UTILISATION DES BIVALVES FILTREURS POUR LE SUIVI DU COUPLAGE PÉLAGO-BENTHIQUE EN ARCTIQUE

USE OF FILTER-FEEDING BIVALVES TO MONITOR PELAGIC-BENTHIC COUPLING IN ARCTIC

Thèse présentée

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« *Chaque difficulté rencontrée doit être l'occasion d'un nouveau progrès.* »

Pierre de Coubertin

À mon Papa…

« *Le commencement de toutes les sciences, c'est l'étonnement de ce que les choses sont ce qu'elles sont.* »

Métaphysique, **Aristote**

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RÉSUMÉ

Le réchauffement climatique global affecte plus fortement et à un rythme accéléré les régions arctiques. Les changements des conditions physiques, tels que le réchauffement de la surface de la mer, la réduction du couvert de glace, l'intensification de la stratification de la colonne d'eau, et la turbidité ont des effets encore mal compris sur les producteurs primaires. L'initialisation, l'intensité et la répartition spatiale des producteurs primaires peuvent être modifiées et avoir des conséquences sur les réseaux trophiques pélagiques et benthiques. Cependant, il est difficile de savoir comment les communautés benthiques répondront à ces changements qui affectent la contribution relative des sources de nourriture (phytoplancton, algues de glace de mer, microphytobenthos, et macroalgues). Il est largement admis que le couplage pélago-benthique sur les plateaux continentaux arctiques est actuellement fort mais devrait s'affaiblir avec la diminution du couvert de glace. En effet, il est attendu que ces systèmes basculent d'une dominance 'algues de glace – benthos' à une dominance de la chaine pélagique 'phytoplancton – zooplancton'. Dans ce contexte, l'objectif principal de cette thèse est de déterminer et suivre les changements potentiels des sources d'alimentation des organismes benthiques par l'étude de trois espèces de bivalves filtreurs dominants les communautés benthiques de l'archipel arctique canadien, *Bathyarca glacialis*, *Astarte elliptica* et *Astarte moerchi*, afin de mieux définir le couplage pélago-benthique dans cette région. Le régime alimentaire de ces bivalves a été caractérisé dans des systèmes côtiers et profonds de l'Arctique canadien (chapitre 1) et un fjord subarctique (chapitre 2). Finalement, la dynamique de croissance d'*Astarte* spp. de la polynie des eaux du Nord a été examinée afin de mieux comprendre la nature du couplage pélago-benthique et les paramètres environnementaux le déterminant (chapitre 3).

Tout d'abord, le chapitre 1 a permis d'identifier les sources principales d'alimentation du bivalve *Bathyarca glacialis* et de décrire le couplage pélago-benthique dans cinq régions de l'Arctique canadien caractérisées par des régimes de production primaire contrastés. L'examen des acides gras marqueurs trophiques indique que *B. glacialis* est un filtreur non sélectif, se nourrissant de microalgues, de zooplancton et de bactéries. Néanmoins des nuances dans le régime alimentaire entre les populations côtières et bathyales peuvent être apportées en raison de conditions environnementales locales différentes et de la variabilité saisonnière. Par ailleurs, la présence d'acides gras non maloniques dans les lipides de *B. glacialis* suggèrerait une réponse physiologique du bivalve pour moduler sa fluidité membranaire face aux contraintes de l'environnement profond, notamment lorsque les acides gras essentiels sont moins disponibles dans son régime alimentaire.

Par une approche multi-marqueurs (isotopes stables, acides gras marqueurs trophiques, et analyse des isotopes stables sur des composés spécifiques), le chapitre 2 a permis de caractériser avec une plus grande précision les sources principales de nourriture pour le bivalve *Astarte elliptica* dans un fjord subarctique (S.-O. Groenland). Les résultats ont montré qu'*A. elliptica* se nourrit sur la matière organique particulaire et contenue dans les sédiments, comprenant des microalgues et des détritus de macroalgues. Nous avons donc pu

établir que malgré le fait qu'elles soient très peu considérées comme des sources de nourriture potentielles, les macroalgues brunes peuvent soutenir de manière significative le réseau trophique benthique arctique.

Finalement, le chapitre 3 présente l'utilisation d'un bivalve *Astarte moerchi* comme bio-archive de la dynamique des ressources trophiques exportées vers le fond marin. À 600 m de profondeur dans le nord de la baie de Baffin, les coquilles d'*A. moerchi* révèlent de fortes anomalies de croissance positives depuis les années 2000, attribuables à un changement dans la disponibilité de la nourriture. D'une part, les acides gras marqueurs trophiques montrent que cette espèce se nourrit principalement sur des microalgues exportées à partir de la zone euphotique vers le fond marin. D'autre part l'analyse de l'élément baryum (ratio Ba/Ca) indique une intensification de l'export de diatomées depuis les années 2000. Les changements observés dans la nature et la force du couplage pélago-benthique peuvent être expliqués, soit par des modifications locales de la dynamique de la glace de mer qui influence la production phytoplanctonique, soit par un décalage entre la floraison du phytoplancton et le broutage par le zooplancton, permettant une exportation accrue de nourriture sur le fond marin.

Cette thèse a permis de mettre en avant le potentiel de bivalves arctiques comme bio-archives de la dynamique de la production primaire présente et passée. Elle a également montré la complexité des relations entre les paramètres environnementaux qui agissent sur la nature et la force du couplage pélago-benthique et leurs impacts sur le benthos. L'importance des macroalgues comme sources d'alimentation pour les bivalves de l'Arctique a été établie et souligne la nécessité de mieux prendre en considération l'ensemble des sources potentielles de nourriture disponible dans un site donné lors d'études trophiques. L'ensemble de ces résultats pourra aider à orienter de futures recherches afin de mieux comprendre les processus qui interfèrent sur le couplage pélago-bentique et la réponse des communautés benthiques des systèmes marins arctiques.

Mots clés : Arctique, couplage pélago-benthique, bivalve, acides gras marqueurs trophiques, isotopes stables, sclérochonologie, sclérochimie, bio-archive

ABSTRACT

Global warming strongly affects and at a faster pace arctic regions. Effects of physical conditions changes on primary production, such as rise of the sea surface temperature, reduced ice cover, increased stratification of the water column and turbidity, are still poorly understood. Timing, magnitude and spatial distribution of primary producers may be modified and have effects on the pelagic and benthic trophic webs. Nonetheless, it is difficult to know how benthic communities will adjust to these changes in terms of relative contribution of food sources (phytoplankton, sea ice algae, microphytobenthos, and macroalgae). It is widely acknowledged that there is a strong pelagic-benthic coupling occurring on continental arctic shelves, which should weaken with diminishing ice cover. Indeed, a shift from an 'ice algae – benthos' domination to a 'phytoplankton – zooplankton" domination of the pelagic web is to be expected. In this context, the main objective of this thesis is to determine and follow potential changes in food sources of benthic organisms through the study of three dominant filter-feeding bivalves species in benthic communities of the canadian arctic archipelago, *Bathyarca glacialis*, *Astarte elliptica* and *Astarte moerchi*, in order to better define the pelagic-benthic coupling in this area. Diets of these bivalves species have been characterized in coastal and deep water systems of the Canadian Arctic (chapter 1) and in a subarctic fjord (chapter 2). Finally, growth dynamics of *Astarte* spp. from the Northern water polynya has been investigated for a better understanding of the pelagic-benthic coupling and the environmental parameters defining it (chapter 3).

First of all, the first chapter allowed to identify primary food sources of the bivalve *Bathyarca glacialis* and describing the pelagic-benthic coupling in five regions of the Canadian Arctic characterized by contrasted primary production regimes. Investigation of fatty acid trophic markers indicates that *B. glacialis* is a non-selective filter feeder, feeding on microalgae, zooplankton and bacteria. Nevertheless, nuances in the diet of coastal and bathyal populations can be adduced on account of differences in local environmental conditions and seasonal variability. Furthermore, the presence of non-methylene interrupted fatty acids in *B. glacialis* lipids suggests a physiological response from the bivalve in order to modulate its membrane fluidity when facing deep ecosystem constraints, especially when essential fatty acids are less available in its diet.

Through a multi-markers approach (stable isotope, fatty acids trophic markers and compound-specific stable isotope analysis), chapter 2 allowed to characterize with an increase precision principal food sources for the bivalve *Astarte elliptica* in a subarctic fjord (S.-W. Greenland). Results have shown that *A. elliptica* feeds on particulate organic matter as well as organic matter trapped into the sediments, including microalgae, and macroalgae detritus. We then were able to establish that even though macroalgae are less considered as potential food sources, brown macroalgae can significantly sustain the arctic benthic trophic web.

Finally chapter 3 presents the use of a bivalve *Astarte moerchi* as bio-archive of the dynamics of exported trophic resources towards the seafloor. At 600m depth in the northern Baffin Bay, *A. moerchi* shells reveal strong positive growth anomalies since 2000s attributable to a change in food availability. On one hand, fatty acids trophic markers show that this species feeds predominantly on microalgae exported from the euphotic zone towards the seafloor. On the other hand, the analysis of the barium compound (Ba/Ca ratio) indicates an increase of diatoms export since 2000s. Observed changes in the nature and strength of the pelagic-benthic coupling can be explained either by local modifications of the sea ice dynamic which influences the phytoplankton production, or by a mismatch between the phytoplankton bloom and the zooplankton grazing allowing an increased food export towards the sea floor.

This thesis allowed shedding light on the potential of arctic bivalves as bioarchive of the present and past primary production dynamics. It also showed the complexity of the interactions between environmental parameters acting on nature and the strength of the pelagic-benthic coupling and their impacts onto the benthos. The importance of macroalgae as food sources for Arctic bivalves was established and underlies the necessity to take into consideration the entirety of potential food sources available in a given study site for trophic studies. The overall results will help to direct future researches in order to better understand the underlying processes of the pelagic-benthic coupling and the response of benthic communities of arctic marine systems.

Key words: Arctic, pelagic-benthic coupling, bivalve, fatty acids trophic markers, stable isotopes, sclerochronology, sclerochemistry, bioarchive

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INTRODUCTION GÉNÉRALE

En réponse aux changements climatiques observés depuis le milieu du siècle passé, de nombreuses modifications des systèmes naturels ont déjà pu être constatées (IPCC 2013). Bien que ce phénomène global affecte l'ensemble des écosystèmes terrestres et aquatiques, les pôles et plus particulièrement l'Arctique, paraissent être les régions du monde les plus affectées par l'augmentation des températures. Les spécialistes prédisent ainsi que l'Arctique continuera de se réchauffer plus rapidement que la moyenne mondiale (IPCC 2013). Le signe le plus visible des changements climatiques en Arctique est la diminution du couvert de glace de mer en termes d'étendue et d'épaisseur (Comiso *et al.* 2008, Parkinson & Comiso 2013). Or, l'une des caractéristiques principales de l'océan Arctique est la présence de cette glace de mer, de façon permanente (ou pluriannuelle) à hautes latitudes et saisonnièrement à plus basses latitudes. Au cours des dernières décennies, la couverture de la glace pluriannuelle est devenue de plus en plus mince (Figure 1) contrairement à la glace saisonnière qui s'est généralisée, bien que sa superficie estivale ait effectivement baissé de près de 50% (Comiso 2012). Les prédictions quant à la diminution du couvert de glace de mer laissent entrevoir un océan Arctique libre de glace, c.à.d. avec une étendue de la glace de mer inférieure à 1 Mkm^2 durant au moins cinq années consécutives, au cours de la saison estivale avant 2050 (IPCC 2014). Les nombreuses modifications des conditions physiques attendues, comme la diminution du couvert de glace, mais aussi l'augmentation de la stratification et de la turbidité de la colonne d'eau, auront une influence sur les producteurs primaires mais leurs effets restent encore mal compris (Wassmann 2011). La distribution spatiale et temporelle des producteurs primaires ainsi que l'amplitude des floraisons printanières peuvent être affectées, modifiant la structure des réseaux trophiques aquatiques (Wassmann & Reigstad 2011). La façon dont les organismes pélagiques et benthiques répondront à ces modifications des conditions environnementales et de disponibilité des ressources trophiques reste encore à éclaircir.

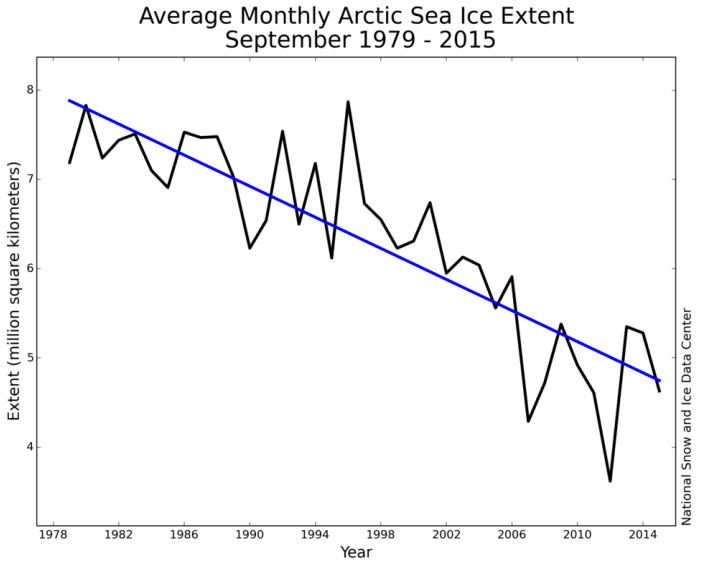

Figure 1. Étendue moyenne de la glace de mer en Arctique atteinte au mois de septembre entre 1979 et 2015, montrant un déclin de 13,4% par décennie relativement à l'étendue moyenne de 1981 à 2010. Image tirée de National Snow and Ice Data Center

L'ENVIRONNEMENT MARIN ET L'ÉCOSYSTÈME BENTHIQUE ARCTIQUE

L'océan Arctique et ses mers épicontinentales couvrent une superficie de près de 14 Mkm^2 (Carroll & Carroll 2003) (Figure 2). Bien qu'étant une des régions océaniques parmi les plus petites au monde, comptant pour seulement 2% du volume total des océans (Carroll & Carroll 2003), les plateaux continentaux arctiques présentent une très large étendue, avec plus de la moitié de l'océan Arctique ayant une profondeur inférieure à 200 m (Gradinger *et al.* 2010). Les mers arctiques sont soumises à une extrême saisonnalité de lumière, de couverture de glace, d'apports fluviaux et de salinité, autant de facteurs abiotiques qui influencent les processus biogéochimiques, la composition des communautés pélagiques et benthiques et entraînent une forte saisonnalité de la production biologique (Carroll & Carroll 2003, Gradinger *et al.* 2010).

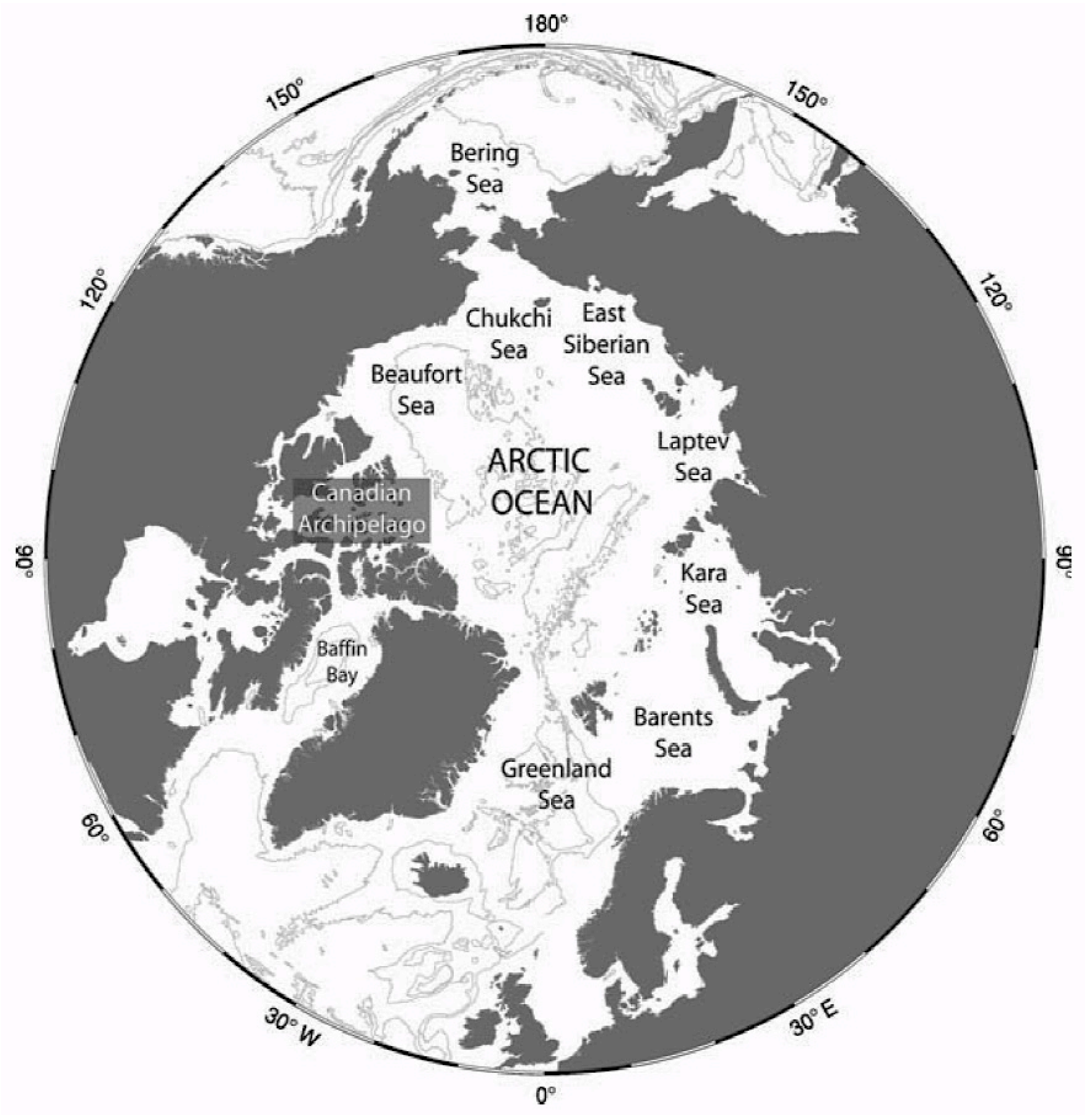

Figure 2. Carte de l'océan Arctique et de ses mers épicontinentales. Image tirée de Piepenburg (2005)

Il est généralement admis que les écosystèmes marins arctiques reposent sur deux producteurs primaires principaux : les algues de glace (production primaire sympagique) se développant en dessous ou au sein même de la glace de mer, et le phytoplancton (production primaire pélagique) qui se développe habituellement dans les eaux ouvertes (Legendre *et al.* 1992, Falk-Petersen *et al.* 2000, Sakshaug 2004, Søreide *et al.* 2006). Néanmoins, il a été récemment montré que les floraisons phytoplanctoniques peuvent aussi avoir lieu sous la glace de mer en raison de l'amincissement de la couverture de glace et des mares de fonte de plus en plus nombreuses, permettant ainsi une meilleure pénétration de la lumière favorable à leur développement (Arrigo *et al.* 2014). Généralement, la croissance de ces deux types de producteurs primaires se déroule sur une période de quelques mois au cours du printemps et de l'été (Søreide *et al.* 2006, Renaud *et al.* 2008a, Iken *et al.* 2010). La floraison des algues de glace dès la fin de la nuit polaire, lorsque la lumière du soleil devient suffisante, jusqu'à la fonte de leur substrat initie la saison productive (Hegseth 1998). La production du phytoplancton commence quant à elle avec la fonte de la glace de mer, créant une discontinuité temporelle entre la production primaire sympagique et pélagique (Hegseth 1998). Cette discontinuité temporelle entre le développement des algues de glace et du phytoplancton permet une production primaire continue durant la saison productive (p. ex. Leu *et al.* 2011). La contribution des algues de glace par rapport au phytoplancton dans la production primaire totale annuelle est très variable, et est dépendante de l'étendue des eaux libres de glace et de la latitude (Legendre *et al.* 1992, Gosselin *et al.* 1997, Hegseth 1998). La production d'algues de glace peut atteindre 25% de la production primaire totale annuelle dans les eaux couvertes de glace de manière saisonnière (Legendre *et al.* 1992, Hegseth 1998, Gradinger 2009), et près de 60% dans l'océan Arctique central où la glace multi-annuelle est présente (Gosselin *et al.* 1997). De par leur développement précoce dans la saison et leur sédimentation rapide, les algues de glace soutiennent de manière efficace, et ce dès le printemps, les réseaux trophiques benthiques des plateaux continentaux arctiques peu profonds et majoritairement couverts de glace saisonnière (Hobson *et al.* 1995, Tamelander *et al.* 2006). Cette contribution des algues de glace devient proportionnellement plus importante dans les zones où la couverture de glace reste plus tardivement dans l'année

(Gosselin *et al.* 1997). Boetius *et al.* (2013) ont d'ailleurs montré qu'un export important d'algues de glace peut avoir lieu depuis la glace de mer jusqu'au fond marin du bassin central arctique à 4400 m, où la glace pluriannuelle est dominante, représentant ainsi une ressource pour les communautés benthiques à de très grandes profondeurs. Cependant, avec l'augmentation des températures et la diminution du couvert de glace observées depuis les dernières décennies, la contribution des algues sympagiques devrait être moins élevée dans les réseaux trophiques arctiques (Leu *et al.* 2011). La floraison printanière du phytoplancton suit la floraison d'algues de glace dès lors que la glace de mer se met à fondre (Leu *et al.* 2011). Durant l'été, la limitation en nutriments supporte une faible biomasse phytoplanctonique (Wassmann & Reigstad 2011), avec cependant des floraisons épisodiques facilitées par des nutriments disponibles occasionnellement (Grebmeier *et al.* 2006). Ces floraisons de phytoplancton, bien que responsables de l'essentiel de la production totale annuelle, sont généralement limitées aux eaux ouvertes bien que Arrigo *et al.* (2012) et Mundy *et al.* (2014) aient observé des floraisons massives de phytoplancton sous la glace de mer.

Outre le phytoplancton et les algues de glace, les microalgues benthiques (ou microphytobenthos) et les macroalgues peuvent également soutenir les réseaux trophiques arctiques dans les systèmes côtiers (Glud & Rysgaard 2007, Glud *et al.* 2009, Woelfel *et al.* 2010). Les macroalgues peuvent contribuer de manière significative à la production primaire totale et même dépasser la production primaire pélagique dans des zones de faibles profondeurs (Glud & Rysgaard 2007, Krause-Jensen *et al.* 2007). À titre d'exemple, Glud & Rysgaard (2007) estiment que la contribution des macroalgues, vivant jusqu'à 50m de profondeur, est légèrement supérieure à 20% relativement à la production primaire totale annuelle dans un fjord du Haut-Arctique (Young Sound, N.-E. Groenland). Ce type de production primaire est particulièrement bénéfique à la croissance des organismes benthiques suspensivores grâce à l'exsudation de carbone organique dissout et l'apport de détritus macroalgaux (Duggins *et al.* 1989, Perez *et al.* 2013, Quartino *et al.* 2015). De plus, Renaud *et al.* (2015) ont récemment montré, dans un fjord de l'archipel du Svalbard, que la plupart des organismes benthiques se nourrissent sur un mélange de matière organique particulaire

et de détritus de macroalgues, même à des profondeurs proches de 400 m. Les bivalves suspensivores, qui généralement sont supposés se nourrir principalement de microalgues ou de phytodétritus (Gosling 2015), ont montré une signature isotopique indiquant une contribution des laminaires et de fucales qui comptaient pour plus de la moitié dans leur alimentation. Le rôle des macroalgues comme sources potentielles de carbone pour les niveaux trophiques supérieurs est d'autant plus primordial à déterminer que leur développement semble être favorisé dans le contexte du réchauffement climatique global (Krause-Jensen & Duarte 2014). En effet, les macroalgues des régions tempérées froides et subarctiques devraient voir leur répartition s'étendre vers le nord (Krause-Jensen *et al.* 2012, Krause-Jensen & Duarte 2014). En outre, le réchauffement observé en Arctique, entraînant des périodes libres de glace plus grandes, devrait permettre une croissance soutenue des macroalgues sur une plus grande période de l'année (Krause-Jensen & Duarte 2014). Weslawski *et al.* (2010) ont par exemple déjà montré que la biomasse de macroalgues a triplé entre 1988 et 2008 sur les côtes rocheuses de l'archipel du Svalbard, en lien avec l'augmentation de la température et de la lumière par la réduction de la couverture de glace de mer. Cependant, l'augmentation prévue des précipitations ainsi que la fonte des glaciers et du pergélisol devraient accroitre la turbidité des eaux douces et pourraient contrecarrer localement, la hausse attendue de la disponibilité en lumière, limitant ainsi le développement des producteurs primaires benthiques en zones côtières (Glud *et al.* 2009, Krause-Jensen & Duarte 2014).

La quantité et la qualité de la production primaire atteignant le fond marin ont un rôle primordial sur les communautés benthiques (Pearson & Rosenberg 1978) et sur le reste du réseau trophique, spécialement dans les systèmes arctiques soumis à une extrême saisonnalité. Les plateaux continentaux arctiques, peu profonds, sont classiquement caractérisés par un couplage pélago-benthique très étroit en raison d'une faible pression de broutage du zooplancton sur la floraison algale dans la colonne d'eau (Grebmeier *et al.* 1988, Grebmeier & McRoy 1989, Renaud *et al.* 2008b, Tamelander *et al.* 2008). D'importantes quantités de matière organique produites dans les couches de surface sont ainsi exportées vers le benthos, et ce, particulièrement au printemps, lorsque la production de microalgues

est plus importante que la consommation du zooplancton (Tamelander *et al.* 2006). Par exemple, en mer de Béring, le zooplancton et la boucle microbienne affectent peu la production phytoplanctonique dans la colonne d'eau, qui est ainsi largement exportée vers le fond marin et soutient une biomasse, une abondance et une diversité d'organismes benthiques élevées (Lovvorn *et al.* 2005). Ces organismes permettent par ailleurs un passage d'énergie vers les niveaux trophiques supérieurs, en servant de proies pour les animaux qui recherchent leur nourriture sur le fond marin comme certains oiseaux (eiders à lunettes) ou mammifères marins (phoques barbus, morses et baleines grises) (Grebmeier & McRoy 1989, Grebmeier *et al.* 2006, Iken *et al.* 2010). La période estivale contraste fortement avec le printemps, par la capacité de broutage du zooplancton sur le phytoplancton qui peut atteindre jusqu'à 97% de la production journalière de chlorophylle dans les eaux de surface de la mer de Barents (Tamelander *et al.* 2006), limitant ainsi l'exportation de carbone pour le benthos. En dehors des moments de productivité intense, la matière organique qui est exportée vers le benthos est principalement formée de pelotes fécales et de débris de zooplancton, de bactéries et de phyto-détritus qui sont autant de sources potentielles de nourriture additionnelles pour les organismes benthiques. L'activité bactérienne qui agit sur les particules exportées vers le fond affecte notamment la quantité mais aussi la qualité de la matière organique qui atteint le fond marin et soutient les communautés benthiques (Forest *et al.* 2010, Wassmann & Reigstad 2011). Dans les zones côtières et sur les plateaux continentaux, l'érosion côtière et les apports des rivières et des glaciers peuvent être des sources importantes de matière organique d'origine terrestre pouvant également servir aux réseaux trophiques benthiques (Dunton *et al.* 2006, Kędra *et al.* 2012, Kuliński *et al.* 2014). Néanmoins, ils limiteraient la production primaire pélagique en raison de la turbidité qui diminue la disponibilité en lumière pour les organismes autotrophes.

Par ailleurs, la quantité et la qualité de la matière organique utilisée par les organismes dépendent de leur capacité de sélection des particules alimentaires. Par exemple, les bivalves peuvent sélectionner des composants nutritifs de leur alimentation mais avec une efficacité dépendante de la taille des particules et variable suivant l'espèce de bivalve considérée, en fonction de la taille des cils qui permettent la capture des particules planctoniques. De plus il

existe une sélection active des aliments par les bivalves en fonction de la qualité et de la quantité des souces de nourriture. Les taux d'ingestion vont ainsi dépendre en partie de la taille et de la concentration des particules alimentaires dans le milieu (v. la revue de Ward & Shumway 2004).

LE COUPLAGE PÉLAGO-BENTHIQUE, QUELS SCÉNARIOS POSSIBLES ?

Le couplage pélago-benthique décrit l'ensemble des interactions pouvant avoir lieu entre la colonne d'eau (pélagos) et les fonds marins (benthos). Il peut s'agir d'échanges de nutriments, de matière organique dissoute et particulaire et le méroplancton. Le terme couplage pélago-benthique se limite, dans le cadre de cette thèse, aux interactions entre des consommateurs primaires (espèces de bivalves filtreurs) et la production primaire pélagique.

Le paradigme le plus largement accepté est que le couplage pélago-benthique est très fort pour la plupart des écosystèmes des plateaux continentaux arctiques, soutenant de grandes richesses spécifiques et biomasses benthiques dans plusieurs régions de l'Arctique (Grebmeier & Barry 1991, Ambrose & Renaud 1995, Hobson *et al.* 2002, Piepenburg 2005, Bluhm & Gradinger 2008). La plupart des études appuyant ce concept ont été réalisées dans des systèmes arctiques éloignés des côtes. Elles contribuent effectivement à apporter une meilleure compréhension des liens entre la production primaire pélagique et sympagique, la pression de broutage par le zooplancton sur cette production et enfin sur la dynamique des flux verticaux impactant la structure et la fonction des communautés benthiques (Grebmeier *et al.* 2006, Morata *et al.* 2008). Plus généralement, les régions couvertes saisonnièrement de glace, les zones en périphérie des glaces et les polynies sont caractérisées par un fort couplage pélago-benthique, comparativement aux endroits plus profonds du centre de l'océan Arctique (Piepenburg 2005). En effet, même si les algues de glace ne constituent qu'une faible part de la production primaire totale, elles sont une source importante dans la matière organique particulaire exportée vers les communautés benthiques au printemps (Grebmeier *et al.* 1995, Grebmeier *et al.* 2006). Les algues de glace ont été décrites comme des sources importantes

de haute qualité nutritive pour les communautés benthiques, notamment au début de la saison de production, avant que la production pélagique ne débute (Ambrose & Renaud 1997, Hargrave *et al.* 2002, Carroll & Carroll 2003). Il a par ailleurs été montré que les algues de glace sont préférentiellement utilisées et rapidement consommées par le benthos (McMahon *et al.* 2006). La nature et la force du couplage pélago-benthique varient spatialement en fonction de nombreux facteurs tels que : les processus physiques qui contrôlent la stratification, la couche de mélange des eaux et les concentrations en nutriments pour la production primaire, la turbidité des eaux, la biomasse et la composition spécifique des algues de glace et du phytoplancton, la composition spécifique et l'efficacité du broutage du zooplancton, l'intensité de la boucle microbienne, et la profondeur de la colonne d'eau qui traduit indirectement l'atténuation des flux verticaux de matière organique particulaire (Wassmann 1997, Dunton *et al.* 2005, Bluhm & Gradinger 2008). Par conséquent, toute perturbation modifiant l'amplitude et la synchronisation entre ces évènements physiques et biologiques a un impact potentiel sur l'intensité du couplage pélago-benthique en Arctique. En réponse aux changements des conditions environnementales induits par le réchauffement global de la planète, de nombreuses études prédisent une diminution de ce couplage pélago-benthique (Carroll & Carroll 2003, Piepenburg 2005, Grebmeier *et al.* 2006, Bluhm & Gradinger 2008, Wassmann 2011, Kedra *et al.* 2015). Plusieurs auteurs suggèrent ainsi que la fonte précoce de la glace annuelle favorisera la chaine trophique pélagique avec un fort couplage phytoplancton – zooplancton au lieu du couplage algues de glace – benthos qui est décrit actuellement dans plusieurs mers épicontinentales de l'Arctique (Carroll & Carroll 2003, Piepenburg 2005, Arrigo *et al.* 2008, Bluhm & Gradinger 2008, Wassmann & Reigstad 2011).

Par conséquent, la transition générale anticipée d'un couplage algues de glace – benthos vers un couplage phytoplancton – zooplancton dans les mers épicontinentales de l'océan Arctique aura un grand impact sur les communautés benthiques et il est donc attendu que les prédateurs d'organismes benthiques (p. ex. morses, phoques barbus) seront désavantagés par rapport aux prédateurs pélagiques (p. ex. poissons, baleines, oiseaux) (Carroll & Carroll 2003, Carmack & Wassmann 2006, Bluhm & Gradinger 2008).

L’abondance et la biomasse des espèces pélagiques, principalement le zooplancton, peuvent augmenter avec l'allongement de la période de production primaire dans la colonne d'eau. En contrepartie, les espèces associées à la glace devraient diminuer car elles seront plus fortement touchées par la hausse des températures et la perte d’habitat. Kedra *et al.* (2015) illustrent les changements possibles qui pourraient affecter la structure des réseaux trophiques le long d’un gradient de couverture de glace : des plateaux continentaux couverts de glace de mer saisonnièrement, de la zone marginale de glace où la glace multi-annuelle disparaît, et le haut arctique, couvert de glace de façon permanente (Figure 3).

Néanmoins, un retrait des glaces qui aurait lieu plus tôt dans la saison et une glace généralement plus mince pourraient entraîner une discontinuité entre le pic de production primaire et celui des consommateurs secondaires pélagiques tels que le zooplancton (Søreide *et al.* 2010, Leu *et al.* 2011). Le décalage temporel entre les floraisons d’algues de glace et d’algues pélagiques sera donc raccourci, ce qui entraîne un décalage potentiel entre la prolifération de phytoplancton et le développement ontogénétique contrôlé par la température de zooplancton tel que *Calanus glacialis* (Søreide *et al.* 2010). Cette hypothèse de décalage temporel entre les floraisons algales et le développement du zooplancton aurait un impact majeur sur la chaîne pélagique, les copépodes étant considérés comme une espèce clé des écosystèmes arctiques, soutenant de nombreux consommateurs de niveaux trophiques supérieurs. Cependant, une quantité plus importante de matière organique pourrait atteindre le fond marin et apporter l’énergie nécessaire aux réseaux trophiques benthiques.

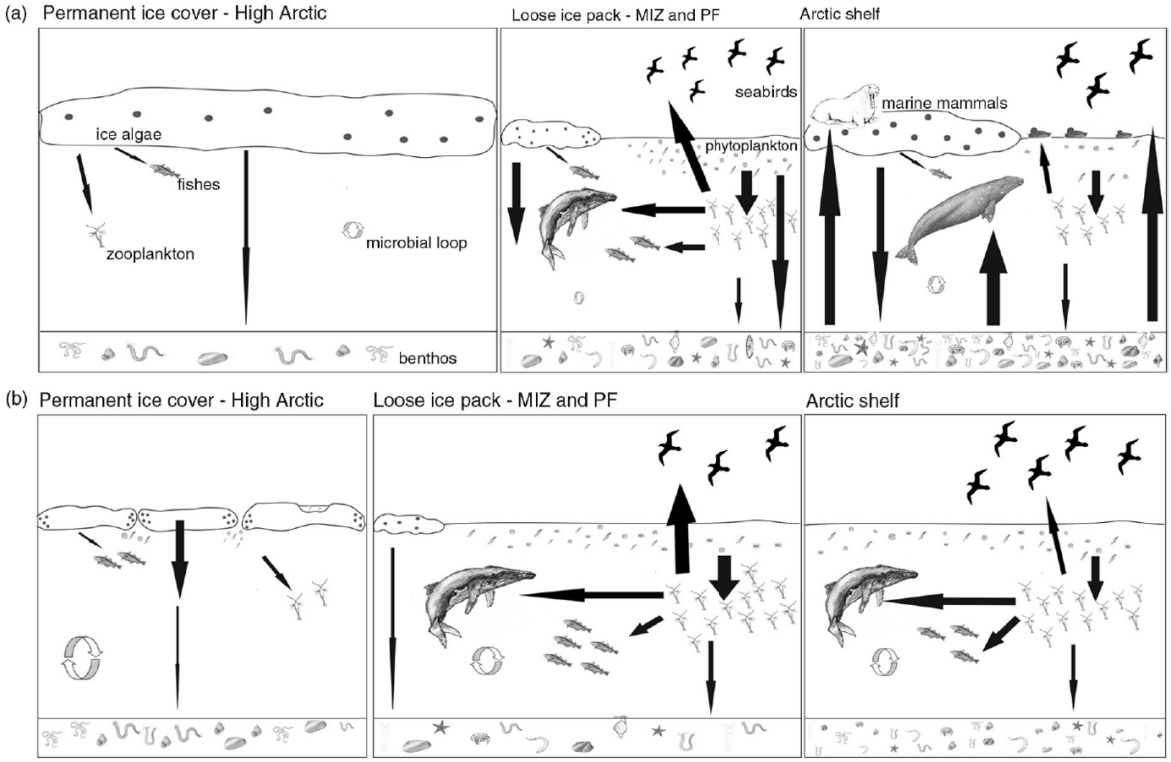

Figure 3. Réseaux trophiques actuels (a) et prédits (b) sur le plateau continental arctique, la zone marginale de glace (MIZ), le front polaire (PF), et le haut arctique avec un couvert de glace permanent. La taille du cadre des images en (b) reflète l'importance des changements prévus dans chaque zone. Image tirée de Kedra *et al.* (2015)

Une deuxième hypothèse a été avancée sur la base d'observations faites à une échelle locale dans le fjord Young Sound (NE Groenland). Cette hypothèse estime qu'actuellement la production d'algues de glace est négligeable et que l'unique prolifération phytoplanctonique survenant au cours de la courte période libre de glace domine largement la production primaire totale. Les copépodes sont responsables de plus de 80% du broutage sur le phytoplancton, et plus de 90% de l'exportation verticale annuelle de la matière organique se produit au moment de la courte période d'eaux libres de glace (Figure 4a). L'augmentation des températures et la diminution du couvert de glace peuvent étendre la saison de production primaire (Tremblay & Gagnon 2009, Slagstad *et al.* 2011) permettant le développement et la succession plus complexe des espèces de plancton (Rysgaard *et al.*

1999). L'intensification de la stratification de la colonne d'eau devrait favoriser les populations de phytoplancton de petite taille (Ardyna *et al.* 2011). Suivant ce scénario, la communauté de zooplancton devrait donc changer d'une dominance de copépodes à une succession bimodale d'espèces zooplanctoniques avec un premier pic principalement formé de copépodes calanoïdes au printemps et un second pic de protozooplancton (ciliés et dinoflagellés hétérotrophes) et de petites espèces de copépodes à la fin de l'été (Levinsen & Nielsen 2002, Riisgaard *et al.* 2014). L'exportation verticale de matière organique serait donc améliorée avec deux épisodes de transfert intense au printemps et à l'automne (Figure 4b) et serait synonyme d'un fort couplage pélago-benthique (Rysgaard & Glud 2007).

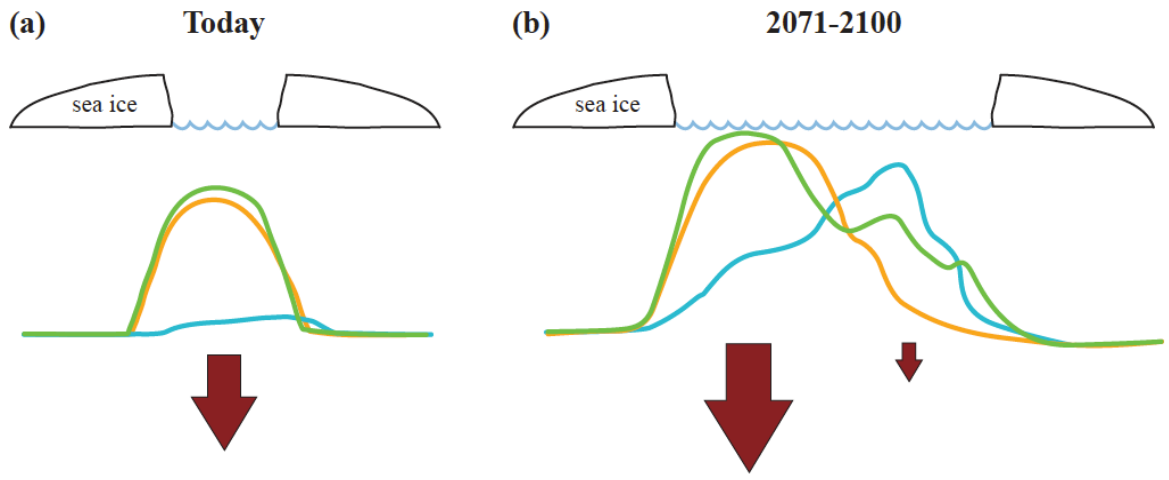

Figure 4. Modèle conceptuel des conditions (a) actuelles et (b) futures de la couverture de la glace de mer, de la production primaire (courbe verte), du broutage exercé par les copépodes (courbe orange) et le protozooplancton (courbe bleue) ainsi que l'exportation verticale vers le benthos (flèches) dans le fjord Young Sound. Image tirée de Rysgaard & Glud (2007)

ESTIMER LES APPORTS DE NOURRITURE AU BENTHOS

Identifier le régime alimentaire des organismes benthiques est essentiel pour caractériser les interactions trophiques et ainsi estimer au niveau des communautés les conséquences des changements biotiques et abiotiques. Dans le milieu marin, l'observation directe de l'alimentation est souvent difficile, voire impossible, de sorte que des méthodes indirectes ont été développées pour étudier les sources de nourriture des organismes. Parmi elles, l'analyse des contenus stomacaux ou des pelotes fécales a largement été utilisée, mais ces méthodes sous-estiment l'importance des aliments réellement ingérés alors qu'elles surestiment les aliments récemment consommés (Jobling 1987, Carss & Parkinson 1996). À l'inverse l'analyse de traceurs biochimiques tels que les acides gras (FA) ou les isotopes stables (SI) ont l'avantage de fournir des informations moins biaisées sur les sources réelles d'alimentation, et ce, sur une échelle de temps plus grande (quelques semaines) (Iverson *et al.* 2004).

Les acides gras marqueurs trophiques

Les FA sont les principaux composants lipidiques de tout organisme vivant et représentent une des plus importantes molécules transférées entre les différents niveaux trophiques au sein des écosystèmes aquatiques (Müller-Navarra *et al.* 2000). Les lipides se divisent en deux catégories, les lipides neutres et les lipides polaires (NL et PL, respectivement). Les NL servent principalement de réserve énergétique (incluant les triglycérides, cétones, cires estérifiées et acides gras libres) pour soutenir le métabolisme et la croissance des organismes, alors que les PL (essentiellement des phospholipides) ont un rôle structurel et fonctionnel puisqu'ils sont les constituants majoritaires des membranes cellulaires (Bergé & Barnathan 2005). L'utilisation des acides gras marqueurs trophiques (FATM) est basée sur l'observation suivante : les producteurs primaires marins se caractérisent par des profils en FA spécifiques qui peuvent être transférés de façon

conservatrice dans les réseaux trophiques aquatiques (Dalsgaard *et al.* 2003). Ainsi, ils peuvent être reconnus dans la fraction lipidique neutre de leurs consommateurs primaires (Dalsgaard *et al.* 2003, Bergé & Barnathan 2005). Parmi ces consommateurs primaires, les bivalves sont capables de synthétiser *de novo* des acides gras saturés et monoinsaturés (SFA et MUFA, respectivement), dont le signal va, de ce fait, souvent se confondre avec les SFA et MUFA procurés par les ressources trophiques sauf pour les SFA ramifiés (structure iso ou antéiso) qui sont des marqueurs typiques des bactéries (Dalsgaard *et al.* 2003). En revanche, les bivalves ne peuvent pas synthétiser les précurseurs 18:2ω6 (acide linoléique) et le 18:3ω3 (acide α-linolénique). De plus, ils ont une capacité très limitée à synthétiser des acides gras polyinsaturés (PUFA) en raison de l'activité réduite d'élongases et de désaturases spécifiques (désaturases Δ12 et Δ15 notamment, Figure 5a) permettant la conversion des précurseurs en acides gras essentiels (EFA), tels que les acides arachidonique (AA, 20:4ω6), eicosapentanoïque (EPA, 20:5ω3) et docosahexaénoïque (DHA, 22:6ω3) (De Moreno *et al.* 1976, Waldock & Holland 1984, Chu & Greaves 1991, Fernández-Reiriz *et al.* 1998, Pirini *et al.* 2007, Glencross 2009). Les microalgues qui possèdent la machinerie enzymatique nécessaire à la production de ces PUFA constituent ainsi les principales sources de 18:2ω6, 18:3ω3, et de PUFA à 20 et 22 carbones (Figure 5b) (Viso & Marty 1993, Zhukova *et al.* 1998) pour les bivalves. Ces derniers doivent donc aller chercher dans leur alimentation les PUFA et EFA nécessaires pour répondre à leurs besoins physiologiques, leur survie, leur croissance et leur reproduction (Chu & Greaves 1991). La composition lipidique et les profils en FA de différents groupes de microalgues ont donc été largement étudiés afin d'être utilisés comme signature taxonomique pour différencier les principaux producteurs primaires dans les milieux marins (Ackman *et al.* 1968, Viso & Marty 1993, Zhukova & Aizdaicher 1995). Par exemple, les diatomées sont riches en EPA (Napolitano *et al.* 1997) et en FA insaturés à 16 carbones. La voie de biosynthèse pour produire le 16:4ω1 à partir du 16:0 est caractéristique de ce groupe de microalgues (Dalsgaard *et al.* 2003). Les dinoflagellés, ainsi que les flagellés, sont souvent dominés par le DHA et des PUFA à 18 carbones tels que le 18:4ω3 (Budge & Parrish 1998, Mansour *et al.* 1999, Dalsgaard *et al.* 2003). Parmi les autres sources possibles de nourriture pour le benthos, se trouvent les bactéries et le zooplancton.

Les FA avec un nombre de carbones impairs et/ou ramifiés (15:0, 17:0, iso- et anteiso- SFA) sont caractéristiques des bactéries (Viso & Marty 1993, Budge & Parrish 1998) et indiquent ainsi une contribution de bactéries hétérotrophes dans les sédiments, la matière organique en suspension, et l'alimentation animale (Meziane & Tsuchiya 2002, Dalsgaard *et al.* 2003). Les MUFA à longue chaîne carbonée (20:1 et 22:1) sont généralement produits et accumulés dans les copépodes. Ils correspondent aux FA dominants chez ces organismes et peuvent donc être utilisés comme traceurs pour les identifier chez les consommateurs (Dalsgaard *et al.* 2003, Kelly & Scheibling 2012). La méthode des FATM a été ainsi largement utilisée pour décrire les réseaux trophiques pélagiques, notamment pour identifier le phytoplancton et caractériser le régime alimentaire d'organismes zooplanctoniques (Dalsgaard *et al.* 2003, Søreide *et al.* 2008). Cependant, contrairement aux systèmes pélagiques, pour lesquels le phytoplancton est la principale source de production primaire, les réseaux trophiques benthiques s'appuient sur de nombreuses sources potentielles de nourriture complexifiant d'autant plus l'analyse trophique de ces systèmes. Des microalgues et des bactéries sont exportées vers le fond depuis la colonne d'eau, s'ajoutant à des producteurs primaires tels que les macroalgues et les plantes vasculaires (Dalsgaard *et al.* 2003). La caractérisation de la ressource *via* l'étude des marqueurs trophiques peut alors s'avérer délicate puisqu'un même FA peut être associé à plusieurs types d'organismes (Tableau 1). Par exemple, l'EPA est un indicateur de diatomées, mais aussi de macroalgues brunes et rouges ; l'AA se retrouve à la fois chez les algues brunes et les algues rouges ; enfin, le 18:3ω3 est présent chez les macroalgues vertes et brunes, et les plantes vasculaires. C'est pourquoi, dans le but de limiter les biais liés à l'attribution d'un FA à une source donnée, il est indispensable d'échantillonner l'ensemble des sources de nourriture potentielles en même temps que les consommateurs dans le milieu concerné. L'interprétation d'un unique FA comme traceur de producteurs primaires doit néanmoins être faite avec précaution (Dalsgaard *et al.* 2003).

En milieu naturel, la ressource trophique est très souvent limitée, notamment dans les systèmes arctiques qui sont caractérisés par une forte saisonnalité et une hétérogénéité spatiale très marquée. Les organismes marins présentent toutefois la capacité de biosynthétiser *de novo* des PUFA particuliers (Figure 5c) : les FA non maloniques ('*non-*

methylene interrupted', NMI) (Paradis & Ackman 1977, Zhukova 1986, Barnathan 2009, Monroig *et al.* 2013). Bien que leur rôle et leur fonction biologiques ne soient pas encore bien compris chez les bivalves, leur prédominance dans les PL suggère qu'ils pourraient être importants pour la structure et la fonction des membranes (Kraffe *et al.* 2004), constituant des PUFA alternatifs pour compenser de faibles apports en EFA par la nourriture (Klingensmith 1982, Zhukova 1991, Pernet *et al.* 2006).

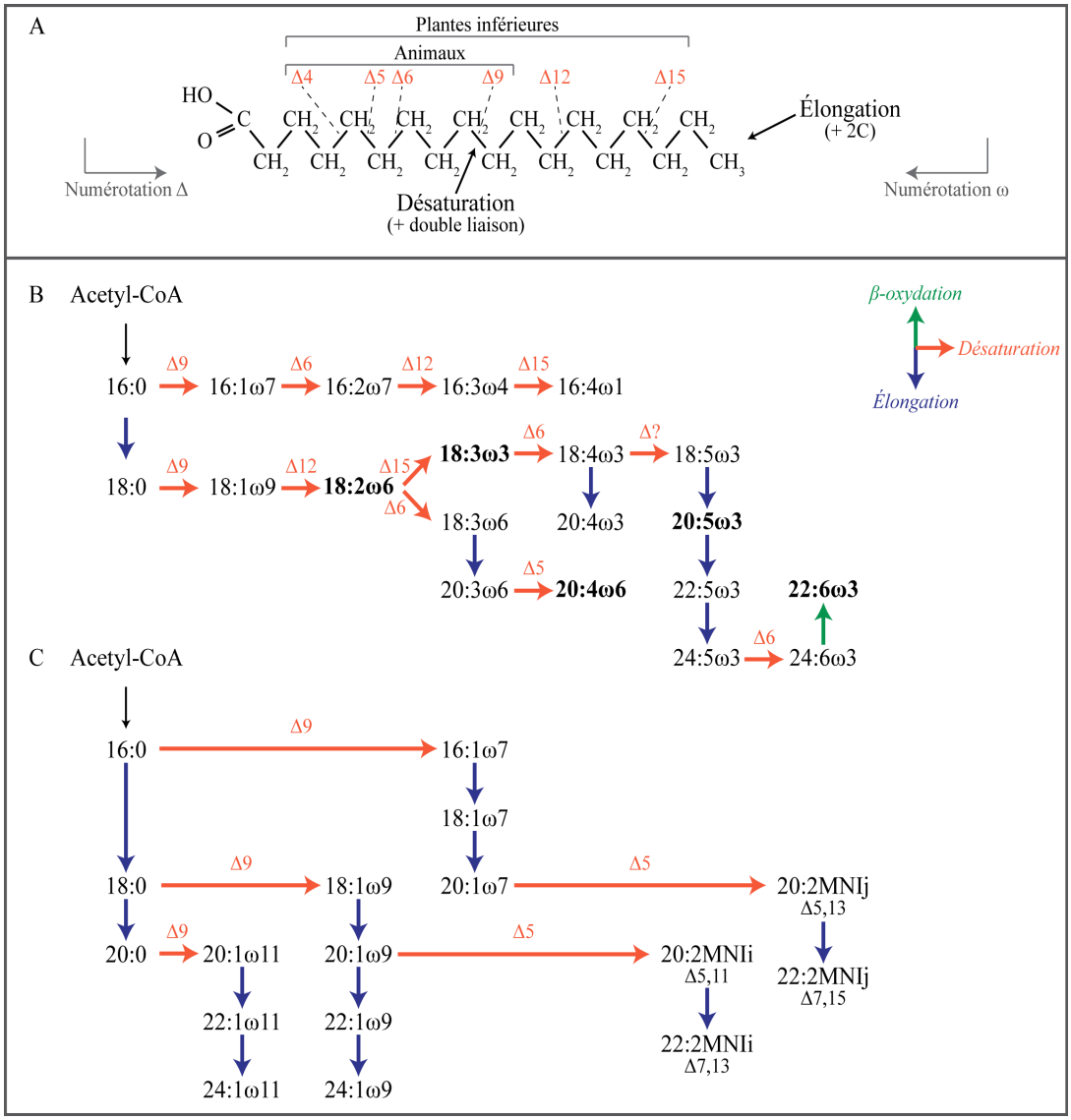

Figure 5. (A) Détail des enzymes désaturases présentes chez les animaux et les plantes inférieures et de leur action sur un acide gras (18:0) et patrons de biosynthèse des acides gras chez (B) les producteurs primaires, et (C) les bivalves. Les acides gras essentiels sont indiqués en **gras**. Extrait et adapté de Dalsgaard *et al.* (2003) et références incluses, et de Zhukova (1991) pour la synthèse des acides gras non maloniques (NMI)

Tableau 1. Liste non exhaustive des acide gras marqueurs trophiques (FATM) utilisés dans les études trophiques

Source	FATM	Références
Bactéries	*iso-* et *anteiso-* SFA, 16:1ω7, 18:1ω7	Viso & Marty (1993), Kharlamenko *et al*. (1995), Budge & Parrish (1998), Stevens *et al*. (2004a)
Détritus	SFA	Fahl & Kattner (1993)
Diatomées	16:1ω7, 16:4ω1, C_{16} PUFA, EPA	Viso and Marty (1993), Napolitano *et al*. (1997), Reuss & Poulsen (2002), Søreide *et al*. (2008), Kelly & Scheibling (2012)
Dinoflagellés	DHA, 18:4ω3, 18:1ω9	Napolitano *et al*. (1997), Mansour *et al*. (1999) , Søreide *et al*. (2008), Kelly & Scheibling (2012)
Phaeocystis spp.	14:0, 16:0, 18:0, 18:1ω9	Claustre *et al*. (1990), Nichols *et al*. (1991), Cotonnec *et al*. (2001), Reuss & Poulsen (2002)
Copépodes	20:1, 22:1	Dalsgaard *et al*. (2003), Lee *et al*. (2006)
Algues vertes	18:3ω3, 18:2ω6, 16:4ω3	Graeve *et al*. (2002), Li *et al*. (2002), Kelly & Scheibling (2012), Wessels *et al*. (2012)
Algues brunes	18:4ω3, AA, EPA, 18:1ω9	Graeve *et al*. (2002), Li *et al*. (2002), Kelly & Scheibling (2012), Wessels *et al*. (2012)
Algues rouges	16:0, EPA	Graeve *et al*. (2002), Li *et al*. (2002), Kelly & Scheibling (2012)

SFA : acides gras saturés ; PUFA : acides gras polyinsaturés ; AA : acide arachidonique (20:4ω6) ; EPA : acide eicosapentanoïque (20:5ω3) ; DHA : acide docosahexaénoïque (22:6ω3)

Les isotopes stables

La méthode du traçage isotopique repose sur les mesures d'abondance naturelle des isotopes stables de certains éléments chimiques dont les plus utilisés en écologie trophique sont le carbone (^{13}C) et l'azote (^{15}N). En écologie trophique, les isotopes stables sont souvent employés pour comprendre la structure des réseaux trophiques car considérés comme des marqueurs efficaces permettant de déterminer l'origine des sources alimentaires et le niveau trophique des espèces (DeNiro & Epstein 1978, 1981, Minagawa & Wada 1984, Cabana & Rasmussen 1996, Post 2002). En effet, la composition isotopique des producteurs primaires dépend des sources de carbone et d'azote disponibles ainsi que des voies métaboliques utilisées lors de l'assimilation de ces éléments. Il en résulte que les grandes classes de producteurs primaires possèdent des signatures isotopiques distinctes, notamment en terme de carbone (p. ex. Hobson *et al.* 2002). A chaque réaction physique, chimique ou biologique, l'isotope léger (^{12}C, ^{14}N) est préférentiellement utilisé par le métabolisme conduisant à un enrichissement de la matière organique en isotope lourd (^{13}C, ^{15}N). Cet enrichissement crée alors une différence de composition isotopique entre la source et son consommateur, définissant le principe du fractionnement isotopique (Peterson & Fry 1987). L'enrichissement en ^{13}C permet d'identifier les sources consommées alors que l'enrichissement en ^{15}N correspond à l'augmentation du niveau trophique (Peterson & Fry 1987, Vander Zanden & Rasmussen 2001, Post 2002). Ainsi, l'utilisation couplée des isotopes stables du carbone et de l'azote permet de comparer les signatures isotopiques des sources potentielles et des consommateurs afin de déterminer par une approche qualitative et quantitative les processus trophiques dans de nombreux systèmes (Peterson & Fry 1987).

Le traçage isotopique révèle cependant certaines limites dans son application à l'étude des relations trophiques. Si la détermination du fractionnement isotopique entre une source et son consommateur apparaît comme primordiale (DeNiro & Epstein 1978, 1981, Peterson & Fry 1987, Post 2002), il s'avère que le degré de fractionnement varie en fonction de plusieurs facteurs (groupes taxonomiques, sources, physiologie...) et est encore aujourd'hui soumis à débat (p. ex. Dubois *et al.* 2007, Martínez del Rio *et al.* 2009). De plus il a été

montré que les méthodes de traitement et d'analyse des échantillons peuvent induire des biais dans les facteurs de fractionnement (McCutchan *et al.* 2003). Par ailleurs, l'identification des sources et la quantification de leurs contributions à travers l'analyse de la composition isotopique d'un consommateur se réalisent de plus en plus à l'aide de modèles de mélange mixte qui requièrent les signatures isotopiques de toutes les sources disponibles pour ce consommateur. Cependant, l'échantillonnage de toutes les sources de matière organique est parfois difficile ou restreint par les possibilités techniques et la validité des résultats issus des modèles de mélange deviennent incertains avec l'augmentation du nombre de sources.

Analyse isotopique de composés spécifiques

Comme mentionné plus haut, les eaux arctiques abritent deux groupes principaux de producteurs primaires : les algues de glace qui vivent en dessous et à l'intérieur même de la glace de mer, et le phytoplancton qui se développe classiquement dans les eaux libres de glace. Les profils en FA des algues de glace et du phytoplancton ainsi que leurs compositions isotopiques ont été utilisés pour mieux comprendre l'écologie trophique de consommateurs dans de nombreuses mers arctiques (p. ex. Falk-Petersen *et al.* 1998, Auel *et al.* 2002, Budge *et al.* 2007, Feder *et al.* 2011, Mayzaud *et al.* 2013). Grâce à l'augmentation de la disponibilité en lumière (Gradinger *et al.* 2009) et d'un milieu où le carbone est limitant dans les canaux fermés de la glace de mer (Schubert & Calvert 2001, Kennedy *et al.* 2002), la matière organique particulaire associée à la glace de mer est enrichie en ^{13}C (le ratio isotopique du carbone, $\delta^{13}C$, est alors plus élevé) par rapport à la matière organique particulaire dérivée du phytoplancton (Hobson *et al.* 1995, Schubert & Calvert 2001, Gradinger 2009).

La combinaison des méthodes d'isotopie et de FATM a conduit à l'analyse de l'isotope stable du carbone sur des FA spécifiques ($\delta^{13}C_{FA}$), le plus souvent marqueurs de diatomées. Cette technique a été essentiellement utilisée dans le but de différencier les diatomées sympagiques des diatomées pélagiques et de déterminer leur contribution relative pour les

consommateurs primaires en Arctique (Budge *et al.* 2008). L'étude des valeurs de $\delta^{13}C$ des FA 16:4ω1 et EPA (20:5ω3) montre qu'elles sont plus élevées pour les algues de glace par rapport au phytoplancton.

SUIVI À LONG TERME DES CHANGEMENTS DE PRODUCTION PRIMAIRE

L'analyse de la composition isotopique et des FATM des tissus ne fournissent des informations sur le régime alimentaire des organismes qu'à court terme (quelques semaines). D'autres techniques doivent donc être envisagées afin d'acquérir des données à plus long terme (plusieurs années ou décennies) afin de suivre les changements que peuvent connaître les écosystèmes arctiques notamment sur la dynamique de la production primaire. Des observations et des collectes de données sur des échelles de temps suffisamment grandes sont ainsi cruciales. Cependant, en raison de sa localisation, des conditions difficiles qui y règnent, ainsi que des coûts relatifs aux campagnes océanographiques, il est compliqué d'étudier une grande partie des régions arctiques. Les systèmes d'observation et d'enregistrement des paramètres environnementaux y sont encore peu nombreux et difficiles à mettre en place (Morison *et al.* 2002). Par conséquent, ils ne fournissent actuellement que peu de données et dans des secteurs limités. Dans ce contexte, l'utilisation de proxies[1] au sein d'archives naturelles est une alternative intéressante pour étendre le suivi instrumenté du climat et de l'environnement sur des échelles de temps et d'espace plus grandes.

Un proxy est une variable, le plus souvent géochimique, dont la valeur est fonction d'un paramètre environnemental tel que la température, la salinité, la concentration en nutriments, l'oxygène ou le dioxyde de carbone, la vitesse des vents ou la productivité (Wefer *et al.* 1999). Les archives naturelles de la variabilité du climat et de l'environnement sont le plus souvent caractérisées par une croissance s'effectuant par dépôts successifs de matériel.

[1] Ce terme, bien qu'étant un anglicisme, sera utilisé continuellement dans la suite du manuscrit. Au singulier, nous parlerons de 'proxy'.

Lorsque la périodicité de ces marques de croissance est connue, il est alors possible de dater chacune d'entre elles et de replacer ainsi les variations du proxy étudié sur une échelle de temps. En milieu continental, les archives les plus couramment utilisées sont les arbres, les glaciers, les sédiments lacustres et les spéléothèmes (stalactites et stalagmites). En milieu océanique, les sédiments et les squelettes carbonatés d'organismes marins (coquilles, otolithes, coraux, algues corallines) sont les plus étudiés (Schöne & Gillikin 2013). Les coquilles de bivalves sont ainsi de plus en plus utilisées pour la reconstruction paléoenvironnementale (Gordillo *et al.* 2014). En effet, les bivalves regroupent de nombreux critères pour être de bons enregistreurs du climat (Goodwin *et al.* 2001, Schöne *et al.* 2005) :

- De part leur sédentarité, ils enregistrent finement les variations de leur habitat comme la température et la salinité mais aussi les sources d'alimentation et les pollutions;
- Les variations des taux de croissance (sclérochronologie) et certaines propriétés chimiques de la coquille (sclérochimie) résultent des variations de paramètres environnementaux;
- Le dépôt successif de couches de carbonates de calcium ($CaCO_3$) au cours de la croissance de l'animal produit en alternance des stries d'arrêt de croissance et des incréments de croissance;
- Certaines espèces, longévives, s'avèrent particulièrement adaptées pour les reconstructions des conditions environnementales à très long terme (plusieurs décennies);
- Enfin, les bivalves présentent une très large distribution biogéographique, des pôles à l'équateur, et bathymétrique.

Au cours des dernières années, les coquilles de bivalves ont largement servi de bio-archives permettant de réaliser des reconstructions paléoenvironnementales de la température de l'eau (Jones 1981, Goodwin *et al.* 2003, Schöne *et al.* 2004, Schöne *et al.* 2011, Royer *et al.* 2013), de la circulation océanique (Ambrose *et al.* 2006, Wanamaker *et al.* 2008b, Butler *et al.* 2013, Carroll *et al.* 2014), d'oscillations climatiques telles que l'oscillation nord-atlantique (NAO) (Schöne *et al.* 2003) ou El Niño – oscillation australe

(ENSO) (Carré *et al.* 2005, Brey *et al.* 2011), des débits fluviaux et de la salinité (Mueller-Lupp *et al.* 2003, Dettman *et al.* 2004, Simstich *et al.* 2005b, Carroll *et al.* 2009), ou encore de pollutions (Gillikin *et al.* 2005). En outre, ces coquilles fournissent de nombreuses données biologiques, relatives notamment à la longévité des bivalves (Garcia-March & Marquez-Aliaga 2007, Wanamaker *et al.* 2008a), à leur métabolisme (Lorrain *et al.* 2004), aux taux de calcification (Lorrain *et al.* 2005, Carré *et al.* 2006, Thébault *et al.* 2009b), aux périodes de croissance (Schöne *et al.* 2005), mais également à celle du recrutement (Richardson *et al.* 2004).

Dans un but de suivi des ressources trophiques des organismes benthiques et du couplage pélago-benthique, la composition isotopique et élémentaire des coquilles de bivalves peut être utilisée comme proxy de la dynamique de la production primaire sur plusieurs années ou décennies suivant la longévité de l'organisme étudié. Les variations des rapports $^{13}C/^{12}C$ (Dettman *et al.* 1999) et Ba/Ca (Stecher *et al.* 1996, Vander Putten *et al.* 2000, Elliot *et al.* 2009, Thébault *et al.* 2009a), ainsi que Li/Ca pour les espèces dont les coquilles sont calcitiques (Thébault & Chauvaud 2013) peuvent effectivement refléter la dynamique de la production primaire, dominées par des diatomées.

L'utilisation de tels proxies n'est justifiée que si une chronologie précise des variations des traceurs géochimiques archivés dans la coquille des bivalves au cours de leur croissance peut être établie. La présence des stries périodiques et de périodicité connue dans (ou sur) la coquille conditionne alors leur utilisation éventuelle comme repères temporels. Plusieurs méthodes peuvent être utilisées pour déterminer la périodicité de formation des marques de croissance présentes dans les coquilles de bivalves, notamment la technique de capture-marquage-recapture en milieu naturel. Cette méthode, permettant de mettre en relation le nombre de stries formées avec le temps écoulé entre les deux captures, a permis de valider la formation annuelle des marques de croissance chez le bivalve *Hiatella arctica* au nord-est du Groenland (Sejr *et al.* 2002). L'utilisation d'un marquage chimique à l'aide de fluorochromes (calcéine) a également pu révéler que les marques de croissance chez les bivalves polaires

Serripes groenlandicus et *Ciliatocardium ciliatum* étaient déposées annuellement (Ambrose *et al.* 2012).

Ces techniques servent plus particulièrement à valider le rythme de croissance de bivalves à courte durée de vie et présentant un taux de croissance relativement rapide mais sont peu adaptées aux bivalves longévifs à faible taux de croissance. L'augmentation du carbone radioactif (ou radiocarbone, ^{14}C) produit par les essais nucléaires atmosphériques dans les années 1950 et 1960 offre l'une des meilleures approches disponibles pour confirmer l'âge et le rythme de croissance des organismes marins longévifs tels que les coraux, les bivalves et les poissons (Kalish 1995, Campana 2001, Kilada *et al.* 2007, Campana *et al.* 2008, Sherwood & Edinger 2009). La technique a en effet été utilisée avec succès pour confirmer les estimations d'âge de plusieurs espèces de poissons (Campana & Jones 1998, Campana 2001), coraux (Sherwood & Edinger 2009) et bivalves (Weidman & Jones 1993).

Les essais nucléaires atmosphériques conduits dans les années 1950 et 1960 ont entrainé une augmentation marquée et généralisée du radiocarbone (^{14}C) dans l'atmosphère et l'océan, facilement détectable dans les squelettes carbonatés des organismes marins. La concentration en ^{14}C dans l'atmosphère a ainsi doublé, atteignant un niveau maximal en 1963 (Figure 6). Les concentrations maximales de carbone radioactif ont été retardées et n'ont été observées qu'à la fin des années 1960 ou au début des années 1970, résultat de l'augmentation progressive de la concentration en ^{14}C dans les eaux marines de surface par les apports fluviaux, les précipitations et les échanges de CO_2 avec l'atmosphère. L'année exacte à laquelle le radiocarbone atteint son maximum et commence à décliner diffère d'un lieu à un autre dans les océans, dépendamment des temps de résidence et de la circulation des masses d'eau qui affectent le mélange des eaux de fond pauvres en ^{14}C et les eaux de surface enrichies en ^{14}C (Weidman & Jones 1993).

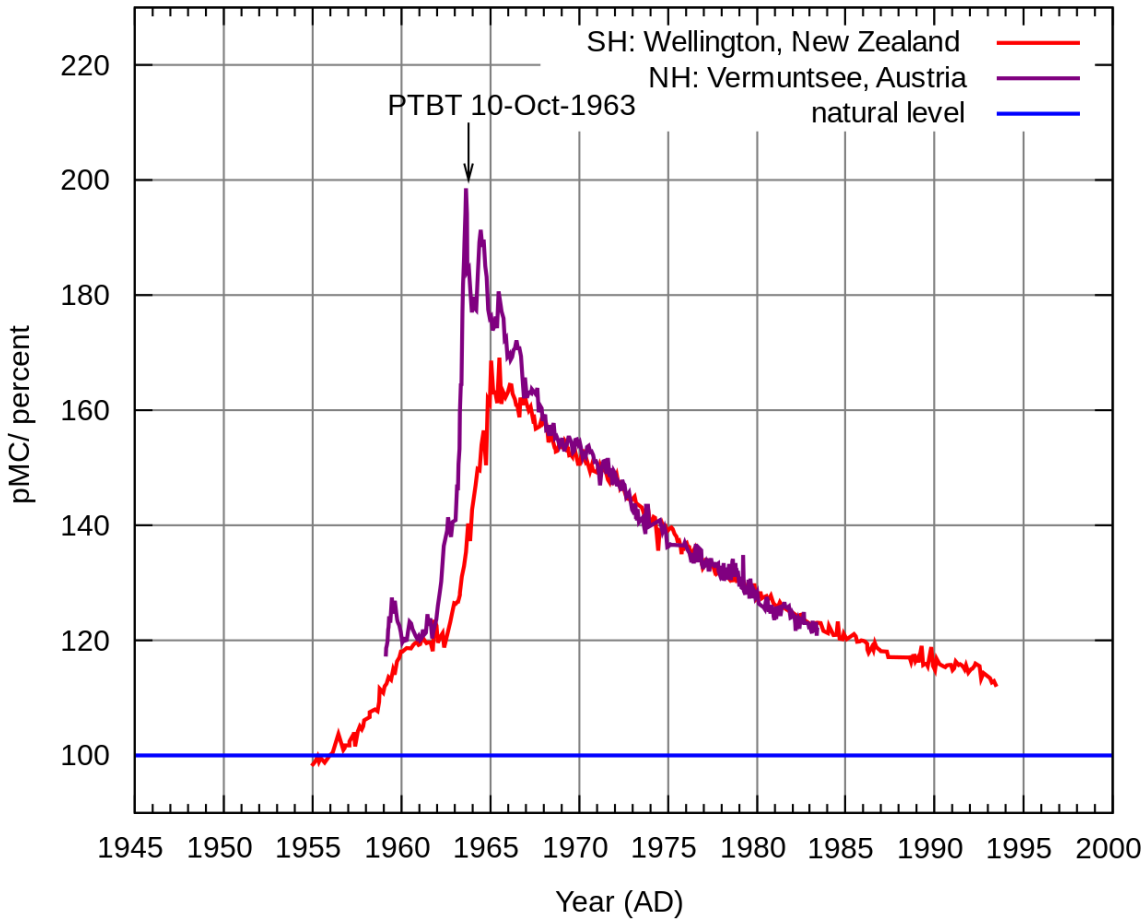

Figure 6 : Augmentation de la concentration en ^{14}C atmosphérique dans l'hémisphère nord et l'hémisphère sud suite aux essais nucléaires

OBJECTIF GÉNÉRAL

Ce projet de recherche s'insère dans les programmes B.B. Polar et Sclerarctic qui visent à utiliser des bivalves marins comme archives biologiques des variations environnementales de l'océan Arctique en analysant les signaux environnementaux qui peuvent être inscrits dans leurs coquilles au cours de leur croissance afin d'obtenir des enregistrements des conditions passées. L'utilisation de telles bio-archives peut ainsi permettre de reconstruire les paramètres de l'environnement arctique à différentes échelles spatiales (du fjord à une échelle pan-arctique) et sur une échelle temporelle importante (jusqu'à un siècle) grâce à l'étude de bivalves longévifs du genre *Astarte spp*.

L'objectif général du présent projet est de déterminer et suivre les changements potentiels des sources d'alimentation des organismes benthiques par l'étude de trois espèces de bivalves filtreurs dominants les communautés benthiques de l'archipel arctique canadien, *Bathyarca glacialis*, *Astarte elliptica* et *Astarte moerchi*, afin de mieux définir le couplage pélago-benthique dans cette région. En raison de sa longévité et de sa faible mobilité, le benthos est considéré comme un bon intégrateur des conditions environnementales (Snelgrove & Butman 1994, McArthur *et al.* 2010). *Bathyarca glacialis* (Gray, 1824) et *Astarte* spp. présentent une très large distribution géographique et bathymétrique. Ces bivalves se rencontrent des régions arctiques à subarctiques, dans des eaux peu profondes jusqu'aux systèmes bathyaux (Oliver & Allen 1980) et peuvent dominer les communautés benthiques (Roy *et al.* 2014). *B. glacialis* et *Astarte* spp. ont été décrits comme filtreurs et déposivores de surface (Iken *et al.* 2005, Renaud *et al.* 2011, Roy *et al.* 2014). Compte tenu de leur large répartition et de leur mode alimentaire, ces deux espèces de bivalves sont des modèles idéaux pour étudier la dynamique des ressources trophiques ainsi que la nature et la force de couplage pélagique-benthique dans des systèmes arctiques contrastés par l'analyse de leurs tissus et de leurs coquilles. Par sa longévité (jusqu'à un siècle, Torres *et al.* 2011) *Astarte* spp. semble particulièrement bien adapté pour la reconstruction des conditions environnementales passées.

Plus spécifiquement, la thèse est divisée en trois chapitres qui présentent à différentes profondeurs (systèmes côtier et bathyal) et à différentes échelles de temps (du saisonnier à des décennies) les sources de nourriture utilisées par ces deux espèces de bivalves en utilisant différents outils permettant la caractérisation et le suivi des sources de production primaire (biomarqueurs et proxies). Les chapitres de la thèse se positionnent selon la Figure 7, ci-dessous.

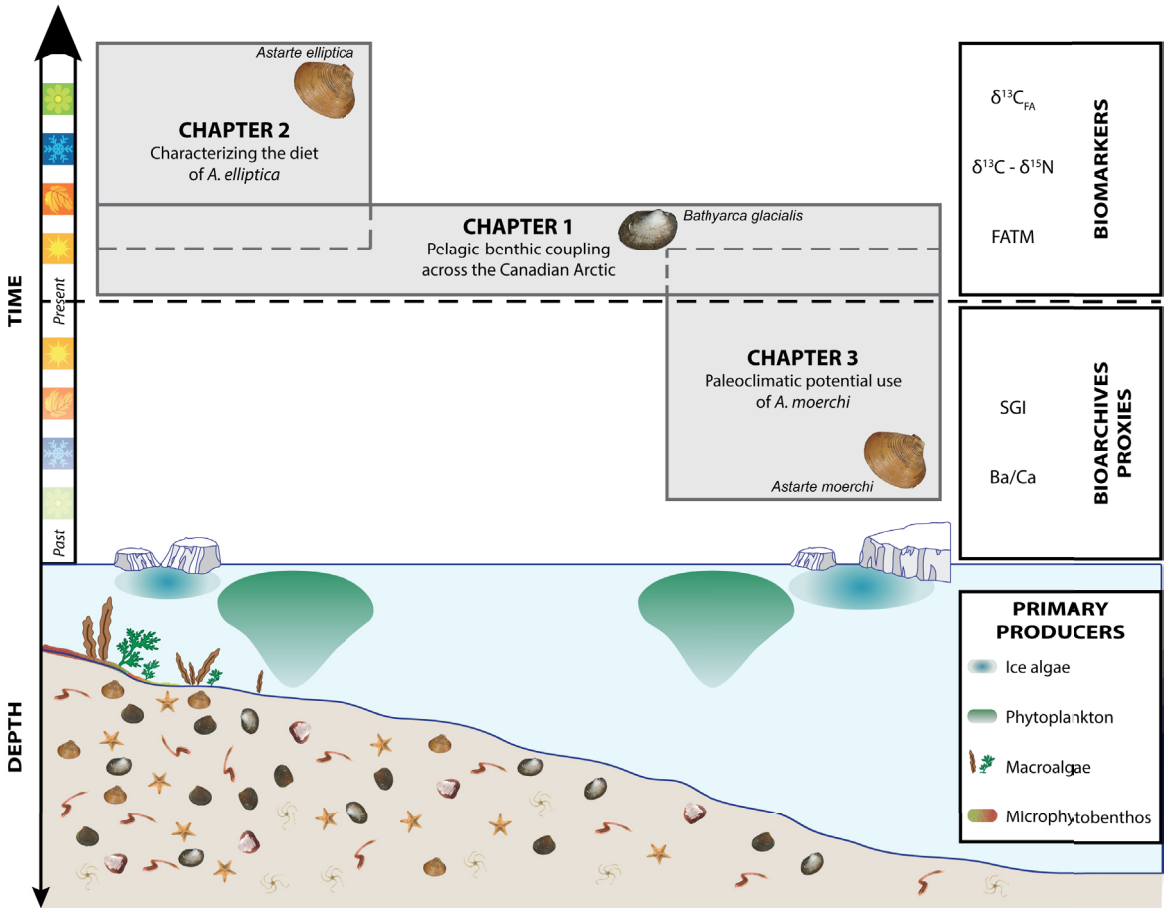

Figure 7. Représentation schématique de la structure de la thèse selon la profondeur étudiée, l'échelle temporelle considérée, et les sources potentielles de nourriture disponibles pour les bivalves afin de définir à l'aide de traceurs la dynamique de la production primaire en Arctique et leurs effets éventuels sur le benthos (couplage pélago-benthique)

OBJECTIFS ET HYPOTHÈSES SPÉCIFIQUES

Chapitre 1 : Traceurs alimentaires dans Bathyarca glacialis de régions trophiques contrastées de l'Arctique canadien

L'objectif principal de ce premier chapitre est d'étudier la nature et la force du couplage pélago-benthique dans des environnements trophiques contrastés (oligotrophique et eutrophique) de l'archipel arctique canadien. Quatre régions caractérisées par des régimes de production primaire différents sont étudiées : le sud-est de la mer de Beaufort, et le détroit de Victoria, décrits comme des régions oligotrophes dominées par des flagellés, et le détroit de Lancaster et le nord de la baie de Baffin, systèmes eutrophes où les diatomées sont dominantes. Par l'utilisation de la méthode des acides gras marqueurs trophiques (FATM), les sources principales de nourriture pour le bivalve *Bathyarca glacialis* sont déterminées et le couplage pélago-benthique dans l'archipel arctique canadien est décrit. Les hypothèses suivantes sont testées : (1) le couplage pélago-benthique est fort dans les systèmes peu profonds, et plus faible en domaine bathyal, (2) *B. glacialis* se nourrit principalement de bactéries et / ou de matériel détritique dans le domaine bathyal, isolé de la zone euphotique, et (3) *B. glacialis* est bien adapté à vivre à différentes profondeurs en changeant sa composition en FA dans la fraction polaire, expliquant la répartition de cette espèce sur de grandes échelles spatiales.

Chapitre 2 : Ressources trophiques du bivalve Astarte elliptica dans un fjord subarctique : une approche multi-marqueurs

L'objectif principal de ce second chapitre est de caractériser le régime alimentaire d'*Astarte elliptica* vivant dans un fjord subarctique par l'utilisation conjointe des FATM, des isotopes stables (SI) et l'analyse du ratio isotopique du carbone d'acides gras spécifiques. Plus spécifiquement, les objectifs sont les suivants: (1) caractériser les sources de nourriture en utilisant leur composition en acides gras et leur signature isotopique, (2) déterminer la (les) source(s) dominante(s) de nourriture et leur contribution relative dans le régime

alimentaire du bivalve *A. elliptica*, et (3) suivre la variabilité saisonnière dans l'alimentation du bivalve. Pour répondre à ces objectifs, les hypothèses suivantes sont posées : (*i*) la matière organique particulaire, les sédiments et les principaux taxons de macroalgues peuvent être différenciés grâce à leurs profils en acides gras et des signatures isotopiques distincts, (*ii*) *A. elliptica*, bivalve filtreur se nourrit principalement sur les microalgues, et (*iii*) le régime alimentaire d'*A. elliptica* change de façon saisonnière en suivant la dynamique de la production phytoplanctonique, montrant ainsi un régime alimentaire opportuniste.

Chapitre 3 : Les changements climatiques en Arctique favorisent la croissance de la coquille du bivalve bathyal Astarte moerchi

L'objectif principal de ce troisième chapitre est de montrer le potentiel du bivalve longévif *Astarte moerchi* en tant que bio-archive des changements environnementaux dans l'Arctique. Plus spécifiquement, les objectifs sont les suivants: (1) valider le fait que la formation des lignes et des incréments de croissance dans les coquilles d'*A. moerchi* se fait annuellement, (2) relier le patron de croissance des coquilles à des indices climatiques régionaux, et (3) expliquer les variations de croissance à l'échelle locale avec des paramètres environnementaux (abiotique et/ou biotiques) inhérents au nord de la baie de Baffin. Nous testons les hypothèses suivantes : (*i*) les indices climatiques NAO et AOO expliquent les anomalies de croissance des coquilles d'*A. moerchi*, (*ii*) le taux de croissance d'*A. moerchi* tend à diminuer (anomalie de croissance négative) au cours des dernières années puisque le couplage algues de glace – benthos devrait être affaibli en raison de la diminution du couvert de glace et d'une plus faible exportation d'algues de glace, et (*iii*) les acides gras marqueurs trophiques dans les tissus et le rapport Ba/Ca dans les coquilles d'*A. moerchi* sont des traceurs pertinents pour suivre la dynamique de la production primaire dans les systèmes marins arctiques profonds.

CHAPITRE 1
TRACEURS ALIMENTAIRES DANS *BATHYARCA GLACIALIS* DE RÉGIONS TROPHIQUES CONTRASTÉES DE L'ARCTIQUE CANADIEN

RÉSUMÉ

Les acides gras marqueurs trophiques (FATM) ont été utilisés pour évaluer les sources de carbone du bivalve *Bathyarca glacialis* et décrire le couplage pélago-benthique dans l'archipel arctique canadien. Quatre régions caractérisées par des environnements trophiques contrastés ont été étudiées : le sud-est de la mer de Beaufort, le détroit de Victoria, le détroit de Lancaster et le nord de la baie de Baffin. Nos résultats suggèrent que *B. glacialis* est un filtreur non sélectif, se nourrissant de microalgues, de zooplancton et de bactéries. Le régime alimentaire était principalement basé sur les microalgues, en particulier pour les populations côtières du sud-est de la mer de Beaufort. Le zooplancton et les bactéries ont toutefois contribué de façon plus importante dans l'alimentation des populations bathyales de *B. glacialis* que dans celle des populations côtières. Les conditions environnementales locales et saisonnières expliquent probablement ces différences dans le régime alimentaire entre les populations. Par ailleurs, des acides gras non maloniques (NMI) étaient présents dans les lipides polaires de *B. glacialis*, et pourraient être produits *de novo* lorsque l'accès à des acides gras essentiels (EFA), nécessaires pour maintenir la structure et la fonction des membranes, est limité. Cette réponse physiologique pourrait aider le bivalve à moduler sa fluidité membranaire face aux contraintes de l'environnement profond telles que les basses températures, la pression élevée, et lorsque les EFA sont moins disponibles dans son régime alimentaire. Cette espèce de bivalve présente certaines capacités pour faire face à de fortes modifications attendues dans la dynamique de la production primaire dues aux changements induits par le climat dans le système marin arctique.

Ce premier article, intitulé « Dietary tracers in *Bathyarca glacialis* from contrasting trophic regions in the Canadian Arctic », fut corédigé par moi-même ainsi que par Tarik

Meziane, Réjean Tremblay, Philippe Archambault, Kara K.S. Layton, André L. Martel, et Frédéric Olivier. Il a été publié dans la revue *Marine Ecology Progress Series* le 29 septembre 2015. En tant que premier auteur, ma contribution à ce travail fut l'essentiel des analyses en laboratoire, le traitement statistique des résultats et la rédaction de l'article. F. Olivier a fournit l'idée originale et réalisé les travaux de terrain. K. Layton et A. Martel ont vérifié l'identification (génétique et taxonomique) de l'espèce. T. Meziane et R. Tremblay ont aidé à l'interprétation des résultats. P. Archambault a contribué au traitement statistique des résultas. L'ensemble des coauteurs ont validé l'interprétation des résultats et aidé à la révision du manuscrit. Une version abrégée de cet article a été présentée dans plusieurs conférences nationales et internationales, lors de *Physiomar-12* à Saint-Jacques-de-Compostelle (Espagne) en Septembre 2012, de *l'Assemblée générale de Québec-Océan* à Montréal (Canada) en Novembre 2012, du Colloque national du Chantier Arctique Français « *Arctique : les grands enjeux scientifiques* » à Paris (France) en Juin 2013 et à *Arctic Change* à Ottawa (Canada) en Décembre 2014.

DIETARY TRACERS IN *BATHYARCA GLACIALIS* FROM CONTRASTING TROPHIC REGIONS IN THE CANADIAN ARCTIC

1. Abstract

This study used fatty acid trophic markers (FATMs) to assess carbon sources of the bivalve *Bathyarca glacialis* and describe the pelagic–benthic coupling in the Canadian Arctic Archipelago. Four regions characterized by contrasting trophic environments were investigated: Southeastern Beaufort Sea, Victoria Strait, Lancaster Sound and Northern Baffin Bay. Our results suggest that *B. glacialis* is a non-selective filter feeder, feeding on microalgae, zooplankton, and bacteria. Diet was based mainly on microalgae, especially for coastal populations of the Southeast- ern Beaufort Sea. However, zooplankton and bacteria contributed more significantly to the diet of *B. glacialis* in bathyal populations than the coastal populations. Local and seasonal environmental conditions likely explain these differences in diet between populations. Furthermore, non-methylene-interrupted (NMI) fatty acids were present in the polar lipids of *B. glacialis*, which could be produced de novo when access to essential fatty acids (EFAs), required for maintaining membrane structure and function, is limited. This physiological response could help the bivalve to modulate its membrane fluidity in the face of constraints of the deep-sea environment such as low temperatures, high pressure, and when EFAs are less available in its diet. This bivalve species thus has certain attributes that could help it to cope with expected strong modifications in primary production dynamics due to climate-induced changes in the Arctic marine system.

Keywords: Fatty acid trophic markers (FATMs); Non-methylene-interrupted fatty acid; Pelagic–benthic coupling; Canadian Arctic Archipelago; Bivalve; *Bathyarca glacialis*

2. Introduction

Arctic regions are experiencing drastic changes in response to global warming. Air and surface ocean temperatures are increasing, ice cover is decreasing, and predictions suggest that these changes will accelerate over the next decades (ACIA 2005, Grebmeier *et al.* 2006, Barber *et al.* 2008, Wassmann *et al.* 2011, IPCC 2013). In the Arctic Ocean, biological processes, especially primary production, exhibit a very pronounced seasonality controlled by light conditions, ice cover and nutrient availability (Carmack *et al.* 2006). One of the major consequences of the rapid decreased area and thickness of Arctic sea ice is that the ecosystem may shift from tight to weaker pelagic–benthic coupling (Carmack & Wassmann 2006). Pelagic–benthic coupling controls the food supply from the overlying water column to the benthos and, hence, directly influences benthic community abundance and biomass (Piepenburg 2005, Darnis *et al.* 2012, Roy *et al.* 2014). Strong pelagic–benthic coupling is characteristic of Arctic ecosystems, in terms of both quantity and quality of organic matter exported to the seafloor (Grebmeier & Barry 1991, Ambrose & Renaud 1995, Renaud *et al.* 2007). Primary production occurs during the spring-to-summer transition, when the ice melts and light availability increases. The quality and quantity of the organic matter exported from the water column and/or from the sea ice to the seabed relies heavily on zooplankton grazing and the microbial food web (Wassmann & Reigstad 2011). When primary producer blooms and large zooplankton stocks coincide in space and time, grazing efficiency is high and sedimentation of intact microalgae is low. When a mismatch occurs between primary production and zooplankton peaks, benthic communities benefit from a non-negligible, ecologically important amount of organic material reaching the seafloor (Carroll & Carroll 2003, Wassmann *et al.* 2006).

In the high Canadian Arctic, most studies on pelagic–benthic coupling have focused on the description of biogeochemical cycles in the water column and/or at the water–sediment interface. For example, Forest *et al.* (2011) were particularly interested in biogenic carbon and nutrient fluxes in the pelagic food web, Link *et al.* (2011) focused on the benthic carbon remineralization function, while other work used sedimentary biomarkers to track changes

in organic matter to the seafloor and its impact on benthic communities (Renaud *et al.* 2007, Morata *et al.* 2008). However, in this area, few studies used biochemical tracer methods such as fatty acid analysis to study pelagic–benthic coupling (Graeve *et al.* 1997, McMeans *et al.* 2013, Søreide *et al.* 2013). Fatty acids (FAs) are major lipid components of all living organisms and form an essential and integral part of neutral and polar lipids (NL and PL, respectively). The principal role of NL is as an energetic reserve (mainly triacylglycerol) to support metabolism and growth of organisms, whereas PL represent lipids structuring membranes (mainly phospholipids; Bergé & Barnathan 2005). The use of fatty acid trophic markers (FATMs) is based on the observation that marine primary producers lay down certain FA patterns that may be conservatively transferred through aquatic food webs. Thus, they can be recognized in the neutral lipid fraction of their primary consumers (Dalsgaard *et al.* 2003, Bergé & Barnathan 2005). Among these primary consumers, bivalves can synthesize *de novo* saturated and monounsaturated fatty acids (SFAs and MUFAs, respectively), but they have a very limited ability to synthesize common polyunsaturated fatty acids (PUFAs) due to the limited activity of specific elongases and desaturases to convert the precursors 18:2ω6 (linoleic acid) and 18:3ω3 (α-linolenic acid) into essential fatty acids (EFAs) such as arachidonic (AA, 20:4ω6), eicosapentanoic (EPA, 20:5ω3) and docosahexaenoic acids (DHA, 22:6ω3) (De Moreno *et al.* 1976, Waldock & Holland 1984, Chu & Greaves 1991, Fernández-Reiriz *et al.* 1998, Pirini *et al.* 2007). Consequently, microalgae, which constitutes the major sources of 18:2ω6, 18:3ω3, C20, and C22 PUFAs (Viso & Marty 1993, Zhukova *et al.* 1998) must provide bivalves with EFAs needed for their survival, growth and reproduction (Chu & Greaves 1991).

Given that microalgae are the principal producers in the marine environment, lipid and FA compositions of these organisms have been extensively studied. FA patterns can be used as taxonomic signatures of particular algal groups. Indeed, this approach has been largely applied to differentiate diatoms and dinoflagellates, 2 major primary producers in marine environments (Ackman *et al.* 1968, Viso & Marty 1993, Zhukova & Aizdaicher 1995). Diatoms are rich in EPA and unsaturated C16. In particular, the biosynthetic pathway producing 16:4ω1 from 16:0 is characteristic of this microalgal group (Dalsgaard *et al.* 2003).

Dinoflagellates, as well as flagellates, are often dominated by C18 PUFAs such as 18:4ω3, and DHA (Budge & Parrish 1998, Mansour *et al.* 1999, Dalsgaard *et al.* 2003). Odd-numbered and branched FAs, such as 15:0, 17:0, *iso*- and *anteiso*-SFAs, are typically dominant in bacterial FA composition and are used as tracers for the contribution of heterotrophic bacteria to sediments, suspended organic material, and animal diets (Meziane & Tsuchiya 2002, Dalsgaard *et al.* 2003). Long-chain MUFAs (20:1 and 22:1) are typically accumulated in calanoid copepods and have been used as tracers to identify them in consumers (Dalsgaard *et al.* 2003, Kelly & Scheibling 2012).

Changes in environmental conditions can induce significant effects on the physiology of aquatic organisms, specifically FA composition in their PL. Physiological acclimation, especially at the level of the cell membrane, can provide an effective response to different environments. FAs, especially those that constitute PL, play important structural and functional roles in cell membranes. Ectotherms can maintain their membrane fluidity by changing the structure of their membranes in response to temperature or pressure variations (Parrish 2013). This process is known as homeoviscous adaptation and requires remodeling of the membrane lipids, including changes in phospholipid to sterol ratios (Crockett 1998) and unsaturation level (Hazel 1995). For example, hard clams change their lipid composition and increase the level of unsaturation of FAs in their gills when environmental temperature decreases (Parent *et al.* 2008).

Bathyarca glacialis (Gray, 1824) is an Arcacea (Mollusca: Bivalvia) that exhibits a very large distribution both geographically and bathymetrically. It extends from the Arctic and sub-Arctic regions and has a wide depth range, from shallow waters to bathyal areas (Oliver & Allen 1980). *B. glacialis* is both a filter feeder and surface deposit feeder (Iken *et al.* 2005, Renaud *et al.* 2011). Given these characteristics, this bivalve acts an ideal model for studying the nature and strength of pelagic–benthic coupling in contrasting environments. In this study, we used FATMs to investigate the following hypotheses: (1) pelagic–benthic coupling is strong in shallow systems, and weaker in bathyal systems; (2) *B. glacialis* feeds mainly on bacteria and/or detrital material in bathyal systems, which are isolated from the

euphotic zone; and (3) *B. glacialis* is well adapted to different depths by changing its FA composition in PL, and this can explain the distribution of this species over large spatial scales.

3. Materials and methods

3.1. Specimen collection

Live *Bathyarca* spp. from the northern Baffin Bay and Lancaster Sound were collected in 2010 and bivalves from the Beaufort Sea and Victoria Strait were sampled in 2011 (Figure 8, Table 2) using an Agassiz trawl deployed from the CCGS 'Amundsen'. Table 2 presents detailed information on the collections of *Bathyarca* spp. Individuals were sorted directly on the ship, stored in plastic bags, and immediately frozen at -80°C. In the laboratory, individuals were dissected on ice to separate shells from soft tissues, which were stored at -80°C until used in analyses.

3.2. Specimen identification

Bathyarca specimens that were collected in the Beaufort Sea and Baffin Bay (Lancaster Sound) were identified as *B. glacialis* using the national mollusk collections at the Canadian Museum of Nature. Adductor muscles from these specimens were dissected and stored in 90% ethanol in preparation for molecular analysis. The barcode region of the cytochrome *c* oxidase subunit 1 (COI) gene was amplified from 7 specimens of *B. glacialis*. Specimen details, sequences, and trace files are available from the Dataset DS-CARBG at dx.doi.org/10.5883/DS-CARBG on BOLD (Barcode of Life Data Systems) (Ratnasingham & Hebert 2007). Sequences have also been deposited in GenBank (Accessions: KP976038 to KP976044). DNA barcoding protocols followed Layton *et al.* (2014) and the primer set that generated an amplicon, along with the primer sequences, are available on BOLD.

Maximum and mean intraspecific divergences were calculated with a K2P distance model (Kimura 1980) using the 'Distance Summary' tool on BOLD (Ratnasingham & Hebert 2007) to confirm that a single species was used in this study.

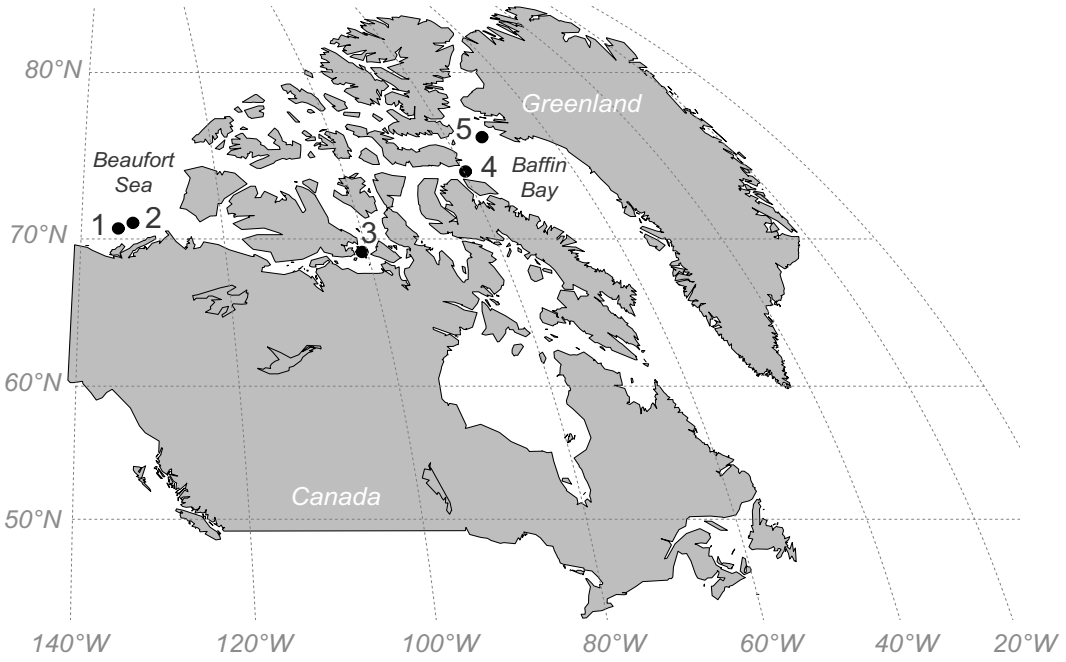

Figure 8. Stations in the Canadian Arctic Archipelago sampled for this study: Stn 1 = BP11-025, Beaufort Sea shelf; Stn 2 = BP11-029, Beaufort Sea shelf; Stn 3 = 312, Victoria Strait; Stn 4 = 323, Lancaster Sound; Stn 5 = 111, northern Baffin Bay

Table 2. Collection information of bivalves *Bathyarca glacialis* with station ID for this study (official designation as in Figure 8), positions, collection dates, and bottom depths

Stn ID	Latitude	Longitude	Date (dd/mm/yyyy)	Depth (m)
1	70°39' N	134°46' W	10/09/2011	052
2	71°01' N	132°41' W	17/09/2011	066
3	69°10' N	100°45' W	09/08/2011	069
4	74°12' N	79°44' W	14/10/2010	780
5	76°17' N	73°17' W	16/10/2010	568

3.3. Fatty acids analysis

Due to limited availability and use of gas-chromatography platforms, we analyzed lipids of B. glacialis either at Muséum National d'Histoire Naturelle (MNHN) in Paris, France (samples collected in 2010), or at Institut des Sciences de la mer (ISMER) in Rimouski, Quebec, Canada (samples collected in 2011) after inter-calibration validation. In both cases, total lipids were extracted using solution dichloromethane:methanol (2:1, v:v) following Folch *et al.* (1957). Lipid extracts were separated into neutral and polar fractions by column chromatography on silica gel micro-columns (30 × 5 mm i.d., packed with Kieselgel 60, 70−230 µm mesh; Merck) using chloroform:methanol (98:2, v/v) to elute NL, followed by methanol to elute PL (Marty *et al.* 1992). This neutral and polar separation method has previously been validated with a mix of triglyceride (tripalmitin) and phospholipids (L-α-phosphatidylcholine) standard. Analysis on chromatography on silica gel-coated glass-chromarods and a flame ionization detection system (Iatroscan MK-VI) demonstrated that 100% of triglycerides were measured in the neutral fraction and 100% of phospholipids in polar fraction. FA profiles were determined on fatty acid methyl esters (FAMEs) using sulphuric acid:methanol (2:98, v:v) and toluene. FAMEs of neutral and polar fractions were concentrated in hexane. FAMEs of the 2010 specimens were separated and quantified with a gas chromatograph (GC; Varian CP-3800 equipped with flame ionization detector). Separation was performed with a Supelco Omegawax 320 column (30 m × 0.32 mm i.d.). Peaks of FAs were identified with a gas chromatograph coupled to a mass spectrometer (GC-MS; Varian 450GC with Varian 220-MS). FAMEs of the 2011 specimens were analyzed in MS scan mode (ionic range: 50 to 650 m/z) on a Polaris Q ion trap coupled to a multichannel gas chromatograph 'Trace GC ultra' (Thermo Scientific) equipped with an autosampler model Triplus, a PTV injector and a mass detector model ITQ900 (Thermo Scientific). The separation was performed with an Omegawax 250 (30 m × 0.25 mm i.d.) capillary column with high purity helium as a carrier gas. In both case, FAMEs were identified by comparing retention times with known standards (Supelco® 37 Component FAME Mix, Supleco). Fatty

acid profiles obtained with the 2 instruments and compared using a SIMPER analysis (Clarke 1993) were similar at a level > 95%.

The unsaturation index (PUI) is a measure of the number of double bonds within a sample and was calculated in PL as the sum of the percentage of each unsaturated FA multiplied by the number of double bonds within the FA (Logue *et al.* 2000).

3.4. Statistical Analysis

Multivariate analyses on total FA composition of each fraction (neutral and polar lipids), including *a posteriori* pair-wise comparison, were done using a distance-based permutational multivariate analysis of variance (PERMANOVA, 9999 permutations) based on Bray-Curtis dissimilarities with 2 sources of variation: Depth (fixed with 2 levels; coastal and bathyal) and Station nested within depth (random with 3 coastal stations [Stns 1, 2, 3] and 2 bathyal stations [Stns 4, 5]), with n = 3 to 5 observations per station. Data were fourth-root transformed before analysis. Variations in FA composition, expressed in percentages, were visualized using non-metric multidimensional scaling (n-MDS) ordination based on Bray-Curtis dissimilarities between samples. The SIMPER procedure was performed to identify FAs explaining the most dissimilarity between Stations. Multivariate analyses were performed using PRIMER 6 (Clarke 1993, Clarke & Gorley 2006) and PERMANOVA+ (Anderson *et al.* 2008).

Based on the FA composition of NL explaining the most dissimilarity between Stations, a variety of trophic markers were calculated. Table 3 summarizes FAs used as dietary markers for our study. Differences in mean value of FATMs (percentages) among Depth and Stations within Depth were tested using analyses of variance (ANOVA) and the same sampling design described above. *A posteriori* comparisons were made using Tukey HSD test. Homogeneity of variance was determined visually on residuals as recommended by Quinn & Keough (2002), and normality was verified using Shapiro-Wilk test. Data were transformed to satisfy both assumptions when necessary. Identical statistical treatments were

used to compare sum of SFAs, MUFAs, PUFAs, EFAs and PUI in the polar lipids. A significance threshold of $\alpha = 0.05$ was adopted for all statistical tests.

Table 3. Fatty acids (FAs) used as dietary tracers in our study (Parrish 2013 and references therein). EPA: eicosapentanoic acid, 20:5ω3; DHA: docosahexaenoic acid, 22:6ω3

Source	Dietary tracer FAs
Diatoms	16:4ω1, EPA
Dinoflagellates	18:4ω3, DHA
Zooplankton	20:1ω11, 20:1ω9, 22:1ω11, 22:1ω9
Bacteria	*i*-15:0, 15:0, *i*-17:0, 17:0

4. Results

The barcode region of COI was amplified from 7 specimens and corresponding sequences ranged in length from 440 to 644 base pairs. Values of intraspecific divergence (K2P) ranged from 0% to 1.15%, with a mean of 0.53%. Low intraspecific divergence at COI (< 2%) confirmed that these 7 specimens, collected from the eastern Canadian Arctic and Beaufort Sea, belong to a single species (*Bathyarca glacialis*).

We compared the FA composition in NL and PL of *B. glacialis* tissues between different depths (coastal vs. bathyal) and populations (i.e. each station nested within the factor Depth) in the Canadian Arctic Archipelago (CAA). Detailed FA profiles for all populations are given in Table 5.

4.1. Diet description by study of NL

FA composition of the NL of *B. glacialis* varied significantly between Depth (coastal and bathyal populations), and among Stations within Depth (PERMANOVA, p(perm) < 0.01; Table 4, Figure 9). Within coastal populations, Stns 2 and 3 were similar (Figure 9; pairwise test, p(perm) = 0.05, Table 6) and both differed from Stn 1 (Figure 9; pairwise test, p(perm) < 0.01, Table 6). FA profiles for the 2 bathyal populations (Stns 4 and 5) were similar (Figure 9; pairwise test, p(perm) = 0.12, Table 6). SIMPER analysis showed that the average of the Bray-Curtis dissimilarities between coastal and bathyal stations was 14.08 (Table 7). Only by looking FATMs in SIMPER results, differences were attributed to a higher contribution of FA markers of microalgae (both FA markers of diatoms – 16:4ω1 and EPA – and dinoflagellates – 18:4ω3 and DHA) in NL of coastal *B. glacialis* specimens, while FA markers of zooplankton (sum of 20:1ω11, 20:1ω9, 22:1ω11, and 22:1ω9) and bacteria (especially, *i*-15:0 and *i*-17:0) were more abundant in NL of bathyal *B. glacialis*. All of these FAs participated to explain 22.35% to the dissimilarity (Table 7). Differences between the Stn 1 and the 2 other coastal stations (Stns 2 and 3) were partly explained by a higher contribution of EPA and 18:4ω3 and a lower contribution of DHA in *B. glacialis* from the Stn 1 compared to *B. glacialis* from the Stns 2 and 3 (Table 7).

In regards to specific trophic markers, proportion of 16:4ω1 (marker of diatoms) was significantly higher in NL of *B. glacialis* from the coastal Stn 3 (mean ± SE: 0.75 ± 0.16%) than in NL of *B. glacialis* from the other coastal and bathyal stations (0.29 ± 0.03% on average) (2-way nested ANOVA, p < 0.01; Figure 10). Significant higher levels of EPA (marker of diatoms) were found in coastal populations (11.65 ± 0.80%) compared to bathyal populations (7.00 ± 0.68%) but no differences were observed among Stations nested within Depth (2-way nested ANOVA, p < 0.01, and p = 0.63, respectively; Figure 10). 18:4ω3, FA marker of dinoflagellates, was more abundant in *B. glacialis* from coastal populations (1.97 ± 0.17%) than in *B. glacialis* from bathyal populations (0.58 ± 0.09%) (2-way nested ANOVA, p < 0.001; Figure 10). Analysis on DHA (marker of dinoflagellates) showed a significant difference among Stations within Depth (2-way nested ANOVA, p < 0.001;

Figure 10). Proportion of DHA in *B. glacialis* from the coastal Stns 2 and 3 (12.58 ± 0.34% on average) was higher than the 3 others stations (7.17 ± 0.65% on average). Significantly higher proportions of FA markers of zooplankton and bacteria distinguished bathyal populations from coastal populations (2-way nested ANOVA, $p < 0.05$ and $p < 0.01$, respectively; Figure 10). Furthermore, bathyal Stns 4 and 5 showed significant level of FA markers of zooplankton (2-way nested ANOVA, $p < 0.01$; Figure 10). Proportions of markers of zooplankton were highest for bathyal Stn 4 (7.26 ± 0.70%), intermediate for bathyal Stn 5 (4.87 ± 0.56%), and lowest for coastal stations (1.78 ± 0.10% on average; Figure 10). Bathyal populations were described by a mean of FA markers of bacteria equal to 1.61 ± 0.28%, while coastal populations presented less than 1%, on average, bacterial markers.

4.2. Physiological aspects by study of PL

FA composition of PL was significantly different between Depth (coastal and bathyal populations), and among Stations within Depth (PERMANOVA, p(perm) < 0.01; Table 4). Within coastal populations, FA composition in PL of *B. glacialis* from Stns 2 and 3 were similar (pairwise test, p(perm) = 0.09; Table 6) and significantly differed from that of *B. glacialis* from Stn 1 (pairwise test, p(perm) < 0.05; Table 6). The 2 bathyal populations showed significant differences in FA composition (pairwise test, p(perm) < 0.05; Table 6). SIMPER analysis indicated that the average of the Bray-Curtis dissimilarities between coastal and bathyal stations is 18.62 (Table 7). The non-methylene-interrupted dienoic FA (22:2 NMI), present in bathyal bivalves, contributed to explain close to 14% to the dissimilarity.

PUI was equal to 342 ± 3 for coastal populations, a value 23% higher than PUI for bathyal populations (263 ± 5) (2-way nested ANOVA, $p < 0.01$; Figure 11). Additionally, no significant difference was found in the sum of SFAs between the depths or among populations (2-way nested ANOVA, $p > 0.05$; Figure 11). PUFAs and EFAs were significantly higher for coastal populations (65.09 ± 0.41% and 54.05 ± 0.69%, respectively) than bathyal populations (58.27 ± 1.23% and 35.13 ± 0.60%, respectively) (2-way nested

ANOVA, $p < 0.05$ and $p < 0.001$; Figure 11). MUFAs showed the highest variability with significant differences between Depths and among Stations nested within Depth (2-way nested ANOVA, $p < 0.05$; Figure 11). Percentages of MUFAs were highest for bathyal populations (17.71 ± 0.34% on average), lowest for coastal Stn 3 (12.38 ± 0.91%), and intermediate for coastal Stns 1 and 2 (14.34 ± 0.59 on average; Figure 11).

Table 4. Results of permutational multivariate analyses of variance (PERMANOVAs) testing the effect of Depth (Z) and Station (Stn) nested within Depth on total fatty acids composition in neutral and polar lipids of *Bathyarca glacialis* based on the Bray-Curtis dissimilarity matrix. Significant Pseudo-*F* values are in **bold**. P-values calculated from the Monte Carlo method

Source of variation	Neutral lipids				Polar lipids			
	df	MS	Pseudo-*F*	p(perm)	df	MS	Pseudo-*F*	p(perm)
Z	1	787.05	**13.32**	< 0.01	1	1838.0	**78.63**	< 0.01
Stn(Z)	3	63.00	**3.13**	< 0.01	3	23.99	**4.03**	< 0.01
Residual	18				19	5.95		

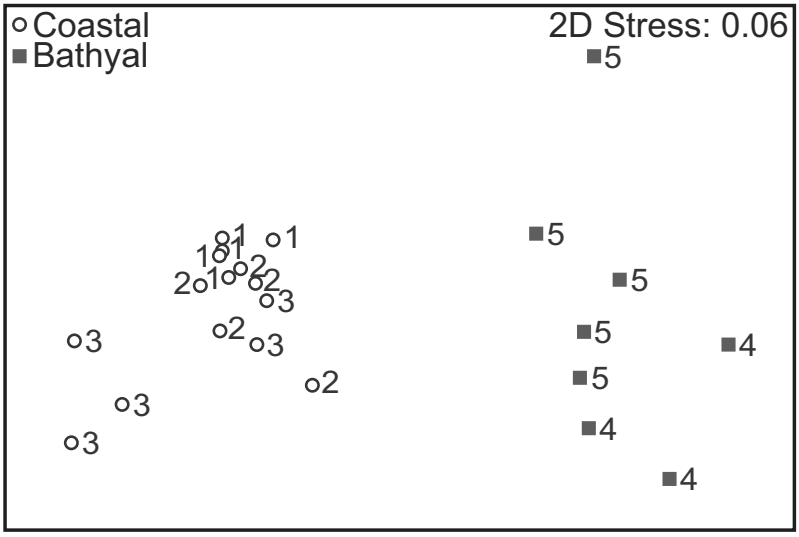

Figure 9. Non-metric multidimensional scaling (n-MDS) plot based on Bray-Curtis dissimilarities matrix calculated on fourth-root transformed data for the total fatty acid composition of neutral lipids in coastal (Stns 1, 2 and 3) and bathyal (Stns 4 and 5) *Bathyarca glacialis* populations

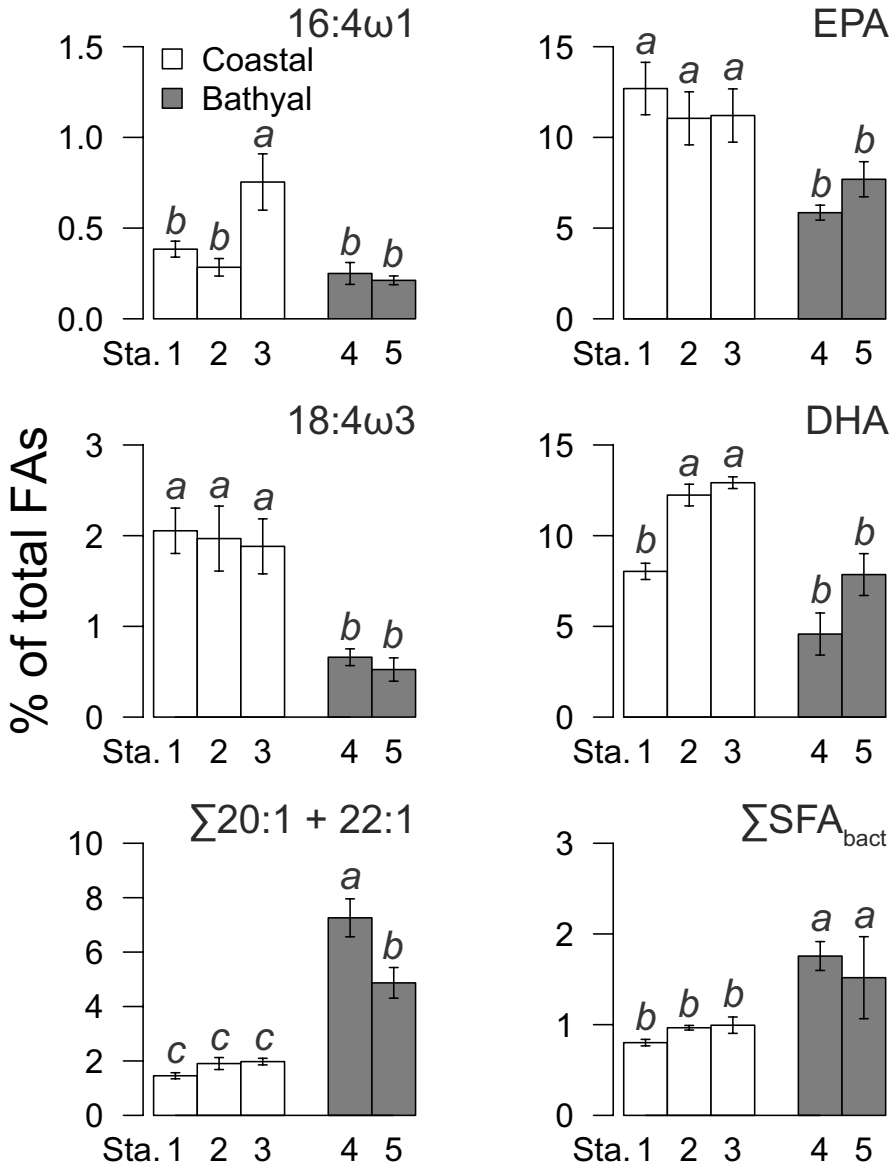

Figure 10. Fatty acid trophic markers (mean ± SE) (see Table 3) in the neutral lipids of *Bathyarca glacialis* from coastal (Stns 1, 2 and 3; white bars) and bathyal (Stns 4 and 5; grey bars) populations. Different letters above bars indicate significant differences (see Table 8 for test results)

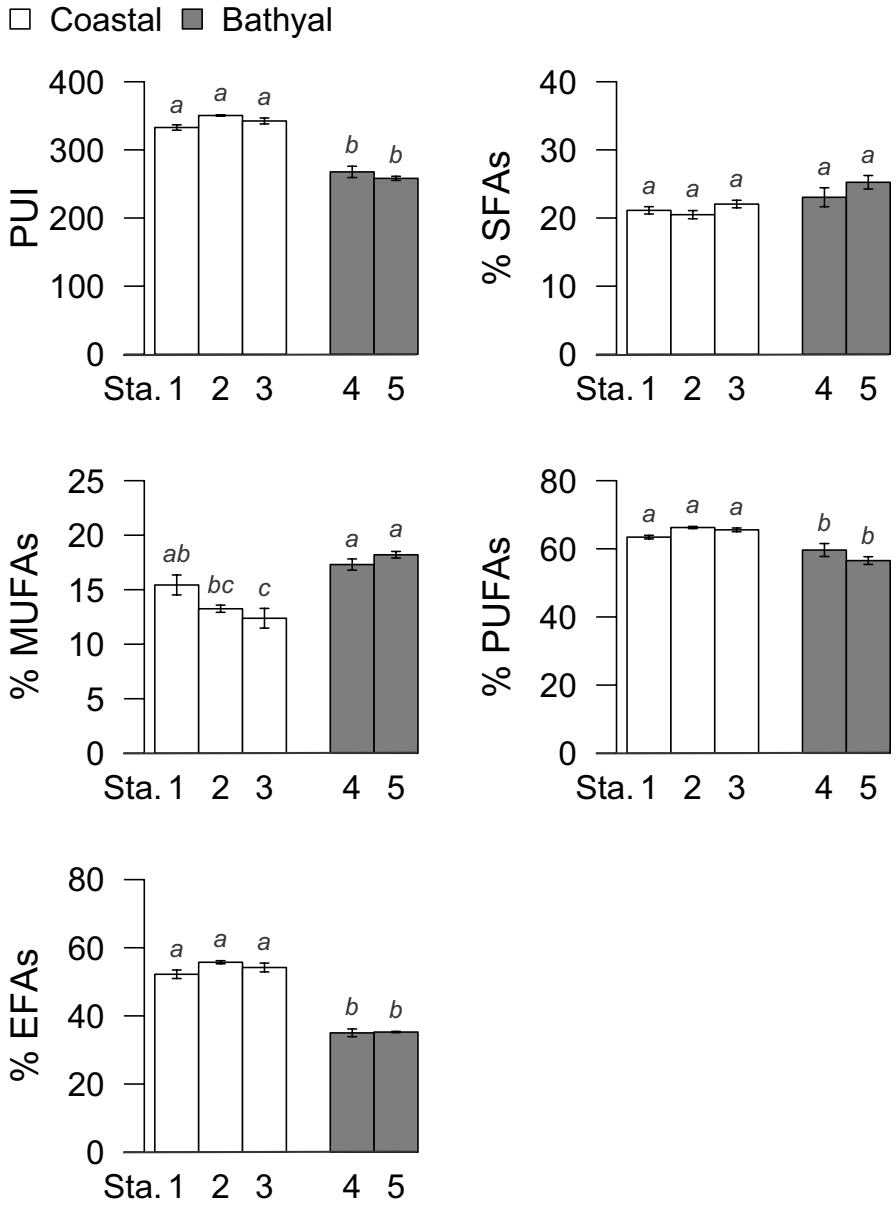

Figure 11. Unsaturation index (PUI), sum of saturated fatty acids (SFAs), monounsaturated fatty acids (MUFAs), polyunsaturated fatty acids (PUFAs) and essential fatty acids (EFAs) in the polar lipids of *Bathyarca glacialis* from coastal (Stns 1, 2 and 3; white bars) and bathyal (Stns 4 and 5; grey bars) populations (mean ± SE). Different letters above bars indicate significant differences (see Table 9 for test results)

5. Discussion

FAs are commonly investigated to study the transfer of organic matter through marine food webs in the Arctic, mostly on sympagic and pelagic taxa (e.g. Scott *et al.* 1999, Stevens *et al.* 2004b, Søreide *et al.* 2008, Wold *et al.* 2011a), and at higher trophic levels (e.g. Karnovsky *et al.* 2008, Thiemann *et al.* 2008, Wold *et al.* 2011b). In contrast, very little research has been conducted on lipids or FAs of Arctic benthic organisms, especially on filter-feeder bivalves (McMahon *et al.* 2006, Sun *et al.* 2009, McMeans *et al.* 2013, Søreide *et al.* 2013). In this paper, we tested 3 hypotheses on bivalves' adaptive capacity in the Arctic by using *Bathyarca glacialis*, largely distributed from Arctic to sub-Arctic regions, and from shallow to bathyal areas. However, the lack of information on the accurate distribution of this species, and constraints with ship availability have led to sampling at different time periods and the 2 trophic systems (eutrophic vs. oligotrophic) at different depths. This sampling design restricts the interpretation of our results. However, this study provide innovative results to increase knowledge in the Arctic and clearly shows the high plasticity of *B. glacialis* to feed on various food sources – even in bathyal environments.

In accordance with our first hypothesis, FATMs supported that pelagic–benthic coupling is more important in shallow systems than in the deepest. Overall, microalgae (both diatoms and dinoflagellates) are more involved in the diet of coastal *B. glacialis* populations from the southeastern Beaufort Sea and Victoria Strait than in bathyal populations from the northern Baffin Bay and Lancaster Sound. Lower levels of PUFAs, such as 18:2ω6, 18:3ω3, 18:4ω3, 16:4ω1, EPA, and DHA, in bathyal bivalves denote a degradation of microalgae during transfer from the euphotic zone to the seafloor, if we consider that the bloom occurs in a similar pattern as in coastal areas. FAs are known to be selectively degraded in the marine environment and therefore may be used as an indicator of degradation processes (Reemtsma *et al.* 1990, Fileman *et al.* 1998). The more rapid degradation of PUFAs with depth compared to saturated and monounsaturated FAs is well established. More generally, the quantity and quality of exported organic matter reaching the benthos are greatly dependant upon the timing of the primary production (ice and plankton algae blooms), consumption (grazing by

heterotrophs), and biological degradation by bacteria in the water column (Forest *et al.* 2010, Wassmann & Reigstad 2011). An efficient pelagic food web reduces the quantity and quality of organic material exported, while processes promoting fast sinking, such as aggregation, enhanced particle density or physical processes, facilitate benthic utilisation and carbon sequestration (Turner 2015 and references therein). However, because PUFAs are highly labile, they can be used to detect recent inputs of fresh matter on the seafloor, even in deeper water (Parrish *et al.* 2005). Although bivalves from northern Baffin Bay and Lancaster Sound were sampled at depths of up to 780 m, levels of PUFAs in their NL are slightly lower than those in NL of coastal *B. glacialis* collected at about 60 m (~29% and ~35%, respectively). Since NL represent major energy reserves in bivalves, and FAs in the NL closely reflect the type of food available (Delaunay *et al.* 1993), presence of PUFAs markers of microalgae in NL of *B. glacialis*, even in deep water, suggest that bivalves benefit from microalgae exported from the euphotic zone.

When only regarding pelagic productivity regimes, the northern Baffin Bay and Lancaster Sound are high productivity areas where large latent-heat polynyas open in spring. Consequently, pelagic primary production estimates based on field and satellite observations are higher in these areas than in the central and western parts of the CAA (Ardyna *et al.* 2011, Bélanger *et al.* 2013). Ardyna *et al.* (2011) defined the Baffin Bay and Lancaster Sound as eutrophic diatom-based systems, and the eastern Beaufort Sea and the central part of the CAA as oligotrophic flagellate-based systems. This intense marine biological productivity in the northern Baffin Bay and Lancaster Sound support a strong pelagic–benthic coupling, even at deep sites, particularly revealed by high sediment chlorophyll *a* contents and benthic boundary fluxes (Kenchington *et al.* 2011, Link *et al.* 2011, Darnis *et al.* 2012). According to these pelagic productivity regimes, we could expect higher levels of microalgae tracers (especially diatoms markers) in tissues of *B. glacialis* from the northern Baffin Bay and Lancaster Sound (eutrophic systems). However, we found higher proportions of FATMs for diatoms (16:4ω1 and EPA) and dinoglagellates (18:4ω3 and DHA) in tissues of *B. glacialis* from the Beaufort Sea and Victoria Strait (oligotrophic systems). Given the late sampling in the northern Baffin Bay and Lancaster Sound (October) and that FATMs providing

information on food ingested over the previous couple of weeks (McMahon *et al.* 2006, Sun *et al.* 2007), we could suggest that FA analysis in tissues of *B. glacialis* do not reflect the spring bloom, which occurs as early as May-June during typical conditions (Tremblay *et al.* 2002). However, high proportions of long-chain MUFAs in tissues of these bivalves likely indicate that they fed on zooplankton, which would have benefited from the spring bloom. High grazing pressure from zooplankton ultimately reduce the potential vertical export of organic matter (from the primary production), but grazers may contribute to the vertical carbon flux via faecal pellets (Wassmann *et al.* 2006). Furthermore, the strong microalgal signature in coastal populations (Beaufort Sea and Victoria Strait) may be directly related to food availability, in terms of quantity and quality, in the overlying water column. *B. glacialis* in shallow waters likely benefits from primary production taking place in the euphotic zone and fresher sinking material than in bathyal areas. Moreover, changes in ice and atmospheric conditions on the Canadian Beaufort Shelf may promote enhanced productivity. Upwelling winds are more frequent and favor repeated inputs of new nutrients that can generate 2 to 4 times the amount of ice algae and phytoplankton in this region (Tremblay *et al.* 2011).

Within coastal populations, *B. glacialis* from the Stn 1 differed from *B. glacialis* from the Stns 2 and 3, due notably by a higher contribution of EPA and 18:4ω3 and a lower contribution of DHA. Variability in FA content in NL of coastal *B. glacialis* suggests a fluctuating regional food supply to the benthos. Spatial and seasonal heterogeneities in pelagic–benthic coupling have already been suggested in the southeastern Beaufort Sea and Amundsen Gulf, based on analyses of primary production, benthic activity and sediment pigments (Forest *et al.* 2011, Link *et al.* 2011). Influence of the Mackenzie River, discharging around 316 km^3 y^{-1} of freshwater (Holmes *et al.* 2012) and 125 x 10^6 t y^{-1} of sediment load (Holmes *et al.* 2002) into the Beaufort Sea, has been also revealed. For example, Morata *et al.* (2008) demonstrates that the Beaufort Sea shelf is under the influence of terrestrial inputs, while in the gulf, material reaching the sea floor is from a more marine origin.

FATMs partially supported our second hypothesis that bacteria and detritus are the main sources of food for *B. glacialis* in bathyal environment. Although odd-numbered and

branched FAs (15:0, 17:0, *i*-15:0 and *i*-17:0), markers of bacteria, contribute more significantly to the diet of bathyal *B. glacialis* populations than to the diet of coastal populations, bathyal bivalves contained also more long-chain MUFAs (up to 7% compared to less than 2% in coastal bivalves). In marine consumers, this is often attributed to consumption of zooplankton, more specifically calanoid copepods (live or recently dead) which product high amounts of 20:1ω9 and 22:1ω11 (Sargent & Falk-Petersen 1988, Dalsgaard *et al.* 2003). Major biomass of dominant copepod species from the western Arctic Ocean has already been observed in a depth range reaching 1500 m (Ashjian *et al.* 2003). Other probable sources of these FAs might be zooplankton faecal pellets. Mayzaud *et al.* (2007) showed that long-chain monounsaturated 20:1 and 22:1 might be effectively transferred to the benthic communities via zooplankton faecal pellets. Alternatively, high concentrations of long-chain 20:1 MUFAs might result from the bivalves' ability to desaturate and elongate *de novo* synthesized SFAs and MUFAs (Paradis & Ackman 1977, Pernet *et al.* 2012), and from degradation of PUFAs that naturally occur in sinking material in the water column.

From a physiological perspective, levels of NMI FA (22:2 NMI) and some specific FAs, especially the docosapentaenoic acid (ω3-DPA, 22:5ω3), supported our third hypothesis that *B. glacialis* is well adapted to depth-related effects by changing its FA composition in PL. A lower unsaturation index related to a lower PUFA content, and more particularly in EPA and DHA, was demonstrated in PL of bathyal *B. glacialis* compared to coastal specimens. Previous works showed that unsaturation level in PL of bivalves increases when environmental temperatures decrease, reflecting a remodelling of the membrane lipid composition to maintain membrane fluidity in response of temperature variations in accordance with homeoviscous adaptation theory (Sargent 1976, Hall *et al.* 2002, Pernet *et al.* 2007). Since differences in mean bottom temperatures are less than 1°C among study sites (P. Guillot, pers. comm.), unsaturation level in PL of *B. glacialis* should have increased with depth, as a response to high pressure. However, our results suggest that bathyal *B. glacialis* populations could use 22:2 NMI to compensate for lower levels of EFAs, especially EPA and DHA. Proportions of 22:2 NMI and its monounsaturated precursors are higher in PL of

bathyal populations compared to coastal populations. The 22:2 NMI FAs are seemingly ubiquitous lipid components in mollusks but the amounts of these vary widely from species to species (Paradis & Ackman 1975, Zhukova 1986, Abad *et al.* 1995, Pazos *et al.* 2003). Whyte (1988) reported for *Crassostrea gigas* that the increase in 22:2Δ7,15 coincided with low levels of EPA and Klingensmith (1982) found an inverse relationship between the ω3-PUFAs, especially EPA and DHA, and NMI FA levels in the hard clam *Mercenaria mercenaria*. Although their biological role and function in bivalves are not clearly understood, the predominance in PL suggests that they may be important for membrane structure and function (Kraffe *et al.* 2004), acting as a substitute for EFAs (Klingensmith 1982, Zhukova 1991). Thus, it is possible that when PUFAs are less available in the diet, NMI FAs may be *de novo* biosynthesized by the bivalves. Fernández-Reiriz *et al.* (2015) also suggested that PUFA deficiencies in mantle of the mussel *Mytilus galloprovincialis* might induce *de novo* biosynthesis of NMI to satisfy reproductive demands. In addition, da Costa *et al.* (2015) showed that larvae of the oyster *Crassostrea gigas* synthesized ω3-docosapentaenoic acid (ω3-DPA, 22:5ω3) in response to an excess of EPA in the diet. Although pronounced elongation of EPA to ω3-DPA was found in larvae, no desaturation of ω3-DPA to DHA was observed. Da Costa *et al.* (2015) therefore suggested that an increase in ω3-DPA might take place to compensate for insufficient dietary supply of DHA. Our results show high proportions of ω3-DPA in PL (2% on average). In this context, *B. glacialis* appears to biosynthesize some PUFAs (ω3-DPA) and NMI FAs when PUFAs provided by diet are less available.

In conclusion, this study has shown that the bivalve *B. glacialis* is able to feed on various food sources including microalgae (diatoms and dinoflagellates), zooplankton, and bacteria, thus demonstrating high diet plasticity. Our analysis also highlighted a stronger pelagic–benthic coupling in shallow regions than in the deeper regions across the CAA. However, we note that, despite *B. glacialis* from the northern Baffin Bay and Lancaster Sound living at a depth close to 800 m, the presence of PUFAs markers of microalgae in their tissues suggest that they benefit from microalgae exported from the euphotic zone. However, some uncertainties remain about the nature of the food particles reaching the seafloor and

used by the bathyal communities. Processes affecting the sinking organic matter and its lipid content through the water column until the seafloor (such as degradation and remineralization) need further investigation. A multi-method approach would be necessary, since complexity of benthic food webs along with lack of unambiguous FATMs limits tracking of trophic relationships with the use of FAs alone. Further investigations, combining fatty acids profiles, bulk isotopes, compound specific isotopic analyses, and pigments would be helpful to determine major carbon sources to benthic organisms and describe the pelagic–benthic coupling along depth gradients and biological productivity regimes specific to the CAA. In addition, *B. glacialis* shows a distinctive physiological response to a lower EFA availability in its diet by the synthesis capacity of NMI FAs. Because of their dietary flexibility, *B. glacialis* may adapt to predicted changes in the quality, quantity, and timing in primary production that could modify their food web. However, climate-related changes may affect their population dynamics, including growth, mortality, and reproduction.

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7. Supporting information

Table 5. Fatty acid composition of neutral (a) and polar (b) lipids of coastal and bathyal populations of *B. glacialis*. Data of each FA are expressed as % of total fatty acids (mean ± SE). Only FAs contributing > 1% in at least one group are reported (excluding odd-branched FAs used as markers for bacteria and 16:4ω1 used as marker for diatoms). Σ22:1 is the sum of 22:1ω11 + 22:1ω9. 22:2ω11 (ω9): position of double bond is uncertain. AA: arachidonic acid, 20:4ω6; EPA: eicosapentanoic acid, 20:5ω3; DHA: docosahexaenoic acid, 22:6ω3. NMI = non-methylene-interrupted; SFAs = saturated fatty acids; MUFAs = monounsaturated fatty acids; PUFAs = polyunsaturated fatty acids

A	Neutral lipids				
	Coastal			Bathyal	
Fatty acids	Stn 1 *n* = 5	Stn 2 *n* = 5	Stn 3 *n* = 5	Stn 4 *n* = 3	Stn 5 *n* = 5
14:0	2.78 ± 0.11	2.82 ± 0.12	2.86 ± 0.16	2.90 ± 0.58	2.18 ± 0.18
i-15:0				0.35 ± 0.58	0.15 ± 0.58
15:0	0.23 ± 0.02	0.26 ± 0.02	0.23 ± 0.03	0.37 ± 0.06	0.20 ± 0.03
16:0	13.85 ± 1.12	13.84 ± 1.16	16.54 ± 1.11	15.06 ± 1.35	15.73 ± 1.17
i-17:0	0.13 ± 0.01	0.18 ± 0.01	0.22 ± 0.01	0.55 ± 0.08	0.70 ± 0.39
16:1ω7	37.39 ± 0.82	32.34 ± 0.37	24.28 ± 1.06	19.42 ± 1.54	20.79 ± 1.58
16:3ω3				1.44 ± 0.76	0.38 ± 0.00
16:4ω1	0.39 ± 0.05	0.28 ± 0.05	0.75 ± 0.16	0.25 ± 0.06	0.21 ± 0.02
17:0	0.44 ± 0.02	0.53 ± 0.03	0.55 ± 0.05	0.72 ± 0.02	0.58 ± 0.03
18:0	1.92 ± 0.12	2.20 ± 0.07	3.19 ± 0.23	3.81 ± 0.25	2.87 ± 0.23
18:1ω9	3.00 ± 0.11	3.26 ± 0.26	3.47 ± 0.49	10.92 ± 0.66	8.50 ± 0.57
18:1ω7	2.73 ± 0.15	2.49 ± 0.09	2.46 ± 0.33	6.43 ± 0.70	5.81 ± 0.53
18:1ω5	0.35 ± 0.01	0.59 ± 0.05	0.52 ± 0.05	1.11 ± 0.08	1.29 ± 0.07
18:2ω6	1.53 ± 0.10	2.01 ± 0.19	2.34 ± 0.16	1.16 ± 0.04	1.09 ± 0.03
18:4ω3	2.05 ± 0.25	1.97 ± 0.36	1.88 ± 0.30	0.66 ± 0.09	0.52 ± 0.13
20:1ω11	0.83 ± 0.10	0.90 ± 0.10	1.08 ± 0.09	3.17 ± 0.19	2.19 ± 0.55
20:1ω9	0.31 ± 0.02	0.52 ± 0.08	0.44 ± 0.04	2.44 ± 0.09	1.60 ± 0.20
20:1ω7	3.62 ± 0.33	4.16 ± 0.15	4.11 ± 0.36	3.77 ± 0.39	3.76 ± 0.89
Σ22:1	0.31 ± 0.02	0.48 ± 0.08	0.46 ± 0.06	1.66 ± 0.42	1.08 ± 0.13
AA	0.75 ± 0.04	1.00 ± 0.08	1.56 ± 0.36	1.75 ± 0.11	1.46 ± 0.22
EPA	12.69 ± 1.44	11.05 ± 1.46	11.21 ± 1.47	5.85 ± 0.41	7.69 ± 0.97
22:2ω11 (ω9)	1.46 ± 0.27	1.43 ± 0.34	2.03 ± 0.44	1.10 ± 0.36	1.03 ± 0.18
22:2 NMI				4.09 ± 0.85	7.44 ± 0.92
22:5ω3	0.61 ± 0.02	0.67 ± 0.03	0.88 ± 0.04	0.87 ± 0.27	0.61 ± 0.05
DHA	8.03 ± 0.45	12.24 ± 0.60	12.92 ± 0.32	4.58 ± 1.16	7.86 ± 1.15
SFAs	19.42 ± 1.10	19.91 ± 1.22	23.63 ± 0.95	24.56 ± 1.34	22.51 ± 0.78
MUFAs	49.57 ± 0.83	45.81 ± 0.53	37.60 ± 1.69	50.87 ± 1.92	46.22 ± 1.85
PUFAs	31.00 ± 1.42	34.28 ± 1.29	38.78 ± 2.59	24.57 ± 2.98	31.27 ± 1.72

Table 5 continued

B	Polar lipids				
	Coastal			Bathyal	
Fatty acids	Stn 1 *n* = 5	Stn 2 *n* = 5	Stn 3 *n* = 5	Stn 4 *n* = 5	Stn 5 *n* = 4
14:0	1.33 ± 0.07	1.17 ± 0.10	1.29 ± 0.09	2.73 ± 0.45	3.39 ± 0.21
i-15:0	0.06 ± 0.00	0.06 ± 0.00	0.07 ± 0.00	0.39 ± 0.04	0.34 ± 0.01
15:0	0.27 ± 0.01	0.32 ± 0.02	0.31 ± 0.02	0.67 ± 0.14	0.68 ± 0.09
16:0	10.64 ± 0.62	10.52 ± 0.77	10.78 ± 0.73	9.13 ± 0.72	11.18 ± 0.53
i-17:0	0.22 ± 0.01	0.25 ± 0.01	0.29 ± 0.00	0.45 ± 0.04	0.31 ± 0.05
16:1ω7	5.25 ± 0.52	3.89 ± 0.26	3.04 ± 0.24	2.52 ± 0.13	2.81 ± 0.14
16:3ω3					
16:4ω1					
17:0	1.01 ± 0.03	1.12 ± 0.03	1.05 ± 0.04	0.97 ± 0.07	1.02 ± 0.05
18:0	7.24 ± 0.16	6.70 ± 0.27	7.79 ± 0.31	7.19 ± 0.06	7.22 ± 0.11
18:1ω9	0.78 ± 0.07	0.79 ± 0.06	0.77 ± 0.07	3.57 ± 0.35	2.98 ± 0.49
18:1ω7	1.77 ± 0.13	1.53 ± 0.11	1.32 ± 0.07	2.37 ± 0.25	2.21 ± 0.19
18:1ω5	0.34 ± 0.01	0.43 ± 0.02	0.35 ± 0.02	0.51 ± 0.03	0.67 ± 0.06
18:2ω6	0.93 ± 0.06	0.99 ± 0.08	0.93 ± 0.04	0.81 ± 0.10	0.72 ± 0.06
18:4ω3	0.58 ± 0.06	0.50 ± 0.03	0.39 ± 0.04	1.13 ± 0.31	0.57 ± 0.08
20:1ω11	1.77 ± 0.16	1.66 ± 0.20	1.84 ± 0.17	2.97 ± 0.14	2.50 ± 0.03
20:1ω9	0.40 ± 0.02	0.45 ± 0.02	0.43 ± 0.02	1.03 ± 0.02	0.58 ± 0.06
20:1ω7	4.90 ± 0.21	4.36 ± 0.23	4.41 ± 0.38	3.16 ± 0.09	3.78 ± 0.18
Σ22:1	0.11 ± 0.01	0.07 ± 0.02	0.13 ± 0.02	0.47 ± 0.11	0.44 ± 0.05
AA	5.83 ± 0.35	6.18 ± 0.47	6.20 ± 0.14	8.43 ± 0.22	7.04 ± 0.14
EPA	19.09 ± 0.97	16.69 ± 1.21	16.73 ± 0.56	9.58 ± 0.56	11.38 ± 0.54
22:2ω11 (ω9)	4.36 ± 0.59	4.37 ± 0.40	4.85 ± 0.66	3.31 ± 0.33	2.24 ± 0.69
22:2 NMI				12.97 ± 0.59	13.25 ± 1.10
22:5ω3	2.18 ± 0.08	1.83 ± 0.19	1.89 ± 0.13	2.56 ± 0.19	1.73 ± 0.17
DHA	27.30 ± 0.49	32.87 ± 0.61	31.27 ± 1.02	17.01 ± 0.91	16.85 ± 0.34
SFAs	21.13 ± 0.53	20.49 ± 0.60	22.05 ± 0.56	23.05 ± 1.39	25.25 ± 0.99
MUFAs	15.44 ± 0.91	13.25 ± 0.33	12.38 ± 0.91	17.31 ± 0.52	18.20 ± 0.30
PUFAs	63.44 ± 0.53	66.25 ± 0.32	65.57 ± 0.55	59.64 ± 1.89	56.55 ± 1.13

Table 6. Pairwise test between stations in neutral and polar lipids of *B. glacialis*. Significant values are in **bold**. See Table 2 and Figure 8 for stations codes

Depth	Station pairs	Neutral lipids		Polar lipids	
		t	p(perm)	*t*	p(perm)
Coastal	Stn 1 x Stn 2	1.74	**0.01**[a]	1.53	**0.03**
	Stn 1 x Stn 3	2.67	**0.01**[a]	2.48	**0.01**
	Stn 2 x Stn 3	1.73	0.05[a]	1.42	0.09
Bathyal	Stn 4 x Stn 5	1.43	0.12[a]	2.30	**0.01**

[a] Monte-Carlo P

Table 7. Fatty acid contribution to total dissimilarity (%) of neutral (a) and polar (b) lipid composition among significantly different *B. glacialis* populations (See Table 4 and Table 6 for test results). In each combination, fatty acids are listed in order of decreasing contribution. AA: arachidonic acid, 20:4ω6; EPA: eicosapentanoic acid, 20:5ω3; DHA: docosahexaenoic acid, 22:6ω3. 20:2ω9 (ω7), and 22:2ω11 (ω9): position of double bond is uncertain. See Table 2 and Figure 8 for stations codes

A	Neutral lipids	
Station pairs	Fatty acids	Contribution (%)
Stn 1 x Stn 2	Total	4.55
	i-16:0	6.50
	i-18:0	6.45
	18:1ω11	6.15
	16:3ω4	5.65
	DHA	5.39
	EPA	4.31
	16:2ω6	3.71
	22:2ω11(ω9)	3.60
	18:4ω3	3.39
	18:1ω5	3.02
	22:1ω11	2.80
Stn 1 x Stn 3	Total	7.58
	18:1ω11	6.92
	i-16:0	5.95
	20:4ω3	5.65
	i-18:0	5.54
	16:1ω9	5.16
	16:1ω7	4.38
	DHA	3.69
	20:2ω6	3.54
	20:3ω6	2.93
	AA	2.91
	18:2ω3	2.88
	22:1ω11	2.83

Table 7 continued

B	Polar lipids	
Station pairs	Fatty acids	Contribution (%)
Stn 1 x Stn 2	Total	3.41
	20:2ω9 (ω7)	9.06
	22:1ω9	6.76
	20:4ω3	6.46
	16:2ω4	4.86
	16:1ω7	4.75
	DHA	4.44
	22:2ω11 (ω9)	4.03
	EPA	3.72
	22:3ω6	3.31
	22:5ω3	3.07
Stn 1 x Stn 3	Total	3.43
	20:2ω9 (ω7)	19.71
	16:1ω7	7.70
	22:2ω11 (ω9)	4.78
	18:4ω3	3.44
	18:1ω7	3.34
	DHA	3.25
	EPA	2.99
	22:3ω6	2.99
	18:2ω3	2.96
Stn 4 x Stn 5	Total	5.56
	18:1ω11	18.84
	16:1ω9	10.13
	22:1ω11	4.68
	22:2ω11 (ω9)	4.56
	16:2ω4	4.55
	18:4ω3	3.77
	20:1ω9	3.25
	21:5ω3	2.91

Table 8. Results of 2-way nested analyses of variance (ANOVAs) testing the effect of Depth (Z) and Station (Stn) nested within Depth on the fatty acids 16:4ω1 and EPA (eicosapentanoic acid, 20:5ω3) markers of diatoms, 18:4ω3 and DHA (docosahexaenoic acid, 22:6ω3) markers of dinoflagellates, Σ20:1 + 22:1 (sum of 20:1ω11 + 20:1ω9 + 22:1ω11 + 22:1ω9) markers of zooplankton, and SFA_{bact} (sum of 15:0 + 17:0 + *i*-15:0 + *i*-17:0) markers of bacteria in neutral lipids of *B. glacialis*. Significant values are in **bold**; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Source of variation	df	16:4ω1 MS	F	df	EPA MS	F
Z	1	0.30	1.56***	1	118.99	**23.06*****
Stn(Z)	3	0.21	**6.15*****	3	4.86	0.59***
Residual	18	0.03		18	8.18	

Source of variation	df	18:4ω3 MS	F	df	DHA MS	F
Z	1	9.47	**149.30*****	1	117.47	4.26***
Stn(Z)	3	0.04	0.11***	3	30.08	**11.30*****
Residual	18	0.34		18	2.66	

Source of variation	df	Σ20:1 + 22:1 MS	F	df	SFA_{bact} MS	F
Z	1	91.86	**25.95*****	1	2.57	**29.39*****
Stn(Z)	3	3.83	**6.40*****	3	0.07	0.29***
Residual	18	0.60		18	0.25	

Table 9. Results of 2-way nested analyses of variance (ANOVAs) testing the effect of Depth (Z) and Station (Stn) nested within Depth on unsaturation index (PUI), and the sum of saturated fatty acids (SFAs), monounsaturated fatty acids (MUFAs), polyunsaturated fatty acids (PUFAs) and essential fatty acids (EFAs) in polar lipids of *B. glacialis*. Significant values are in **bold**; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Source of variation	PUI df	PUI MS	PUI F	SFAs df	SFAs MS	SFAs F	MUFAs df	MUFAs MS	MUFAs F
Z	1	34785.30	**108.85*****	1	47.74	8.56***	1	93.33	**10.72*****
Stn(Z)	3	326.76	2.82***	3	5.64	1.54***	3	8.84	**4.02*****
Residual	19	115.71		19	3.67		19	2.20	

Source of variation	PUFAs df	PUFAs MS	PUFAs F	EFAs df	EFAs MS	EFAs F
Z	1	272.55	**19.46*****	1	1995.54	**195.08*****
Stn(Z)	3	14.31	2.70***	3	10.41	2.08***
Residual	19	5.30		19	5.00	

CHAPITRE 2
RESSOURCES ALIMENTAIRES DU BIVALVE *ASTARTE ELLIPTICA* DANS UN FJORD SUBARCTIQUE : UNE APPROCHE MULTI-MARQUEURS

RÉSUMÉ

Généralement, le couplage pélago-benthique est considéré étroit sur les plateaux continentaux de l'Arctique. Cependant, ce paradigme est principalement basé sur le fait que le phytoplancton et les algues de glace sont présumés être les principales sources de carbone pour les communautés benthiques. Les changements liés au climat devraient entraîner des modifications dans la contribution relative des sources de nourriture, y compris les macroalgues, pour les organismes benthiques. Dans cette étude, une approche multi-marqueurs (isotopes stables, acides gras marqueurs trophiques, et analyse des isotopes stables sur des composés spécifiques) a été utilisée pour déterminer les sources de nourriture parmi la matière organique particulaire des eaux de surface et des eaux de fond, la matière organique contenue dans les sédiments, et six espèces de macroalgues dans le régime alimentaire du bivalve *Astarte elliptica* d'un fjord subarctique (Kobbefjord, Groenland). Les résultats ont montré qu'*A. elliptica* se nourrit de la matière organique particulaire et des sédiments incluant des détritus de macroalgues. Ces résultats indiquent que les macroalgues brunes peuvent soutenir de manière significative le réseau alimentaire benthique arctique. Comme la biomasse des macroalgues devrait augmenter dans les systèmes côtiers, en réponse à l'élévation de la température et la réduction de la couverture de glace de mer, une meilleure compréhension de la contribution relative des composants benthiques et pélagiques pour le réseau trophique benthique est nécessaire. L'approche multi-marqueurs peut ainsi aider à déterminer et tracer toutes les sources potentielles de carbone et de suivre leur variabilité temporelle dans le régime alimentaire des organismes benthiques pour étudier la stratégie d'alimentation face aux changements de la dynamique de la production primaire.

Ce second article, intitulé « Food resources of the bivalve *Astarte elliptica* in a subarctic fjord: a multi-biomarkers approach », fut corédigé par moi-même ainsi que par les professeurs Tarik Meziane, Réjean Tremblay, Philippe Archambault, Martin E. Blicher, Laurent Chauvaud, Søren Rysgaard, et Frédéric Olivier. Il a été soumis pour publication dans la revue *Marine Ecology Progress Series* le 15 février 2016. En tant que premier auteur, ma contribution à ce travail fut l'essentiel de la recherche (travaux sur le terrain et analyses en laboratoire), le traitement statistique des résultats et la rédaction de l'article. T. Meziane et R. Tremblay ont aidé à l'interprétation des résultats et ont contribué à la révision de l'article. P. Archambault a contribué à l'approche statistique des données et à la révision de l'article. M. Blicher a contribué aux travaux sur le terrain ainsi qu'à la révision de l'article. L. Chauvaud et S. Rysgaard ont contribué à la révision de l'article. F. Olivier a contribué à l'idée originale, l'interprétation des résultats et à la révision de l'article. Une version abrégée de cet article a été présentée dans plusieurs conférences nationales et internationales, lors de *Physiomar-14* à La Serena (Chili) en Novembre 2014, de *l'Assemblée générale de Québec-Océan* à Rivière-du-Loup (Canada) en Novembre 2014 et à *Arctic Change* à Ottawa (Canada) en Décembre 2014.

FOOD RESOURCES OF THE BIVALVE *ASTARTE ELLIPTICA* IN A SUBARCTIC FJORD: A MULTI-BIOMARKERS APPROACH

1. Abstract

It is generally admitted that the pelagic-benthic coupling is tight on Arctic shelves. However, this paradigm is mainly based on the assumption that phytoplankton and ice algae are the main sources of carbon for the benthic communities. Climate change is expected to alter the relative contribution of food sources for benthic organisms. In this study, a multi-biomarkers approach (stable isotopes, fatty acid trophic markers, and compound-specific stable isotope analysis) has been applied to link potential sources of carbon including particulate organic matter from subsurface and bottom waters, sediment organic matter, and six macroalgae species to the diet of the bivalve *Astarte elliptica* from a subarctic fjord (Kobbefjord, Greenland). Results showed that *A. elliptica* feeds on particulate and sediment organic matter and that brown macroalgae significantly support Arctic benthic food web. Since macroalgae biomass is predicted to upsurge in near-shore systems in response to increased temperature and reduced sea ice cover, a better understanding on the relative contribution of benthic and pelagic components in benthic food web is needed. Multi-biomarkers approaches help to determine and trace all potential sources of carbon and track temporal variability in the diet of benthic organisms to study food regime strategies in response to changing primary production dynamics.

Keywords: trophic ecology, stable isotopes, fatty acid trophic markers, compound-specific stable isotope analysis, subarctic fjord, bivalve

2. Introduction

Unprecedented changes of natural systems are happening in response to the observed global warming since the mid-20th century with the poles being the most affected regions (IPCC 2013). Changes in physical conditions, including warming of the sea surface, decreasing of the sea ice cover, and changes in water column stratification are expected to affect primary production (Rysgaard *et al.* 1999, Wassmann 2011, Krause-Jensen *et al.* 2012). Timing, magnitude and spatial distribution of primary producers may be modified and consequently have effects on the trophic pathways supporting pelagic and benthic consumers (Wassmann & Reigstad 2011, Gaillard *et al.* 2015). Two divergent hypotheses are presently put forward to predict changes of the primary production and food web in the future Arctic. The first one is based on the current importance of ice algal production at a pan-Arctic scale, which efficiently provide food for benthic communities. The decline in sea ice extent and thickness could lead to a shift from the present ice algae – benthos dominance to a predicted phytoplankton – zooplankton prevalence (Carroll & Carroll 2003) and thus a weaker pelagic-benthic coupling (Carmack & Wassmann 2006). The second one, based on smaller (local) scale observations, considers that the sea-ice algal production is negligible and that the single phytoplankton bloom occurring during the short ice-free period currently far dominates. In the future, the longer open-water period would induce a more extensive bloom and may lead to a shift in the pelagic food web structure. This will enhance the vertical export of organic matter during the spring bloom due to copepod grazing and faecal pellet export, and a second vertical export event in autumn, resulting to a stronger pelagic-benthic coupling (Rysgaard & Glud 2007). It is also hypothesized that in shallow areas, microphytobenthos production will be greater (Glud *et al.* 2009). Until now, macroalgae have not been considered in arctic food web studies. However, it has been shown, especially in suspension feeders from temperate coastal systems (Perez *et al.* 2013), that they can substantially contribute to the total primary production and even exceed pelagic primary production at shallow depths in the Arctic (Glud & Rysgaard 2007, Krause-Jensen *et al.* 2007). Glud & Rysgaard (2007) estimate the relative contribution of macroalgae to nearby 20% of the annual total primary

production in an ecosystem of Young Sound (NE Greenland), dominated by phytoplankton production (65%). This macroalgal primary production enters food webs through direct grazing (Blicher *et al.* 2007), exudation of dissolved organic carbon and as detritus, and could be especially beneficial to benthic suspension feeders' growth (Duggins *et al.* 1989, Perez *et al.* 2013). The role of macroalgae as potential sources of carbon for higher trophic levels is even more important to determine since warming of the Arctic is expected to favour them (Krause-Jensen & Duarte 2014). Indeed, cold temperate and sub-Arctic macroalgae are predicted to extend their distribution onto the Arctic Ocean with global change (Hop *et al.* 2012, Kortsch *et al.* 2012, Krause-Jensen *et al.* 2012, Krause-Jensen & Duarte 2014). Changes in macroalgal community composition have already been noted in fjords of the Svalbard archipelago. The dominance of calcareous algae, well adapted to low-light and cold-water regimes, has been replaced by a rapid expansion of erect boreal macroalgae in response to increased sea surface temperature and improved light availability (Kortsch *et al.* 2012). In addition, warming of the Arctic will likely favour macroalgal growth that could start earlier and extend the growing season in response to the longer ice-free period (Krause-Jensen & Duarte 2014). A threefold increase in the biomass of macroalgae was observed between 1988 and 2008 in the rocky shore of Svalbard, along with increases in temperature and decreases in sea ice cover (Weslawski *et al.* 2010). On the other hand, future climate with greater glacial meltwater is expected to increase particle load in the surface waters of Greenlandic fjords (Godthåbsfjord and Young Sound; Murray *et al.* 2015). Moreover, the special feature of the freshwater coming from glacial melt and feeding these fjords is that it contains low concentrations of nutrients (Murray *et al.* 2015). Increased runoff and turbidity with low levels of nutrients may negatively influence primary production. Yet, it remains unclear how benthic communities will respond to those changes in food sources (phytoplankton, sea ice algae, microphytobenthos, and macroalgae). In the context of changing primary production, it is essential to achieve a better understanding of the dominant sources and their contribution to the benthic food web.

Our study combined fatty acids, stable isotopes, and compound-specific stable isotope analysis to characterize and trace sources of food and their fate towards benthos in a subarctic

fjord. More specifically, the objectives were to: (1) characterize sources of food using their fatty acid composition, (2) determine dominant source(s) of food and their relative contribution in the diet of a bivalve *Astarte elliptica*, dominant species of the subarctic macrofaunal assemblages, and (3) show seasonal variability in the diet of the bivalve. We hypothesized that (*i*) particulate organic matter (POM), sediment organic matter and major macroalgae taxa are distinguishable because of their different fatty acid profiles and isotopic signatures, (*ii*) as filter feeder, *A. elliptica* mainly feeds on microalgae, and (*iii*) the diet of *A. elliptica* changes along with seasonal phytoplankton pattern, showing an opportunistic feeding strategy in the context of changing primary production.

3. Methods

3.1. Study site

This study was conducted in the sub-arctic Kobbefjord, in southwest Greenland (Figure 12). This sill fjord is a part of the Godthabfjord system and is ca. 17 km long and 0.8 to 2 km wide. The innermost part of the Kobbefjord is usually sea ice covered, with extensive inter-annual variation (Mikkelsen *et al.* 2008). Sea surface temperature ranges from ca. -1.5°C during winter to ca. 8°C in late summer (Blicher *et al.* 2009).

3.2. Field sampling

Sampling of the bivalve *Astarte elliptica*-complex and its potential sources of food were carried out on 15 May and 2 September 2013. Alive *A. elliptica* were collected using a triangular dredge at a depth of 50 to 60 m in the outer region of Kobbefjord (64°07'N, 51°38'W; Figure 12) in a shell substrate with high densities of scallops (*Chlamys islandica*) and sea urchins (*Strongylocentrotus droebachiensis*). Specimens were frozen at -80°C shortly after being collected and kept at -80°C until further analysis. 50 and 49 specimens

were collected in May and in September, respectively. For each sampling period, 17 individuals were randomly selected and were dissected on ice to separate soft tissues (digestive gland and foot) from shells.

Because sediment sampling was impossible using a hand corer on *A. elliptica* habitat, we collected sediment cores (n = 3 for both sampling periods) at a depth of 110 m in a sedimentation basin in the middle section of the fjord (64°10'N, 51°31'W; Figure 12) using a Kajak sampler (KC-Denmark). The upper 1 cm was retained and frozen at -80°C until further analysis.

To characterize suspended particulate organic matter (POM), both from the subsurface waters (5 m depth, s-POM) and from 5 m above the bottom (b-POM), we collected 10L water samples (n = 3 for both sampling periods) at the study site using Niskin bottles. Three sub-samples for each type of analysis (*i.e.*, fatty acid / isotopic carbon ratio on specific fatty acid, and bulk stable isotopes) were made from initial 10L samples. On average 2L sub-samples were filtered onto pre-combusted (450°C during 4h) 47 mm diameter Whatman GF/F glass-fiber filters (pore size 0.7 µm). All POM filters were kept at -80°C until analyses.

Lastly, the most abundant macroalgae were collected in May (Phaeophyceae: *Agarum clathratum*, *Ascophyllum nodosum*, *Dictyosiphon foeniculaceus*, *Fucus vesiculosus*, *Laminaria* spp.; Chlorophyta: *Ulva lactuca*) using grab hook or by hand on the field. Three specimens were collected for each species. Salt and epibionts were then removed with Milli-Q and samples were frozen at -80°C until further analysis.

3.3. Analysis of stable nitrogen and carbon isotopes

Stable isotopes analyses were performed on potential sources of food available at the time of sampling (*i.e.*, pelagic-POM (including s-POM and b-POM), sediment, and macroalgae) and on the digestive gland of *A. elliptica*. All samples were freeze-dried before any treatment and analyses. Digestive glands were then ground to a homogeneous powder, and ca. 1 mg weighted in tin capsules for analyses. Filters, sediments and macroalgae samples

were duplicated: one untreated, and one acid fumed or acid washed to remove carbonate (Harris *et al.* 2001). Both were analyzed for C and N. Filters were treated following the acid fume method, while sediment and macroalgae samples were treated by the acid washing method. Samples were then dried at 60°C during 24h and weighted in tin capsules before analyses. $\delta^{13}C$ and $\delta^{15}N$ composition were determined at the UC Davis Stable Isotope Facility (Department of Plant Sciences, University of California at Davis, Davis, California) using a PDZ Europa ANCA-GSL elemental analyzer interfaced with a PDZ Europa 20/20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Isotopic ratios for carbon and nitrogen were expressed using the standard δ notation according to the following equation:

$$\delta X = \left[\left(R_{sample}/R_{reference}\right) - 1\right] \times 1000\ (‰)$$

where X is ^{13}C or ^{15}N of the sample, and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The reference for carbon was Vienna Pee Dee Belemnite, and atmospheric N2 for nitrogen. The analytical precision was 0.2‰ and 0.3‰ for carbon and nitrogen, respectively.

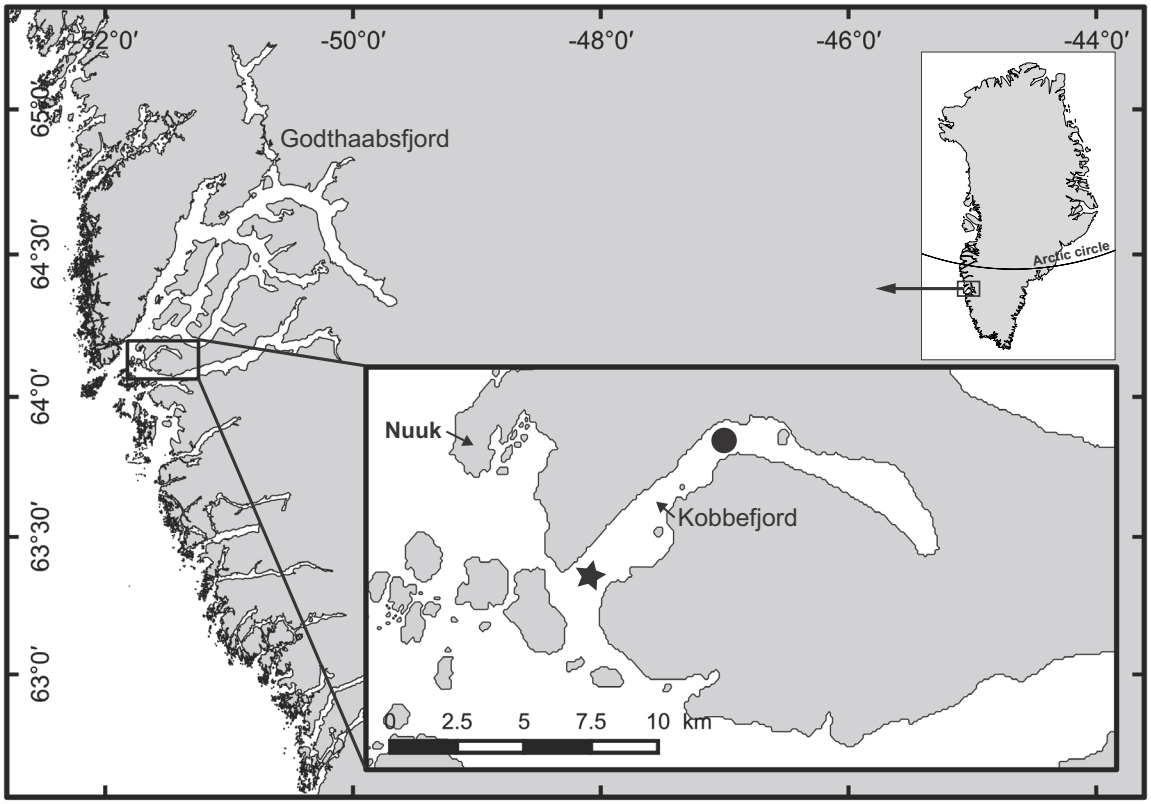

Figure 12. Study site and sampling stations. *A. elliptica* and its potential sources of food were sampled in the outer region of Kobbefjord (star) except for sediments collected in the center part of the fjord (circle)

3.4. Fatty acid analysis

Fatty acids analysis was performed on potential sources of food, and on digestive gland and foot of *A. elliptica*, following the method of Bligh & Dyer (1959) as slightly modified in Meziane & Tsuchiya (2002). Briefly, samples were freeze-dried overnight, and lipids extracted via ultrasonication for 20 min in distilled water:$CHCl_3$:MeOH (1:1:2, v:v:v) after addition of an internal standard (23:0). Lipids were concentrated under N_2 flux, and saponified with a mixture of NaOH:MeOH (1:2, v:v) at 90°C during 90 min to separate fatty acids. Saponification was stopped with HCl (35%) and $CHCl_3$ was added to recover fatty acids. Fatty acids were concentrated under N_2 flux and converted to methyl esters by incubation with BF_3-MeOH at 90°C during 10 min. Fatty acid methyl esters (FAMEs) were extracted with addition of mixture distilled water:$CHCl_3$ (1:1, v:v), and concentrated under N_2 flux to transfer in hexane. 1 µL of sample was injected to a gas chromatograph (GC, Varian CP-3800 equipped with flame ionization detector) equipped with a Supelco OMEGAWAX 320 column (30 m × 0.32 mm i.d., 0.25 µm film thickness) and helium as carrier gas to separate and quantify fatty acids. Fatty acids were identified by comparison of the retention time with analytical standards (Supelco® 37 Component FAME Mix, Supelco Inc., USA) and analysis of the sample in a gas chromatograph coupled to mass spectrometer (GC–MS, Varian 450GC with Varian 220-MS). Each fatty acid was given as a percentage of total fatty acids.

3.5. Stable carbon isotope analysis of specific fatty acids

Carbon stable isotope ratios of FAME samples (expressed as $\delta^{13}C$ values in ‰) were analyzed at the UC Davis Stable Isotope Facility (Department of Plant Sciences, University of California at Davis, Davis, California). Isotopic analyses of individual FAME were carried out under a continuous helium flow using a gas chromatograph (GC, Agilent 6890N) equipped with a BPX70 column (60 m x 0.25 mm o.d., 0.25 µm film thickness) coupled to an isotope ratio mass spectrometer (IR-MS, Thermo Finnegan MAT 253). Once separated,

samples were converted to CO_2 in an oxidation reactor at 950°C, and CO_2 entered the IRMS. FAME $\delta^{13}C$ were corrected for the methyl group addition during methylation according to the following formula:

$$\delta^{13}C_{FA} = \frac{(x+1) \times \delta^{13}C_{FAME} - \delta^{13}C_{MeOH}}{x}$$

where $\delta^{13}C_{FAME}$ and $\delta^{13}C_{MeOH}$ are the $\delta^{13}C$ values of the measured FAME and methanol used during methylation, respectively. $\delta^{13}C_{FA}$ represents the $\delta^{13}C$ of the given fatty acid prior to methylation, and x is the number of carbon atoms in the (non-methylated) fatty acid. In this study, the $\delta^{13}C$ value of the methanol used for the FAME preparation was equal to -38.43‰. All $\delta^{13}C$ values are reported relative to VPDB using standard δ notation.

3.6. Data analysis

Effect of acid treatment on bulk carbon isotopic ratio of sources of food was tested using paired Student's *t*-test. Effect of 'Season' (fixed with two levels: May and September) and 'Depth' (fixed with two levels: subsurface and bottom) on $\delta^{13}C$ and $\delta^{15}N$ in POM was assessed with 2-way crossed ANOVAs. Effect of 'Season' (fixed with two levels: May and September) on $\delta^{13}C$ and $\delta^{15}N$ in sediment and in digestive gland was tested with 1-way ANOVAs. Differences in isotopic signatures between the six macroalgae 'Species' (fixed with six levels: *A. clathratum*, *A. nodosum*, *D. foeniculaceus*, *F. vesiculosus*, *Laminaria* spp., *U. lactuca*) were identified using 1-way ANOVAs followed by Tukey HSD *post hoc* test. $\delta^{13}C_{FA}$ values of 7 fatty acids in tissues of *A. elliptica* were analysed with 3-way crossed ANOVAs to assess effect of 'Fatty acid' (fixed with seven levels, 18:1ω9, 18:2ω6, 18:3ω3, 18:4ω3, 20:4ω6, 20:5ω3, 22:6ω3), 'Tissue' (fixed with two levels: digestive gland and foot), 'Season' (fixed with two levels: May and September), and their interactions. Normality and homogeneity of variance of the residuals were assessed using the Shapiro-Wilk test and explanatory checks of plots of residuals against predicted values as suggested by Quinn & Keough (2002), respectively. When required, a logarithmic transformation was applied to the data and indicated.

To investigate fatty acid composition between the two sampling periods and among the different samples, permutational multivariate analyses of variance (PERMANOVA, 9999 permutations) were performed using PRIMER 6 (Clarke 1993, Clarke & Gorley 2006) and PERMANOVA+ (Anderson *et al.* 2008). Multivariate homogeneity of group dispersion was verified before each analysis (PERMDISP, 9999 permutations) and data were transformed when necessary. In case of significant PERMANOVA tests, post-hoc tests were carried out. Pairwise multiple comparison tests were used to identify differences among levels of source of variation. Multivariate analyses on total fatty acid composition, including *a posteriori* pair-wise comparison, were performed using a distance-based permutational multivariate analysis of variance (PERMANOVA, 9999 permutations) based on Bray-Curtis dissimilarities. The variation in fatty acid composition of tissues of *A. elliptica* was investigated, based on the 48 fatty acids identified, with two sources of variation: 'Season' (fixed with two levels: May and September) and 'Tissue' (fixed with two levels: digestive gland and foot). Fatty acid compositions of the pelagic-POM were examined, based on 27 fatty acids identified, with two sources of variation: 'Season' (fixed with two levels: May and September) and 'Depth' (fixed with two levels: subsurface and bottom). Fatty acid composition of sediment was examined, based on determined 52 fatty acids, with one source of variation: 'Season' (fixed with two levels: May and September), and the variation in fatty acid composition was studied among macroalgae 'Species' (fixed with six levels: *A. clathratum*, *A. nodosum*, *D. foeniculaceus*, *F. vesiculosus*, *Laminaria* spp., *U. lactuca*), based on 45 fatty acids. The number of replicates varied between 3 to 7. Variations in fatty acid composition, expressed in percentages, were visualized using non-metric multidimensional scaling (n-MDS) ordination based on Bray-Curtis dissimilarities between samples after standardization of data. The SIMPER (SIMilarity PERcentages) procedure (Clarke, 1993) was performed on untransformed data to identify fatty acids explaining the most dissimilarity between significant different levels.

To seek differentiation in FATM contents between the two seasons and among the digestive gland of *A. elliptica* and its potential sources of food, a two-way PERMANOVA with 'Sample' (fixed with four levels: s-POM, b-POM, sediment, and digestive gland) and

'Season' (fixed with two levels: May and September) as sources of variation were performed on twelve specific fatty acids used as dietary tracers. Multivariate homogeneity of group dispersion was verified before each analysis (PERMDISP, 9999 permutations).

A significance threshold of $\alpha = 0.05$ was adopted for all statistical tests.

4. Results

4.1. Seasonal $\delta^{13}C$ and $\delta^{15}N$ variability

No significant difference in $\delta^{13}C$ was shown between acid-treated and untreated samples of sediment and macroalgae (paired *t*-test, $p > 0.05$). Paired *t*-test showed, however, significant differences in $\delta^{13}C$ between acidified and non-acidified samples of POM (both s-POM and b-POM, $p < 0.05$) collected in September. Statistical tests were therefore performed on acid-treated samples for $\delta^{13}C$, and on untreated samples for $\delta^{15}N$, respectively. Significant interaction between season and depth was observed in POM $\delta^{13}C$ (two-way ANOVA, $p < 0.01$; Figure 13). $\delta^{13}C$ values were similar in May between sub-surface and bottom samples (-22.00 ± 0.06‰, on average), while s-POM was more enriched in ^{13}C (-24.26 ± 0.11‰) than b-POM (-25.49 ± 0.21‰) in September. No significant effect of season and depth or interaction was shown in POM $\delta^{15}N$ (two-way ANOVA, $p > 0.05$; Figure 13). Surface sediment $\delta^{13}C$ and $\delta^{15}N$ values were similar between May and September (one-way ANOVA, $p = 0.36$ and $p = 0.82$, respectively; Figure 13). Mean $\delta^{13}C$ and $\delta^{15}N$ values were -20.87 ± 0.04‰ and 6.08 ± 0.03‰, respectively. $\delta^{13}C$ values of six macroalgae species were determined and significantly differed (one-way ANOVA, $p < 0.001$; Figure 13). The Chlorophyceae *U. lactuca* was the most enriched in ^{13}C ($\delta^{13}C$ = -16.44 ± 0.05‰), while *D. foeniculaceus* was the macroalgae the most depleted in ^{13}C ($\delta^{13}C$ = -22.44 ± 0.37‰). $\delta^{15}N$ in macroalgae also differed significantly among species (one-way ANOVA, $p < 0.001$; Figure 13). $\delta^{15}N$ values were highest in *U. lactuca* and *Laminaria* spp. (7.12 ± 0.30‰, on average), lowest in *A. nodosum* and *F. vesiculosus* (3.73 ± 0.12‰, on average), and

intermediate in *D. foeniculaceus* and *A. clathratum* (5.56 ± 0.59‰, on average). Isotopic signature of the digestive glands of *A. elliptica* was not significantly different between May and September (one-way ANOVA, $p = 0.48$ and $p = 0.13$ for $\delta^{13}C$ and $\delta^{15}N$, respectively; Figure 13). $\delta^{13}C$ was equal to -21.23 ± 0.17‰ and $\delta^{15}N$ was equal to 5.54 ± 0.13‰, on average.

4.2. Fatty acid analysis

Fatty acid profiles of macroalgae were significantly different (PERMANOVA, $P < 0.001$; Table 10, Figure 14). Each of the six species had a specific fatty acid composition (Pair-wise tests, $P < 0.05$). Table 11 presents detailed fatty acid composition for each species and the five major fatty acids contributing to explain more than 60% of the average similarity (AD) within each species group. We grouped brown macroalgae in order to seek fatty acid markers of major taxa (*i.e.*, Phaeophyceae *vs.* Chlorophyta). SIMPER analysis indicated that 16:4ω3, 18:3ω3, 18:4ω3 were more abundant in *Ulva* spp., whereas 14:0, 18:2ω6, 20:4ω6, 20:5ω3 were present in higher proportion in Phaeophyceae (Table 11). These seven fatty acids explained more than 60 % of AD between the two taxa.

Detailed fatty acid composition in POM is given in Table 15A. SFA largely dominated POM samples (> 85% of total fatty acids), but with significantly different fatty acid composition between sub-surface and bottom samples, and between May and September (PERMANOVA, $P < 0.01$; Table 10). No interaction between depth and season was observed (Table 10). SIMPER analysis showed that the average of Bray-Curtis dissimilarities among depths and among seasons was 14.6 and 15.5, respectively and that the same set of fatty acids explained the differences. Levels of SFA (16:0 and 18:0) were more important in b-POM and in September, while unsaturated fatty acids (especially 16:1ω7, 16:4ω1, 18:4ω3, 20:5ω3, and 22:6ω3) showed higher proportions in s-POM and in May (Table 15A).

No significant differences were found in sediment total fatty acid composition between the two sampling periods (PERMNOVA, P = 0.07; Table 10), with 16:1ω7 (17.2 ± 0.7%),

16:0 (14.1 ± 0.3%), 20:5ω3 (10.2 ± 0.4%), and 18:1ω7 (7.2 ± 0.5%) as major fatty acids (Table 15B).

An n-MDS was performed using all sampled trophic sources (data from the two seasons and from the two depths for POM were included in these analyses) and SIMPER analysis to determine which fatty acids contributed to the dissimilarities observed in our study site (Figure 14). SIMPER indicated the large influence of 18 carbon unsaturated fatty acids (18:1ω7, 18:3ω3 and 18:4ω3) in *U. lactuca*, the importance of SFA (16:0 and 18:0) in POM, and the isolation of sediment samples was based primarily on the presence of 16:1ω7 and 20:5ω3. The other macroalgae (Phaeophyceae) were divided into three groups. The first one included *A. nodosum* and *F. vesiculosus* mainly due to higher proportions of 18:1ω7 and 18:2ω6 compared to all the other groups. The second cluster was made of *D. foeniculaceus* and *Laminaria* spp. because of their higher contents in 20:4ω6 and 20:5ω3, and *A. clathratum* is distinct based on its higher contents of 16:0, 16:1ω7 and 18:1ω9.

Complete fatty acid compositions of the digestive gland and the feet of *A. elliptica* are given in Table 15C and showed significant differences between tissues and seasons (PERMANOVA, $P < 0.01$; Table 10, Figure 15) but no interaction between tissues and seasons (Table 10). SIMPER analysis showed the influence of long-chain PUFAs (20 and 22 carbons) in the feet of *A. elliptica*, while unsaturated fatty acids with 16 and 18 carbons were more abundant in its digestive glands. Higher proportions of 18:4ω3, 16:4ω1, and 16:1ω7 was observed in May, while 18:2ω3, 20:4ω6, and 20:1ω9 showed higher levels in September (Figure 15).

We looked at variations of twelve fatty acids commonly used as dietary tracers between seasons and between the digestive gland of *A. elliptica* and its potential sources of food (Table 12). Proportions of 18:1ω7 and 18:3ω3 were similar between May and September for all groups. Sum of 20:1ω9 and 22:1ω11 and levels of 16:4ω1, 18:2ω6, 20:4ω6, and 20:5ω3 significantly differed between May and September for all groups (PERMANOVA, $P < 0.05$; Table 13). Proportions of 20:1ω9, 22:1ω11, and 20:4ω6 significantly increased between May and September, while levels of the three others FATMs (16:4ω1, 18:2ω6, and 20:5ω3)

decreased (Table 13). Proportions of 16:1ω7 significantly decreased in POM (both s-POM and b-POM, from 4.9 ± 0.7 to 1.4 ± 0.2% and from 4.4 ± 0.3 to 0.5 ± 0.1%, respectively) and in sediment (from 18.5 ± 0.5 to 15.9 ± 0.8%) between May and September as well (Table 13). Proportions of 18:4ω3 in b-POM, sediment and digestive gland of *A. elliptica* were significantly lower in September compared to May, while they were similar in s-POM (Table 13). Levels of 18:1ω9 were the same in POM (both s-POM and b-POM) for the two periods, while sediment and digestive gland of *A. elliptica* showed reverse trends with a lower proportion in sediment and a higher proportion in digestive glands in May compared to September (Table 13). Levels of 22:6ω3 were significantly higher in s-POM and digestive gland of *A. elliptica* in September compared to May (Table 13). Levels of 22:6ω3 decreased in b-POM between May and September and remained stable in sediment. Seasonal difference in proportions of branched fatty acids, used as marker of bacteria, was only found in b-POM (Pairwise test, $t = 3.82$, $P = 0.02$), with higher proportion in May (0.5 ± 0.1%) compared to September (0.1 ± 0.0%) (Table 13).

As result of significant interaction between the two factors 'Season' and 'Sample' (PERMANOVA, $P < 0.5$), branched fatty acids, sum of 20:1ω9 and 22:2ω11, 16:1ω7, 18:4ω3, and 22:6ω3 varied in a different way between b-POM, s-POM, sediment, and the digestive glands of *A. elliptica* in May and in September (Table 13). A higher variability was observed in September compared to May since the four groups were often significantly different from each other, with the exception of the sum of 20:1ω9 and 22:2ω11 that significantly differed between sediment and digestive gland in May, and became similar in September (Table 13). Proportions of 18:1ω9, 18:1ω7, and 16:4ω1varied in the same way among the four groups (both in May and in September), with the lowest proportions in POM, intermediate proportions in digestive gland of *A. elliptica*, and the highest proportions in sediment (Table 13). Levels of 20:5ω3 remained lower in POM, intermediate in sediment and higher in the digestive glands of *A. elliptica*, levels of 18:2ω6 were intermediate in s-POM, lower in b-POM and sediment, and higher in the digestive glands, and proportions of 20:4ω6 were significantly higher in sediment than in the digestive glands of *A. elliptica* (Table 13).

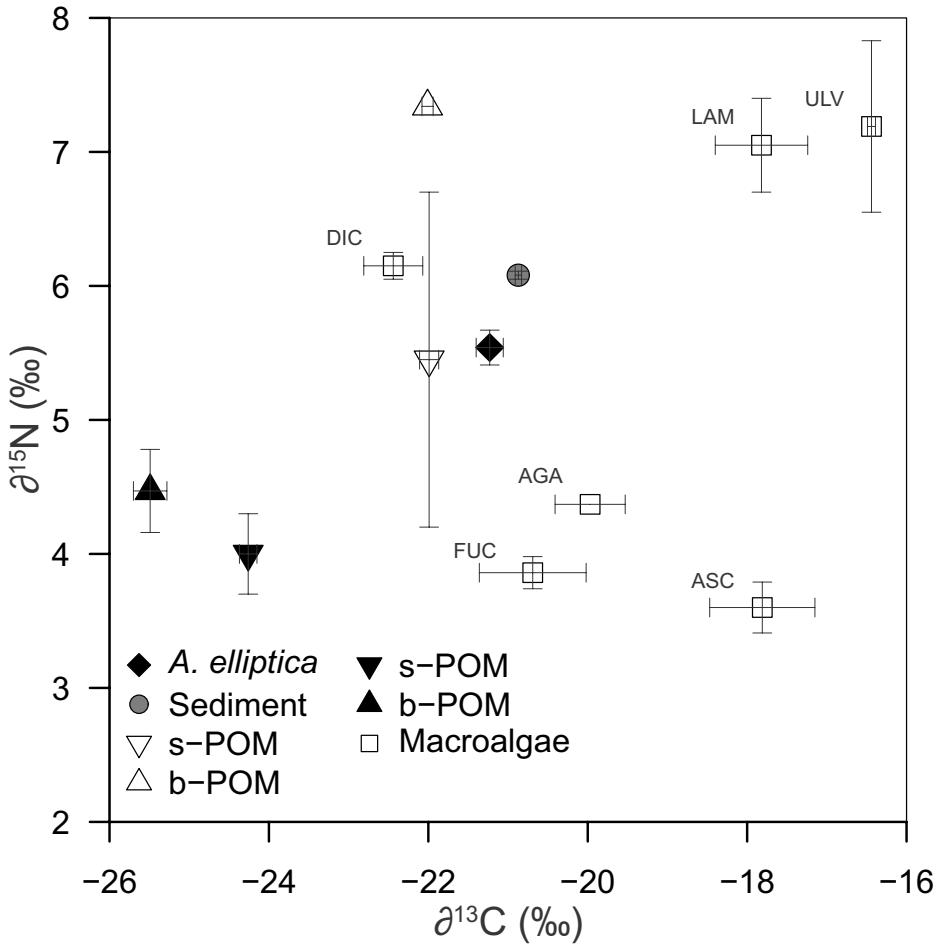

Figure 13. Carbon and nitrogen isotopic composition of digestive glands of *A. elliptica* and its potential sources of food: particulate organic matter (POM, including s-POM and b-POM) collected in May (open triangles) and September (black triangles), sediment and six macroalgae species (AGA = *A. clathratum*; ASC = *A. nodosum*; DIC = *D. foeniculaceus*; FUC = *F. vesiculosus*; LAM = *Laminaria* spp.; ULV = *U. lactuca*) collected in Kobbefjord. Data from May and September were pooled for sediment and digestive glands of *A. elliptica* since no significant difference was found (one-way ANOVA)

Table 10. Results of permutational multivariate analyses of variance (PERMANOVAs) on total fatty acid composition of *A. elliptica*'s tissues (digestive gland and foot) and potential sources of food (*i.e.*, POM (including s-POM and b-POM), sediment, and six macroalgae species) collected in Kobbefjord in May and September 2013 based on the Bray-Curtis dissimilarity matrix. Significant values (*p*-value < 0.05) are in **bold**; ** p < 0.01, *** p < 0.001

Source of variation	df	*A. elliptica*[a] MS	Pseudo-F	Source of variation	df	POM MS	Pseudo-F
Tissue (T)	1	1488.300	**48.856*****	Depth (D)	1	361.680	**10.667*****
Season (S)	1	299.030	**9.816*****	Season (S)	1	504.760	**14.886*****
T × S	1	39.719	1.304***	D × S	1	28.428	0.838***
Residual	22	30.463		Residual	8	33.908	

	df	Sediment MS	Pseudo-F		df	Macroalgae MS	Pseudo-F
Season	1	136.130	3.241***	Species	5	2829.200	**43.228*****
Residual	4	42.001		Residual	12	65.449	

[a] Data were log(x + 1) transformed prior to analysis

Table 11. Fatty acid composition, expressed as mass % of total fatty acids, of six macroalgae species (AGA = *A. clathratum*; ASC = *A. nodosum*; DIC = *D. foeniculaceus*; FUC = *F. vesiculosus*; LAM = *Laminaria* spp.; ULV = *U. lactuca*) collected in Kobbefjord in May 2013. Only FA > 3% are shown. Average similarity within each species group and the main fatty acids responsible for similarities (SIMPER outputs) are given in bold. MTFA = mass of total fatty acid expressed in mg g^{-1}; SFA = saturated fatty acid; MUFA = monounsaturated fatty acid; PUFA = polyunsaturated fatty acid '-' not determined. Values are mean (SE)

Average similarity	AGA 80%	ASC 95%	DIC 94%	FUC 96%	LAM 88%	ULV 92%
14:0	5.0 (0.6)	**12.7 (0.3)**	7.0 (0.5)	**12.9 (0.3)**	**10.3 (0.4)**	1.0 (0.1)
16:0	**28.7 (3.0)**	**13.3 (0.6)**	**18.0 (0.4)**	**11.5 (0.0)**	**20.6 (1.2)**	**20.1 (1.4)**
Σ SFA	36.4 (3.4)	28.1 (1.0)	27.1 (1.0)	26.0 (0.3)	33.2 (0.5)	24.0 (1.6)
16:1ω7	**11.9 (3.2)**	1.3 (0.0)	1.7 (0.1)	1.6 (0.1)	2.2 (0.2)	2.1 (0.3)
17:1ω9	0.1 (0.0)	0.2 (0.0)	0.1 (0.0)	0.3 (0.0)	-	5.7 (0.5)
18:1ω9	**8.2 (1.1)**	-	8.9 (0.5)	**14.8 (0.8)**	-	0.8 (0.1)
18:1ω7	0.6 (0.1)	**28.2 (0.7)**	0.2 (0.1)	7.0 (0.4)	**11.0 (0.6)**	**8.0 (0.3)**
Σ MUFA	24.0 (2.7)	32.7 (0.8)	13.4 (0.7)	28.3 (0.4)	15.0 (0.6)	19.2 (0.9)
16:4ω3	0.3 (0.0)	-	0.2 (0.1)	0.2 (0.0)	-	**15.7 (0.5)**
16:4ω1	3.8 (0.9)	-	0.0 (0.0)	0.1 (0.0)	-	0.3 (0.0)
18:2ω6	5.7 (2.1)	**8.7 (0.2)**	**8.6 (0.1)**	**12.2 (0.3)**	7.2 (0.6)	2.1 (0.2)
18:3ω3	2.9 (0.9)	3.9 (0.3)	**9.2 (0.6)**	6.0 (0.2)	6.3 (1.1)	**17.8 (2.3)**
18:4ω3	1.3 (0.4)	3.3 (0.2)	9.6 (1.2)	4.3 (0.2)	9.5 (2.8)	**13.1 (0.8)**
20:4ω6	**7.1 (0.6)**	9.0 (0.6)	**17.8 (0.7)**	**9.8 (0.2)**	**11.0 (2.6)**	0.2 (0.0)
20:5ω3	**7.2 (2.4)**	**9.7 (0.6)**	**12.0 (0.6)**	9.2 (0.1)	**15.2 (0.8)**	2.6 (0.2)
22:5ω3	3.1 (0.5)	-	-	-	-	2.7 (0.2)
Σ PUFA	39.6 (6.1)	39.2 (1.5)	59.6 (1.7)	45.8 (0.2)	51.8 (1.1)	56.8 (2.4)
MTFA	6.5 (1.9)	3.0 (0.4)	9.1 (0.8)	7.6 (1.2)	7.5 (0.9)	9.4 (2.4)

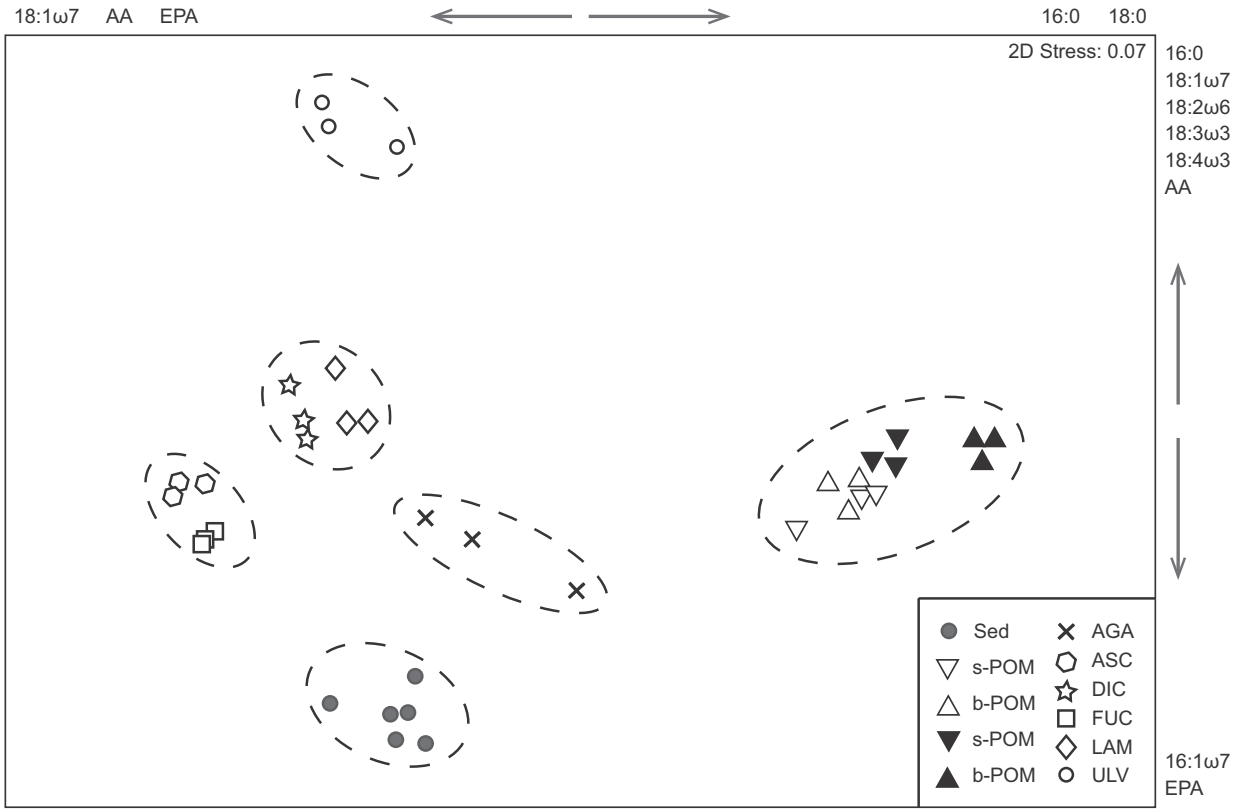

Figure 14. Non-metric multidimensional scaling (n-MDS) ordination based on Bray-Curtis dissimilarity matrix calculated on untransformed data for potential sources of food: POM (including s-POM and b-POM) collected in May (open triangles) and September (black triangles), sediment (Sed), and six macroalgae species (AGA = *A. clathratum*; ASC = *A. nodosum*; DIC = *D. foeniculaceus*; FUC = *F. vesiculosus*; LAM = *Laminaria* spp.; ULV = *U. lactuca*) collected in Kobbefjord. The factor 'Season' is not shown for sediment data since no significant difference was found (PERMANOVA, Table 10). Arrows and fatty acids indicate the main component explaining the group dissimilarities (SIMPER outputs). Dashed ellipses represent samples similar at 70%

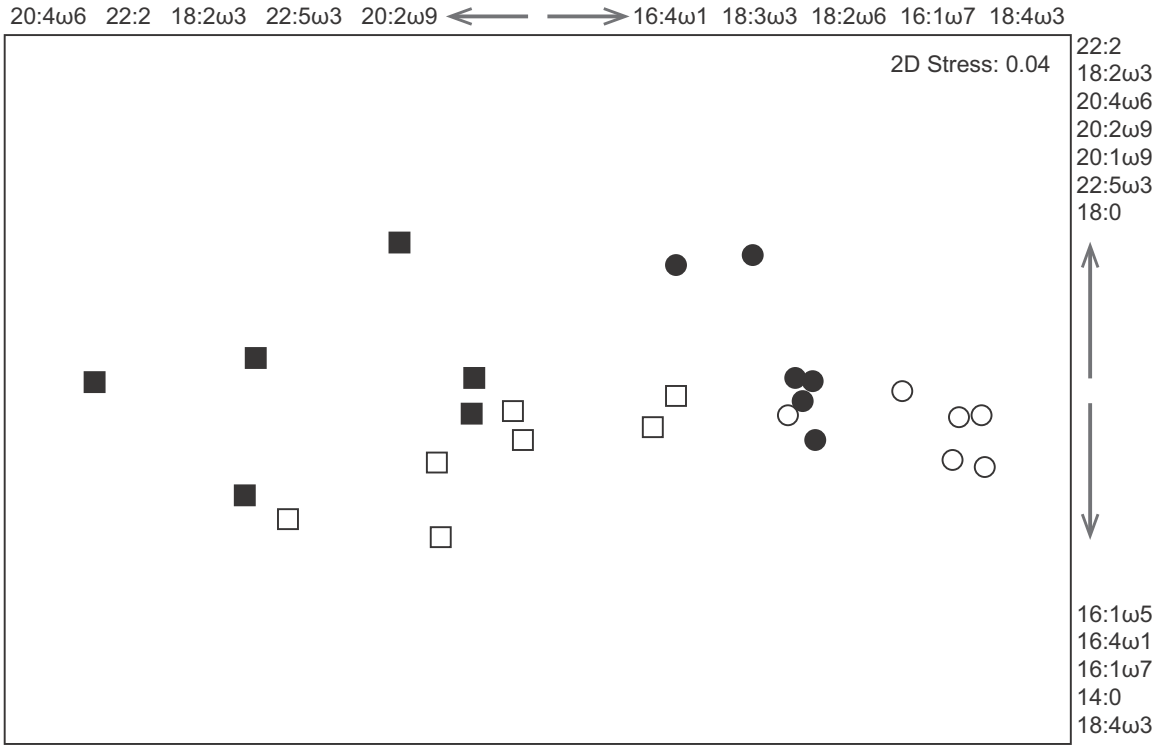

Figure 15. Non-metric multidimensional scaling (n-MDS) ordination based on Bray-Curtis dissimilarity matrix calculated on log(x + 1) transformed data for *A. elliptica* tissues, digestive glands (squares) and feet (circles) collected in Kobbefjord in May (open symbols) and September (black symbols). PERMANOVA results are given in Table 10. Arrows and fatty acids indicate the main component explaining the group dissimilarities (SIMPER outputs)

Table 12. Summary of selected fatty acids (FAs) used as dietary tracers in our study

Source	FATMs	References
Bacteria	Σ *i*-FA + *ai*-FA, 18:1ω7, 16:1ω7	Viso & Marty (1993), Kharlamenko *et al.* (1995), Budge & Parrish (1998), Stevens *et al.* (2004a)
Diatoms	16:4ω1, 16:1ω7, 20:5ω3	Viso & Marty (1993), Napolitano *et al.* (1997), Reuss & Poulsen (2002), Søreide *et al*. (2008), Kelly & Scheibling (2012)
Dinoflagellates	22:6ω3, 18:4ω3, 18:1ω9	Napolitano *et al.* (1997), Mansour *et al.* (1999), Søreide *et al*. (2008), Kelly & Scheibling (2012)
Copepods	Σ 20:1ω9 + 22:1ω11	Dalsgaard *et al*. (2003), Lee *et al*. (2006)
Chlorophyta	18:3ω3, 18:2ω6	Graeve *et al*. (2002), Kelly & Scheibling (2012), Wessels *et al*. (2012)
Phaeophyceae	18:4ω3, 20:4ω6, 20:5ω3, 18:1ω9	Graeve *et al*. (2002), Kelly & Scheibling (2012), Wessels *et al*. (2012)

Table 13. Average values (%) of 12 FATMs in POM (including s-POM and b-POM), sediment, and digestive gland (DG) of *A. elliptica* collected in Kobbefjord in May and September 2013. Letters indicate significant differences between groups in May and September, and symbols indicate significant differences among seasons (Pairwise tests, $P < 0.05$). '-' = not determined. Values are mean (SE)

	May				September			
FA	s-POM	b-POM	Sediment	DG	s-POM	b-POM	Sediment	DG
Σ *i*-FA + *ai*-FA	0.6 (0.2) ^{ab}	0.5 (0.1) ^{a}	16.3 (0.1) ^{b}	12.0 (0.1) ^{c}	0.5 (0.1) ^{a} ❖	0.1 (0.0) ^{b} ❖	17.3 (0.7) ^{c} ❖	12.4 (0.1) ^{d} ❖
16:1ω7	4.9 (0.7) ^{ab}	4.4 (0.3) ^{a}	18.5 (0.5) ^{b}	15.2 (0.2) ^{a}	1.4 (0.2) ^{a} ❖	0.5 (0.1) ^{b} ❖	15.9 (0.8) ^{c} ❖	14.4 (0.3) ^{d} ❖
18:1ω9	1.0 (0.1) ^{ab}	1.1 (0.0) ^{a}	15.7 (0.2) ^{b}	11.4 (0.0) ^{c}	1.0 (0.2) ^{a} ❖	1.1 (0.2) ^{a} ❖	13.8 (0.0) ^{b} ❖	11.7 (0.0) ^{c} ❖
18:1ω7	0.6 (0.1) ^{ab}	0.9 (0.1) ^{a}	16.7 (0.2) ^{b}	14.0 (0.2) ^{c}	0.6 (0.1) ^{a} ❖	0.3 (0.1) ^{a} ❖	17.6 (1.1) ^{b} ❖	14.5 (0.2) ^{c} ❖
Σ 20:1ω9 + 22:1ω11	-	-	10.8 (0.0) ^{a}	12.3 (0.1) ^{b}	-	-	14.3 (0.7) ^{a} ❖	13.5 (0.4) ^{a} ❖
16:4ω1	0.9 (0.2) ^{ab}	1.0 (0.2) ^{a}	11.5 (0.2) ^{b}	11.4 (0.1) ^{c}	0.3 (0.0) ^{a} ❖	0.0 (0.0) ^{a} ❖	11.1 (0.2) ^{b} ❖	10.6 (0.0) ^{c} ❖
18:2ω6	0.7 (0.1) ^{ab}	0.4 (0.0) ^{b}	10.5 (0.0) ^{b}	11.4 (0.0) ^{c}	0.5 (0.1) ^{a} ❖	0.3 (0.1) ^{b} ❖	10.3 (0.1) ^{b} ❖	11.5 (0.1) ^{c} ❖
18:3ω3	0.2 (0.1) ^{ab}	0.1 (0.0) ^{b}	10.4 (0.1) ^{c}	10.8 (0.0) ^{d}	0.4 (0.0) ^{a} ❖	0.1 (0.0) ^{b} ❖	10.5 (0.1) ^{c} ❖	10.7 (0.1) ^{d} ❖
18:4ω3	0.8 (0.2) ^{ab}	0.7 (0.0) ^{a}	11.5 (0.2) ^{b}	10.0 (0.7) ^{c}	1.1 (0.1) ^{a} ❖	0.1 (0.0) ^{b} ❖	10.9 (0.1) ^{a} ❖	16.1 (0.5) ^{c} ❖
20:4ω6	-	-	11.9 (0.1) ^{a}	11.0 (0.1) ^{b}	-	-	14.4 (2.0) ^{a} ❖	11.4 (0.1) ^{b} ❖
20:5ω3	1.8 (0.3) ^{ab}	2.8 (0.5) ^{a}	10.7 (0.3) ^{b}	24.7 (0.5) ^{c}	1.6 (0.1) ^{a} ❖	0.4 (0.2) ^{a} ❖	19.8 (0.8) ^{b} ❖	23.1 (0.2) ^{c} ❖
22:6ω3	0.6 (0.1) ^{ab}	0.6 (0.0) ^{a}	12.9 (0.3) ^{b}	19.5 (0.1) ^{c}	1.3 (0.1) ^{a} ❖	0.2 (0.1) ^{b} ❖	12.7 (0.3) ^{c} ❖	10.7 (0.5) ^{d} ❖

4.3. Carbon stable isotope of individual fatty acids

Isotopic signatures of seven fatty acids in tissues (digestive glands and feet) of *A. elliptica* are shown in Figure 16. A significant effect of the interaction between the two factors 'Fatty Acid' and 'Tissue' was observed on $\delta^{13}C$ values, while no effect of the factor 'Season' was detected (3-way ANOVA, *p*-value < 0.01; Table 14). The highest $\delta^{13}C$ values (-25.0 ± 0.4‰) were found for the fatty acid 22:6ω3 and the lowest $\delta^{13}C$ values (-37.2 ± 0.8‰) were obtained for 18:3ω3, both in foot of *A. elliptica* (Figure 16). Range of $\delta^{13}C$ values in digestive gland of *A. elliptica* was smaller, from -25.4 ± 1.0‰ for 22:6ω3 to -31.0 ± 0.6‰ for 18:2ω6 (Figure 16). 18:2ω6 and 18:3ω3 were significantly more depleted than the other fatty acids in the foot, while they had about equal $\delta^{13}C$ values to the other fatty acids in the digestive gland (Figure 16). Whether in digestive gland or in foot, $\delta^{13}C$ values of 20:4ω6, 20:5ω3, and 22:6ω3 tended to decrease with unsaturation, although no significant difference was observed (Figure 16).

$\delta^{13}C$ values of ten fatty acids used as dietary tracers are shown in Figure 17. In *A. elliptica*, $\delta^{13}C$ values widely varied, from -37.5 ± 0.9‰ for 18:3ω3 to -24.7 ± 0.1‰ for 22:6ω3. Among all sources of food, $\delta^{13}C$ values ranged between -32.2‰ for 20:4ω6 in POM and -19.1 ± 1.5‰ for 20:5ω3 in the Chlorophyta *U. lactuca*.

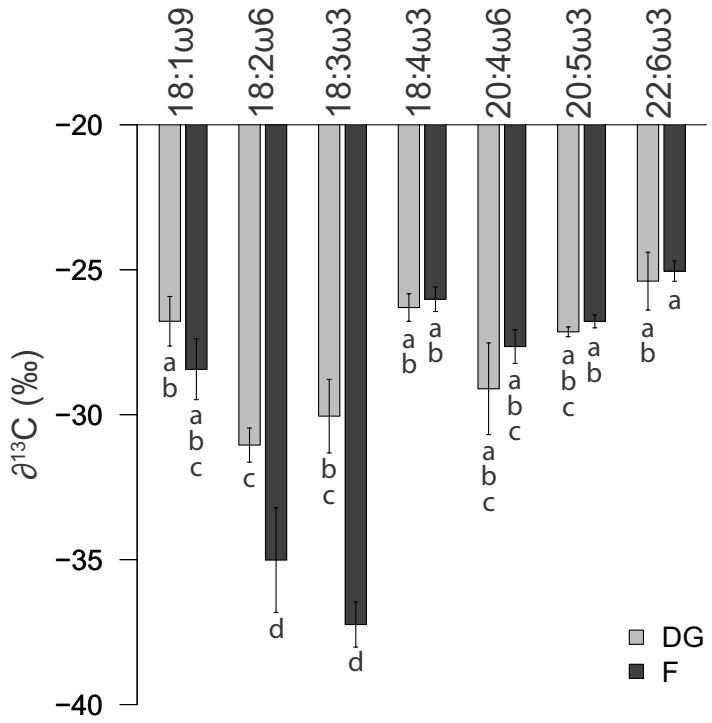

Figure 16. Average values of the carbon isotope ratio of fatty acids (‰, ± SE) in *A. elliptica* tissues (DG = digestive gland and F = foot). Different letters indicate significant differences for the interaction between tissue and fatty acid (p-value < 0.05 after Tukey's HSD *post-hoc* test)

Table 14. Results of 3-way ANOVAs testing the effect of Fatty Acid (FA), Tissue (T), and Season (S) and their interactions on the carbon isotopic ratio of 7 fatty acids in *A. elliptica*. Significant values are in **bold**; ** $p < 0.01$, *** $p < 0.001$

Sources of variation	df	MS	F
FA	6	161.139	**22.416*****
T	1	72.212	**10.046*****
S	1	14.205	1.976***
FA × T	6	27.919	**3.884*****
FA × S	6	3.210	0.447***
T × S	1	27.289	3.796***
FA × T × S	6	7.355	1.023***
Residual	105	7.188	

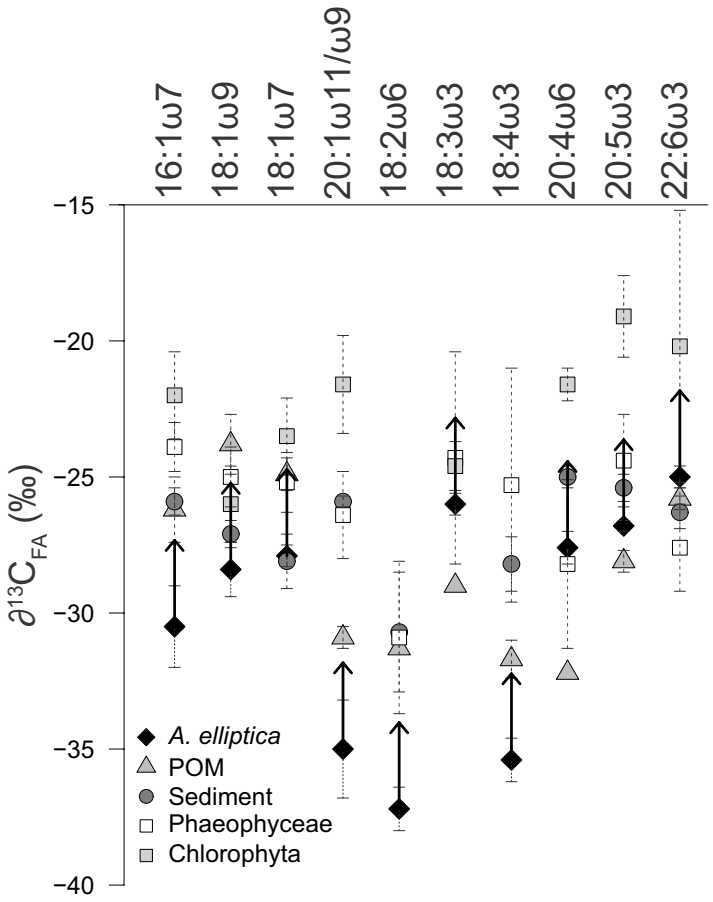

Figure 17. Average stable carbon isotopic values of 10 fatty acids ($\delta^{13}C_{FA}$) in feet of *A. elliptica* and its potential sources of food (POM, sediment, and macroalgae) collected in Kobbefjord in May and September 2013. Data from different depths (for POM) and from the two seasons were pooled. Values are mean (SE). Arrows indicate fractionation constant (3.17‰) applied on $\delta^{13}C_{FA}$ as a result of a decrease in the isotope ratio of the consumer's tissue compared to that of the food resource, as described by Gladyshev et al. (2014)

5. Discussion

In accordance with our first hypothesis, trophic resources (organic matter from the water column and the sediment, and macroalgae) were distinguishable in terms of fatty acid compositions and isotopic signatures (bulk stable isotopes, and carbon isotopic ratio on individual fatty acids). Thus, these biological and chemical segregations allowed us to trace these resources in the benthic food web and to accurately identify the diet of the bivalve *A. elliptica* in a subarctic fjord. However, in contrary to our second hypothesis, the multiple biomarker approach showed that *A. elliptica* did not feed only on microalgae, but rather on a mixture of POM, including microalgae and macroalgal (mainly brown algae) detritus. Moreover, $\delta^{13}C$ signatures in *A. elliptica* tissues suggest that isotopic composition was not the most appropriate tool to track seasonal variability in its diet, whereas total fatty acid profiles and FATM showed marked differences between the two sampling periods. Thus, combination of both tools seems to be a useful method to understand trophic strategy in response to changing primary production dynamics as proposed in our third hypothesis.

5.1. Characterization of trophic resources

Our study included nine potential sources of food available at the time of samplings (*i.e.*, pelagic POM, including s-POM and b-POM, surface sediment, and 6 six macroalgae species) that presented distinct fatty acid compositions and isotopic signatures. As observed by Khotimchenko *et al.* (2002) and Li *et al.* (2002), the green algae *U. lactuca* showed typical fatty acid composition containing higher concentration of C_{18} PUFAs (especially 18:3ω3 and 18:4ω3) and lower levels of C_{20} PUFAs than brown macroalgae. Furthermore, we found high levels of 16:4ω3 (up to 15%) that is characteristic in the Ulvales order (Fleurence *et al.* 1994, Khotimchenko *et al.* 2002), making this fatty acid a relevant biomarker of this green algae species in primary consumers. Brown algae were characterized and distinguishable from green algae by relatively high levels of 20:4ω6, 20:5ω3, 18:2ω3, and 18:1ω9 as already shown in previous studies (Graeve *et al.* 2002, Khotimchenko *et al.* 2002, Li *et al.* 2002).

The clear differences between the two macroalgal taxa and also between species since the six algae species had distinctive fatty acid compositions, make these lipids a suitable tracer of algal resources for studies of benthic food web. However, considerable variability in fatty acid composition has been found in macroalgae among species, sites, and seasons (Nelson *et al.* 2002, Dethier *et al.* 2013). Sampling for fatty acid characterization ideally should span all seasons to capture this variation and how it propagates up through consumers in food webs. Despite these variations, fatty acid biomarkers could readily distinguish macrophyte phyla (Dethier *et al.* 2013).

Stable isotope compositions of POM was in the range of values observed in other Arctic studies (Hobson *et al.* 1995, Tamelander *et al.* 2006, Søreide *et al.* 2008, Renaud *et al.* 2011, Oxtoby *et al.* 2013). No significant depth effect was found on $\delta^{15}N$ even if suspended material sinks to the seafloor in various manners, such as phytodetritus, faeces of pelagic grazers or marine snow, which affect the isotopic composition of the settling material (Mintenbeck *et al.* 2007). In particular, increased POM $\delta^{15}N$ values with depth may be a consequence of zooplankton grazing and microbial degradation (Ostrom *et al.* 1997). POM showed also variations in $\delta^{13}C$ and more ^{13}C-depleted values in September than in May (see discussion on seasonal variability below). Although microalgal species were not identified in POM samples, the algal class composition can be partially deduced using fatty acid biomarkers (e.g. reviewed in Dalsgaard *et al.* 2003, Kelly & Scheibling 2012). POM fatty acid composition was largely dominated by SFAs. It has already been shown that marine detritus contains significant quantities of SFAs between 14 and 18 carbons (Fahl & Kattner 1993). Dominance of fatty acids 14:0, 16:0 and 18:0 are also characteristic of Prymnesiophyceae such as *Phaeocystis* spp. (Claustre *et al.* 1990, Nichols *et al.* 1991, Cotonnec *et al.* 2001). Generally, diatoms (particularly the diatom genera *Chaetoceros* and *Thalassiosira*) dominates the microplankton assemblage during the spring bloom in late April/early May in the Godthåbsfjord system and were complemented by haptophytes (Juul-Pedersen *et al.* 2015, Krawczyk *et al.* 2015). Haptophytes, represented by *Phaeocystis* spp., were already observed during spring seasons with a maximum contribution as high as 72% of the microplankton assemblage composition (for instance in April–May 2010; Krawczyk *et al.*

2015). This dominance of fatty acid markers of *Phaeocystis* spp. in POM is consistent with observations conducted during the monitoring program of Godthåbsfjord since *Phaeocystis* spp. dominated the phytoplankton community composition from March to June (86% on average) and in September (78%) 2013 (Jensen & Christensen 2014). Higher levels of SFAs and lower levels of unsaturated fatty acids in b-POM compared to s-POM could explain depth-related differences in fatty acid composition of POM samples. FAs are known to be selectively degraded in the marine environment and may be used as an indicator of degradation processes (Reemtsma *et al.* 1990, Fileman *et al.* 1998). The more rapid degradation of PUFAs with depth compared to saturated and monounsaturated FAs is well established although lower degradation rates have been shown in cold environment (Fileman *et al.* 1998). Lower levels of PUFAs likely denoted degradation of pelagic organic matter during transfer through the water column.

Sediment had higher $\delta^{13}C$ values than POM, likely related to sinking phytodetritus that may be slightly ^{13}C-enriched through recycling processes across the microbial loop (Hobson *et al.* 1995). The relatively high $\delta^{13}C$ values in sediment may also result from the influence of macroalgae (especially *F. vesiculosus* and *A. chlathratum*), which were mostly enriched in ^{13}C. The ^{13}C composition of the sediment indicates therefore that phytoplankton and detritus from brown algae both contribute to the organic material buried in the sediment of the Kobbefjord. Alternatively, with regard to fatty acid composition, relatively high levels of 16:1ω7 (17.2 ± 0.7 %), 16:4ω1 (1.3 ± 0.1 %), and 20:5ω3 (10.2 ± 0.4 %) in sediment may reflect the presence of diatoms which are major taxa of microplankton during the blooms (Krawczyk *et al.* 2015), and in microphytobenthos (Wulff *et al.* 2009 and references therein, but see discussion about 20:5ω3 origin below) although we did not isolate this trophic source. Indeed, we did not sample three potential additional sources that may contribute to Arctic food webs: terrestrial carbon, sea ice algae and microphytobenthos. The POM samples (from -22.00 to -25.49‰) clearly had a marine $\delta^{13}C$ signature (marine $\delta^{13}C$ from -22 to -25‰, terrestrial $\delta^{13}C$ from -27 to -31‰; Dunton *et al.* 2006) and sea ice algae contribute less than 1% of total (sympagic plus pelagic) primary production annually in Kobbefjord (Mikkelsen *et al.* 2008). Microphytobenthos, however, may exhibit significant rates of primary

production at shallow depths that is comparable to the primary production in the water column above (Glud *et al.* 2009, Woelfel *et al.* 2010, Attard *et al.* 2014) and, hence, it could be considered as a potentially important carbon source for benthos in coastal areas. Furthermore, based on stable carbon isotope composition, Oxtoby *et al.* (2013) concluded that microphytobenthos may be distinct from terrestrial and sympagic origins but indistinguishable from marine pelagic POM, which may cause microphytobenthos to be overlooked as an important source of carbon to the benthic community. However, microphytobenthos can be assumed to be of minor importance at the sampling depth of *A. elliptica*.

5.2. Diet of A. elliptica

Coupled approaches of bulk isotopic, fatty acid, and compound-specific isotope analyses showed that *A. elliptica* feeds on a mixture of suspended POM and brown macroalgae detritus. Carbon and nitrogen stable isotopes are particularly useful to trace pathways of organic matter in food webs, and to determine the contribution of various food items to organisms' diet (Fry 2007). $\delta^{15}N$ is used to assess the mean trophic position of organisms in a food web (DeNiro & Epstein 1981, Peterson & Fry 1987, Hobson & Welch 1992, Vander Zanden & Rasmussen 2001), while the $\delta^{13}C$ values can provide information on major carbon sources of consumers (Peterson & Fry 1987, Vander Zanden & Rasmussen 2001, Post 2002). Indeed, the conservative transfer of carbon isotopic compositions (< 1‰) to the animal from its diet can be useful in tracing food webs in systems where food sources show large differences in $\delta^{13}C$ values, such as marine *vs.* terrestrial systems, or coastal *vs.* oceanic systems (DeNiro & Epstein 1978, Peterson & Fry 1987, Vander Zanden & Rasmussen 2001). Based on this assumption, three sampled sources of food (suspended POM, in May, and the two brown algae *F. vesiculosus* and *D. foeniculaceus*) are likely to support the bivalve *A. elliptica* in Kobberfjord. Fatty acid composition and FATM analyses supported these results since digestive glands of *A. elliptica* contained high levels of fatty

acid markers of microalgae, both diatoms and dinoflagellates (16:1ω7, 18:4ω3, 20:5ω3 and 22:6ω3), and brown macroalgae (C_{18} PUFAs, 20:4ω6 and 20:5ω3).

The only use of fatty acids as trophic markers is sometimes limiting since a unique fatty acid tracer assigned to a given taxonomic group is a relatively rare situation. Compound-specific isotope analysis appeared to be more successful than the other trophic markers when different food sources have similar bulk carbon isotope and fatty acid signatures (Gladyshev *et al.* 2012). In our study, we analysed $\delta^{13}C$ on seven fatty acids, both in digestive glands and feet of *A. elliptica*. As observed by Gladyshev *et al.* (2012) in organisms of a four-link food chain from the Yenisei River, a parabolic dependence of $\delta^{13}C$ values of fatty acids on their degree of unsaturation/chain length occurred, with 18:2ω6 and 18:3ω3 in its lowest point. However, our results showed that the parabolic pattern of $\delta^{13}C_{FA}$ was less pronounced in the digestive glands than in feet of *A. elliptica*. Since bivalves have a very limited or no ability to synthesize PUFAs (especially EFAs, such as 20:4ω6, 20:5ω3, and 22:6ω3) from the precursors 18:2ω6 and 18:3ω3 contained in their food (De Moreno *et al.* 1976, Waldock & Holland 1984, Fernández-Reiriz *et al.* 1998), we suggest that dissimilarities in $\delta^{13}C$ values between the tissues of *A. elliptica* is likely caused by a differential isotopic fractionation, as is the case for bulk stable isotopes study. Indeed, different tissues show different isotopic enrichment, depending on their turnover rate (Lorrain *et al.* 2002, Cabanellas-Reboredo *et al.* 2009, Deudero *et al.* 2009). When investigating trophic dynamics on different timescales, tissues with higher metabolic activity, such as the digestive gland or gonad, are more appropriate to elucidate recent bivalve diet, while tissues with lower metabolic activity, such as muscle, provide an 'average' of dietary source over a longer period of time (Paulet *et al.* 2006). Since $\delta^{13}C$ values on individual fatty acids from feet of *A. elliptica* showed a larger range, compound-specific isotope analysis in this tissue seems to be more appropriate to determine and distinguish the trophic source of the fatty acids. Fatty acids in *A. elliptica* lipids were generally ^{13}C-depleted compared with their counterpart in trophic resources. This depletion in ^{13}C content of fatty acids, especially EFAs, appeared to be a widespread common phenomenon (Bec *et al.* 2011, Gladyshev *et al.* 2012). Gladyshev *et al.* (2014) have therefore proposed a fractionation constant equal to 3.17‰ on $\delta^{13}C$ values of PUFAs, as a result of a

decrease in the isotope ratio of the consumer tissues compared to that of the trophic resource. After applying this fractionation constant, our compound-specific isotope data reinforce results from bulk isotope analysis and fatty acid analysis, and indicate that the diet of *A. elliptica* is comprised of POM and sediment organic matter including macroalgal material. *A. elliptica* probably feeds unselectively on macroalgae detritus and the dominance of brown algae signature in their tissues is likely related to the dominant biomass of brown algae species in Kobberfjord. This supports that even suspension feeders, generally presumed to feed mainly on phytodetritus, incorporate significant amounts of resuspended macroalgae detritus.

In Arctic food web studies, isotope analysis on individual fatty acids has been mainly investigated to distinguish diatoms originating from the pelagic and sympagic habitats, and assess their relative contribution in consumer diet (Budge *et al.* 2008, Wang *et al.* 2014). It has been established that sea ice algae $\delta^{13}C_{FA}$ (especially 16:4ω1 and 20:5ω3, which are common fatty acids used as diatoms marker) values were higher than in phytoplankton. In our study, however, high levels of 20:5ω3 in brown macroalgae (> 7%, compared to 0.4 – 2.8% in POM) combined with $\delta^{13}C_{20:5\omega3}$ values in tissues of *A. elliptica* (following application of the fractionation constant) indicated that the bivalve incorporate 20:5ω3 rather from brown algae than diatom-derived organic matter from microphytobenthos (sediment) or pelagic primary production (POM). Furthermore, sampling and characterization of all trophic resources in a given study site seems to be essential since $\delta^{13}C_{FA}$ can be similar between two resources. For instance, our results showed that the green algae *U. lactuca* had a carbon isotopic ratio on the fatty acid 20:5ω3 (-19.1 ± 1.5‰) in the range of that in ice algae (-18.3 ± 2.0‰, Budge *et al.* 2008). In areas where a large number of food sources are available and may contribute to primary consumers diet, compound-specific stable isotope analysis can help to distinguish trophic resources.

5.3. Seasonal variability

POM showed high seasonal $\delta^{13}C$ and $\delta^{15}N$ variability. The large range of POM $\delta^{13}C$ values has been related to several factors, such as phytoplankton growth conditions, changes in species composition, temperature, water masses, and aqueous CO_2 limitation (Descolas-Gros & Fontungne 1990, Rau *et al.* 1992, Kopczyńska *et al.* 1995, Ostrom *et al.* 1997, Michener & Kaufman 2007). In our study, POM $\delta^{13}C$ variability may directly reflect variations in nutrients availability. During the spring bloom, the intense phytoplankton growth leads to reduced nutrients levels. As concentrations of CO_2 decrease, phytoplankton cells are forced to incorporate ^{13}C-enriched CO_2 resulting in a higher carbon isotopic ratio (Rau *et al.* 1992, Ostrom *et al.* 1997). Depletion in ^{13}C in September could, hence, be explained by the replenishment of nutrients as a consequence of the decreased primary production combined with a weakening of stratification at the end of the summer (Jensen & Christensen 2014). A seasonal variability has also been observed in POM fatty acid composition, despite the large dominance of SFAs likely explained by the high occurrence of *Phaeosyctis* spp. in phytoplankton communities during the studied year (Jensen & Christensen 2014). Slightly higher levels of fatty acid markers of microalgae, both diatoms (16:1ω7, 16:4ω1 and 20:5ω3) (Viso & Marty 1993, Reuss & Poulsen 2002, Kelly & Scheibling 2012) and dinoflagellates (18:4ω3 and 22:6ω3) (Napolitano *et al.* 1997, Mansour *et al.* 1999, Kelly & Scheibling 2012), as well as markers of brown macroalgae (18:4ω3 and 20:5ω3) (Graeve *et al.* 2002, Kelly & Scheibling 2012, Wessels *et al.* 2012) were found in May. POM contained more diatoms, dinoflagellates and/or macroalgae-derived organic matter in May, while higher levels of saturated fatty acids in September suggest a more degraded material. The lower concentration of total fatty acids (nearby 30%) and the decreased level of unsaturated fatty acids in September compared to May, as well as the $\delta^{13}C$ variability well depict bloom and post-bloom conditions in Kobbefjord.

In contrast, sediment organic matter showed identical $\delta^{13}C$ and $\delta^{15}N$ values and fatty acid composition in May and September. Stability in isotopic composition of sediment organic matter may reflect heterogeneity of carbon sources reaching the seafloor and its long-

time persistence. This accumulation of phytodetritus can create a sediment 'food bank' (Mincks *et al.* 2005), that is available and can sustain benthic organisms with continuous supplies of food that offset the effects of the strong seasonality of primary production in the Arctic marine system (McMahon *et al.* 2006, Norkko *et al.* 2007). In areas where macroalgae biomass is relatively important, the pool of phytodetritus can be supplemented by macroalgae-derived material, which can then be exploited by deposit and suspension feeders (Hop *et al.* 2002, Quijón *et al.* 2008, Legeżyńska *et al.* 2012).

Digestive glands of *A. elliptica* showed very stable $\delta^{13}C$ and $\delta^{15}N$ values at the time of sampling periods. This highlights that bulk stable isotope analysis is a well-adapted method to integrate isotope signature of trophic resources, either very specifically on one source of food having a similar carbon isotopic ratio compared to the bivalve, or the carbon isotopic ratio of *A. elliptica*, as a non-selective feeder, reflects heterogeneity of available sources of food. This temporal stability of $\delta^{13}C$ values in *A. elliptica* suggests, however, that bulk isotopes are not the appropriate approach to characterise seasonal variability in food supply to bivalves. The low (< 1‰) or no seasonal variability in benthic organism $\delta^{13}C$ has been already recorded in previous Arctic studies (Dunton *et al.* 1989, Kędra *et al.* 2012, Legeżyńska *et al.* 2012, Carroll *et al.* 2014, Roy *et al.* 2015). Fatty acid profiles and FATMs showed, however, differences between the two sampling periods and seems therefore a useful method to look into food regime strategy in response to changing primary production dynamics. We tracked more specifically changes in relative levels of FATMs between May and September in digestive gland, which is a tissue with relatively high turnover rates, leading to rapid changes in biochemistry with diet quality (Shin *et al.* 2008, Stead *et al.* 2013). Diet can be therefore particularly traceable in the digestive glands of bivalves since it is the primary place of nutrient absorption and storage (Napolitano & Ackman 1992) and, hence, represents recent ingested food. Overall, seasonal variability in the diet of *A. elliptica* is related to a smaller contribution of microalgae, especially diatoms (lower levels of 16:1ω7 and 16:4ω1), and macroalgae (general decreased levels of C_{18} PUFAs) in September compared with May. In addition, *A. elliptica* showed a higher consumption of zooplankton, more specifically calanoid copepods (associated to increased proportion of 20:1ω9 and

22:1ω11) and bacteria (due to higher levels of branched fatty acids) in September. Benthic organisms depend of processes that take place in the water column and affect the organic matter, in terms of quantity and quality, and sinking to the seafloor (pelagic-benthic coupling processes). Exported organic matter is strongly dependent upon the timing and the diversity of the primary producers, consumption (grazing by heterotrophs), and biological degradation by bacteria in the water column (Forest *et al.* 2010, Wassmann & Reigstad 2011). Hence, *A. elliptica* seems to rather quickly respond to changes in organic matter reaching the benthos, by behaving opportunistically to get its food.

Macroalgae communities are expected to be favoured in Arctic coastal systems in response to increased temperature and reduced sea ice cover (Krause-Jensen *et al.* 2012, Krause-Jensen & Duarte 2014). Higher biomass and northward-expanded distribution may already be occurring in some areas (Weslawski *et al.* 2010, Kortsch *et al.* 2012). Recent studies (McMeans *et al.* 2013, Renaud *et al.* 2015) and our results indicate that macroalgal detritus can contribute significantly to the diet of arctic benthic organisms in coastal areas and also to filter feeders traditionally considered relying completely on phytoplankton. Nevertheless, further investigations are needed to determine the relative contributions of benthic and pelagic components (*i.e.* macroalgae, microphytobenthos, phytoplankton, and sea ice algae) in benthic coastal food webs and how the diet of suspension feeders could be modified in a changing Arctic.

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7. Supporting information

Table 15. Fatty acid composition, expressed as mass % of total fatty acids, of (A) the particulate organic matter (POM) in sub-surface (s-POM) and bottom (b-POM) waters, (B) sediments and (C) tissues of *A. elliptica* (DG = digestive gland and F = feet) collected in Kobbefjord in May and September 2013. Sediment data were average since no significant difference was found between May and September (PERMANOVA, p(perm) = 0.07; Table 10). Fatty acids > 1% were included. MTFA = mass of total fatty acid expressed in mg g^{-1}; SFA = saturated fatty acid; MUFA = monounsaturated fatty acid; PUFA = polyunsaturated fatty acid. Values are mean (SE)

(A)	s-POM		b-POM	
	May	September	May	September
12:0	10.0 (0.3)	7.7 (2.8)	4.1 (2.1)	2.7 (2.0)
14:0	10.1 (0.7)	7.5 (0.4)	8.5 (0.3)	5.5 (0.9)
16:0	30.3 (1.4)	32.0 (1.4)	33.5 (1.0)	37.7 (1.0)
18:0	34.7 (1.5)	41.9 (2.2)	38.7 (2.2)	49.4 (1.5)
Σ SFA	87.0 (2.2)	91.1 (0.7)	86.8 (0.8)	97.0 (0.8)
16:1ω7	4.9 (0.7)	1.4 (0.2)	4.4 (0.3)	0.5 (0.1)
18:1ω9	1.0 (0.1)	1.0 (0.2)	1.1 (0.0)	1.1 (0.2)
Σ MUFA	7.0 (0.9)	3.4 (0.4)	6.8 (0.5)	1.9 (0.4)
18:4ω3	0.8 (0.2)	1.1 (0.1)	0.7 (0.0)	0.1 (0.0)
20:5ω3	1.8 (0.3)	1.6 (0.1)	2.8 (0.5)	0.4 (0.2)
22:6ω3	0.6 (0.1)	1.3 (0.1)	0.6 (0.0)	0.2 (0.1)
Σ PUFA	6.1 (1.2)	5.5 (0.3)	6.5 (0.6)	1.0 (0.4)
MTFA	95.4 (3.6)	66.4 (14.4)	98.6 (7.1)	71.0 (14.1)

Table 15 continued

(B)	Sediment	(C)	DG		F	
			May	September	May	September
14:0	6.2 (0.3)	14:0	2.3 (0.1)	1.5 (0.1)	1.0 (0.1)	0.6 (0.1)
15:0	1.4 (0.1)	16:0	9.5 (0.3)	9.4 (0.4)	11.6 (0.3)	10.6 (0.5)
i-15:0	1.4 (0.1)	17:0	0.6 (0.0)	0.8 (0.0)	1.2 (0.1)	1.3 (0.1)
ai-15:0	2.8 (0.1)	*i*-17:0	0.8 (0.0)	0.9 (0.1)	1.3 (0.1)	1.4 (0.1)
16:0	14.1 (0.3)	18:0	2.5 (0.1)	2.8 (0.1)	3.8 (0.2)	4.4 (0.3)
18:0	3.0 (0.1)	Σ SFA	17.3 (0.5)	17.2 (0.4)	21.4 (0.5)	21.6 (0.5)
22:0	1.6 (0.2)					
24:0	1.5 (0.2)	16:1ω7	5.2 (0.2)	4.4 (0.3)	3.7 (0.5)	2.5 (0.3)
Σ SFA	36.9 (0.9)	Σ 18:1[b]	7.1 (0.2)	7.6 (0.3)	8.0 (0.3)	7.3 (0.4)
		Σ 20:1[c]	8.2 (0.3)	10.4 (1.1)	9.3 (0.2)	10.3 (1.1)
Σ 16:1[a]	21.6 (0.7)	Σ MUFA	22.6 (0.5)	24.4 (0.9)	22.7 (1.0)	20.8 (0.7)
18:1ω9	4.8 (0.4)					
18:1ω7	7.2 (0.5)	Σ 18:2[d]	2.3 (0.2)	2.6 (0.2)	1.4 (0.2)	3.4 (0.7)
22:1ω11	1.9 (0.8)	18:4ω3	10.0 (0.7)	6.1 (0.5)	3.3 (0.3)	1.8 (0.4)
Σ MUFA	39.5 (0.4)	20:2ω9	1.2 (0.1)	1.9 (0.2)	2.3 (0.1)	3.0 (0.2)
		20:4ω6	1.0 (0.1)	1.4 (0.1)	3.0 (0.5)	4.2 (0.4)
16:4ω1	1.3 (0.1)	20:5ω3	24.7 (0.5)	23.1 (0.2)	20.7 (1.3)	15.9 (1.4)
18:4ω3	1.2 (0.1)	21:5ω3	2.1 (0.0)	2.0 (0.1)	1.7 (0.1)	1.5 (0.1)
20:4ω6	3.1 (1.0)	Σ 22:2[e]	2.8 (0.2)	4.4 (0.6)	6.2 (0.7)	8.7 (1.1)
20:5ω3	10.2 (0.4)	22:6ω3	9.5 (0.1)	10.7 (0.5)	12.1 (0.7)	13.4 (0.8)
22:6ω3	2.8 (0.2)	Σ PUFA	60.2 (0.8)	58.4 (0.6)	55.9 (0.9)	57.6 (0.5)
Σ PUFA	23.6 (1.1)					
MTFA	0.1 (0.0)	MTFA	29.3 (3.5)	23.3 (3.4)	12.2 (1.8)	8.6 (1.5)

[a] Σ 16:1 is the sum of 16:1ω9, ω7, and ω5
[b] Σ 18:1 is the sum of 18:1ω9, ω7, and ω5
[c] Σ 20:1 is the sum of 20:1ω9, ω7, and ω5
[d] Σ 18:2 is the sum of 18:2ω6 and ω3
[e] Σ 22:2 is the sum of 22:2ω9 and ω6

CHAPITRE 3
LES CHANGEMENTS CLIMATIQUES EN ARCTIQUE FAVORISENT LA CROISSANCE DE LA COQUILLE DU BIVALVE BATHYAL *ASTARTE MOERCHI*

RÉSUMÉ

Les changements climatiques en Arctique peuvent conduire à affaiblir le couplage pélago-benthique actuellement étroit. En réponse à la diminution de la couverture de glace de mer, les systèmes marins de l'Arctique devraient basculer d'une dominance 'algues de glace – benthos' à une dominance 'phytoplancton – zooplancton'. Nous avons utilisé des coquilles de mollusques comme bio-archives et des acides gras marqueurs trophiques pour estimer les effets de la réduction de la couverture de glace de mer sur la nourriture exportée vers le fond marin. Le bivalve bathyal *Astarte moerchi,* vivant à 600 m de profondeur dans le nord de la baie de Baffin, révèle de fortes anomalies de croissance positives dans la coquille depuis les années 2000 que nous attribuons à un changement dans la disponibilité de la nourriture. Les acides gras marqueurs trophiques montrent que cette espèce se nourrit principalement sur des microalgues exportées à partir de la zone euphotique vers le fond marin. Nous suggérons que les changements dans le couplage pélago-benthique sont probablement dus, soit à des changements locaux dans la dynamique de la glace de mer, par l'influence exercée par la glace de mer sur la production phytoplanctonique, soit à un décalage entre la floraison du phytoplancton et le broutage par le zooplancton, permettant une exportation accrue de nourriture sur le fond marin.

Ce troisième article, intitulé « Arctic climate change fosters bathyal bivalve *Astarte moerchi* shell growth », fut corédigé par moi-même ainsi que par Frédéric Olivier, Julien Thébault, Tarik Meziane, Réjean Tremblay, Dany Dumont, Simon Bélanger, Michel Gosselin, Aurélie Jolivet, Laurent Chauvaud, André L. Martel, Søren Rysgaard et Philippe Archambault. Il sera soumis pour publication dans la revue *Global Change Biology* à l'hiver

2016. En tant que premier auteur, ma contribution à ce travail fut l'essentiel des analyses en laboratoire le traitement statistique des résultats et la rédaction de l'article. F. Olivier a contribué à l'idée originale, à l'échantillonnage, à l'interprétation des résultats et à la révision de l'article. J. Thébault, A. Jolivet et L. Chauvaud ont contribué aux analyses sclérochronologiques, à l'interprétation des résultats et à la révision de l'article. T. Meziane et R. Tremblay ont aidé à l'interprétation des résultats et ont contribué à la révision de l'article. D. Dumont, S. Bélanger et M. Gosselin ont fourni les données physiques, de télédétection et de production primaire. Ils ont également contribué à l'interprétation des résultats et à la révision de l'article. P. Archambault a contribué à l'approche statistique des données et à la révision de l'article. A. Martel et S. Rysgaard ont contribué à la révision de l'article. Une version abrégée de cet article a été présentée dans plusieurs conférences internationales, lors de la *Conférence de l'Année polaire internationale 2012 – De la connaissance à l'action* à Montréal (Canada) en Avril 2012, à la *3ème Conférence Internationale de Sclérochronologie* à Caernarfon (Pays de Galles) en Mai 2013, ainsi qu'à la conférence *Ocean Sciences Meeting* à Honolulu (États-Unis) en Février 2014.

ARCTIC CLIMATE CHANGE FOSTERS BATHYAL BIVALVE *ASTARTE MOERCHI* SHELL GROWTH

1. Abstract

Climate changes in the Arctic may lead to weaken the currently tight pelagic-benthic coupling. In response to decreasing sea ice cover, arctic marine systems are expected to shift from a 'sea-ice algae-benthos' to a 'phytoplankton-zooplankton' dominance. We used mollusc shells as bio-archives and fatty acids trophic markers to estimate the effects of the reduction of sea ice cover on the exported food to the seafloor. Bathyal bivalve *Astarte moerchi* that lives at a 600 m depth in northern Baffin Bay reveals strong positive shell growth anomalies since 2000s that we relate to a change in food availability. Fatty acid trophic markers show that this species feeds mainly on microalgae exported from the euphotic zone to the seabed. We suggest that changes in pelagic-benthic coupling are likely due to either local changes in sea ice dynamics, mediated through bottom-up regulation exerted by sea ice on phytoplankton production or a mismatch between phytoplankton bloom and zooplankton grazing, that allows an increased export of food to the seabed.

Keywords: Arctic, climate change, pelagic-benthic coupling, match/mismatch hypothesis, bivalve growth

2. Introduction

The Arctic region is experiencing strong changes since the last several decades. Annual average near-surface air temperatures have risen by 2°C to 3°C since the 1950s (ACIA 2005) and the rate at which sea ice extent has declined is accelerating (Kerr 2012). Polynyas are large areas of open water or reduced ice cover surrounded by thick pack ice. By remaining open in winter or becoming ice-free early in spring, polynyas are also local 'oases' for biological production and biodiversity that support large populations of arctic birds and mammals (Stirling 1997). The ephemeral nature of polynyas makes them interesting regions for the study of large-scale processes related to climate changes (Smith & Barber 2007). By monitoring the evolution of such sensitive areas, Smith & Barber (2007) suggest that polynyas can act as model system for studying the impact of global changes on polar marine environments. The North Water (NOW) polynya, located in northern Baffin Bay, is the largest polynya in the Arctic ($5\text{-}8 \cdot 10^4$ km^2) that opens in early to late spring. The opening of the polynya is caused and maintained by persistent northerly winds and currents that carry ice away from an ice bridge between Greenland and Ellesmere Island (Barber *et al.* 2001, Dumont *et al.* 2009), with secondary contributions of sensible heat from the West Greenland Current and upwelling in the east (Melling *et al.* 2001, Dumont *et al.* 2010). In order to assess the effects of climate change on Arctic marine ecosystems, observations, data collection and monitoring over seasonal to decadal time scales are needed. Strictly speaking, characterizing climate changes requires past records of environmental conditions over multiple 30 year long periods during which conditions can be assumed to be stationary. While such records exist for surface physical variables like sea ice or temperature, the situation is more difficult concerning ecosystem indicators. In this context, biogenic archives provide a valuable assessment of the variability of marine ecosystems over the long term. Because of its longevity and its low mobility, benthos is considered a good integrator of environmental conditions (Snelgrove & Butman 1994, McArthur *et al.* 2010). Seafloor communities can therefore act as models to examine impact of environmental changes since relationship between water column and benthic processes is often closely linked (Grebmeier *et al.* 1988,

Ambrose & Renaud 1995, Piepenburg *et al.* 1997, Dunton *et al.* 2005, Tamelander *et al.* 2006). Particularly, long-lived, sessile benthic organisms may be relevant monitor of processes variation in the overlying water column (*e.g.* Dunton *et al.*, 2005, (Kröncke *et al.* 1998). Furthermore, bivalves that often dominate the benthic biomass in Arctic (*e.g.* (Feder *et al.* 1994, Sejr *et al.* 2000, Conlan *et al.* 2008) incorporate in their shells ambient environmental conditions at the time of shell formation (Richardson 2001). For instance, long-lived bivalves (from decades to centuries) have already been used to reconstruct past climate at regional scale by relating their growth patterns with regional climate indices such as the North Atlantic Oscillation (NAO) and the Arctic Ocean Oscillation (AOO), as well as local conditions such as ice cover and precipitation (Schöne *et al.* 2003, Ambrose *et al.* 2006, Sejr *et al.* 2009, Carroll *et al.* 2011a, Butler *et al.* 2013). Shells of most bivalves exhibit periodic banding, or growth lines (Pannella & MacClintock 1968, Rhoads & Pannella 1970) that have proved valuable in developing a history of environmental changes in marine systems (Jones *et al.* 1989, Witbaard *et al.* 1997, Müller-Lupp & Bauch 2005). The rate and timing of bivalve shell growth is controlled by regional and local environmental factors (Schöne *et al.* 2003, Wanamaker *et al.* 2008b) such as temperature (Pannella & MacClintock 1968, Jones *et al.* 1989), age and reproductive cycle (Sato 1995), tidal cycle (Lutz & Rhoads 1980), and nutrient and food availability (Coe 1948), which can translate into a wide variety of annual and sub-annual (seasonal, lunar, fortnightly, daily, and disturbance) growth patterns. Furthermore, minerals and chemicals incorporated into bivalve shells can reflect specific environmental conditions at the time of shell formation. It is generally accepted that stable isotope composition of biogenic carbonates can serve as a proxy for ambient environmental conditions. For instance, many studies have used stable isotope oxygen profiles from bivalve shells to reconstruct seasonal water temperature cycles, water masses, river discharge and salinity (Israelson *et al.* 1994, Goodwin *et al.* 2003, Carroll *et al.* 2009). Barium has been used as a tracer for productivity and deep-water circulation (Lea & Boyle 1989). Most bivalve Ba/Ca profiles seem to exhibit seasonal peaks in Ba which appear associated with changes in particulate Ba, dissolved Ba or phytoplankton productivity (Lazareth *et al.* 2003, Gillikin *et al.* 2006, Thébault *et al.* 2009a).

In the present study, we focus on the bathyal bivalve *Astarte moerchi*, one of dominant taxa in terms of biomass in community inhabiting deep soft substratum characteristic of NOW (Roy *et al.* 2014). As a long-lived (up to a century) (Torres *et al.* 2011) species, we investigate the potential of *A. moerchi* as recorder of long term environmental changes in Arctic. More specifically the objectives were to: (1) validate that the formation of successive growth lines and increments is annual, (2) relate growth pattern with regional climate indices, and (3) explain growth variations at a local scale with environmental (abiotic and/or biotic) parameters inherent to northern Baffin Bay. We hypothesized that (*i*) climate indices NAO and AOO governed growth anomalies in shells of *A. moerchi*, (*ii*) *A. moerchi* growth rate tends to decrease (negative growth anomaly) in recent years since the tight sympagic-benthic coupling is expected to be weakened in response to diminishing sea ice cover and export of ice algae (Carroll & Carroll 2003, Bluhm & Gradinger 2008), and (*iii*) fatty acid trophic markers in tissues and Ba/Ca ratio in shells are relevant tracers to monitor primary production dynamics in deep arctic marine systems.

3. Materials and methods

3.1. Specimens collection

Live *Astarte moerchi* were collected October 16, 2010, from a depth of 568 m in northern Baffin Bay (Sta. 111; 76°11’ N; 73°12’ W; Figure 18) using an Agassiz trawl deployed from the R/V Amundsen. Individuals were sorted directly on the ship and then immediately frozen at -80°C. In the laboratory, individuals were dissected on ice to separate soft tissues from shells. Tissues were stored at -80°C until lipid analyses, and shells were gently washed and air-dried until further analysis.

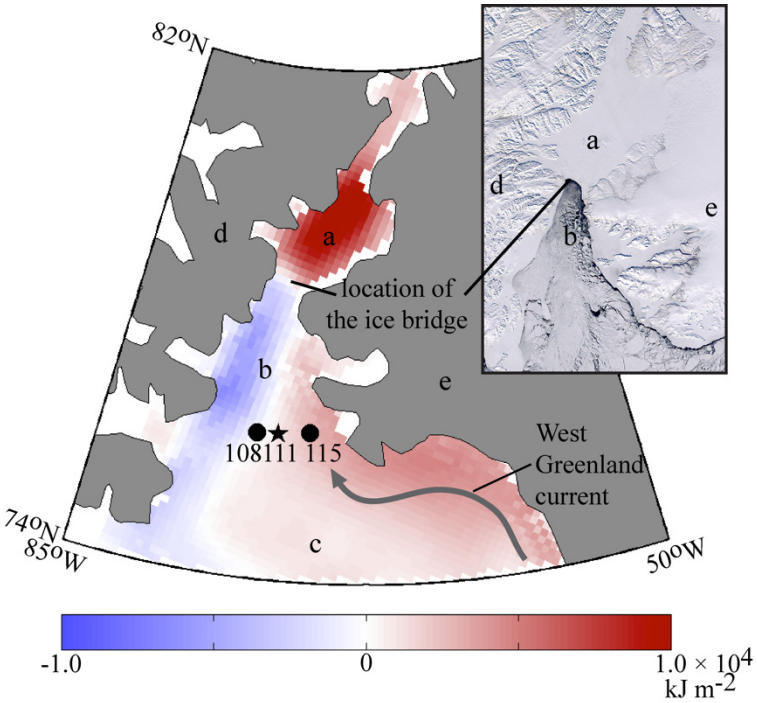


Figure 18. Location of Sta. 108, 111, and 115 in northern Baffin Bay. The map shows the difference between the average cumulated short-wave radiation (SWR) at the sea surface, expressed in kJ m^{-2}, for years without polynya (1990, 1993, 1995, 2007, 2009, and 2010) and the climatological SWR (1979-2010). The anomaly appears as a dipole centered over the average ice bridge location. Inset: A Moderate Resolution Imaging Spectroradiometer (MODIS) image of the open polynya on 23 April 2002. The ice bridge prevents sea ice from drifting in the polynya. (a) Kane Basin; (b) Smith Sound; (c) Baffin Bay; (d) Ellesmere Island, Canada; (e) Greenland

4. Preparation of shell cross sections

Shell cross-sections were made for analyses of growth and chemistry (isotopic and elemental analyses). A low-speed precision saw (Secotom-10, Struers; rotation speed: 300 revolution per minute; feed rate: 75 µm s^{-1}) with a 0.6 mm thick diamond-coated blade, cooled and kept wet using MilliQ water, was used to cut epoxy-embedded left valves along the line of maximum growth. These cross-sections were then mounted on glass slides, manually ground (800 and 1200 grit size) and polished with either Al_2O_3 powder (1 µm grain size) or a diamond suspension (1 µm grain size) for sclerochronological and sclerochemical analyses, respectively. Sections were then ultrasonically rinsed with MilliQ water to remove any adhering grinding powder. For sclerochronological analyses, sections were ground and polished down to an average thickness of 160 µm and images of the hinge sections of the shell taken with a microscope at 40X magnification. For isotopic and elemental analyses, cross-sections were thicker (ca. 800 µm and ca. 750 µm, respectively). All samples were imaged and stitched (software AxioVision) using a stereomicroscope connected to a 5 mega-pixel camera at 80X magnification.

4.1. Radiocarbon analysis

We have undertaken radiocarbon analyses on six shells in order to establish whether or not the growth increments observed in shells of *A. moerchi* from northern Baffin Bay are annual. Sampled were collected on four resin-embedded and two non-embedded right valves to evaluate potential risk of contamination by epoxy resin on radiocarbon signal (Stewart *et al.* 2006). Three samples were collected from each shell (weight range: 1.3 – 4.3 mg) using a Merchantek computer-controlled MicroMill and a Dremel hand-held drill equipped with a 300 µm tungsten carbide drill bit on embedded and non-embedded shells, respectively. The first sample was taken close to the hinge of shell equivalent to the older part of shell and presumed pre-bomb period; the second sample was taken in the central part of the shell in presumed 1960s – 1970s and the abrupt increase of bomb radiocarbon signal; finally the third

sample was taken close to the margin ventral equivalent to recent years of formation and post-bomb period. Position of samples was assessed from presumed annual growth lines counting on hinge cross-sections. Radiocarbon measurements were performed on graphite targets at the Centre for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory. Results include a background and $\delta^{13}C$ correction and are reported as $\Delta^{14}C \pm 1\sigma$ error according to Stuiver & Polach (1977). We compared our results with three reference chronologies based on fish otoliths whose age was either known or could be estimated based on their length. The Northwest Atlantic (NWA) reference chronology is based on three fish species from the eastern coast of Canada and a bivalve from Georges Bank. The NWA chronology is a good proxy for the $\Delta^{14}C$ DIC history of the NWA. Radiocarbon data obtained from otoliths of the Greenland cod (*Gadus odac*) and Greenland halibut (*Reinhardtius hippoglossoides*) are used as radiocarbon reference chronologies for surface marine waters and deeper waters (300 m on average) of Davis Strait and western Greenland (see Campana *et al.* (2008) for details). We used locally weighted least square (LOESS) regressions to visualize bomb radiocarbon pattern over time.

4.2. Growth pattern analyses

Increments in the hinge sections of the shell were dated considering that the last increment was produced in 2010 (year of sampling). Variability in growth lines counting between three readers was evaluated using the coefficient of variation (CV) (Campana 2001). Increment widths were subsequently measured from images of the hinge section using the image analysis software ImageJ (Rasband 1997-2012, http://imagej.nih.gov/ij/). Because bivalve growth naturally declines with age, we removed this ontogenetic trend to isolate environmental signals from annual growth increment time series. Thus, we used methods developed by dendrochronologists and adapted to mollusc shells by Schöne (2003), based on calculation of Standardized Growth Index (SGI) for each year of life of individuals. SGI involves both measured and predicted increment widths calculated from a growth function. Shell growth was modeled by fitting the generalized von Bertalanffy growth function

(gVBGF) to age and hinge length by an iterative nonlinear least-square method (Brey, 2001, http://www.thomas-brey.de/science/virtualhandbook). The generalized von Bertalanffy growth function is:

$$L(p)_t = L(p)_\infty \times (1 - e^{-k(t-t_0)})^D \qquad (1)$$

where t = age (y); $L(p)_t$ = predicted hinge length at age t (mm); $L(p)_\infty$ = predicted asymptotic hinge length (mm); k = Brody growth coefficient (y^{-1}); D = shape of the curve; and t_0 = theoretical age when L = 0 mm (y).

To remove age-dependence, a growth index was constructed by dividing measured increment widths by predicted increment widths from the fitted generalized von Bertalanffy growth function:

$$\mathrm{GI}_t = \frac{L_{t+1} - L_t}{L(p)_{t+1} - L(p)_t} \qquad (2)$$

where GI_t = individual growth index at year t; L_{t+1} = the measured hinge length (mm) at time t+1 (year) ; L_t is the measured hinge length at time t (mm), $L(p)_{t+1}$ is the predicted hinge length at time t+1 (mm), and $L(p)_t$ = predicted hinge length at time t (mm).

SGI (for each year and each individual) is calculated as:

$$\mathrm{SGI}_t = \frac{\mathrm{GI}_t - \bar{X}_{\mathrm{GI}_t}}{S_{\mathrm{GI}_t}} \qquad (3)$$

where $\bar{X}_{\mathrm{GI}_t}$ = mean of growth indices of the individual; and S_{GI_t} = standard deviation of these same indices.

The mean SGI for each calendar year was calculated by averaging across all individuals. For a given year, a positive SGI indicates better than expected growth whereas a negative value indicates a worse than expected growth, suggesting either a positive or a negative influence of environmental parameters on shell growth.

4.3. Shell oxygen isotope analysis

Stable isotope oxygen analyses were performed on cross-sections of three *A. moerchi* shells. The oxygen isotope composition ($\delta^{18}O$) was measured on aragonite samples drilled in the outer shell layer of cross-sections using a Merchantek MicroMill equipped with a 300 μm tungsten carbide drill bit (model H71.104.003, Gebr. Brasseler GmbH & Co. KG). Due to spatial resolution limits set by the milling device and increment widths, each aragonite sample covers 1 to 3 years of shell growth. Between 42 and 55 samples were collected from each shell (mean weight = 112 μg). Samples were then analysed using a Finnigan MAT 253 continuous flow isotope ratio mass spectrometer (CF-IRMS) coupled to a GasBench II at the Institute of Geosciences of the University of Mainz, Germany. They were measured against an in-house Carrara marble calibrated against the international isotopic reference standard. Shell isotopic ratios are reported in conventional delta (δ) notation relative to the Vienna Pee Dee Belemnite (VPDB) standard (Epstein *et al.* 1953). Internal precision and accuracy were 0.07 and 0.04‰ VPDB, respectively.

4.4. Laser ablation for Ba/Ca determination

Trace element profile for Ba was obtained using Laser Ablation Inductively Coupled Plasma Mass Spectrometry (LA-ICP-MS). The analyses were performed on the outer shell layer of the cross-sections. Immediately before elemental analysis, the sample was pre-ablated in a fast-scanning mode to remove shell surface contamination (spot diameter of 80 μm and plate movement speed of 50 μm s^{-1}). The measurements were obtained by operating in a continuous sample mode at a translation speed of 5 μm s^{-1} (spot diameter of 80 μm). Signal intensities were recorded for ^{43}Ca and ^{138}Ba. ^{43}Ca was used as an internal standard to correct for variations in ablation yield because of laser energy drift and sample density. Three standards were measured before each sample analysis to obtain a calibration to determine elemental concentrations. Absolute concentrations were converted to molar ratios (Ba/Ca),

assuming 100% $CaCO_3$. Detection limits were estimated from the signal intensities of argon blanks (3σ) and were 0.16 μmol mol^{-1} for Ba/Ca ratio.

4.5. Fatty acid analysis

Lipids were extracted using a solution of dichloromethane:methanol (2:1, v:v) following the Folch procedure (Folch *et al.* 1957). Extracts were separated by column chromatography on silica gel micro-columns (30 × 5 mm inner diameter (i.d.) Kieselgel 70–230 mesh Merck) using chloroform:methanol (98:2, v:v) to elute neutral lipids (Marty *et al.* 1992). Neutral lipids fractions represent energetic lipids (mainly triacylglycerol) stored by the bivalves to support metabolism and growth. Fatty acid profiles were determined on fatty acids methyl esters (FAMEs) using sulphuric acid:methanol (2:98, v:v) and toluene. FAMEs of neutral lipids were concentrated in hexane and analysed in mass spectrometry scan mode (ionic range: 50–650 m/z) on a Polaris Q ion trap coupled to a multichannel gas chromatograph 'Trace GC ultra' (Thermo Scientific) equipped with an autosampler model Triplus, a PTV injector and a mass detector model ITQ900 (Thermo Scientific). The separation was performed with an Omegawax 250 (30 m × 0.25 mm i.d.) capillary column with high purity helium as a carrier gas. FAMEs were identified by comparing retention times with known standards (Supelco® 37 Component FAME Mix and menhaden oil; Supleco Inc., Belfonte, PA, USA) with the use of Xcalibur v.1.3 software (Thermo Scientific). The mass of total FA (MTFA) was expressed in mg g^{-1} of tissue dry mass and FA composition was expressed by the relative proportion of each fatty acid.

4.6. Physical data and remote sensing

Annual spatially averaged values of surface air temperature were obtained from the National Centre for Environmental Prediction (NCEP) Re-analysis. Cumulative shortwave radiation was calculated using total cloud cover data from the European Centre for Medium-Range Weather Forecasting (ECMWF) ERA-Interim Re-analysis and sea ice concentration

from the MyOcean Ocean and Sea Ice Satellite Application Facility (OSI-SAF). Ice charts from the Canadian Ice Service (CIS) and from the Danmarks Meteorologiske Institute (DMI) were used to assess the break-up date of the ice bridge and its variability over a 45 years period (1968-2010).

Monthly maps of primary production (PP) were calculated from satellite observations of ocean colour, sea ice and cloud cover based on the approach developed by Bélanger *et al.* (2013). Briefly, PP was estimated using a common photosynthesis-irradiance model (*i.e.*, P *vs.* I curve) proposed by Platt *et al.* (1980). The light-saturated chlorophyll *a* (Chl *a*)-normalized carbon fixation rate ($P^B_{\max}$) was set at 2 mg C (mg Chl)$^{-1}$ h^{-1} based on the work of Harrison & Platt (1986) and Huot *et al.* (2013) in the Canadian Arctic and the saturation irradiance (E_k, µmol photons m^{-2} s^{-1}) modelled as a function of the averaged photosynthetic usable radiation at each depth following Arrigo *et al.* (1998). Surface Chl *a* and diffuse attenuation of downwelling irradiance (K_d) were derived from monthly ocean colour observations at 9.28 km resolution from SeaWiFS starting in 1998 to 2010 using semi-analytical algorithms: Garver-Siegel-Maritorena (GSM) for Chl *a* (Maritorena *et al.* 2002) and quasi-analytical algorithm (QAA) for K_d (Lee *et al.* 2005). Downwelling spectral irradiance available for phytoplankton photosynthesis was estimated accounting for the presence of sea ice, total ozone concentration, cloud fraction, and cloud optical thickness. The latter two were derived every 3 h from satellite data (mainly from the advanced very high resolution radiometer; (Schweiger *et al.* 1999) following the method developed by Zhang *et al.* (2004) and were obtained from the International Satellite Cloud Climatology Project web site. Daily satellite-derived SIC data from the Defense Meteorological Satellite Program (DMSP) Scanning Multichannel Microwave Radiometer (SMMR), F8 and F13 Special Sensor Microwave Imager (SSMI) (1984–2007) and F17 Special Sensor Microwave Imager/Sounder (SSMIS) (2008–2010) sensors were obtained from the National Snow and Ice Data Center (NSIDC) (Bélanger *et al.* 2013).

Trends in monthly PP over the 13 year SeaWiFS time series from 1998 to 2010 were calculated for each pixel using a nonlinear trends estimator as described in Zhang *et al.*

(2000). This is a non-parametric method that removes autocorrelation and outliers from the time series before calculating the trend using the Theil-Sen approach (TSA; Sen's slope). The Mann-Kendall non-parametric test was then run on the resulting time series to test the significance of the trends.

4.7. Phytoplankton production and taxonomic composition

During the autumns of 1999 and 2005-2010, particulate primary production rates were measured at 7 depths within the euphotic zone (100, 50, 30, 15, 5, 1 and 0.2% of surface photosynthetically active radiation using the ^{14}C-uptake method (Knap *et al.* 1996, Gosselin *et al.* 1997) at stations108 and 115 (Figure 18). Samples containing ^{14}C were incubated for 24 h under simulated *in situ* conditions in a deck incubator with running surface seawater. Primary production rates were integrated for euphotic zone depths using trapezoidal integration. Production rates of small (0.7-5 μm) and large (≥ 5 μm) phytoplankton cells were considered. Detailed information about primary production measurements can be found in Klein *et al.* (2002) and Ardyna *et al.* (2011). In the autumns of 2005-2010, phytoplankton samples were also sampled from surface waters and at the depth of the subsurface maximum fluorescence and preserved in acidic Lugol's solution (Parsons *et al.* 1984). Cells (> 2 μm) were identified to the lowest possible taxonomic level using the inverted microscope method (Lund *et al.* 1958).

4.8. Statistical analysis

The quality of the annual average SGI chronology we assessed using the Cronbach α coefficient (Bland & Altman 1997) for the available growth data on a common set of years (1950–2010). Cronbach α is a useful coefficient for assessing internal consistency of scaled datasets such that:

$$\propto = \frac{k}{k-1}\left(1 - \frac{\sum s_i^2}{s_T^2}\right) \qquad (4)$$

where k is the number of items, s_i^2 is the variance of the i^{th} item and s_T^2 is the variance of the total score formed by summing all the items. Values higher than 0.6 are considered to be reliable (Carroll *et al.* 2011b). Pearson correlation coefficients were calculated to assess correlations between SGI, climate indices time-series and physical parameters between 1950 and 2010. Statistical computations were carried out with the free software R (2011). Variations in phytoplankton community structure among years was evaluated using a distance-based permutational multivariate analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarities and visualized using non-metric multidimensional scaling (nMDS) ordination using PRIMER 6 (Clarke 1993, Clarke & Gorley 2006).

5. Results

5.1. Radiocarbon results

$\Delta^{14}C$ values from resin-embedded and non-embedded samples were similar during pre-bomb and post-bomb periods. We can therefore consider that resin contamination on $\Delta^{14}C$ values was negligible. $\Delta^{14}C$ values ranged between -82.02 ± 5.33 and 8.34 ± 4.80‰ (Figure 19). Despite smaller amplitude, $\Delta^{14}C$ pattern in the shells of *A. moerchi* was similar to bomb radiocarbon reference chronologies with relatively low and stable pre-bomb values (prior 1957 in theory) followed by increasing values after 1960. Pre-bomb values in shells of *A. moerchi* were virtually identical at a $\Delta^{14}C$ of about –70‰ in the NWA and Arctic deepwater (Greenland halibut) chronologies. $\Delta^{14}C$ levels after 1960 differed substantially between shells of *A. moerchi* and reference chronologies. Highest $\Delta^{14}C$ values were reached later than in NWA and arctic water reference chronologies.

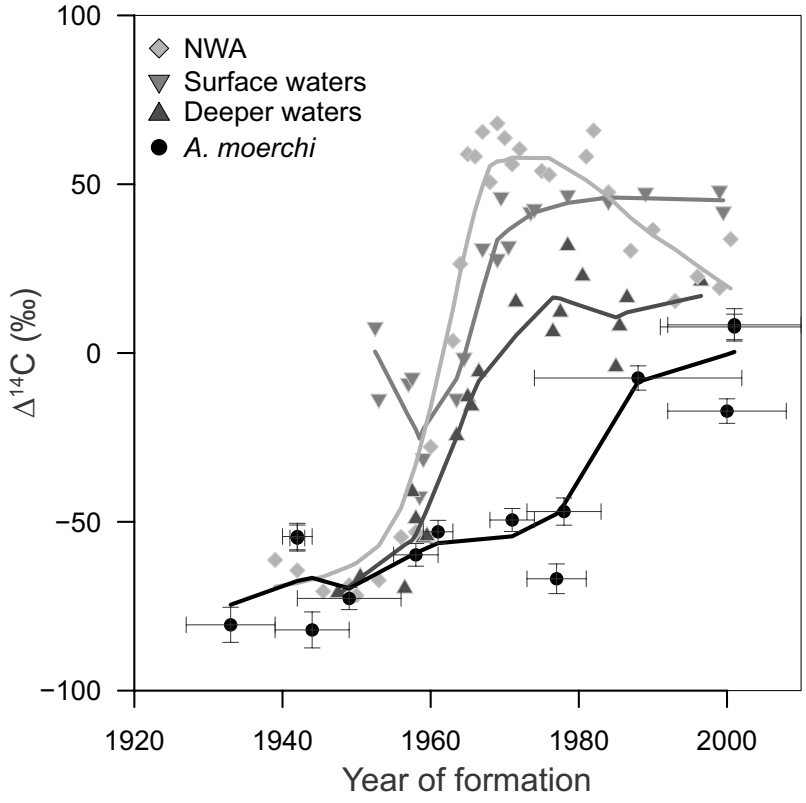


Figure 19. Bomb radiocarbon chronologies for *Astarte moerchi*. Horizontal bars are estimated sampled period for $\Delta^{14}C$ analysis. Fitted lines are locally weighted least square (LOESS) regressions. Reference chronologies are from Campana *et al.* (2008): marine Northwest Atlantic (NWA) reference chronology, arctic marine surface waters (0-100 m), and arctic marine deep waters (300 m on average)

5.2. Sclerochronology and sclerochemistry

Sclerochronological analyses were performed on 15 specimens of *Astarte moerchi* collected in the North Water polynya area. The precision (CV) between counts in hinge region from three readers was 8.0%. The minimum and maximum ages of individuals used to build the mean Standardized Growth Index (SGI) chronology were 61 and 103 years, respectively (Figure 20A). The generalized von Bertalanffy equation yielded a high R^2 value (R^2 = 0.99), indicating that this growth model was an excellent descriptor of *A. moerchi*

growth (Figure 20B). However, due to the reduction of the sample density before 1950, the average growth for the period 1908-1950 is less reliable. We have therefore chosen to limit the sclerochronological analyses to the period 1950-2010 to which all the 15 individuals contribute. As the Cronbach α coefficient is 0.74, the annual average SGI chronology can be considered to be reliable (> 0.6) for this period. Values above or below the abscissa line correspond to either positive (growth greater than expected) or negative (growth less than expected) growth anomalies. Mean annual SGI varied from –0.530 in 1983 to 1.476 in 2010. The annual average SGI chronology shows alternating positive (1965-1970) and negative (1950-1960, 1975-1990) growth anomalies between 1950 and 2010. However, the most notable result is that *A. moerchi* growth is much greater than expected over the last decade (Figure 21A).

No ontogenetic trends were observed for oxygen stable isotopes. The $\delta^{18}O$ profiles displayed low variability along the three shells (CV = 5.28%, n = 3) (Figure 22). Although the mean $\delta^{18}O$ value from shell 98 (5.06 ± 0.27‰) was significantly greater than that of shells 41 and 76 (4.95 ± 0.26‰ and 4.84 ± 0.46‰, respectively) (Mann-Whitney test, $p < 0.05$), values remained stable for a 50-year period. In contrast, time-series of Ba/Ca ratio for the three specimens, ranging from 1.33 to 50.08 μmol mol^{-1}, showed relatively similar patterns with a flat background level interrupted by several sharp peaks. The frequency and intensity of Ba/Ca peaks from the three shells tend to increase since 1990 (Figure 23).

5.3. Fatty acids

The main food sources of *A. moerchi* were determined using fatty acid trophic marker methods in neutral lipids from the digestive gland of the filter feeders. The detailed fatty acid composition is presented in Table 16. Saturated fatty acids (SFA) were dominated by 16:0 and 18:0. Branched fatty acids proportions were very low (< 1%), monounsaturated fatty acids (MUFA) were dominated by 16:1ω7, 20:1ω7 and 18:1ω7 and polyunsaturated acids (PUFA) were mainly 20:5ω3 (EPA), 22:6ω3 (DHA) and 20:4ω6 (AA).

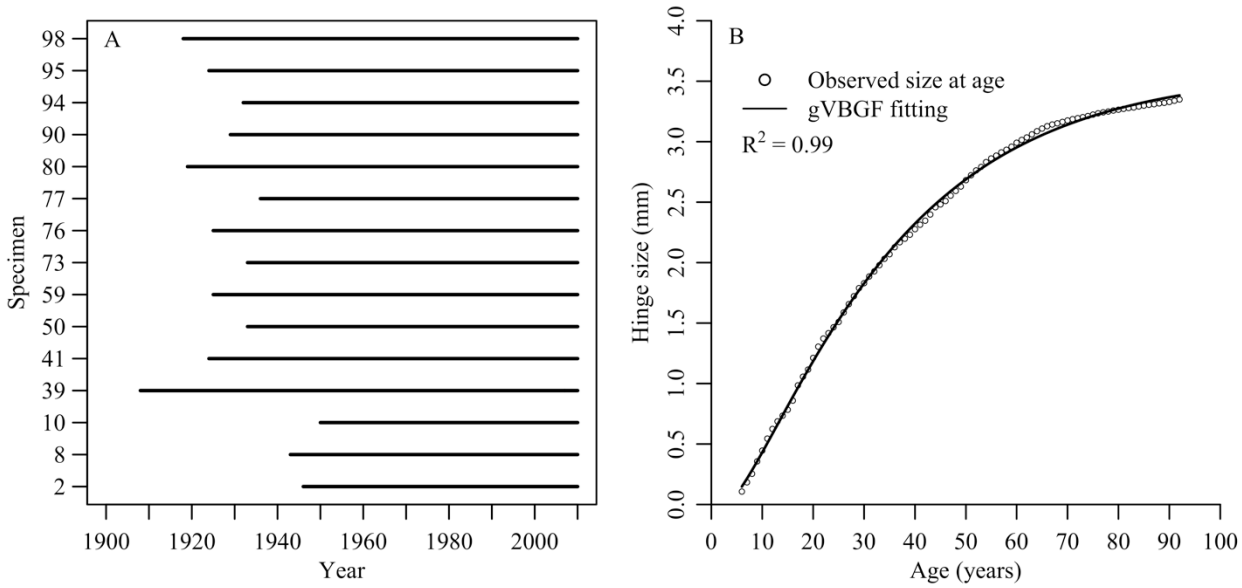


Figure 20. (A) Schematic diagram showing the lifespan of each of the 15 *A. moerchi* specimen used for sclerochronological analyses; (B) Hinge length at age for the *A. moerchi*'s shell number 41 and the associated fitted generalized von Bertalanffy growth function. Individual growth parameters are added in the legend. The mean growth parameters (± SE) calculated for the 15 shells are as follow: L_∞ = 4.66 (± 0.50) mm, k = 0.03 (± 0.004) y^{-1}, D = 4.87 (± 2.07), and t_0 = -2.72 (± 3.58) y

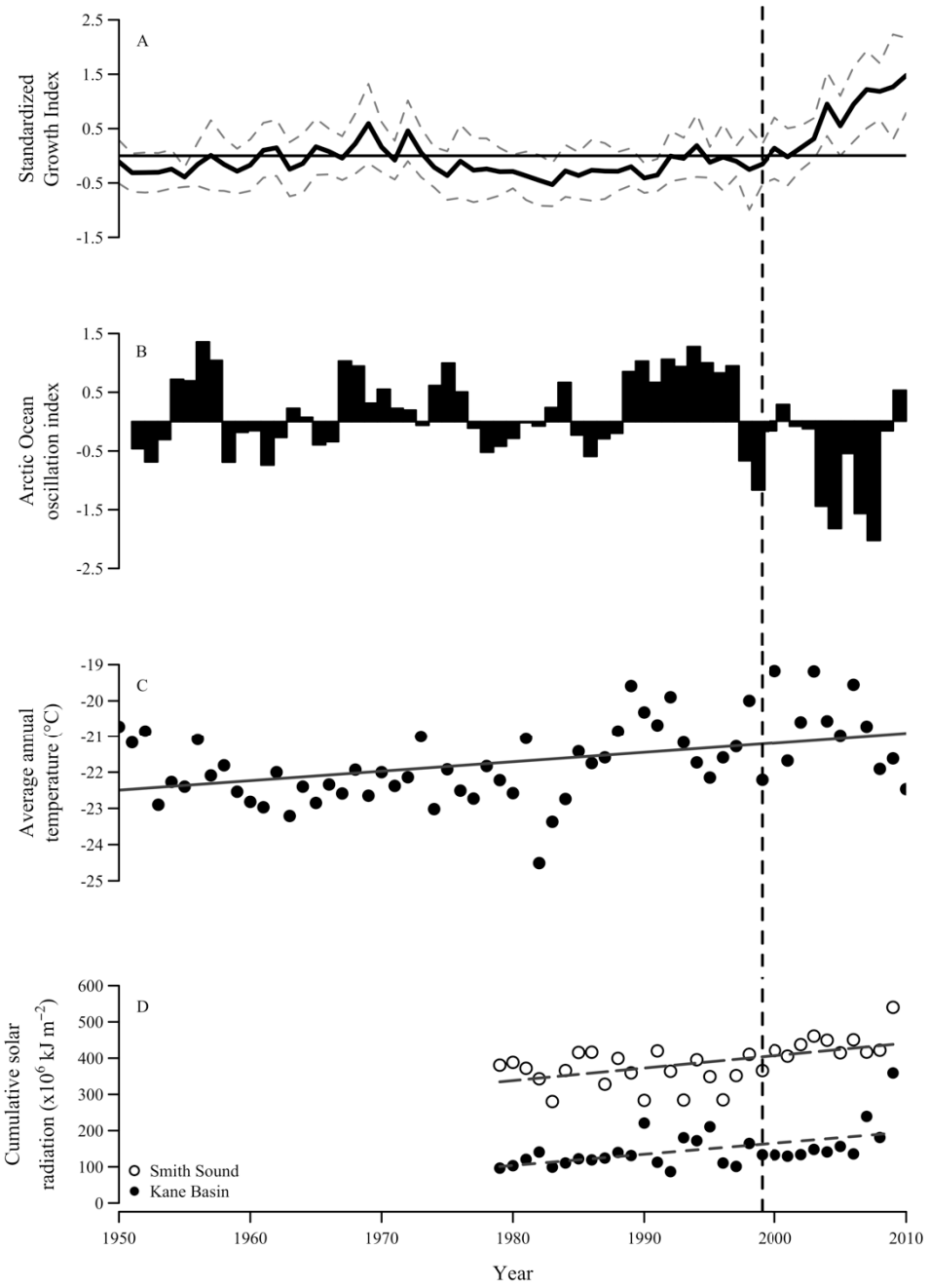


Figure 21. Time series of (A) average annual SGI, (B) AOO index, (C) average annual temperature, and (D) cumulative short-wave radiation at the sea surface in Smith Sound and Kane Basin. In (A), the black line represents average annual SGI and the grey dashed lines indicate the distribution limits at a 95% confidence interval. In (B), the bars represent two-year running means (previous and present year) of the AOO index. SGI and two-year running means of AOO index are negatively correlated ($r_p = -0.35$, $p < 0.01$). In (C, D), dashed lines represent the linear regressions

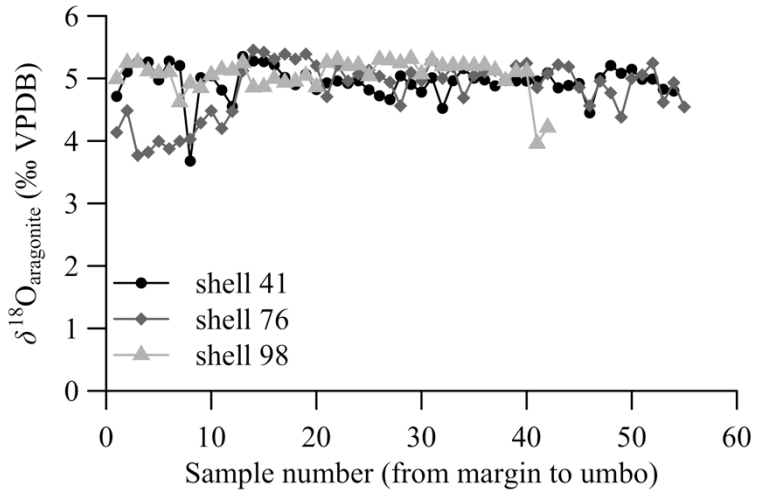


Figure 22. Stable isotope oxygen profiles from cross-sections of three *A. moerchi* shells from northern Baffin Bay (Sta. 111)

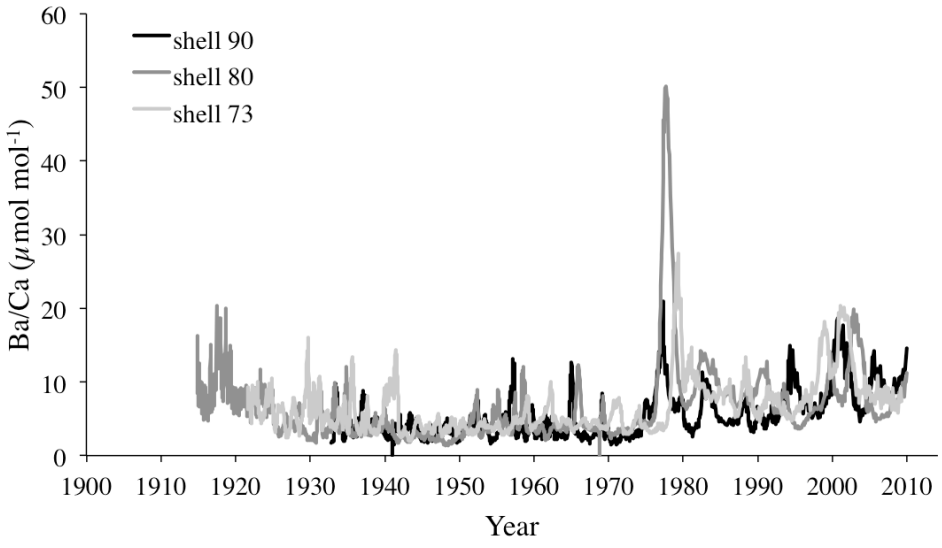


Figure 23. Ba/Ca profiles from cross-sections of three *A. moerchi* shells from northern Baffin Bay (Sta. 111)

Table 16. Relative fatty acid composition of the neutral fraction of *Astarte moerchi*'s digestive gland. Fatty acid values are mean % of the mass of total fatty acids ± standard error (SE). Only FA > 1% are shown, excluding branched FA. Important trophic markers are highlighted in **bold**: branched fatty acids are bacterial markers, 16:1ω7 and 20:5ω3 are markers of diatoms, 18:4ω3 and 22:6ω3 are markers of dinoflagellates, and 20:1ω9 is marker of zooplankton. *i-*: iso- fatty acid; *ai-*: anteiso- fatty acid; SFA: saturated fatty acids; MUFA: monounsaturated fatty acids; PUFA: polyunsaturated fatty acids; AA: arachidonic acid; EPA: eicosapentaenoic acid, DHA: docosahexaenoic acid, MTFA: mass of total fatty acids

Fatty acid	Relative proportion (mass % ± SE)
***i*-15:0**	0.08 ± 0.04
***i*-16:0**	0.85 ± 0.23
16:0	10.61 ± 0.32
***i*-17:0**	0.80 ± 0.08
***ai*-17:0**	0.47 ± 0.08
***i*-18:0**	0.33 ± 0.12
18:0	3.36 ± 0.95
Σ SFA	18.64 ± 1.69
16:1ω7	15.31 ± 3.06
18:1ω9	1.96 ± 0.24
18:1ω7	4.11 ± 0.40
18:1ω5	3.75 ± 0.29
20:1ω11	2.27 ± 0.21
20:1ω9	1.10 ± 0.16
20:1ω7	6.82 ± 0.93
20:1ω5	2.78 ± 0.20
Σ MUFA	40.39 ± 1.83
22:2[a]	1.50 ± 0.36
22:2[a]	10.51 ± 0.84
18:4ω3	1.73 ± 0.28
20:4ω6 (AA)	2.07 ± 0.69
20:5ω3 (EPA)	15.28 ± 1.76
22:6ω3 (DHA)	4.30 ± 0.09
Σ PUFA	40.97 ± 1.05

Table 16 continued

Ratios	
16:1ω7/16:0	1.46 ± 0.29
$\Sigma C_{16}/\Sigma C_{18}$	1.68 ± 0.26
EPA/DHA	3.57 ± 0.42
MTFA mg g-1	6.28 ± 2.78

[a] double bond position currently unknown

5.4. Climate indices and physical environment

Correlations between SGI and climate indices from 1950 to 2010 were calculated. SGI was not correlated with the winter North Atlantic Oscillation or the winter Arctic Oscillation but was negatively correlated to the Arctic Ocean Oscillation (AOO) index (Figure 21A, B; Table 17). Figure 21C shows a 62 year time series of annual mean surface air temperature in Kane Basin. This period is characterized by a slight warming trend, which becomes more obvious over the last three decades. The same trend is observed for the cumulative short-wave radiation at the sea surface (in kJ m^{-2}) with a 23% increase in Smith Sound and of 38% in Kane Basin between the periods 1979-1990 and 2000-2010 (Figure 21D). Figure 18 illustrates the difference in short-wave radiation (SWR) at the sea surface between years with and without polynya, knowing that years during which the polynya did not form at all were all in the last 23 years (1990, 1993, 1995, 2007, 2009, and 2010). The SWR is also averaged over two regions, *i.e.*, north and south of the ice bridge position, over the 1979-2009 period. It is significantly increased in Smith Sound, owing to a reduction of summer ice concentrations, but even more so in Kane Basin over the last ten years due to the ice arch forming less often and for a shorter period of time, thus reducing the landfast ice cover.

Monthly summer (May, June and July) primary production trends in northern Baffin Bay and Smith Sound from 1998 to 2010 computed for each SeaWiFS 9.28 x 9.28 km pixel are shown in Figure 24. Positive values (in red) indicate increasing trends in the monthly PP, which was the case in May with increasing trends reaching ~1 g C m^{-2} $month^{-1}$ $year^{-1}$ between 1998 and 2010. In June and July, in contrast, we observed strongly negative trends (in blue) suggesting that the monthly PP has declined at rates as great as 2 g C m^{-2} $month^{-1}$ $year^{-1}$ during the period considered. This negative trend, estimated from satellite-based methods, is also confirmed by *in situ* observations. PP measured during the autumns of 1999, 2005, 2006, 2007, 2008, and 2010 decreased on the Greenland side of the northern Baffin Bay. At Sta. 108, PP decreased from 2.36 g C m^{-2} d^{-1} in 1999 to 0.05 g C m^{-2} d^{-1} in 2010, whereas the decrease was less pronounced at Sta. 115, decreasing from 0.72 g C m^{-2} d^{-1} to 0.04 g C m^{-2} d^{-1} between 1999 and 2010 (Figure 25A, B). Moreover, this trend was associated with a

decrease in the contribution of large (> 5 µm) and small (0.7-5 µm) cells to total phytoplankton production (Figure 25). But, since 2005, the structure of phytoplanktonic assemblages was highly variable. Figure 26 showed that there is no clear evolution of phytoplankton assemblages between 2005 and 2010 (*e.g.*, from a majority of diatoms to more flagellates), suggesting that bivalve growth was better explained by changes in PP quantity than in species assemblages over the last decade. More importantly, the positive PP trend in May followed by a decreasing trend in June-July suggests that the phytoplankton bloom now occurs earlier in the season than it did previously in northern Baffin Bay (Figure 24).

Table 17. Pearson correlation coefficients between standardized growth index (SGI) and climate indices from 1950 to 2010: The North Atlantic Oscillation (WNAO) and the Arctic Oscillation (WAO) in winter (December, January, February, and March) and the Arctic Ocean Oscillation (AOO). Significant correlations are given in bold (*: $p < 0.05$; **: $p < 0.01$)

	SGI	
WNAO		
Present year	r = -0.17	
1 year lag	r = -0.07	
Running mean	r = -0.14	
WAO		
Present year	r = -0.06	
1 year lag	r = 0.08	
Running mean	r = 0.02	
AOO		
Present year	r = -0.26	*
1 year lag	r = -0.25	*
Running mean	r = -0.35	**

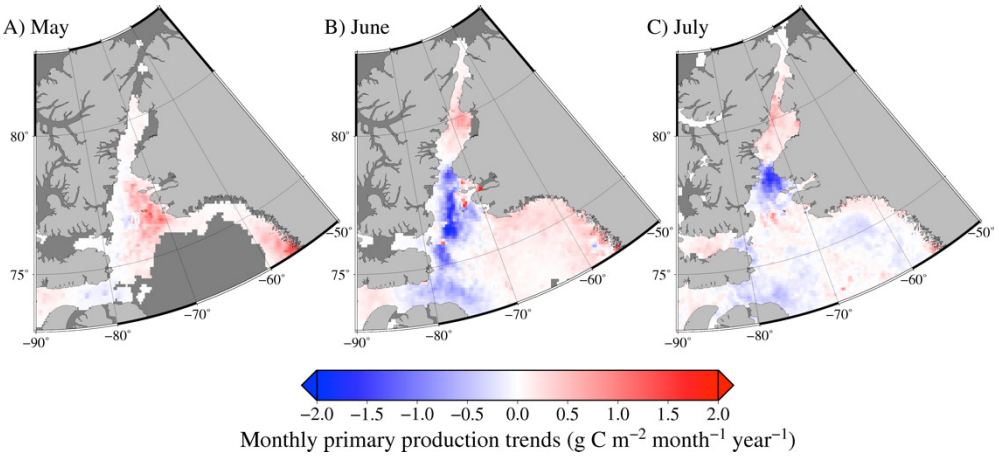


Figure 24. Trends in monthly primary production (in g C m^{-2} $month^{-1}$ $year^{-1}$) in northern Baffin Bay and Smith Sound from 1998 to 2010 as assessed by remote sensing following Bélanger *et al.* (2013) with SeaWiFS monthly data

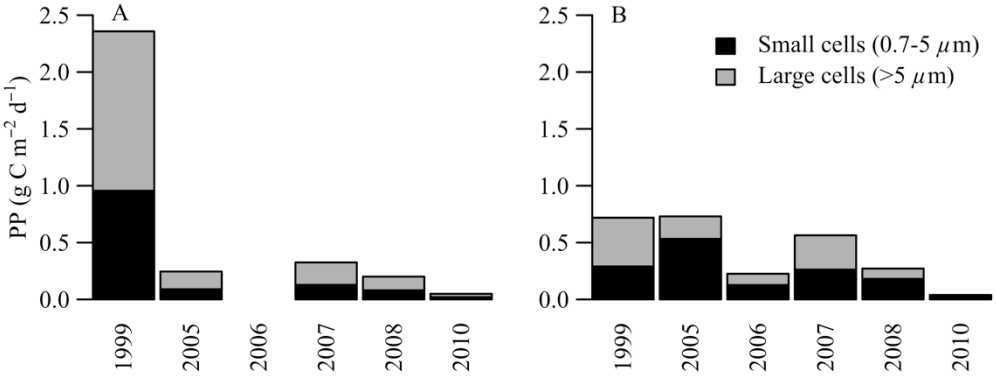
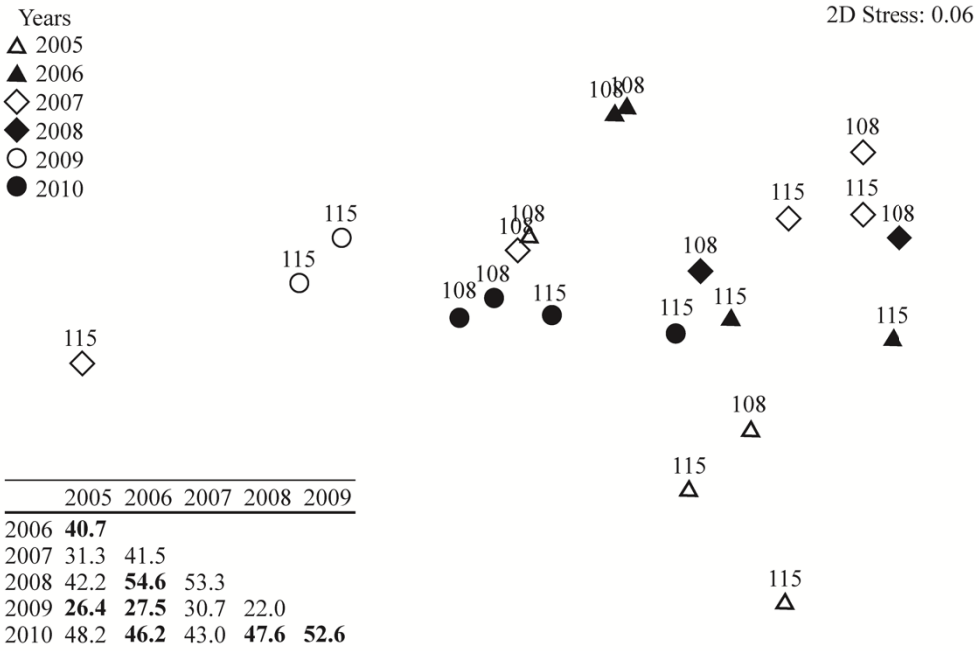


Figure 25. Variations in primary production (PP) for small (0.7–5 µm) and large (> 5 µm) cells integrated over the euphotic zone at Sta. (A) 108 and (B) 115 during autumn. Data of 1999 are from Klein *et al.* (2002)



	2005	2006	2007	2008	2009
2006	**40.7**				
2007	31.3	41.5			
2008	42.2	**54.6**	53.3		
2009	**26.4**	**27.5**	30.7	22.0	
2010	48.2	**46.2**	43.0	**47.6**	**52.6**

Figure 26. Non-metric multidimensional scaling (nMDS) ordination based on the Bray-Curtis dissimilarity matrix calculated on untransformed protist group (> 2 µm) abundances. Samples were collected at Sta. 108 and 115 between 2005 and 2010. Before performing the nMDS, the taxa were grouped into six categories: (1) C-diatoms (*Chaetoceros* spp.), (2) T-diatoms (chain-forming centric diatoms), (3) M-diatoms (filament-forming diatoms), (4) dinoflagellates, (5) flagellates, and (6) ciliates, including Tintinids. The table indicates the average percentage similarity between years. Years that differ significantly ($p < 0.05$) are highlighted in **bold**

6. Discussion

Shell growth rate is largely governed by temperature and food availability (Richardson 2001). It is generally assumed that high-latitude species deposit darker growth lines in winter (Gröcke & Gillikin 2008) when low temperatures and lack of food cause individuals to stop growing or grow very slowly. In the present study, we used bomb radiocarbon to confirm or infirm that growth lines deposition in shells of *A. moerchi* was annual. We observed delayed and reduced amplitude of $\Delta^{14}C$ values compared to reference chronologies. However, since shells were collected in approximately 600 m depth water, this may result from transit time of bomb signal from surface waters to deeper waters and reservoir effect (Weidman & Jones 1993). $\Delta^{14}C$ values showed that formation of at least one growth line every year is impossible since the more ^{14}C-depleted data related to pre-bomb signal would be after the 1970s. In the other hand, one growth line every two years is very unlikely in view of stable abiotic conditions in surrounding deep environment habitat of *A. moerchi* (temperature, salinity, light availability, etc.). To our knowledge, only primary production dynamics exhibiting an annual rhythmicity resulting in a strong seasonal variation of food availability in Arctic systems may lead *A. moerchi* to produce clearly separated growth increments. Hence, radiocarbon analysis confirmed that the formation of growth lines in shells of *A. moerchi* was annual.

The oxygen isotopic composition ($^{18}O/^{16}O$) of marine carbonate is controlled by the temperature and isotopic composition of the ambient water ($\delta^{18}O_{water}$) from which it precipitated. The $\delta^{18}O_{water}$ is influenced primarily by the amount of freshwater runoff, direct precipitation, sea ice formation, and glacial melt (Alkire 2010). By establishing oxygen isotopic profiles along the axis of maximum growth of the carbonate shells, it is possible to obtain hydrographic time series information on the bivalve's habitat. Low ontogenetic variations in the oxygen isotope composition of *A. moerchi* shells demonstrate that water temperature and salinity were both very stable through the bivalve's lifetime, which is expected at a 600 m depth in the ocean. In this context, we hypothesize that food supply is

the main environmental factor explaining the recent strong positive growth anomaly of the bivalve *A. moerchi*.

The presence and combinations of certain FA can be characteristic, and thus have potential as markers, for particular algal classes. Diatoms are characterized by high proportions of 16:1ω7, C_{16} PUFA, and 20:5ω3, while flagellates and dinoflagellates are characterized by elevated C_{18} PUFA (particularly 18:4ω3) and C_{22} PUFA (especially 22:6ω3) (Søreide *et al.* 2008). While we expected detrital or bacterial markers with high proportions of branched FA (iso- and anteiso- FA) for these filter-feeder bivalves living in a deep system, this is not what we observed. Fatty acids suggest that the greatest contribution to *A. moerchi*'s diet is microalgae (mainly diatoms) exported from the euphotic zone to the seabed. These results confirm observations made on the bivalve *Bathyarca glacialis* across the Canadian Arctic archipelago (Gaillard *et al.* 2015). Furthermore, Ba/Ca ratio results, used in coastal areas as a proxy for the timing and magnitude of diatom blooms (Thébault *et al.* 2009a), support the hypothesis of a succession of blooms during the whole life of the bivalve. Frequency and intensity of Ba/Ca peaks from three *A. moerchi* shells tend to increase since 2000.

Despite the lack of available data on pelagic communities, especially for zooplankton, these results contradict the current hypothesis arguing that climate change will benefit the pelagic food chain (phytoplankton – zooplankton), but be detrimental to the zoobenthos (Grebmeier *et al.* 2006, Wassmann *et al.* 2011). The present work suggests that the pelagic-benthic coupling in the northern Baffin Bay may have intensified over the last decade.

6.1. Local physical conditions

If causal connections relate climate to the growth of filter-feeding bivalves at 600 m depth, they should ensue from local dynamics of primary producers. The growth pattern of *A. moerchi* is thus possibly related to large-scale environmental patterns affecting sea ice, and this could become apparent in the correlation between the SGI and the AOO. The AOO

index (Proshutinsky & Johnson 1997) is based on a circulation model assessment of the sea level height difference anomaly between the North Pole and the Beaufort Sea, which is indicative of variations in the Arctic ice and ocean circulation. However, the correlation with the AOO does not tell how and what environmental conditions would favour or hinder the growth of bivalves, and an interpretation involving the complex dynamics of the Arctic Ocean would be difficult to corroborate. It rather suggests that the main drivers are acting at a regional or local scale and that these drivers may be linked to the Arctic climate in some way. In the case under investigation, the presence of a recurrent polynya constitutes a strong driver that deserves closer evaluation.

The NOW polynya forms when persistent northerly winds push ice away from the landfast ice covering Kane Basin. The southern limit of this landfast ice cover is often referred to as an ice bridge. This bridge plays a central role in the formation of the polynya as without it, sea ice flows continuously following winds and currents and the polynya simply does not exist as a persistent and localized feature. The position and shape of the ice bridge are very stable, but the time of formation and break-up are highly variable from one year to another (D. Dumont pers. comm.). This means that the ice bridge exerts a control on the timing and the area over which light will or will not penetrate the ocean. Since landfast ice is immobile by definition, the ice thickness and strength are mostly controlled by thermodynamics, which are determined in a large extent by the local surface air temperature. During a cold winter, the ice is likely to grow thick, be resistant to stronger forces and to survive longer during the melt season. The relation between surface air temperature, which tends to increase, and ice distribution in the area is not linear but depends, for instance, upon the highly nonlinear and heterogeneous dynamic ice behavior. Two kinds of changes are nonetheless expected: in the timing and in the quantity of ice over the spring-summer period, both of which affect the spatio-temporal distribution of light penetration into the ocean. Based on ice charts produced by the Canadian Ice Service over the last five decades, we conclude that the ice bridge broke up on average two weeks earlier during the 1994-2012 period compared to the 1968-1993 period. In addition, the frequency of occurrence of the NOW polynya decreased from almost 100% (1968-1993) down to 70% (2002-2012). When

the ice bridge does not form, sea ice flows uninterruptedly through the channel so that the concentration of ice in Kane Basin drops while that of Smith Sound increases slightly compared to the climatology. Changes in the spatio-temporal distribution of sea ice have significant effects on light availability. This is quantified by integrating the incident short-wave radiation (SWR) that effectively reaches the ocean surface, i.e., after being attenuated by clouds and sea ice over time from January to October. This is shown in Figure 18 in the cumulative shortwave radiation anomaly between polynya vs. no-polynya years. In fact, higher cumulated SWR means a larger potential for PP. Recently, Arrigo *et al.* (2008) argued that the general reduction of Arctic sea ice will lead to an increase in PP in the Arctic Ocean and its marginal seas due to enhanced light availability for photosynthesis. As a result of the controlling effect of sea ice on phytoplankton production and, hence, food availability for the bivalves, correlations between local sea ice cover and the growth rate of benthic organisms have been already observed. Very high concentrations of sea ice can be viewed as an inhibitor of primary production and growth of consumers, and, by contrast, a low sea ice cover leads to increased primary productivity and food availability for the benthos. For example, sea urchin (*Strongylocentrotus droebachiensis*) growth performance is limited by food, especially in high-Arctic areas where sea ice cover influences annual primary productivity (Blicher *et al.* 2007). This trend is supported by a study by Sejr *et al.* (2009) that showed a correlation between an annual index of ice cover and the growth rate of the Arctic cockle *Clinocardium ciliatum*. Changes in sea ice cover in the northern Baffin Bay may affect the growth performance of bivalves through bottom-up regulation of phytoplankton production.

6.2. Spatio-temporal mismatch hypothesis

In response to the reduction in sea ice thickness and cover at a pan-Arctic scale, marine ecosystems are likely to be more productive and the pelagic food webs (phytoplankton-zooplankton) promoted (Carroll & Carroll 2003). Our results suggest, however, that global environmental change can induce contrasting effects at a smaller spatial scale with unknown local effects on benthic productivity.

In northern Baffin Bay, phytoplankton communities have declined in terms of biomass, production and size structure over the last decade and PP in Smith Sound declined over the period 1998-2010 (Bélanger *et al.* 2013). Overall, regional patterns of change in sea ice conditions, induced by a large-scale air temperature warming, suggest that optimal conditions for pelagic PP have shifted both in time (earlier in the season) and space (displaced northward). When associated with the strong positive growth anomaly of the *A. moerchi* population in northern Baffin Bay, this leads us to suggest that this spatio-temporal shift in the pelagic PP could have promoted a match between pelagic food production and the benthic filter feeders. Despite uncertainties about horizontal ocean currents from the surface to the bottom and the vertical sinking velocity profiles of phytoplankton cells, it can be presumed that a horizontal shift in the food source could change its location of arrival to the bottom.

Such changes in the phytoplankton communities in northern Baffin Bay could alter both the quality and quantity of the food supply exported to higher trophic levels, especially within the benthic environment. The high variability of phytoplanktonic assemblages since 2005 suggests changes in PP quality from year to year but does not explain the observed growth pattern. In other words, regardless the phytoplankton composition exported to the seabed, growth anomalies observed in *A. moerchi* shells have remained positive since 2005. While a decline in the quantity of food supplied to the benthos was expected (because of the decline of the PP in surface waters), the observed growth anomaly in bivalve shells leads us to hypothesise that a larger amount of microalgae reaches the seabed. One possible mechanism to account for this is a mismatch (Cushing 1990) between phytoplankton and zooplankton dynamics. Grazing by herbivorous zooplankton largely determines the contribution of primary producers for the benthic systems. Recent Arctic studies that focus on links between primary and secondary producers in a changing sea ice cover in the Arctic suggest a potential mismatch between the phytoplankton bloom and the temperature-controlled ontogenetic development of zooplankton (mainly *Calanus glacialis*) (Søreide *et al.* 2010, Leu *et al.* 2011). Recently, Boetius *et al.* (2013) advanced the hypothesis that the current sea-ice thinning may enhance under-ice productivity and ice-algae export. However, years with less ice coverage, caused by earlier ice break-up, reduced ice and snow cover or

both, will thus lead to a shorter temporal time lag between the ice algal and phytoplanktonic blooms, resulting in a potential mismatch (Leu *et al.* 2011). Timing is the single most essential factor controlling the recruitment and development success or the failure of pelagic secondary producers (Cushing 1990). Timing will therefore determine how efficient the biomass and energy transfer to higher pelagic trophic levels or a greater export to the bathyal benthic communities will be, and this will likely continue in northern Baffin Bay until the North Water polynya disappears completely. The timing of phytoplankton productivity in northern Baffin Bay may have shifted earlier in the season, as revealed by satellite-derived PP time series. In addition, earlier phytoplankton blooms have been observed in other locations across the subarctic seas (Kahru *et al.* 2011).

In conclusion, the marine bivalve *A. moerchi* shows an unexpected higher growth since the 2000s that may be explained by a greater availability of food on the sea floor, resulting either from a mismatch between phytoplankton growth and zooplankton grazing in the water column or from an increased contribution of microalgae due to the reduction of the sea ice cover. It is now well established that global climate change is altering physical settings in the Arctic Ocean (currents, water masses, winds, ice coverage, etc.). Yet, we do not clearly understand how it will affect high latitude marine ecosystems. We suggest that the main influence will change food webs dynamics, through cascading effects from primary producers to higher trophic levels. Effects on the benthos depend on the level of a match-mismatch between phyto- and zooplankton as well as on the influence of the sea ice cover through bottom-up regulation of phytoplankton production. Further studies should focus on the fate of the phytoplankton bloom at shorter temporal and spatial scales to better understand variation in the quality and quantity of food reaching the sea floor, and on interactions between physical and biological parameters governing Arctic benthic ecosystems under sea ice cover.

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CONCLUSION GÉNÉRALE

Dans le contexte des changements climatiques, plusieurs études ont tenté de mieux comprendre et d'évaluer la nature et la force du couplage pélago-benthique et l'influence que cela entraine sur les communautés benthiques arctiques. Bien que le terme couplage pélago-benthique regroupe tous les échanges qui puissent avoir lieu entre la colonne d'eau et les fonds marins (nutriments, matière organique, etc.), il se limite, dans le cadre de ce travail, aux interactions entre la production primaire pélagique et des consommateurs primaires tels que les bivalves suspensivores. Le paradigme actuel est que le couplage pélago-benthique est fort sur les plateaux continentaux arctiques en raison principalement d'une proportion élevée de la production primaire non utilisée par le zooplancton et par conséquent directement disponible pour le benthos après export dans la colonne d'eau (p. ex. Dunton *et al.* 2005, Renaud *et al.* 2008b, Tamelander *et al.* 2008). C'est le cas, par exemple, des mers de Barents, des Tchouktches et de Béring, qui sont peu profondes et où la production primaire est importante (Sakshaug 2004). Néanmoins, les autres régions de l'Arctique présentent d'importantes inégalités avec un couplage pélago-benthique fort, c.-à-d. un important export de matière organique issue de la production primaire de surface vers les fonds marins, généralement associé aux zones de remontée d'eaux profondes ('*upwellings*'), des zones marginales de glace et les polynies (Piepenburg 2005). Une baisse de ce fort couplage pélago-benthique est prédite en raison de la contribution plus faible des algues de glace qui sont habituellement rapidement exportées depuis la zone euphotique et soutiennent de manière efficace le benthos. En contrepartie, la chaine pélagique serait favorisée avec une plus grande production phytoplanctonique largement utilisée par le zooplancton. Par ailleurs, il reste à savoir dans quelle mesure d'autres sources de matière organique d'origine terrestre, le microphytobenthos ou les macroalgues peuvent supporter les réseaux trophiques benthiques. Dans ce contexte, l'objectif général de cette thèse était de déterminer et suivre les changements potentiels des sources d'alimentation des organismes benthiques de régions arctiques et subarctiques par l'étude de trois espèces de bivalves *Bathyarca glacialis*, *Astarte elliptica* et *Astarte moerchi*. Le régime alimentaire de ces bivalves a été caractérisé dans des

systèmes côtiers et profonds de l'Arctique canadien (chapitres 1 et 3) et un fjord subarctique (chapitre 2), permettant d'avoir des connaissances complémentaires sur le couplage pélago-benthique dans des environnements contrastés sur une période de temps courte (saison). La dynamique de croissance d'*Astarte moerchi* de la polynie des eaux du Nord a été examinée afin de mieux comprendre les paramètres environnementaux à des échelles régionale et/ou locale qui affecteraient depuis les dernières décennies les ressources trophiques exportées vers le benthos en termes de qualité et quantité et ainsi déterminer la nature et la force du couplage pélago-benthique (chapitre 3).

CONTRIBUTION DE L'ÉTUDE

Détermination du régime alimentaire de *B. glacialis* et d'*Astarte* spp.

Les sources principales de nourriture pour les trois espèces de bivalves étudiées ont pu être caractérisées dans des environnements à la fois très différents par leur bathymétrie et les caractéristiques de leurs assemblages phytoplanctoniques (oligotrophe vs. eutrophe) dans l'archipel canadien (chapitre 1), le Nord de la baie de Baffin (chapitre 1 et 3) et un fjord subarctique (chapitre 2). Le régime alimentaire de *B. glacialis* et *Astarte* spp. révèle une grande plasticité en étant basé sur diverses ressources trophiques incluant les microalgues (diatomées et dinoflagellés), le zooplancton, les bactéries, et le matériel dérivé de macroalgues (détritus, exsudats). Néanmoins, le manque d'acides gras marqueurs trophiques (FATM) spécifiques à une source de nourriture limite notre interprétation quant aux relations trophiques. L'inconvénient lié à cette méthode a été en partie comblé dans le chapitre 2 par une approche multi-marqueurs combinant les profils en FA, les isotopes stables (SI) sur le matériel entier ('*bulk stable isotopes*'), et l'analyse isotopique d'acides gras individuels. En effet, les ressources trophiques (matière organique de la colonne d'eau et des sédiments, et six espèces de macroalgues) ont pu être différenciées grâce à leur composition en FA et des signatures isotopiques distinctes. La présence de ces composants spécifiques à chacune des

ressources (biomarqueurs) dans les tissus des consommateurs a permis de déterminer avec plus de précision et de robustesse le régime alimentaire du bivalve *A. elliptica* dans un fjord subarctique. L'un des points majeurs avancé dans le chapitre 2 est l'importance des macroalgues brunes qui peuvent contribuer significativement à la diète d'*A. elliptica*. Alors qu'elles n'étaient que très peu considérées comme sources potentielles de carbone pour les organismes benthiques filtreurs, un intérêt grandissant leur est accordé pour avoir une meilleure compréhension de la structure des réseaux trophiques des systèmes côtiers arctiques (McMeans *et al.* 2013, Renaud *et al.* 2015). Par ailleurs, les valeurs stables de $\delta^{13}C$ dans les tissus d'*A. elliptica* suggèrent que la composition isotopique n'est pas l'outil le plus approprié pour suivre la variabilité saisonnière de son régime alimentaire. Les FATM, quant à eux, fournissent des informations sur la nourriture ingérée pendant quelques semaines (McMahon *et al.* 2006, Sun *et al.* 2007) et paraissent donc une méthode utile pour étudier la stratégie d'alimentation en réponse à la dynamique de la production primaire sur une échelle de temps relativement courte. L'approche multi-marqueurs est donc à privilégier pour obtenir le plus d'informations possibles qui facilitent la caractérisation des réseaux trophiques et pour suivre leur évolution au fil des saisons et des années.

Par ailleurs, le chapitre 1 a mis en évidence la capacité des populations profondes de *B. glacialis* à synthétiser *de novo* des acides gras non maloniques ('*non-methylene-interrupted*', NMI) pour faire face aux contraintes de l'environnement telles que les basses températures, la pression, mais surtout lorsque leurs apports en acides gras essentiels sont insuffisants en raison d'une plus faible disponibilté des ressources trophiques. De par son régime alimentaire non sélectif et sa capacité de biosynthèse de NMI, *B. glacialis* semble ainsi capable de s'adapter aux éventuels changements dans la qualité, la quantité et le moment de la production primaire qui sont prédits en Arctique.

Le couplage pélago-benthique

Il a été mis en évidence un couplage pélago-benthique plus fort dans les systèmes peu profonds de l'ouest de l'Arctique canadien et du Kobbefjord (chapitres 1 et 2) par rapport aux systèmes bathyaux du détroit de Lancaster et du nord de la baie de Baffin (chapitre 1). Ces résultats sont consistants avec la littérature qui décrit très largement le fort couplage pélago-benthique sur les plateaux continentaux arctiques, à l'inverse des eaux ouvertes qui sont caractérisées par un faible export de carbone vers le fond marin et donc un couplage pélago-benthique réduit (p. ex. Moran *et al.* 2012). En effet, de par la plus grande disponibilité en lumière et l'accessibilité au substrat pour les espèces benthiques, une plus grande diversité de producteurs primaires se trouve dans les zones côtières peu profondes. Dans l'océan ouvert, à de plus grandes profondeurs, les organismes benthiques suspensivores dépendent essentiellement de la production pélagique. Il est ainsi difficile, voire impossible, de discerner l'influence de la profondeur et la disponibilité en ressources alimentaires sur la matière organique exportée et utilisée par les organismes benthiques. Les apports de nourriture au benthos en termes de qualité et de quantité ne peuvent donc être dissociés des effets de la profondeur. Certaines incertitudes demeurent quant à la nature des particules alimentaires qui atteignent le fond marin et sont ensuite utilisées par les communautés benthiques. Les processus, tels que la dégradation et la reminéralisation, affectant la matière organique lors de son transfert dans la colonne d'eau nécessitent des investigations complémentaires. Néanmoins, ce travail apporte de nouvelles données, en particulier pour l'est et le centre de l'archipel canadien qui sont des régions de l'Arctique sous-représentées dans les études du couplage pélago-benthique, ainsi qu'une approche originale avec l'utilisation conjointe des marqueurs trophiques pour l'exploration des liens trophiques à court terme et des techniques de scléro–chronologie/–chimie pour le suivi à long terme.

L'étude du patron de croissance des coquilles d'*A. moerchi* du nord de la baie de Baffin, à près de 600 m de profondeur, a montré que les bivalves grandissaient plus que la normale depuis le début des années 2000 (chapitre 3). Du fait que leur environnement immédiat est stable, ces anomalies de croissance positives s'expliqueraient par un apport plus important

de nourriture grâce à une forte production primaire et une exportation de cette production hors de la zone euphotique, vraisemblablement aidée par de forts courants pour transporter cette production même à de grandes profondeurs. Ces observations sont par ailleurs soutenues par les informations fournies par les FATM, puisque la présence d'acides gras marqueurs de microalgues, notamment de diatomées, dans les tissus de *B. glacialis* et *A. moerchi*, montre que les bivalves, même à 600 m de fond, bénéficient de la production primaire issue de la zone euphotique. Cet export accru de matière organique pour le benthos serait dû, soit à des modifications de la dynamique locale de la glace de mer qui influence la production phytoplanctonique en modulant la disponibilité en lumière, soit à un décalage entre la floraison du phytoplancton et le broutage par le zooplancton. Ces résultats ont montré qu'il était difficile de conclure sur les relations environnement – communautés benthiques à une échelle régionale (faible corrélation entre les indices climatiques et le patron de croissance d'*A. moerchi*) car les conditions physiques et biologiques à l'échelle locale interfèrent avec les tendances données à grande échelle. Bien que les études à grande échelle spatiale (p. ex. à l'échelle de l'Arctique canadien, échelle pan-arctique), soient essentielles pour définir les principaux facteurs environnementaux ou climatiques qui influencent les systèmes marins arctiques, des études à des échelles spatiales plus petites doivent être également menées pour mieux décrire certains processus (p. ex. le couplage pélago-benthique) en raison des conditions locales.

Le potentiel d'*A. moerchi* en tant que bio-archive pour des études paléo-climatiques

Parmi les espèces du genre *Astarte*, celles rattachées au complexe *A. borealis* ont déjà fait l'objet d'études pour retracer, à partir de la composition en isotope stable de l'oxygène de la coquille, les conditions hydrographiques (effets de dessalure) en mer de Laptev (Mueller-Lupp *et al.* 2003, Müller-Lupp & Bauch 2005), en mer de Kara (Simstich *et al.* 2005a), dans le détroit de Béring (Khim *et al.* 2001), et dans un fjord de l'est du Groenland (Israelson *et al.* 1994). Cependant, une très grande variabilité de la longévité existe pour cette

espèce. Dans le chapitre 3, nous avons pu observé qu'*A. moerchi* déposait succesivement et régulièrement des incréments et des lignes de croissance pour lesquels la rythmicité annuelle a pu être validée grâce à la méthode du radiocarbone issu des essais nucléaires atmosphériques. Cette espèce, qui peut vivre au delà d'une centaine d'année, représente ainsi un modèle idéal pour les reconstructions des conditions environnementales à long terme, d'autant plus que les espèces arctiques ordinairement utilisées (*Clinocardium ciliatum* ou *Serripes groenlandicus*) pour les études sclérochronologiques et sclérochimiques ont une durée de vie assez moyenne (40 ans). En outre, les coquilles d'*A. moerchi* ont montré des profils en baryum (ratio Ba/Ca) typiques avec une ligne de base faible régulièrement entrecoupée de pics d'amplitude variable. Ces derniers représentent les variations temporelles de production primaire car les pics de baryum ont été associés aux floraisons microalgales dominées par des diatomées (Stecher *et al.* 1996, Elliot *et al.* 2009, Thébault *et al.* 2009).

PERSPECTIVES

Approfondir les études sur les algues de glace comme source de carbone pour les réseaux trophiques benthiques arctiques

Plusieurs études récentes ont suggéré l'importance des algues de glace comme sources de carbone pour les communautés benthiques (p. ex. Søreide *et al.* 2013, Carroll *et al.* 2014, Roy *et al.* 2015). Néanmoins, la composition en isotope stable du carbone, mesurée sur les tissus musculaires ou l'ensemble de l'organisme, a montré une certaine stabilité dans le temps chez les invertébrés benthiques arctiques. Cela en fait un outil biochimique tout à fait pertinent pour l'étude de la variabilité spatiale du régime alimentaire des organismes benthiques mais peu adapté pour suivre les variations saisonnières. Par ailleurs, il ne permet pas d'affirmer avec certitude que le benthos a bien assimilé des algues de glace. Søreide *et al.* (2014) ont notamment montré la grande variabilité des valeurs isotopiques de la matière

organique particulaire associée au couvert de glace ou à la colonne d'eau entre les différentes régions de l'Arctique, rendant l'interprétation des réseaux trophiques complexe. À l'inverse des isotopes, les acides gras permettent de suivre les variations temporelles des apports en carbone pour le benthos. Cependant, cette méthode ne permet de distinguer que les grandes classes de producteurs primaires, dont les diatomées, mais sans différentiation possible de leur origine entre la colonne d'eau ou la glace de mer. Bien que largement utilisée dans de récentes études, l'étude du ratio isotopique sur des acides gras spécifiques marqueurs de diatomées pour distinguer leur origine sympagique ou pélagique (Budge *et al.* 2008, Wang *et al.* 2014) ne paraît pas si facile et sans équivoque. Le ratio isotopique du carbone pour l'acide gras 20:5ω3 des diatomées sympagiques peut être particulièrement semblable et confondu avec celui des algues vertes du genre *Ulva* (chapitre 2). Le marqueur lipidique IP_{25} ('*ice proxy*' avec 25 atomes de carbone), spécifique aux algues de glace, pourrait être ainsi utilisé de façon complémentaire, puisque sa présence dans les tissus des consommateurs indique précisément et sans équivoque que ces derniers ont assimilé du matériel organique dérivé des algues de glace. En effet, l'IP_{25} a été spécifiquement associé à certaines espèces de diatomées sympagiques et l'accumulation de ce marqueur dans la glace de mer coïncide effectivement avec la floraison printanière des diatomées sympagiques, lorsque la fonte de la glace de mer crée des canaux permettant leur croissance. C'est pourquoi, la présence de l'IP_{25} dans les autres composantes de l'écosystème reflèterait davantage une couverture de glace saisonnière plutôt que des conditions d'eaux libres de glace ou de glace permanente. Ce marqueur de diatomées sympagiques a été utilisé avec succès pour démontrer l'importance des algues de glace comme sources de nourriture (directes ou indirectes) pour les communautés benthiques (Brown & Belt 2012b, Brown *et al.* 2012), le zooplancton (Brown & Belt 2012a) ou encore les mammifères marins (Brown *et al.* 2013). De manière analogue, la méthode 'H-Print' repose sur la distribution de sept isomères de lipides isoprénoïdes fortement ramifiés (HBI, '*higly branched isoprenoid lipids*') produits par certaines espèces de diatomées et dont la distribution varie en fonction de la composition spécifique et des conditions environnementales, permet de distinguer facilement les diatomées pélagiques des diatomées sympagiques, ainsi que la matière organique dérivée et

transférée dans les différents compartiments et niveaux trophiques des systèmes arctiques incluant la glace de mer, la colonne d'eau, les sédiments, les organismes benthiques, démersaux, pélagiques et les oiseaux (Brown *et al.* 2014).

Alors que la diminution du couvert de glace laisse présager une baisse de l'importance de la contribution des algues de glace pour le compartiment benthique (Carroll & Carroll 2003, Grebmeier *et al.* 2006, Bluhm & Gradinger 2008), le couplage algues de glace – benthos pourrait temporairement augmenter dans certaines régions de l'Arctique canadien où la glace multiannuelle est actuellement présente. Boetius *et al.* (2013) ont d'ailleurs montré qu'un export important d'algues de glace peut avoir lieu depuis la glace de mer jusqu'au fond marin du bassin central arctique à une profondeur de 4400 m. La production d'algues de glace est dépendante de plusieurs facteurs environnementaux, dont l'épaisseur de la glace de mer et la couverture de neige qui atténuent la lumière (Michel *et al.* 2006). Ainsi, la diminution continue de l'épaisseur et de l'étendue de la glace de mer, et l'épaisseur du couvert de neige, favoriseraient la production d'algues de glace dans ces régions dans un avenir proche, bien qu'à long terme l'apport amoindri d'algues de glace prédit pour le benthos à l'échelle de l'Arctique semble inévitable. Un suivi saisonnier afin de définir l'importance des algues de glace dans le régime alimentaire des organismes benthiques et leur cycle annuel ainsi qu'un suivi à long terme de l'évolution du régime alimentaire suivant la diminution du couvert de glace multiannuelle pourraient être envisagés par l'utilisation conjointe des différents marqueurs biochimiques décrits plus haut.

Mieux estimer l'importance des producteurs primaires benthiques : microphytobenthos et macroalgues

Glud *et al.* (2009) ont recensé seulement dix études révisées par les pairs et trois études non publiées sur la production des microalgues benthiques (ou microphytobenthos) dans les eaux arctiques. Malgré ce nombre limité, ces études suggèrent que les microalgues benthiques contribuent de manière significative à la production primaire dans les

écosystèmes côtiers arctiques. La productivité des microalgues benthiques est d'une ampleur similaire ou peut même dépasser la productivité pélagique dans les zones côtières peu profondes (< 30 m). L'ensemble de l'Arctique est cependant nettement sous-échantillonné et montre d'importantes disparités. Aucune étude n'a par exemple été conduite sur la production des microalgues benthiques dans l'archipel canadien. D'autres études sur la production primaire benthique devraient être ainsi encouragées. La couverture de la glace de mer diminuant rapidement en Arctique (Serreze *et al.* 2007), et étant donné le rôle important qu'exerce la couverture de glace sur la production primaire marine (Rysgaard *et al.* 1999), la productivité pélagique devrait augmenter dans les systèmes marins arctiques en raison de la plus grande disponibilité en lumière. La compétition pour les nutriments entre les producteurs primaires benthiques et pélagiques serait par conséquent accrue mais le développement du microphytobenthos serait davantage favorisé dans les régions côtières de l'Arctique avec des nutriments limitants (Glud *et al.* 2009). Cependant, l'augmentation prévue des précipitations ainsi que la fonte du pergélisol devraient accroitre l'apport d'eau douce riche en nutriments et la turbidité, ce qui pourrait limiter la production primaire benthique et pélagique et contrecarrer localement la hausse attendue avec la disponibilité de la lumière (Weslawski *et al.* 2011). Le bilan net est difficile à prévoir et ne peut être élucidé qu'avec des mesures à long terme de la production primaire benthique côtière.

Parmi les producteurs primaires benthiques, les communautés de macroalgues devraient être aussi favorisées dans les systèmes côtiers de l'Arctique en réponse à l'augmentation de la température et la réduction de la couverture de glace de mer (Krause-Jensen *et al.* 2012, Krause-Jensen & Duarte 2014). Une biomasse supérieure et une répartition de plus en plus nordique se manifestent déjà dans certaines régions (Weslawski *et al.* 2010, Kortsch *et al.* 2012). Des études récentes (McMeans *et al.* 2013, Renaud *et al.* 2015) et nos résultats (chapitre 2) indiquent que les détritus de macroalgues peuvent contribuer de manière significative à l'alimentation des organismes benthiques arctiques même à de grandes profondeurs (400 m). D'autres investigations sont nécessaires pour compléter cette étude et déterminer le rôle d'une plus importante couverture macroalgale sur la structure et le fonctionnement des communautés benthiques des systèmes côtiers arctiques. Ces résultats

soulignent par ailleurs la nécessité d'échantillonner toutes les sources potentielles de carbone pour la réalisation des études trophiques et la description du couplage pélago-benthique dans les systèmes côtiers. En considérant uniquement la matière organique particulaire (et parfois les algues de glace) comme sources probables de carbone pour la chaine alimentaire benthique, les études trophiques ont une vision incomplète du « fort » couplage pélago-benthique qui est largement mis en avant.

Préciser la qualité et la quantité de la matière organique exportée vers le benthos

Une des limitations pour décrire la nature du couplage pélago-benthique en termes de qualité et de quantité de matière organique exportée vers le benthos selon le régime de productivité primaire (systèmes oligotrophes vs. eutrophes) considéré est due aux effets confondus de la profondeur. Les particules alimentaires qui atteignent les communautés benthiques sont affectées par un certain nombre de processus lors de leur transfert dans la colonne d'eau, comme la dégradation ou la reminéralisation par les bactéries qui nécessiteraient des études complémentaires. Il serait, par exemple, intéressant de caractériser le flux vertical de matière organique exporté depuis les eaux de surface jusqu'au benthos en utilisant des pièges à particules placés à différentes profondeurs dans des systèmes trophiques contrastés. L'approche multi-marqueurs (acides gras marqueurs trophiques, isotopes stables du carbone et de l'azote et isotope du carbone sur des composés spécifiques) est ainsi à privilégier pour obtenir le plus d'informations possible facilitant la caractérisation de la matière organique et suivre sa transformation avec la profondeur. Elle peut être, par ailleurs, complétée par des analyses pigmentaires en chromatographie liquide à haute performance (HPLC) afin de suivre avec plus de précision la dynamique des communautés microalgales et leur devenir lors de leur transfert dans la colonne d'eau. En effet, les pigments photosynthétiques (chlorophylles, caroténoïdes, phéopigments et les phicobiliprotéines) sont aussi communément utilisés comme marqueurs des classes algales. Récemment, McTigue *et al.* (2015) ont mesuré la teneur en pigments des sédiments de la mer des Tchouktches afin de

déterminer les voies de dégradation de la matière organique qui est ensuite utilisée par les organismes benthiques.

Alors que ces analyses ne fourniraient que des indications sur la qualité de la matière organique, elles pourraient également être mises en parallèle avec les études existantes ou futures portant sur les flux de carbone réalisées dans différentes régions de l'Arctique (voir la revue de Turner 2015) afin de discuter de l'aspect quantitatif du couplage pélago-benthique.

L'ensemble de ces études complémentaires sur le devenir de la production phytoplanctonique offriraient donc une meilleure compréhension des changements qualitatifs et quantitatifs de la nourriture qui atteint les communautés benthiques. Leur réalisation à haute fréquence dans des systèmes contrastés tels que les plateaux continentaux avec une couverture de glace saisonnière (p. ex. la mer de Béring et la mer des Tchouktches), les systèmes influencés par les apports terrestres (p. ex. la mer de Beaufort), les régions ouvertes dominées par la production pélagique, ou encore les zones où il y a de la glace multi-annuelle (p. ex. Haut-Arctique), permettrait une meilleure interprétation des interactions entre les paramètres physiques et biologiques qui régissent les écosystèmes benthiques arctiques. Enfin, l'étude de la dynamique de la production primaire dans les régions plus subarctiques, comme le Kobbefjord, peut apporter un début de réponse à ce que pourraient devenir certains systèmes arctiques dans le futur, en réponse aux changements climatiques.

Élargir l'utilisation d'*Astarte* spp. comme outil paléoenvironnemental

Le chapitre 3 a démontré que le bivalve longévive *A. moerchi* est un modèle prometteur pour la reconstruction passée de l'environnement. Toutefois des études complémentaires peuvent être envisagées. Tout d'abord, des analyses sur de plus jeunes individus (30 à 40 ans) permettraient de réaliser une calibration du modèle *A. moerchi*. En effet, la datation des incréments serait moins complexe et leur largeur serait plus appropriée d'un point de vue

résolution temporelle pour tenter de relier paramètres de croissance et éléments chimiques de la coquille à des paramètres environnementaux. Néanmoins, cela demande d'avoir des données environnementales acquises *in situ* sur une échelle de temps suffisamment grande pour permettre la comparaison. Nous avons effectué les analyses sclérochronologiques et sclérochimiques sur des *A. moerchi* de la polynie des eaux du Nord. Bien que cette région soit considérée comme un site privilégié pour étudier l'impact des changements climatiques sur le fonctionnement et la structure des écosystèmes marins arctiques en raison de sa caractéristique éphémère, il serait intéressant de comparer les patrons de croissance de la même espèce sur une large échelle spatiale en considérant les différents régimes de production primaire et les gradients de profondeurs. Dans l'archipel canadien, les sites pourraient être les mêmes que ceux indiqués dans la partie 'couplage pélago-benthique' plus haut : les plateaux continentaux influencés par la couverture de glace saisonnière (p. ex. la mer de Béring et la mer des Tchouktches), les systèmes influencés par les apports terrestres (p. ex. la mer de Beaufort), les régions ouvertes dominées par la production pélagique, ou encore les zones où subsiste de la glace multiannuelle (p. ex. Haut-Arctique). Dans ces systèmes très différents où les ressources trophiques principales ne sont pas les mêmes et en nombre variable, la croissance des organismes benthiques devrait être différente et pourrait être estimée par l'étude des patrons de croissance des bivalves. *Astarte moerchi* pourrait ainsi être utilisé à une échelle plus large, sur l'ensemble de l'archipel canadien ou même à une échelle panarctique, affin d'apprécier la dynamique spatio-temporelle des effets du changement global sur la disponibilité des ressources trophiques pour le compartiment benthique.

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