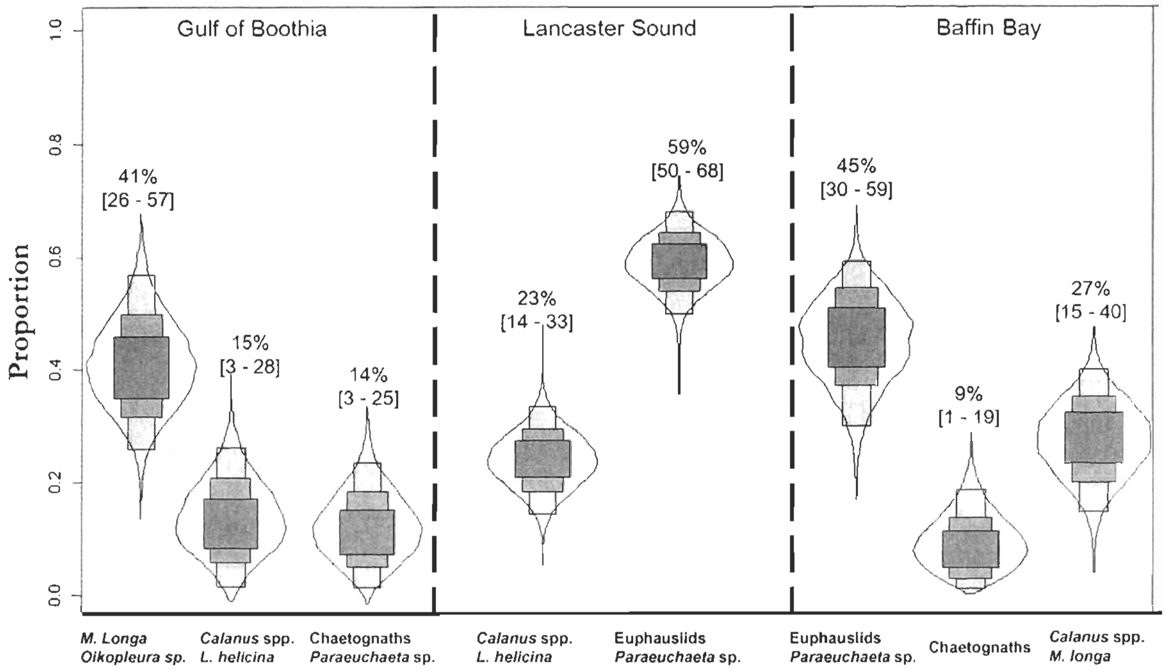


Figure 7. Important prey items (CI 50-75-95%) of bowhead whale cluster group 4

4.6 DISCUSSION

Our study revealed a significant amount of inter-individual diet variability in bowhead whales and indicated that for a given group of animals, targeted prey was mainly the same regardless of the region potentially exploited. The lack of a clear structure in the sample as to sampling sites, age or sex classes, even when natural groupings of individuals were revealed through cluster analysis, suggest that there is no ontogenic shift nor sex differences in diet among the bowhead whales sampled in this study.

Ontogenic shifts in trophic niche are common in animals that exhibit large increases in size throughout their lifetime (Jackson et al. 2004) as predator body size is one of the main factors influencing predator-prey relationships (Peters 1983, Werner & Hall 1988, Persson & Hansson 1999). They have been documented in a number of marine mammal species including killer whales (Newsome et al. 2009), sea lions (Hobson & Sease 1998, Drago et al. 2009, Orr et al. 2011), sperm whales (Mendes et al. 2007) and bottlenose dolphins (Knoff et al. 2008). Considering that the diet of bowhead whales is composed primarily of zooplankton (Finley 2001, Lowry et al. 2004, Pomerleau et al. 2011b), a very small prey relative to the size of the predator, the species might not adhere to this pattern. In bowhead whales from the western Arctic, a greater variability in isotopic signatures over the approximately 15 year record represented by their baleen suggests the use of a wider range of habitat by sub-adults compared to adults (Lee et al. 2005). However, their muscle tissue suggests that both age classes acquire their food largely from the same area (the Bering-Chukchi Sea) and likely similar trophic levels. Thus, our findings for the EC-WG population of exploitation of a similar isotopic niche by sub-adult and adult bowhead whales are consistent with what has been described previously for the species.

Differences in trophic niche between males and females may occur as a result of a significant body size dimorphism between genders, differences in spatial distribution and habitat use and other factors including energy requirements and intra-specific competition (Ruckstuhl & Neuhaus 2005). Bowhead whales exhibit only a small and reversed size dimorphism, with females being slightly larger than males (Koski et al. 1993). Given the similarity in diet documented in many monomorphic species (Michaud 2005), the absence of a difference in isotopic niche between male and female bowhead whales in this study was not totally unexpected. Similar results were obtained for marine mammal species with mild or no sexual dimorphism, including bowhead whales from the western Arctic (Todd et al. 1997, Whiteveen et al. 2009, Hicks et al. 2005, Lawson & Hobson 2000, Lowry et al. 2004, Budge et al. 2008). In bowhead whales of this population, stomach contents of males and females were nearly identical (Lowry et al. 2004) suggesting similar diets among gender class, a result supported by the similarity of the dietary fatty acid composition of their blubber (Budge et al. 2008).

Differences in spatial distribution and habitat use among age and sex classes have been documented in bowhead whales, including the EC-WG population (Cubbage & Calambokidis 1987, Heide-Jørgensen et al. 2010). Baffin Bay and Davis Strait is generally used by adult males and resting or pregnant females from Disko Bay, West Greenland, whereas the Hudson Bay complex, including Prince Regent Inlet and the Gulf of Boothia, is also used by nursing females, calves and sub-adults. During the autumn, bowhead whales either travel southeast from Foxe Basin toward Hudson Strait (Reeves & Mitchell 1990, Ferguson et al. 2010) or move along the east coast of Baffin Island and/or travel towards the West Greenland coast (Reeves et al. 1983). Bowhead whales overwinter in Hudson Strait, Cumberland Sound, West Greenland and the North Water Polynya (Koski et al. 2006, Ferguson et al. 2010, Wiig et al. 2011). Little is known about spring movements, but the lack of difference in isotopic niche among sex and age classes for a period likely representing mostly spring and early summer feeding may indicate a more diffuse spatial structure of age and sex classes at that time when movements between wintering and spring/summer feeding grounds are likely to occur (Heide-Jørgensen et al. 2003, 2006). Mating is thought to occur during late winter (Heide-Jørgensen et al. 2006), suggesting a co-occurrence of adults from both sex classes. The spring migration may be spatially structured, as suggested by observations of bowhead whales in the western Arctic, where sub-adult whales migrate past Point Barrow, Alaska first, and mother-calf groups last (Koski et al. 1993, George et al. 2004). While spring movements of adult males relative to females and sub-adults remain largely undocumented, there is no reason to believe they cannot overlap with those of females and younger individuals. Animals wintering in Hudson Strait could be moving west and north as the ice retreats to reach Foxe Basin in late spring and early summer (Heide-Jørgensen et al. 2010). It is also possible that these animals moved into Foxe Basin from the North via Lancaster Sound, Prince Regent Inlet, the Gulf of Boothia and Fury and Hecla Strait.

Bowhead whales sampled during summer, and mostly in northern Foxe Basin, were unlikely to have used Davis Strait or Disko Bay as a feeding ground in the preceding months, as indicated by the mixing model results, and acknowledging the predominance of one sampling site in our study. The results from the mixing models might have been different if more samples were obtained from other areas such as Disko Bay. Whether bowhead whales sampled in Foxe Basin in summer foraged in Lancaster Sound, Baffin

Bay, the Gulf of Boothia or in other areas in the spring or early summer, the period reflected by the skin isotopic ratios, could not be ascertained. No zooplankton samples were available from Hudson Strait and Foxe Basin, which prevented us from estimating diet composition based on these prey assemblages.

The cluster analysis identified isotopically distinct groups among the bowhead whales, which indicate variability in diet among individuals within the population. The similarities observed in diet composition for a given bowhead whale group, regardless of the biogeographic region against which it was evaluated, suggest that differences in diet composition among groups of bowhead whales were unlikely driven by the region exploited, but more by a preference of each of these groups for specific sets of prey species. This inter-individual variability was also unlikely related to the timing of sampling and thus, period reflected by the sampled tissue, given that the vast majority of the whales were sampled in late summer (July-August). It was also not related to sampling site given that diet was similar for a given group regardless of the area considered as a feeding ground.

Since the years of prey collection (2007–2009) did not always corresponded to those of bowhead whales (1994-2009), the observed group differences in diet should be interpreted with caution. Differences in $\delta^{15}N$ among the four clusters may result from regional difference at the base of the food web (Post 2002). Spatial and temporal variations in primary producers strongly depend on differences in productivity, including nitrogen sources, and may influence the isotopic values in consumers (Montoya 2007, Aurioles-Gamboa et al. 2009). Thus, variability in $\delta^{15}N$ is derived from diet but is also influenced by foraging locations. Future studies should include concurrent sampling of primary producers and zooplankton.

Bowhead whales relied exclusively on zooplankton, and on a limited number of these species, and thus had a relatively restricted or specialized diet compared to some pinnipeds or odontocetes consuming tens of different species (Lawson & Hobson 2000, Loseto et al. 2008). The range of potential diet solutions and estimations of zooplankton species contributions generated by the mixing models generally concur with the results from the small number of studies on bowhead whale diet in the Eastern Arctic (Finley 1993; Finley et al. 2001; Pomerleau et al. 2011b). This, combined with the variability in diet composition among groups of whales, suggests that bowhead whales as a population, although relatively specialized on zooplankton, may be considered generalists of Type B, i.e., groups of bowhead whales feed out of a subgroup of zooplankton species. This is in opposition to Type A generalist where all individuals exploit the same set of prey, and to specialist populations where all individuals eat the same and reduced number of prey (Bearhop et al. 2004). The different prey assemblages and prey proportions of each group may be influenced by prey availability and abundance. Predators may feed randomly on the most abundant prey in their environment or exert selective feeding on a certain aggregation of preys despite their abundance (MacLeod et al. 2006). Some of the variations found between groups of bowhead whales may be a sign of individual and persistent specialization, a known mechanism of intra-population variation (Roughgarden 1972, Bolnick et al. 2003). However, it was not possible in this study to examine the degree of temporal specialization of individual whales given the absence of longitudinal records for each whale.

Bowhead whales are adapted to the extreme seasonal variability in sea ice cover and associated productivity, but they may be impaired by ongoing climate warming (Neibauer & Schell 1993). Results from this study indicate that bowhead whales specialize on zooplankton, relying generally on large arctic calanoid copepods (*C. hyperboreus, C. glacialis, M. longa* and *Paraeuchaeta* spp.), mysids and euphausids, with some degree of flexibility in the species consumed within this group. One group of bowhead whales depended largely on sea ice plankton species. Zooplankton community composition and abundance are tightly coupled with water mass characteristics, thus highly influenced by changes in water temperature and salinity and freshwater/sea ice melt water inputs (Hagen & Auel 2001, Fetzer et al. 2002, Beaugrand et al. 2002). The Arctic sea ice has been drastically decreasing over the last decade and this trend may lead to ice-free summers in the Arctic within 20 years (Perovich & Richter-Menge 2009). The arctic food web is characterized by key ice-covered adapted species driving a lipid rich system (Falk-Petersen et al. 2007), where *Calanus spp.* likely play an important role. Changes in sea ice regimes will impact the timing of bloom events, which are tightly linked with the reproductive cycles of *Calanus* spp. (Kattner & Hagen 2009), including the two species (*C. glacialis* and *C. hyperboreus*) that are important prey of bowhead whales. Along with another prey, the ice amphipods, they have large amounts of lipids and are known to feed under the sea ice (Runge & Ingram 1991). The warming of the Arctic is expected to favor smaller and leaner zooplankton species from more temperate water, thus changing the lipid flux within the food web. Two groups of bowhead whales consumed the arctic pteropod *Limacina helicina*. By the end of this century, *L. helicina* may have disappeared as a result of ocean acidification (Comeau et al. 2011). Bowhead whales, as zooplankton specialists, will have to cope with potentially large spatio-temporal changes in productivity and associated prey assemblages.

4.7 CONCLUSION

Dietary information from the model results provided new insights in diet and potential foraging grounds of bowhead whales from the EC-WG population during summer in the Canadian Arctic. Our study established that diet of bowhead whales varied among groups of individuals, and that for a given group, targeted prey were largely the same regardless of the region exploited. Modeled diets infer the existence of regional differences in prey selection as each whale group exhibited preferences in prey species. The model results from this study may not apply to the entire EC-WG bowhead whale population and reflects spring and early summer feeding behaviour and diet. Thus, further investigation of the seasonal variation of stable isotope ratios in bowhead whale skin sample, especially in fall, winter and early spring, will improve our understanding of the feeding ecology of this species throughout the year.

Sea-ice habitat loss together with increase in predation exposure and increased competition for food resources through migration of non-Arctic baleen whales species within their range as a result of longer ice-free summers may leave them vulnerable to forthcoming environmental changes (ICES 2008). Bowhead whales encounter different water masses and associated prey assemblages in their summer range (Pomerleau et al. 2011c). Results indicate that Lancaster Sound, the Gulf of Boothia and Baffin Bay may constitute spring and early summer feeding grounds, although their importance relative to other potential feeding sites such as Hudson Strait or Foxe Basin could not be ascertained. Bowhead whales from all four groups relied to some extent on large arctic calanoid copepods species (e.g., *C. hyperboreus, C. glacialis, M. longa* and *Paraeuchaeta* spp.). The continuous warming trend in the Arctic may cause the replacement of the larger arctic copepods *C. glacialis* and *C. hyperboreus* by the smaller and leaner *C. finmarchicus* (Beaugrand et al. 2002, 2009). Smaller calanoid copepods from more temperate (*C. helgolandicus*) and boreal waters (*C. finmarchicus*) are mostly limited to Davis Strait with scarce abundance in the Canadian Arctic (*C. finmarchicus*). How these smaller and less lipid-rich species will expand their range into that of bowhead whales and whether the latter can adapt to the shift in distribution or disappearance of Arctic prey species is uncertain and needs to be monitored.

4.8 ACKNOWLEDGEMENTS

Funding was provided by C3O, CFL, and GWAMM – Canadian International Polar Year projects as well as Nunavut Wildlife Research Trust Fund, Fisheries and Oceans Canada, UQAR, and a Weston Garfield scholarship to CP. We thank the officers and crew of the CCGS Louis S. St-Laurent and CCGS DesGroseilliers for all of their support during the scientific missions. We also thank hunters from the following communities for their help during whale biopsy field campaigns: Arctic Bay, Igloolik, Pangnirtung, Kangirsujuaq, Hall Beach, Pelly Bay, Repulse Bay, Cape Dorset and Coral Harbour. We also thank B. Leblanc and L. Dueck for collecting biopsies.

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CHAPITRE 5

ESTIMATION DE LA DIETE DE LA BALEINE BORÉALE (*BALAENA MYSTICETUS*) DANS L'ARCTIQUE DE L'EST CANADIEN A PARTIR DE LA COMPOSITION EN ACIDES GRAS DU TISSU ADIPEUX SOUS-CUTANÉ

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En révision dans *Arctic* (Novembre 2012)

5.1 RÉSUMÉ

La population de baleine boréale (*Balaena mysticetus*) de l'est du Canada et de l'ouest du Groenland (EC-WG) se remet lentement de la chasse commerciale intensive. Cependant, les effets des changements climatiques sur la glace de mer et la disponibilité des proies pourraient affecter le rétablissement de la baleine boréale. Afin d'approfondir les connaissances sur la diète et l'écologie alimentaire de la baleine boréale de la population EC-WG, nous avons examiné la composition en acides gras de la couche de graisse sous-cutanée d'animaux échantillonnés durant les étés 2008 et 2009. Les baleines boréales étaient riches en certains acides gras (AG) notamment; 14:0, 16:0, 16:1n-7, 18:0, 18:1n-11, 18:1n-9, 18:1n-7, 20:1n-11, 20:1n-9, 20:1n-7, 20:5n-3, 22:1n-11, 22:1n-9, 22:5n-3 et 22:6n-3. Ces 15 acides gras constituaient 91% de tous les acides gras identifiés. Nous avons identifié cinq groupes de baleines en utilisant les scores des facteurs d'une analyse composée principale dans une analyse de fonction discriminante. Les acides gras Oméga-3 polyinsaturés (PUFAs) (20:5n-3, 22:5n-3 et 22:6n-3), ainsi que les acides gras monoinsaturés à longue chaîne (MUFAs) (20:1n-9, 20:1n-11, 22:1n-9 et 22:1n-11) étaient responsables de la majorité de la variance entre les cinq groupes de baleines. Les groupes 1, 3 et 5 étaient caractérisés par de fortes abondances de MUFAs à longue chaîne (C20 et C22), tandis que les groupes 2 et 4 avaient de grandes quantités de 16:1n-7, 18:1n-9 ainsi que de PUFAs. Les résultats d'une analyse de variance multiple ont révélé qu'il n'y avait pas de différences significatives dans la composition en acides gras des mâles et des femelles, ce qui suggère qu'ils ont une diète similaire. Les copépodes calanoides semblent être une proie majeure des baleines boréales inclus dans cette étude, et ce résultat corrobore des résultats précédents (contenus stomacaux et isotopes stables) sur la diète de cette population de baleines boréales. Les biomasses de copépodes calanoides pourraient être compromises dans l'Arctique et diminuer en réponse aux changements climatiques soutenus dans cette région du globe. Il est incertain si les espèces spécialistes de l'Arctique, telles que la baleine boréale, va réussir à s'adapter aux nombreux changements survenant

Mots clés: Arctique; acides gras; baleine boréale; *Balaena mysticetus*; couche de graisse; copépodes calanoides; diète; écologie alimentaire; lipides; zooplancton

Ce dernier article, intitulé « *Estimating diet of bowhead whales (Balaena mysticetus) from the Eastern Canadian Arctic waters using blubber fatty acid composition* », fut corédigé par moi-même ainsi que par mes deux co-directrices, Véronique Lesage et Gesche Winkler, Bruno Rosenberg et mon directeur Steven H. Ferguson. Il fut soumis le 18 juillet 2012 à la revue *Polar Biology* et est présentement en révision. En tant que premier auteur, ma contribution à ce travail fut une partie des collectes de données sur le terrain et des analyses en laboratoire, les analyses statistiques ainsi que la rédaction de l'article. Véronique Lesage a fourni plusieurs commentaires quant à l'écriture de l'article de même que Gesche Winkler, troisième auteur. Le quatrième auteur, Bruno Rosenberg à effectué la majorité des analyses des acides gras en laboratoire et le dernier auteur, Steven Ferguson, a dirigé le projet de recherche.

5.2 ABSTRACT

The Eastern Canada – West Greenland (EC–WG) bowhead whale (*Balaena mysticetus*) population is slowly recovering from intensive commercial whaling. However, climate change, through its effects on ice conditions and prey availability, might affect bowhead whale recovery. Diet and feeding ecology of EC–WG bowhead whales (Balaena mysticetus) were examined using fatty acid composition of the outer blubber layer of animals sampled during the summers of 2008 and 2009. Bowhead blubber was rich in the following fatty acids (FAs): 14:0, 16:0, 16:1n-7, 18:0, 18:1n-11, 18:1n-9, 18:1n-7, 20:1n-11, 20:1n-9, 20:1n-7, 20:5n-3, 22:1n-11, 22:1n-9, 22:5n-3 and 22:6n-3, that together accounted for 91% of total fatty acids identified. Using principal components factor scores as input variables into a discriminant function analysis resulted in the identification of five groups of whales. Omega-3 polyunsaturated fatty acids (PUFA) (20:5n-3, 22:5n-3 and 22:6n-3) together with long-chain monounsaturated fatty acids (MUFA) (20:1n-9, 20:1n-11, 22:1n-9 and 22:1n-11) accounted for most of the variance among the five whale groups. Groups 1, 3 and 5 were characterized by very high levels of long-chain C20 and C22 MUFAs, whereas Groups 2 and 4 had high amounts of 16:1n-7, 18:1n-9 and the PUFAs. A multivariate analysis of variance revealed no significant difference in fatty acid composition between gender, which suggests that males and females have a similar diet. Calanoid copepods were likely a major prey item for these bowheads whales, a result which is coherent with dietary conclusions reached from stable isotope and stomach content analysis for this population. Calanoid copepods biomasses are expected to decline in the Arctic as a result of climate change. How specialist feeders such as bowhead whales will adapt to these changes is unknown and warrant close monitoring.

Keywords: Arctic, Bowhead whale, *Balaena mysticetus*, Blubber, Calanoid copepods, Diet, Fatty acids, Feeding ecology, Lipids, Zooplankton

5.3 INTRODUCTION

The bowhead whale occurs in two separate populations in the Canadian Arctic: the Bering–Chukchi–Beaufort (BCB) and the Eastern Canada–West Greenland (EC–WG) population (Nowak 2003). The EC–WG bowhead whale (*Balaena mysticetus*) population is slowly recovering from intensive commercial whaling of the 16th to 20th centuries. However, climate change, through its effects on ice conditions and prey availability, might affect bowhead whale recovery. The lack of understanding of their foraging ecology, feeding behaviour and diet hampers our ability to predict how ongoing changes in the environment might affect this species, which is endemic to the Arctic.

Diet of the EC–WG population has been inferred from short-term, indirect and qualitative approaches such as observation of surface feeding, stomach content analysis, plankton net sampling and dive data (Finley 2001; Lowry et al. 2004; Lee et al. 2005; Laidre et al. 2007; Pomerleau et al. 2011a). Bowhead whales are specialist feeders on zooplankton, but the specific prey they actually consume in the eastern Arctic are largely unknown. Diet of the BCB bowhead whale population has been characterized previously using stable isotopes, stomach contents, and more recently using fatty acids to complement the other approaches (Lee et al. 2005, Budge et al. 2008). Similar insights into the feeding ecology and diet of EC–WG bowhead whales could be gained from these techniques, especially if used in complement to one another.

Fatty acids (FAs) can be used both qualitatively and quantitatively to infer diet ecology of free-ranging predators (Iverson 2008). While some FAs can be used as markers for ingestion of specific prey, it is often the relative abundance of the various long-chain FAs that is used to infer predator-prey relationships and food web structure (Iverson et al. 1997; Dahl et al. 2000; Hooker et al. 2001; Best et al. 2003; Dalsgaard et al. 2003, Iverson et al. 2004, Thiemann et al. 2008). However, particularly specific long-chain FAs (PUFAs), biosynthesized by primary producers (Sargent et al. 1987) are transferred in a relatively conservative way to consumers (Dalsgaard et al. 2003). This characteristic makes it possible to qualitatively determine the reliance of higher trophic level consumers on food webs originating from various microalgal groups (Lee et al. 2006). For instance, the FAs 20:5n-3 and 22:6n-3 are a diatom and a dinoflagellate marker, respectively (Kates and Volcani 1966; Yin et al. 2000; Graeve 1993). Similarly, the abundance of long chain monounsaturated FAs (MUFAs) of 20:1 and 22:1 FAs in marine food webs are formed de novo by biosynthesis in calanoid copepods (Kattner and Hagen 1995) and thus, can be used to ascertain dependency on this taxon, either by direct consumption of copepods or consumption of their predators.

Blubber in marine mammals is a dynamic tissue that serves several functions, including insulation and fat storage (Iverson et al. 1995). Marine mammal blubber reflects the diet composition and dietary intake of prey over a period of weeks to months (Iverson 1995; Iverson et al. 2004). Vertical stratification of FAs in the blubber layer of marine mammals has been documented in pinnipeds (Best et al. 2003; Thiemann et al. 2004) as well as cetaceans (Thiemann et al. 2008; Strandberg et al. 2008), although the degree of stratification appears to be less in larger cetaceans (Hooker et al. 2001, Koopman et al. 2007). In general, the outer layer is composed of a larger proportion of biosynthesized components and MUFA less than 18 carbons in length compared to the inner blubber layer, the most metabolically active layer. In counterpart, MUFA greater than 18 carbons in length, as well as non-branched saturated FA (SFA) and many PUFAs are found in higher amounts in the inner layer (Koopman et al. 1996; Smith and Worthy 2006). In bowhead whales, the FA composition of the inner and outer layers differ, but the extent of the stratification is relatively small (Budge et al. 2008) and makes general inferences about diet possible based on the outer layer alone (Budge et al. 2008).

The objectives of this study was to gain insights into the feeding ecology and diet of EC–WG bowhead whales, including inter-individual and inter-class variability, from examination of FA composition of their blubber outer layer, and comparisons with dietary inferences made using other dietary techniques.

5.4 METHODS

5.4.1 Study area and sample collection.

Bowhead whale blubber samples (n = 51) were collected in July–September of 2008 (n = 7) and 2009 (n = 44) at five locations within the known summer range of the EC–WG bowhead whale population in the Eastern Canadian Arctic (Figure 1; Table 1). The vast majority of the samples came from northern Foxe Basin (n = 39). Blubber samples consisted in the outer layer and were obtained from live individuals using a crossbow darting system (n= 45) (Brown et al. 1991), or from dead carcasses through subsistence harvests (n = 6). Outer blubber layer was measured from the skin (skin not included) and blubber samples were on average 1 cm thick. All samples were preserved frozen in liquid nitrogen until lipid analysis.

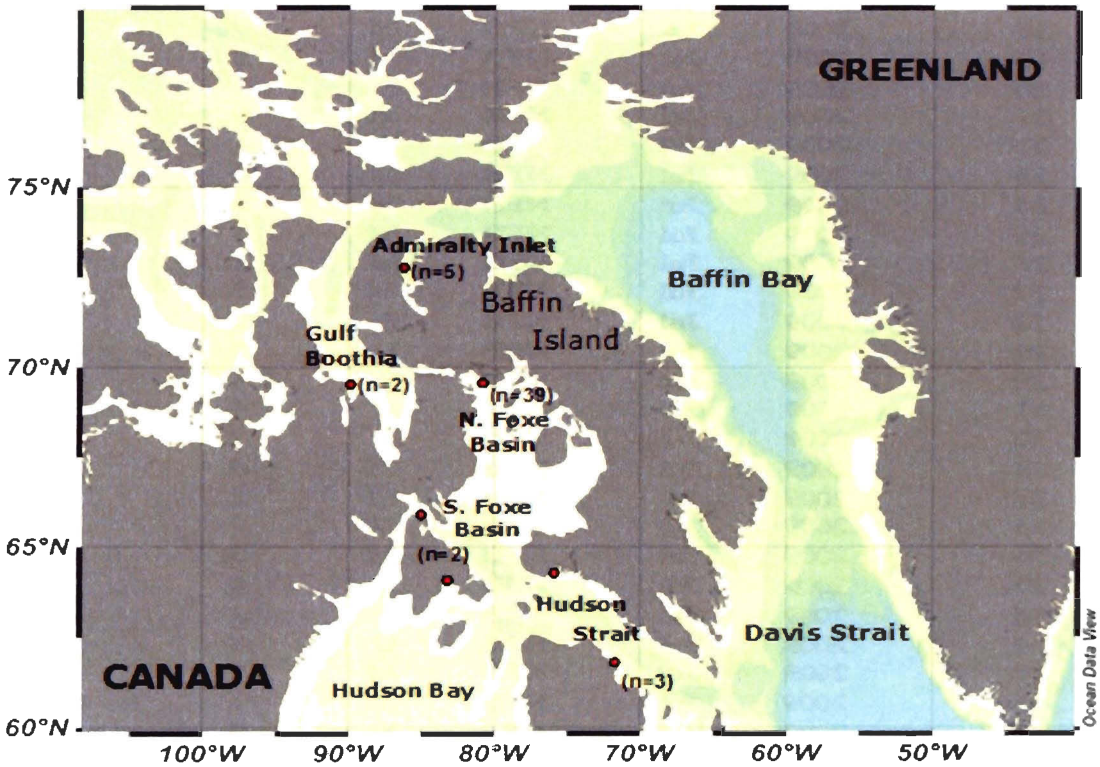
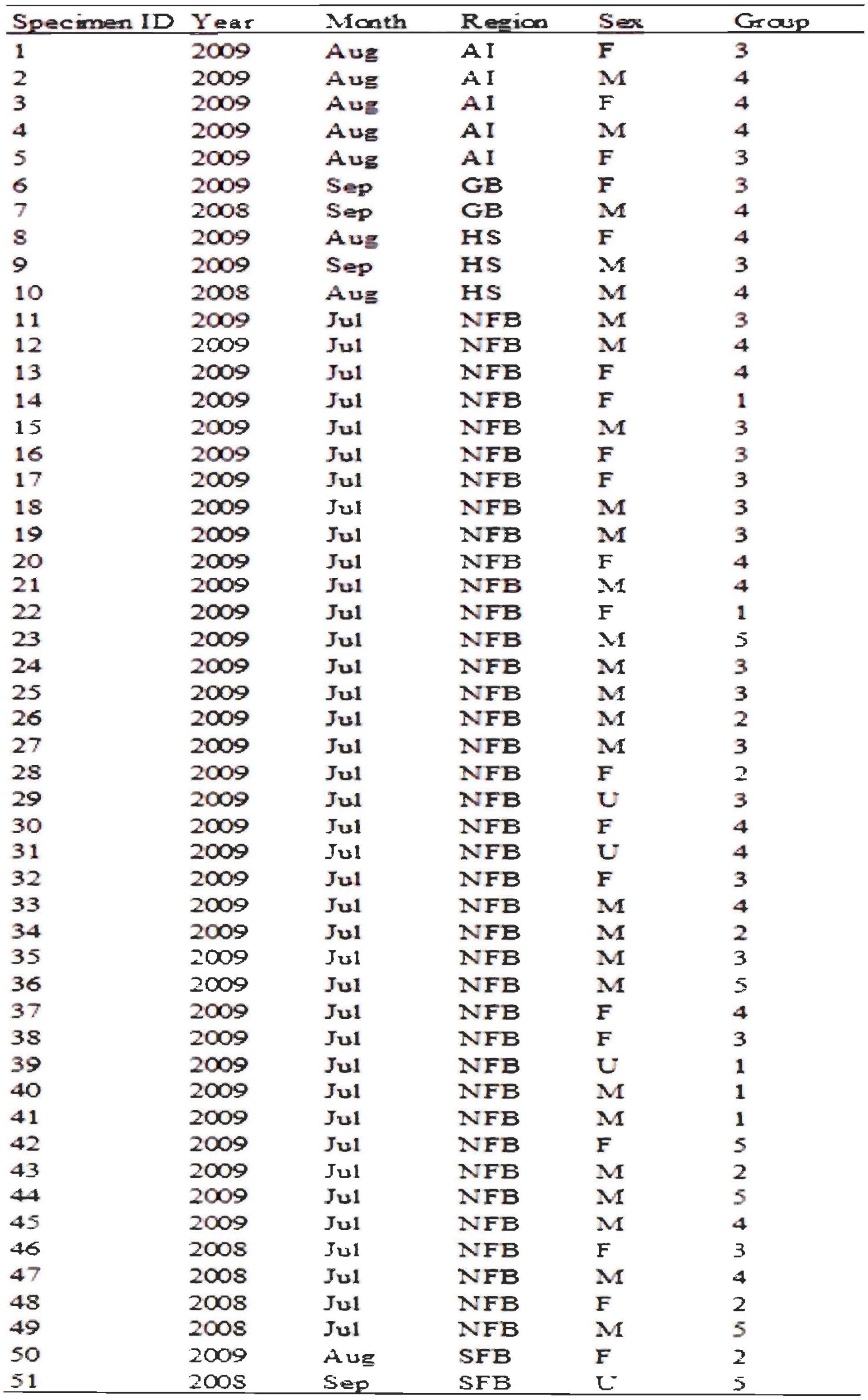


Figure 1. Bowhead whale sampling locations in the eastern Canadian Arctic including the following five regions; Northern Foxe Basin (NFB), Southern Foxe Basin (SFB), Admiralty Inlet (AI), Gulf Boothia (GB) and Hudson Strait (HS).

Table 1. Specimen data including bowhead whale ID, year, month collected and geographical region of sampling collection; Northern Foxe Basin (NFB), Southern Foxe Basin (SFB), Admiralty Inlet (AI), Gulf Boothia (GB) and Hudson Strait (HS) (See Figure 1). Groups are identified by the DAPC analysis (See Figure 3).



Specimen ID	Year	Month	Region	Sex	Group
1	2009	Aug	AI	F	3
2	2009	Aug	AI	M	4
3	2009	Aug	AI	F	4
4	2009	Aug	AI	M	4
5	2009	Aug	AI	F	3
6	2009	Sep	GB	F	3
7	2008	Sep	GB	M	4
8	2009	Aug	HS	F	4
9	2009	Sep	HS	M	3
10	2008	Aug	HS	M	4
11	2009	Jul	NFB	M	3
12	2009	Jul	NFB	M	4
13	2009	Jul	NFB	F	4
14	2009	Jul	NFB	F	1
15	2009	Jul	NFB	M	3
16	2009	Jul	NFB	F	3
17	2009	Jul	NFB	F	3
18	2009	Jul	NFB	M	3
19	2009	Jul	NFB	M	3
20	2009	Jul	NFB	F	4
21	2009	Jul	NFB	M	4
22	2009	Jul	NFB	F	1
23	2009	Jul	NFB	M	5
24	2009	Jul	NFB	M	3
25	2009	Jul	NFB	M	3
26	2009	Jul	NFB	M	2
27	2009	Jul	NFB	M	3
28	2009	Jul	NFB	F	2
29	2009	Jul	NFB	U	3
30	2009	Jul	NFB	F	4
31	2009	Jul	NFB	U	4
32	2009	Jul	NFB	F	3
33	2009	Jul	NFB	M	4
34	2009	Jul	NFB	M	2
35	2009	Jul	NFB	M	3
36	2009	Jul	NFB	M	5
37	2009	Jul	NFB	F	4
38	2009	Jul	NFB	F	3
39	2009	Jul	NFB	U	1
40	2009	Jul	NFB	M	1
41	2009	Jul	NFB	M	1
42	2009	Jul	NFB	F	5
43	2009	Jul	NFB	M	2
44	2009	Jul	NFB	M	5
45	2009	Jul	NFB	M	4
46	2008	Jul	NFB	F	3
47	2008	Jul	NFB	M	4
48	2008	Jul	NFB	F	2
49	2008	Jul	NFB	M	5
50	2009	Aug	SFB	F	2
51	2008	Sep	SFB	U	5

5.4.2 Fatty acid extraction.

Lipids were extracted from 0.5 g of the outer blubber layer of bowhead whales with 2:1 chloroform-methanol containing 0.01% butylated hydroxytoluene (BHT) (v/v/w) (Folch et al., 1957). The lipid phase was collected, washed, and filtered through anhydrous sodium sulphate and evaporated under nitrogen to obtain the total lipid weight. Extracted lipids were used to prepare the fatty acid methyl esters (FAME) by transesterification with Hilditch reagent (0.5 N H2SO4 in methanol). Samples were heated for 1 h at 100 °C. Gas chromatographic (GC) analyses were performed with an Agilent Technologies 6890N GC equipped with a 30 m J&W DB-23 column (0.25 mm I.D; 0.25 μm film thickness). The GC was coupled to an Agilent 5973 Mass Selective Detector (MSD) running in Electron Ionization/Selected Ion Monitoring (EI/SIM) mode. Helium was the carrier gas and flow was 0.7 ml min-1. The split/splitless injector was heated to 250 °C and run in splitless mode. Peaks were quantified with Agilent Technologies ChemStation software following the method developed by Thurnhofer and Vetter (2005). Saturated FAs were quantified using ion 87 with 74 as the qualifying ion. Monoenoic (one double bond) FAs were quantified using 74 with 87 as the qualifier and polyenoic (2 or more double bonds) FAs were quantified using the sum of ions 79 and 81. Each result was corrected to fullscan mode following Thurnhofer and Vetter (2005). FA standards were obtained from Supelco (37 component FAME mix) and Nuchek (54 component mix GLC-463). Sixty-nine FAME were identified with verification via ion mass spectroscopy and known standard mixtures and are reported as percent weight of total FA. The shorthand nomenclature of A:Bn-X is used to describe each FA, with A representing the number of carbon atoms, B the number of double bonds and X the position of the double bond closest to the terminal methyl group.

5.4.3 Statistical analyses.

Statistical analyses were performed using R version 2.14.1 (R Development Core team 2010). Only the most abundant FAs or those known to be associated with diet (Iverson et al. 2004) were used in our analyses. Fifteen FAs (> 1.0 % of total FA content) accounting for ~ 91% of total FAs were retained for statistical analyses: 14:0, 16:0, 16:1n-7, 18:0, 18:1n-11, 18:1n-9, 18:1n-7, 20:1n-11, 20:1n-9, 20:1n-7, 20:5n-3, 22:1n-11, 22:1n-9, 22:5n-3 and 22:6n-3 (Table 2). Values for the retained FAs were first renormalized over 100 %, then proportional FA data were transformed using the centered log ratio transformation (Aitchison 1983; 1986; Budge et al. 2008): xt=log (xi/g(x)), where xi is a given FA expressed as percent of total FA, g(x) is the geometric mean of the FA data for the sample and xt represents the transformed FA data. A discriminant analysis of principal components (DAPC) was performed to identify individuals with similar FA composition. This method aims to identify and describe relationships between groups of observations (Jombart et al. 2010). First, a principal components analysis (PCA) (covariance matrix) was used on the 15 transformed FAs to reduce their number to a set of uncorrelated principal components retaining most of the variance in the original data. The number of clusters best describing our bowhead whale sample, and individual memberships were determined using a k-means cluster analysis and the Bayesian Information Criterion (BIC). The variables analyzed in a DAPC are the principal components of a PCA. The linear combinations of the original 15 FAs best separating the groups identified through the k-means cluster analysis were identified using a linear discriminant function analysis. Genetic data on sex was available for 32 whales sampled in July 2009 in Northern Foxe Basin. Comparisons of FA profiles between males and females were made using a multiple analyse of variance (MANOVA) using all 15 FAs simultaneously.

Table 2. Proportions (mean ± standard deviation) of FAs in bowhead whales from five regions of the Eastern Canadian Arctic (see Figure 1) for 42 FAs contributing > 0.1% in percent weight of total FAs.

	Northern Foxe Basin n=39	Southern Foxe Basin n=2	Gulf Boothia n=2	Hudson Strait n=3	Admiralty Inlet n=5	Average
Saturated						
14:0	3.18 ± 0.35	4.35 ± 0.79	3.35 ± 0.30	3.43 ± 0.44	2.93 ± 0.24	3.22 ± 0.43
14:0 iso	0.09 ± 0.02	0.13 ± 0.00	0.09 ± 0.00	0.10 ± 0.01	0.14 ± 0.06	0.10 ± 0.03
15:0	0.17 ± 0.01	0.21 ± 0.01	0.16 ± 0.01	0.17 ± 0.03	0.17 ± 0.01	0.17 ± 0.02
16:0	5.09 ± 0.52	6.16 ± 0.60	5.03 ± 0.85	4.70 ± 1.04	4.44 ± 0.63	5.04 ± 0.63
18:0	1.12 ± 0.24	1.22 ± 0.33	1.01 ± 0.25	0.73 ± 0.08	0.88 ± 0.31	1.08 ± 0.26
20:0	0.11 ± 0.02	0.10 ± 0.01	0.10 ± 0.01	0.10 ± 0.02	0.12 ± 0.02	0.11 ± 0.02
23:0	0.24 ± 0.06	0.32 ± 0.15	0.34 ± 0.04	0.29 ± 0.06	0.18 ± 0.08	0.24 ± 0.07
Subtotal	9.91 ± 0.17	12.36 ± 0.32	9.99 ± 0.21	9.42 ± 0.23	8.72 ± 0.19	9.96 ± 0.31
Monounsaturated						
14:1n-5	0.63 ± 0.13	1.29 ± 0.13	0.62 ± 0.08	0.67 ± 0.09	0.57 ± 0.07	0.65 ± 0.18
16:1n-11	0.41 ± 0.05	0.17 ± 0.03	0.28 ± 0.03	0.25 ± 0.05	0.51 ± 0.19	0.39 ± 0.10
16:1n-9	0.29 ± 0.04	0.27 ± 0.02	0.25 ± 0.03	0.24 ± 0.01	0.29 ± 0.06	0.28 ± 0.04
16:1n-7	20.02 ± 1.93	24.27 ± 3.60	18.17 ± 0.07	18.59 ± 2.88	18.01 ± 1.19	19.83 ± 2.21
16:1n-5	0.28 ± 0.03	0.31 ± 0.02	0.27 ± 0.00	0.27 ± 0.03	0.25 ± 0.03	0.28 ± 0.03
18:1n-11	4.44 ± 0.56	1.71 ± 0.10	3.72 ± 0.10	3.86 ± 1.25	5.05 ± 0.92	4.33 ± 0.85
18:1n-9	10.67 ± 1.32	13.12 ± 2.53	8.38 ± 0.48	8.87 ± 1.46	9.36 ± 1.19	10.44 ± 1.56
18:1n-7	3.23 ± 0.41	4.35 ± 0.20	3.06 ± 0.14	2.72 ± 0.49	2.68 ± 0.61	3.19 ± 0.51
18:1n-5	0.62 ± 0.06	0.59 ± 0.23	0.60 ± 0.04	0.55 ± 0.04	0.54 ± 0.07	0.60 ± 0.07
20:1n-11	3.64 ± 0.46	1.74 ± 0.04	3.01 ± 0.22	2.84 ± 0.59	4.39 ± 0.90	3.57 ± 0.70
20:1n-9	16.00 ± 1.74	10.37 ± 0.52	15.56 ± 1.50	16.70 ± 3.15	18.44 ± 3.04	16.04 ± 2.32
20:1n-7	1.94 ± 0.21	1.23 ± 0.00	1.80 ± 0.07	1.90 ± 0.27	2.15 ± 0.31	1.93 ± 0.26
22:1n-11	8.91 ± 2.64	5.98 ± 0.16	10.58 ± 2.01	9.67 ± 2.45	11.64 ± 1.72	9.17 ± 2.65
22:1n-9	1.95 ± 0.50	1.35 ± 0.06	2.08 ± 0.37	2.27 ± 0.52	2.64 ± 0.57	2.02 ± 0.54
22:1n-7	0.35 ± 0.10	0.28 ± 0.03	0.44 ± 0.06	0.43 ± 0.10	0.47 ± 0.08	0.37 ± 0.11
24:1n-9	0.10 ± 0.04	0.17 ± 0.04	0.12 ± 0.01	0.12 ± 0.00	0.11 ± 0.02	0.11 ± 0.04
Subtotal	73.48 ± 0.68	67.21 ± 0.48	68.94 ± 0.33	69.95 ± 0.83	77.10 ± 0.73	73.20 ± 0.75
Polyunsaturated						
16:2n-4	0.58 ± 0.06	0.61 ± 0.09	0.68 ± 0.02	0.61 ± 0.01	0.51 ± 0.08	0.58 ± 0.06
16:3n-4	0.18 ± 0.02	0.26 ± 0.07	0.25 ± 0.01	0.23 ± 0.04	0.18 ± 0.02	0.19 ± 0.03
16:4n-3	0.11 ± 0.02	0.09 ± 0.00	0.10 ± 0.03	0.06 ± 0.01	0.09 ± 0.03	0.11 ± 0.02
16:4n-1	0.30 ± 0.06	0.53 ± 0.16	0.51 ± 0.01	0.41 ± 0.07	0.28 ± 0.06	0.32 ± 0.09
18:2n-6	0.86 ± 0.14	1.19 ± 0.15	0.80 ± 0.08	0.97 ± 0.24	0.67 ± 0.06	0.86 ± 0.16
18:2n-4	0.12 ± 0.02	0.17 ± 0.06	0.14 ± 0.00	0.11 ± 0.02	0.10 ± 0.04	0.12 ± 0.03
18:3n-6	0.13 ± 0.02	0.15 ± 0.01	0.15 ± 0.00	0.17 ± 0.01	0.12 ± 0.02	0.14 ± 0.02
18:3n-4	0.16 ± 0.05	0.18 ± 0.07	0.22 ± 0.03	0.19 ± 0.08	0.11 ± 0.06	0.16 ± 0.05
18:3n-3	0.32 ± 0.05	0.28 ± 0.08	0.34 ± 0.03	0.31 ± 0.04	0.28 ± 0.07	0.32 ± 0.05
18:4n-3	0.72 ± 0.14	0.94 ± 0.32	1.08 ± 0.00	1.05 ± 0.18	0.67 ± 0.18	0.76 ± 0.18
18:4n-1	0.43 ± 0.11	0.42 ± 0.14	0.62 ± 0.09	0.42 ± 0.16	0.32 ± 0.20	0.43 ± 0.13
20:2n-9	0.12 ± 0.01	0.10 ± 0.03	0.12 ± 0.01	0.11 ± 0.02	0.12 ± 0.01	0.12 ± 0.01
20:2n-6	0.17 ± 0.03	0.18 ± 0.01	0.14 ± 0.04	0.15 ± 0.03	0.12 ± 0.02	0.16 ± 0.03
20:3n-6	0.12 ± 0.01	0.13 ± 0.02	0.13 ± 0.01	0.15 ± 0.00	0.13 ± 0.02	0.13 ± 0.02
20:4n-6	0.29 ± 0.04	0.30 ± 0.09	0.24 ± 0.01	0.26 ± 0.02	0.27 ± 0.05	0.28 ± 0.04
20:4n-3	0.41 ± 0.11	0.44 ± 0.08	0.59 ± 0.04	0.57 ± 0.16	0.36 ± 0.16	0.42 ± 0.12
20:5n-3	5.49 ± 0.11	7.32 ± 1.35	7.83 ± 0.60	7.84 ± 1.33	4.69 ± 1.65	5.71 ± 1.40
22:5n-3	1.95 ± 0.44	2.15 ± 0.59	2.38 ± 0.14	2.04 ± 0.48	1.51 ± 0.86	1.94 ± 0.50
22:6n-3	3.07 ± 0.63	3.79 ± 1.32	3.72 ± 0.50	3.79 ± 0.37	2.61 ± 0.86	3.12 ± 0.70
Subtotal	15.53 ± 0.15	19.23 ± 0.24	20.04 ± 0.09	19.44 ± 0.17	13.13 ± 0.22	15.87 ± 0.23
Total	99.00 ± 0.20	98.89 ± 0.12	99.08 ± 0.07	98.89 ± 0.18	99.11 ± 0.09	99.03 ± 0.18

5.5 RESULTS

A total of 69 FAMEs were identified from the outer blubber layer of bowhead whales. The 42 most abundant FAs (> 0.1%) are presented for each of the five regions (Table 2). Generally, MUFAs were the most abundant with an average of 71.4 ± 3.9 % of the total FA content. The most abundant MUFAs were 16:1n-7, 20:1n-9, 18:1n-9 and 22:1n-11. PUFAs comprised 17.5 ± 3.0 % of the total FA content and were dominated by 20:5n-3, 22:6n-3 and 22:5n-3. SFAs were the least abundant class of FAs, with an average of 10.1 ± 0.4 % of total FA content, and 14:0, 16:0 and 18:0 as the dominant SFAs.

Regional patterns in FA composition could not be investigated given the small sample size for all regions, except northern Foxe Basin. A PCA reduced the 15 FAs to three uncorrelated PCs retaining 89% of the total variance (Figure 2; Table 3).The first PC separated individuals largely on the basis of their content in 22:5n-3, 18:0, and 20:5n-3, which were negatively but strongly correlated with content in 22:1n-11, 22:1n-9 and 20:1n-9. FAs strongly correlated with PC2 included 18:1n-11, 20:1n-11 and 18:0 (positive correlation) and 22:1n-11, 14:0 and 22:1n-9 (negative correlation). Finally, 22:6n-3, 20:5n-3, 22:5n-3 were positively correlated with PC3, whereas 18:1n-9, 16:1n-7, 18:1n-7 were negatively correlated with this factor.

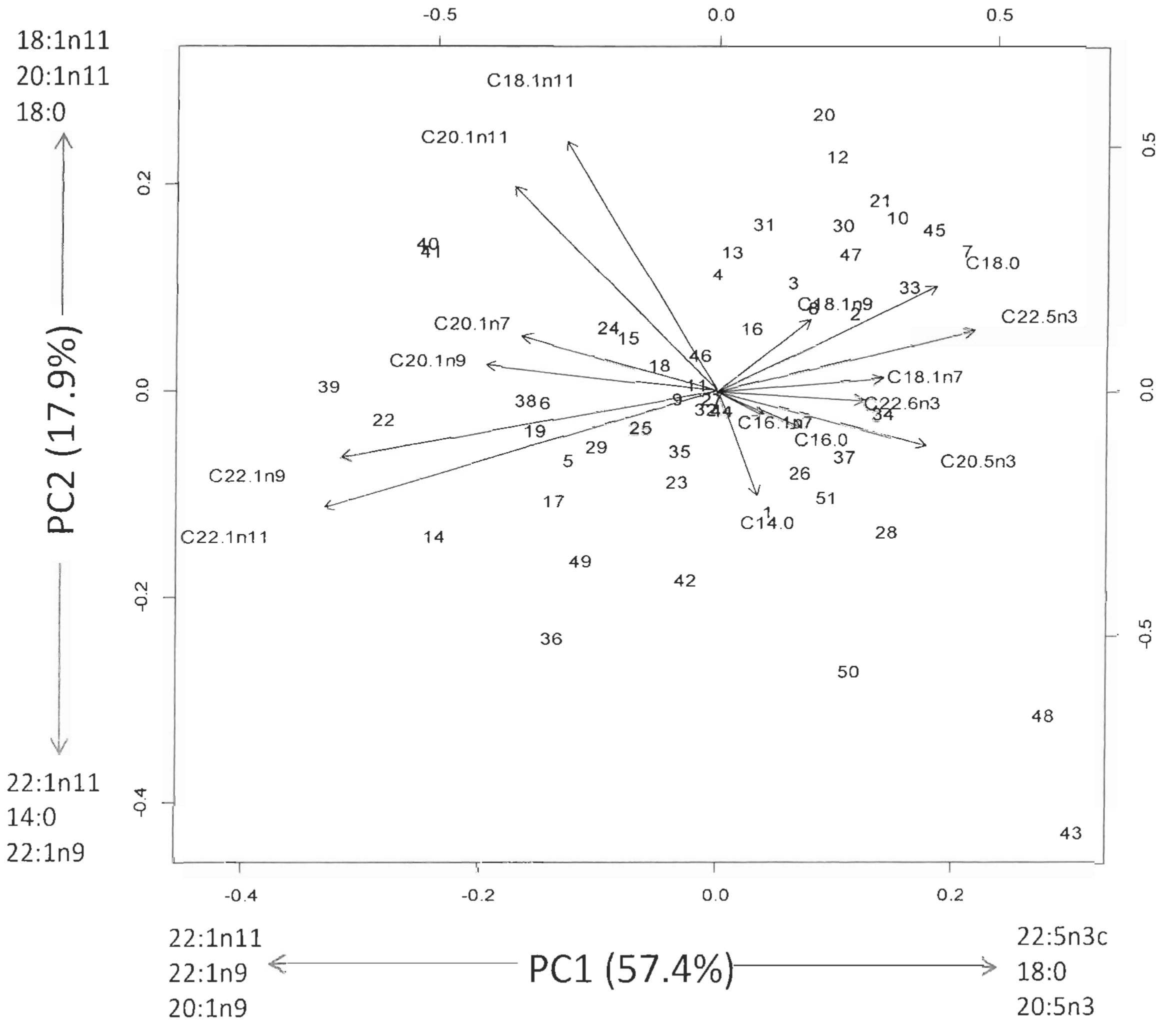


Figure 2. Biplot of the first and second PC derived from the 15 FAs (see Table 3) of individual bowhead whales (n=51). PC1 explained 57.4 % of the variability among individuals. PC2 explained 17.9% of the variability. Arrows indicate FAs contributing most of the variation affecting the distribution of individuals along each principle component

Table 3. Summary of the key variables contributing to the first three principal components of the principal component analysis of the 15 FAs (see Figure 2) in 51 whales.

PC	Loading	Variable	Proportion of variance (%)	Cumulative variance (%)
PC1	+	22:5n-3, 18:0, 20:5n-3	57.4	57.4
	-	22:1n-11, 22:1n-9, 20:1-n9		
PC2	+	18:1n-11, 20:1n-11, 18:0	17.9	75.3
	-	22:1n-11, 14:0, 22:1n-9		
PC3	+	22:6n-3, 20:5n-3, 22:5n-3	13.4	88.7
	-	18:1n-9, 16:1n-7, 18:1n-7		

Five distinct groups of bowhead whales, composed of an approximately equal number of males and females, were identified using PC scores in a k-means cluster analysis (Table 1, Figure 3). All individuals of Group 1 (n = 5), Group 2 (n = 6), and Group 5 (n = 6) were sampled in the northern Foxe Basin. Group 3 encompassed 18 individuals with 14 from northern Foxe Basin, two from Admiralty Inlet, one from the Gulf Boothia and one from Hudson Strait. Group 4 was similar in size to Group 3 (n = 16) and included three whales from Admiralty Inlet and two from Hudson Strait. None of the groups was clearly biased towards one particular sex, except for Group 5 which comprised a larger number of males than females (4 males and 1 female). The lack of difference in FA composition between males and females was confirmed through a MANOVA (Pillai = 0.627, F = 1.79, p = 0.1295).

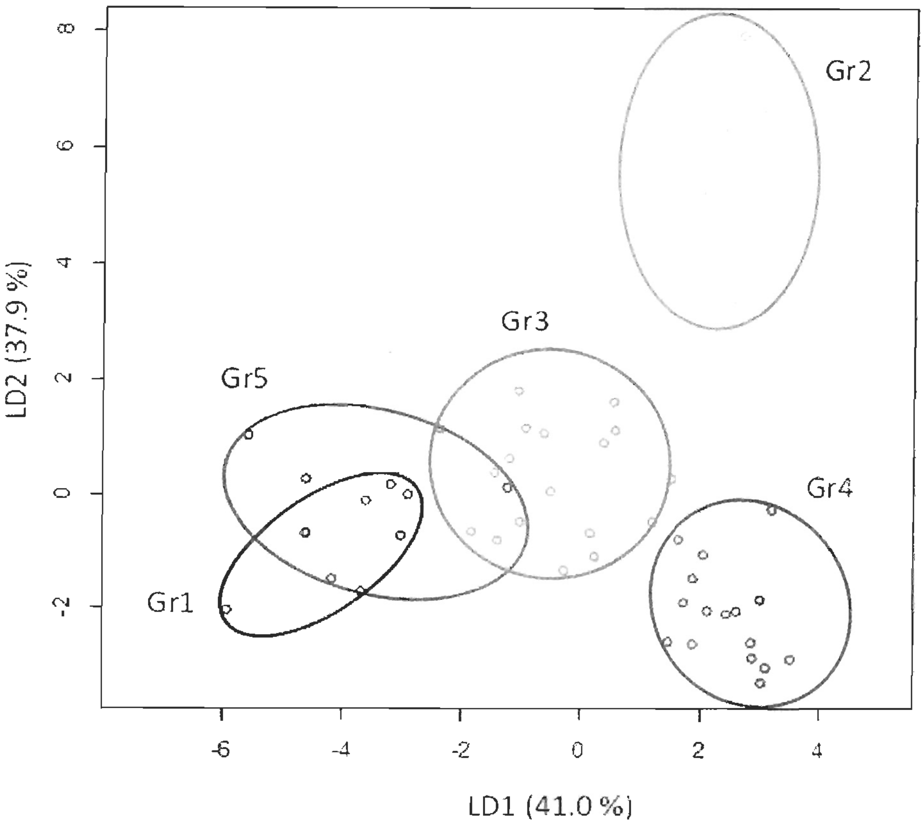


Figure 3. Discriminant analysis of principle component using the most abundant 15 FAs identifying five groups of bowhead whales (see Table 3). Scatterplot shows the first 2 of 15 discriminant functions explaining 78.9% of the variance.

The first three discriminant functions of the DAPC achieved 96% separation among the 5 groups of whales. The FAs that had the highest discrimination power were 14:0, 18:0, 22:5n-3 and 22:6n-3 for the first discriminant axis (41% separation), FAs 14:0, 18:1n-11, 20:1n-11 and 22:5n-3 for the second axis (38%), and FAs 18:1n-9, 20:5n-3, 22:1n-11, 22:5n-3 for the third one (17%). While Groups 1, 2 and 5 were all comprised of individuals from northern Foxe Basin, they varied in FA composition. Overall, Group 1 had the highest amount of long chain MUFA (e.g., 20:1n-9, 20:1n-11, 22:1n-9 and 22:1n-11), but the smallest level of PUFA compared to all other groups. Groups 5, along with group 4, had the highest levels of PUFA (Figure 4, Table 4), whereas Group 2 had the smallest quantity of long chain MUFA, but the highest amount of 16:1n-7, 14:0 and 16:0. Groups 5, along with Group 3, also had large amounts of long chain MUFA.

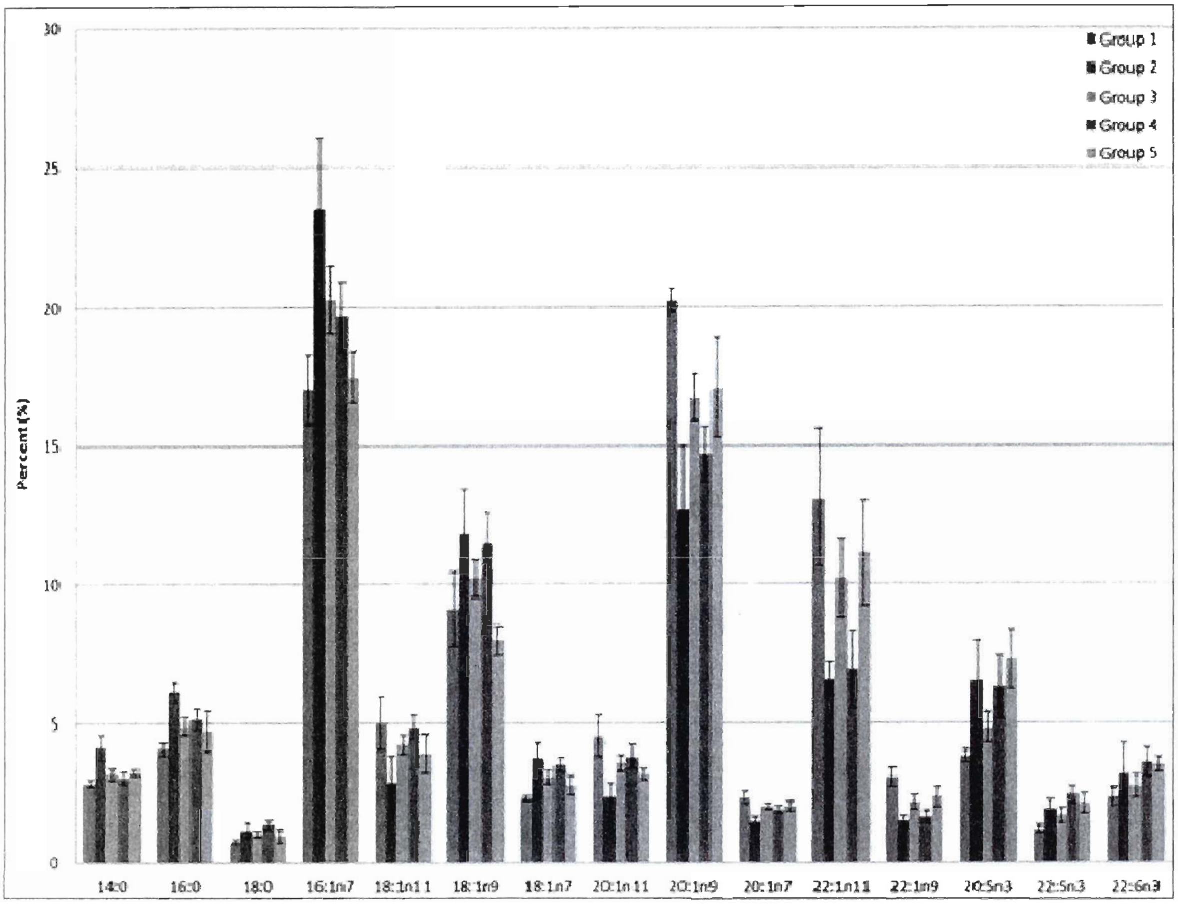
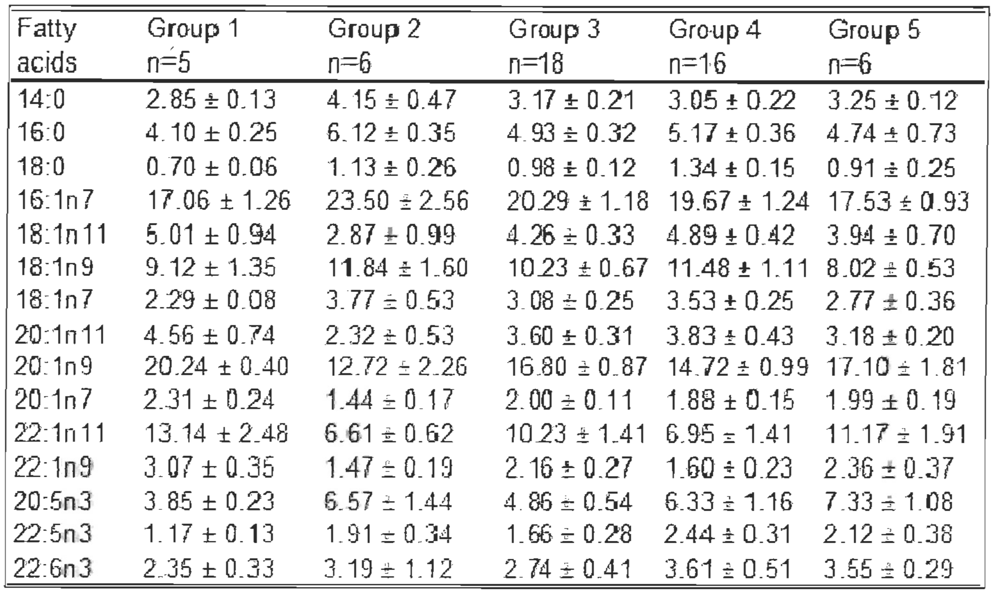


Figure 4. Values (mean ± standard deviation) of the 15 FAs for each of the five groups of bowhead whales.

5.6 DISCUSSION

The FA composition of the outer blubber layer of bowhead whales from the Eastern Canadian Arctic comprised typical marine FAs and was similar to the common array of FAs found in other species of marine mammals including pinnipeds (e.g., Iverson et al. 1997), odontocetes (e.g., Dahl et al. 2000; Hooker et al. 2001; Smith et al. 2006) and mysticetes (Lockyer et al. 1984; Borobia et al. 1995). Bowhead whales from the EC–WG population shared some similarities in their blubber FA composition with those from the BCB population, although some differences were also noted. The 15 most abundant FAs identified in the outer blubber layer of bowhead whales in this study were the exact same most abundant FAs found in the outer blubber of bowhead whales from the western Arctic

Table 4. Values (mean ± standard deviation) of the 15 FAs for each of the five groups of bowhead whales



Fatty acids	Group 1 n=5	Group 2 n=6	Group 3 n=18	Group 4 n=16	Group 5 n=6
14:0	2.85 ± 0.13	4.15 ± 0.47	3.17 ± 0.21	3.05 ± 0.22	3.25 ± 0.12
16:0	4.10 ± 0.25	6.12 ± 0.35	4.93 ± 0.32	5.17 ± 0.36	4.74 ± 0.73
18:0	0.70 ± 0.06	1.13 ± 0.26	0.98 ± 0.12	1.34 ± 0.15	0.91 ± 0.25
16:1n7	17.06 ± 1.26	23.50 ± 2.56	20.29 ± 1.18	19.67 ± 1.24	17.53 ± 0.93
18:1n11	5.01 ± 0.94	2.87 ± 0.99	4.26 ± 0.33	4.89 ± 0.42	3.94 ± 0.70
18:1n9	9.12 ± 1.35	11.84 ± 1.60	10.23 ± 0.67	11.48 ± 1.11	8.02 ± 0.53
18:1n7	2.29 ± 0.08	3.77 ± 0.53	3.08 ± 0.25	3.53 ± 0.25	2.77 ± 0.36
20:1n11	4.56 ± 0.74	2.32 ± 0.53	3.60 ± 0.31	3.83 ± 0.43	3.18 ± 0.20
20:1n9	20.24 ± 0.40	12.72 ± 2.26	16.80 ± 0.87	14.72 ± 0.99	17.10 ± 1.81
20:1n7	2.31 ± 0.24	1.44 ± 0.17	2.00 ± 0.11	1.88 ± 0.15	1.99 ± 0.19
22:1n11	13.14 ± 2.48	6.61 ± 0.62	10.23 ± 1.41	6.95 ± 1.41	11.17 ± 1.91
22:1n9	3.07 ± 0.35	1.47 ± 0.19	2.16 ± 0.27	1.60 ± 0.23	2.36 ± 0.37
20:5n3	3.85 ± 0.23	6.57 ± 1.44	4.86 ± 0.54	6.33 ± 1.16	7.33 ± 1.08
22:5n3	1.17 ± 0.13	1.91 ± 0.34	1.66 ± 0.28	2.44 ± 0.31	2.12 ± 0.38
22:6n3	2.35 ± 0.33	3.19 ± 1.12	2.74 ± 0.41	3.61 ± 0.51	3.55 ± 0.29

(Budge et al. 2008), although they varied in proportions. SFAs and PUFAs accounted for a larger proportion of total FAs in bowhead whales from the BCB compared to the EC–WG population. In contrast, the proportion of long-chain MUFA (e.g., 20:1n-9, 22:1n-9 and 22:1n-11), indicative of calanoid copepod direct or indirect consumption, was much higher in EC–WG than in BCB bowhead whales suggesting a greater dependence of bowhead whales from the eastern Arctic on food web incorporating these species.

Marine diatoms, which comprise both ice algae and planktonic species, are rich in the FA 14:0, 16:0, 16:1n-7 and 20:5n-3 (Kates and Volcani 1966; Yin et al. 2000). In counterpart, dinoflagellates tend to be poor in 16:1n-7, but rich in 22:6n-3, 18:4n-3 and 18:5n-3 (Harrington et al. 1970; Graeve 1993). The high levels of diatom and dinoflagellate marker FAs, i.e., 16:1n-7, 20:5n-3 and 22:6n-3 in EC–WG bowhead whales suggest they depend on food webs relying on these two primary producers. In order to discernate the contribution of ice algae from phytoplankton in blubber of bowhead whales, future works should use compound-specific stable isotope analysis to determine the carbon isotopic composition of individual algal markers.

In marine mammals, the long-chain MUFAs (e.g., 20:1n–9 and 22:1n–11) and the PUFAs (20:5n-3, 22:5n-3 and 22:6n-3) are assimilated exclusively from the diet (Iverson et al. 2004). These long chain MUFAs are formed *de novo* by biosynthesis in calanoid copepods (e.g., *C. hyperboreus, C. glacialis* and *C. finmarchicus*) (Kattner and Hagen 1995). Very high levels of 20:1n-9 and 22:1n-11 in a predator occupying low trophic levels such as bowhead whales, may indicate a reliance on herbivorous calanoid copepods as a food source (Sargent and White 1981; Lee et al. 2006). Relatively high levels of 20:1n-7, such as those detected in bowhead whales, may suggest the consumption of *Limnocalanus macrurus*, which is known to biosynthesize the highest amounts of this specific MUFA compared to other calanoid copepod species (Hirche et al. 2003). *L. macrurus* is common in the coastal waters of the Canadian Arctic and has been identified as an important prey item in bowhead whales from the Beaufort Sea (Pomerleau et al. 2011a). There is also some evidence that omnivorous and carnivorous zooplankton may play a role in the diet of bowhead whales. A certain number of FAs, including the SFAs 16:0 and 18:0 and the MUFAs 14:1n-5, 16:1n-7 and 18:1n-9, can be produced endogenously but, with the exception of 14:1n–5, also originate significantly from the diet in marine mammals (Iverson 1993; Kirsch et al. 2000). SFAs 16:0 and 14:0 are the most common alcohols of wax esters found in omnivorous and carnivorous zooplankton, and were the most abundant SFAs in bowhead whales. Similarly, the endogenously produced MUFA 18:1n-9 (oleic acid), is also a major FA in omnivorous and/or carnivorous zooplankton including euphausids and amphipods (Falk-Petersen et al. 2000), and was observed in high levels in bowhead whales. This FA may derive from the sympagic food web (Soreide et al. 2008), because ice amphipod species, such as *Apherusa* sp., *Gammarus* sp. and *Onisimus* sp. are usually richer in 16:1n-7 and 18:1n-9 compared to herbivorous copepods.

While only quantitative analysis of FA composition can ascertain the diet inferences made through examination of FA relative abundances, our results are in accordance with the recent findings on bowhead whale diet based on stable isotopes. Pomerleau et al. (2012) found that the EC–WG population feeds on a small array of species, including large arctic calanoid copepods, euphausids and mysids. Diet composition appeared unrelated to gender or maturity status as groups of whales with similar isotopic signatures were composed of a mix of individuals of different age or sex classes. Similarly, five groups of EC-WG bowhead whales were revealed in this study based on FA composition, suggesting within-species variability in diet composition. The segregation among some of the groups was mostly on the basis of some diatom and copepod markers suggesting some differences among groups in relative dependency on the various food webs.

No clear spatial patterns were found in the individuals analysed in this study, because animals from different areas clustered together based on their FA composition. One potential explanation may arise from the integration of diet over a time period where animals did not feed in in the same area. The approximate blubber FA turnover rate is in the order of 1.5 to 3 months (Nordstrom et al. 2008), but has not been established in large whales like the bowhead whale (Koopman et al. 2003). Satellite telemetry data indicate that EC−WG bowhead whales perform extensive seasonal migrations throughout the Canadian eastern Arctic and West Greenland (Heide-Jørgensen et al. 2003). Although the vast majority of whales included in this study were sampled in northern Foxe Basin, five groups of individuals were found, which may reflect feeding in other parts of their distribution range in the eastern Arctic prior to their arrival in Foxe Basin or differences in diet composition. A recent zooplankton assemblage study showed high spatial variability in species composition across the distribution range of EC−WG bowhead whales (Pomerleau et al. 2011b). Thus animals included in this study may have been feeding on different prey assemblages before moving into Foxe Basin from the North via Lancaster Sound, Prince Regent Inlet, the Gulf of Boothia and Fury and Hecla Strait or from the South via Hudson Strait.

5.7 CONCLUSION

FAs were used as a semi-quantitative tool to investigate diet variability among individual bowhead whales. Bowhead whales need roughly 4000 to 5000 kg of lipids annually to complete their annual cycle, and they must feed on lipid rich, abundant and densely aggregated prey to meet their energy requirements (Brodie 1981, Lowry 1993).

Results from this study suggest the existence of a trophic linkage between bowhead whales and the arctic food web fuelled by large cell diatoms that sustains lipid-rich arctic calanoid copepods. Bowhead whales also feed on other omnivorous and carnivorous zooplankton species that are abundant in polar waters including euphausids and amphipods. A recent study suggests that with a warming climate, lipid-rich Arctic copepod species may be progressively replaced by lower quality prey items (Swalethorp et al. 2011). Sampling of food web components remain a challenge in the Arctic due to logistical constraints. However, in the context of accelerating climate change, monitoring of bowhead whale diet using multiple dietary approaches and their potential prey is central to the understanding of their adaptability to the ongoing changes in their environment.

5.8 ACKNOWLEDGEMENTS

Funding was provided by CFL and GWAMM – Canadian International Polar Year projects as well as Nunavut Wildlife Research Trust Fund, Fisheries and Oceans Canada, and a Weston Garfield scholarship to CP. We thank Dr. Suzanne Budge for advice on data analysis. We thank hunters from the following communities for their help during whale biopsy field campaigns: Arctic Bay, Igloolik, Pangnirtung, Kangirsujuaq, Hall Beach, Pelly Bay, Repulse Bay, Cape Dorset and Coral Harbour. We also thank B. Leblanc, L. Dueck and J. Higdon for collecting biopsies.

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CONCLUSION GÉNÉRALE

Il est prévu que le réchauffement global amplifiera les changements climatiques dans les régions polaires et entraînera de profondes modifications de l'environnement arctique qui se répercuteront sur les espèces qui y vivent. Afin de mieux prévoir les conséquences de ces changements sur l'écosystème arctique, et notamment sur les espèces endémiques, il est essentiel d'accroitre les connaissances sur l'écologie de ces espèces. Celles-ci sont demeurées en général peu étudiées en raison de la difficulté d'accès et des coûts associés aux études nordiques. Cette thèse de doctorat présente des données uniques sur l'écologie alimentaire de la baleine boréale de la population de l'est du Canada et de l'ouest du Groenland (EC-WG).

Les aires probables d'alimentation estivale d'individus de la population EC-WG ont été définies dans le premier chapitre de recherche. Cette étude a révélé l'importance du golfe de Boothia vers lequel des baleines provenant de régions séparées par plusieurs centaines de kilomètres convergent leurs activités pendant l'été. Nous avons démontré que les baleines passaient la majorité de leur temps à de faibles profondeurs lorsqu'elles sont dans le golfe de Boothia. Des études antérieures ont démontré que les plus fortes concentrations de zooplancton, en particulier celles des copépodes calanoides, sont plus importantes à de faibles profondeurs pendant l'été dans l'Arctique (ex. Tande et Bamstedt 1985, Blachowiak-Samolyk et al. 2006). Les résultats de notre étude suggèrent que cette région de l'archipel Arctique est probablement utilisée comme site d'alimentation, (ex. sur des concentrations de zooplancton situées près de la surface), et offre une barrière de protection avec son couvert de glace modéré. Nous avons mis en lumière l'apparente importance du golfe de Boothia pour la baleine boréale en saison estivale (juillet-octobre). Dans le contexte actuel du déclin soutenu du couvert de glace estival en Arctique, cette analyse devrait être reprise dans un futur rapproché, en augmentant significativement la taille de l'échantillon ainsi que la durée des données de transmission pour chaque baleine. Cela permettrait de tester l'effet du couvert de glace, variable clé de l'écosystème arctique, sur le comportement de la baleine boréale. Par ailleurs, un plus grand effectif permettrait de révéler l'existence et l'importance de d'autres zones géographiques pour l'alimentation estivale de la baleine boréale. Somme toute, malgré la faible taille de l'échantillon utilisé dans cette étude, les résultats de ce chapitre fournissent de l'information essentielle pour la conservation de cette population de baleine boréale. Dans le contexte de l'essor du développement industriel en Arctique, il serait important de maintenir l'intégrité écologique du golfe de Boothia.

Afin de mieux comprendre l'écologie alimentaire et la diète de la baleine boréale de la population EC-WG, nous avons fait la première caractérisation à grande échelle des assemblages des compositions spécifiques du mésozooplankton et de leurs signatures isotopiques en carbone et azote dans les régions arctiques et subarctiques de l'est du Canada. Cette étude a démontré des liens entre les patrons spatiaux des différentes masses d'eau, la composition spécifique des communautés planctoniques et leurs signatures isotopiques en azote ($\delta^{15}N$). Les valeurs de température et de salinité nous ont permis de définir cinq grandes masses d'eau à travers notre vaste aire d'étude qui s'étendait de la mer du Labrador jusqu'à la portion ouest de l'archipel Arctique. La composition des communautés de zooplancton variait spatialement et nous avons distingué huit assemblages spécifiques qui correspondent pour la vaste majorité à des régions distinctes. Les variations observées dans les communautés planctoniques de même que dans les ratios isotopiques peuvent être attribuées en partie aux variations de la température et de la salinité des masses d'eau. Nous avons trouvé des abondances élevées de *Calanus finmarchicus* en lien avec l'influence des eaux Atlantiques dans la mer du Labrador, tandis que les plus fortes abondances d'espèces de copépodes arctiques (*Calanus hyperboreus, Calanus glacialis* et *Metridia longa*), correspondaient aux eaux froides polaires du centre de la baie de Baffin et de l'est de l'archipel Arctique. Nous avons démontré que les valeurs de $\delta^{15}N$ variaient spatialement chez les quatre espèces omniprésentes dans notre aire d'étude. Ces résultats pourraient être liés à des variations spatiales dans la structure trophique des communautés planctoniques, ou encore à la saisonnalité ou la présence de fronts océaniques, ce qui reste à être déterminé par des études plus approfondies sur la structure trophique des communautés dans les différentes régions subarctiques et arctiques. Ces résultats fournissent des données de base afin de suivre l'évolution des communautés zooplanctoniques et des caractéristiques des masses d'eau. Par ailleurs, il serait important de faire le suivi des communautés de zooplancton dans les régions subarctiques et arctiques afin de voir l'évolution de la structure de ces communautés ainsi que des changements dans la biogéographie de certaines espèces. Il serait intéressant d'utiliser d'autres techniques, notamment l'analyse isotopique de composés spécifiques (*compound-specific stable isotope analysis*) (ex. Hannides et al. 2009), afin de mieux interpréter les variations des signatures isotopiques du zooplancton en lien avec les différences au niveau de la structure trophique, et d'étudier l'efficacité du transfert d'énergie à travers les différentes composantes de la chaîne alimentaire. Somme toute, les données présentées dans cette portion de la thèse ont également permis de dresser le premier portait des valeurs isotopiques des proies potentielles de la baleine boréale dans la majorité de leur aire de répartition estivale.

Cette thèse de doctorat a employé diverses approches afin de mieux comprendre l'écologie alimentaire de la baleine boréale et d'accroître les connaissances sur les proies de cette espèce. Les résultats provenant de l'analyse des contenus stomacaux ont démontré que les baleines boréales pouvaient s'alimenter de proies pélagiques et épi-benthiques, et ont révélé l'importance de *Mysis oculata,* qui était la proie dominante de l'échantillon de l'estomac d'une femelle adulte chassée dans le détroit d'Hudson et d'un mâle juvénile, chassé dans le golfe de Boothia. Les résultats obtenus suggèrent que ces deux baleines se sont alimentés sur de larges agrégations de cette espèce épi-benthique. Malgré le fait que l'analyse des contenus stomacaux comporte des biais engendrés par la digestion des différentes proies, cette technique d'analyse du régime alimentaire est directe et a permis d'identifier les proies récemment ingérées par les animaux.

L'utilisation de traceurs écologiques (isotopes stables et acides gras) a permis d'étudier la diète de la baleine boréale plus en profondeur. Les résultats d'une analyse de classification hiérarchique basée sur la signature isotopique en carbone et en azote de la peau de baleine ont révélé quatre groupes d'individus, mais aucune différence entre les mâles et les femelles ni selon le niveau de maturité (ex. immature vs. adulte). Les modèles de mélange isotopiques ont révélé des informations tant au niveau de l'identité des proies que des contributions proportionnelles de celles-ci à la diète de cette espèce et ont révélés que les baleines boréales des quatre groupes dépendent de copépodes arctiques (ex. *C. hyperboreus, C. glacialis, M. longa* et *Paraeuchaeta* spp.). Les modèles ont également révélés que les mysidacés, euphausiacés et chaetognathes de même que les ptéropodes et les amphipodes sympagiques étaient des proies importantes pour certains groupes de baleines. Les résultats provenant de l'analyse de la composition en acides gras du tissu adipeux sous-cutané des baleines boréales arrivent à des conclusions similaires aux modèles de mélanges isotopiques. Nous avons déterminé cinq groupes de baleines basés selon leur constitution en acides gras et tout comme pour les isotopes stables, les résultats ont démontré qu'il n'y avait aucune différence dans la composition en acides gras des mâles et des femelles, ce qui suggère qu'ils ont une diète similaire. L'analyse de la composition en acides gras a mis en lumière l'existence d'un lien trophique entre les diatomées, les copépodes calanoides et les baleines boréales. Les résultats indiquent une contribution importante des copépodes calanoides à la diète de la baleine boréale, soit par ingestion directe ou encore par leurs prédateurs, ainsi que d'autres espèces de zooplancton omnivores et carnivores. Les résultats présentés dans cette thèse au niveau de la diète des baleines boréales de la population EC-WG corroborent avec ceux de la diète des baleines boréales de la population des mers Béring-Chuckchi-Beaufort. Dans l'arctique de l'ouest, les baleines boréales s'alimentent principalement de copépodes calanoides et d'euphausiacés, et d'autres espèces de zooplancton pélagiques et épi-benthiques dont des mysidacés, des isopodes et des amphipodes (Lowry et Frost 1984, Schell et al. 1987, Lowry 1993, Schell et Saupe 1993, Lowry et al. 2004, Budge et al. 2008).

L'utilisation de traceurs écologiques a révélé qu'au printemps et en été, la diète des baleines boréales varie entre les individus et indépendamment du sexe ou du degré de maturité, et se caractérise par un petit nombre de proies, notamment des copépodes calanoides, des euphausiacés, des mysidacés et des amphipodes sympagiques. Les résultats de cette thèse de doctorat suggèrent que la population EC-WG pourrait être considérée généraliste de Type B (Bearhop et al. 2004), c'est-à-dire que les baleines boréales ne mangent pas toutes les mêmes proies, mais s'alimentent de petits groupes de proies différentes; un comportement alimentaire qui peut être potentiellement influencé par la variation spatio-temporelle dans la disponibilité et l'abondance des proies. La difficulté d'accès, la logistique et les coûts reliés à l'échantillonnage en Arctique, limitent parfois les tailles d'échantillons et les campagnes de collecte de données sont souvent restreintes aux mois d'été. Conséquemment, les résultats de cette thèse ne peuvent être extrapolés à l'ensemble de l'année. Les résultats basés sur les modèles de mélanges isotopiques ont démontré que les baleines boréales incluses dans notre étude ne semblent pas s'alimenter dans la baie de Disko au Groenland ni dans le détroit de Davis, au printemps et à l'été. Toutefois, il est possible qu'elles utilisent ces secteurs durant d'autres saisons. D'autre part, les résultats suggèrent que le détroit de Lancaster de même que le golfe de Boothia et la baie de Baffin constituent des aires plausibles d'alimentation printanières et estivales. Les résultats et les conclusions des analyses isotopiques de même que ceux provenant des acides gras, ne peuvent s'appliquer à la totalité de la population de baleine boréale de l'est du Canada et de l'ouest du Groenland. Ces résultats reflètent les habitudes alimentaires d'un segment de la population au printemps et au début de l'été. En conséquence, d'autres travaux de recherche devraient être entrepris afin d'étudier les variations saisonnières des ratios d'isotopes stables dans la peau de la baleine boréale, ainsi que de la composition en acides gras, particulièrement à l'automne, à l'hiver et au début du printemps, afin d'améliorer notre compréhension de l'écologie alimentaire de cette espèce d'un point de vue annuel.

Cette thèse de doctorat a présenté des données uniques sur l'écologie alimentaire de la baleine boréale dans l'arctique de l'est et les résultats de cette recherche ont mis en lumière l'importance de certaines espèces de zooplancton arctique dans leur diète, particulièrement des copépodes calanoides (*C. hyperboreus, C. glacialis* et *M. longa*), ainsi que d'autres organismes dont les mysidacés, les euphausiacés, les chaetognathes et les amphipodes sympagiques. Le réchauffement aux hautes latitudes devrait s'accentuer et l'océan Arctique pourrait être libre de glace en été d'ici la prochaine décennie (Meier et al. 2011). La diminution, voir même la disparition du couvert de glace en saison estivale, auront des impacts majeurs sur l'écosystème marin arctique tant au niveau physique, chimique que biologique (Duarte et al. 2012). Les biomasses et la composition spécifique des communautés de zooplancton sont grandement influencées par les modifications dans la structure des masses d'eau, notamment par les fluctuations dans la température et la salinité, de même que par les apports d'eau douce (Fetzer et al. 2002, Beaugrand et al. 2002). Les changements climatiques pourraient entraîner le remplacement progressif des copépodes de grande taille et riches en lipides, *C. hyperboreus et C. glacialis*, par des copépodes plus petits et moins riches en lipides, tel que *C. finmarchicus*, dont l'abondance est présentement éparse en Arctique (Swalethorp et al. 2011). L'abondance et la distribution d'autres espèces de zooplancton importantes à la diète de la baleine boréale, tel que les euphausiacés et les amphipodes sympagiques, risquent également d'être affectées par le réchauffement de la température de la surface des océans et les modifications dans le régime de glace (Richardson 2008). La baleine boréale aura fort probablement à faire face à des changements en termes de disponibilité, d'abondance et d'assemblages de ses proies. Le réchauffement aux hautes latitudes entraine également le déplacement vers le nord de plusieurs espèces marines des régions tempérés en saison estivale, ce qui augmentera le risque de compétition pour les ressources alimentaires entre la baleine boréale et des espèces de cétacés à fanons des eaux plus tempérées. Il est prévu que les premières réponses à court terme des vertébrés arctiques face aux modifications environnementales seront l'adaptation par l'intermédiaire de la plasticité phénotypique et dans la distribution géographique (Gilg et al. 2012). Il est possible que les changements en court dans le régime de la glace de mer provoquent des modifications dans la répartition saisonnière des baleines boréales, et que celles-ci étendent leur distribution plus au nord. Bref, l'avenir des mammifères marins endémiques à l'arctique face aux modifications environnementales majeures induites par le réchauffement global, dépendra probablement de leur capacité et de leur degré d'adaptation au cours des prochaines décennies.

Cette thèse de doctorat a permis de grandement élargir les connaissances sur l'écologie alimentaire la baleine boréale de la population de l'est du Canada et de l'ouest du Groenland et ces nouvelles informations définissent un besoin d'un suivi rigoureux afin de déterminer *si* et *comment* les baleines boréales, en tant que spécialistes de zooplancton, vont s'adapter aux multiples transformations qui surviennent dans leur milieu.

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