Vol. 536: 175–186, 2015
doi: 10.3354/meps11424

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published September 29

Dietary tracers in *Bathyarca glacialis* from contrasting trophic regions in the Canadian Arctic

Blandine Gaillard[1,*], Tarik Meziane[2], Réjean Tremblay[1], Philippe Archambault[1], Kara K. S. Layton[3], André L. Martel[4], Frédéric Olivier[2]

[1]Institut des Sciences de la Mer, Université du Québec à Rimouski, 310 Allée des Ursulines, Rimouski, Québec G5L 3A1, Canada
[2]Unité Mixte de Recherche 'Biologie des organismes et écosystèmes aquatiques' (BOREA, UMR 7208), Muséum national d'Histoire naturelle, Université Pierre et Marie Curie, Université de Caen Basse-Normandie, Centre National de la Recherche Scientifique, Institut de Recherche pour le Développement-207; CP53, 61 rue Buffon, 75005 Paris, France
[3]Centre for Evolutionary Biology, University of Western Australia, 35 Stirling Highway, Crawley, Western Australia 6009, Australia
[4]Research and Collections, Canadian Museum of Nature, PO Box 3443, Station D, Ottawa, Ontario K1P 6P4, Canada

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 Southeastern 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.

KEY WORDS: Fatty acid trophic markers · FATMs · Non-methylene-interrupted fatty acid · Pelagic–benthic coupling · Canadian Arctic Archipelago · Bivalve · *Bathyarca glacialis*

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 ben-

*Corresponding author: blandine.gaillard5@gmail.com

thos 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 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

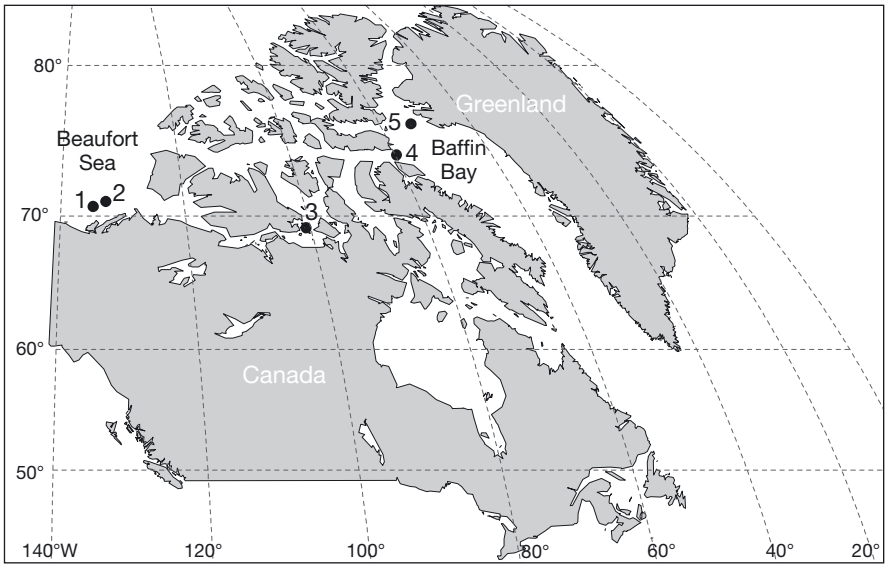

Fig. 1. Stations in the Canadian Arctic Archipelago sampled for this study: Stn 1 = BP11-025, Beaufort Sea shelf; Stn 2 = BP11-029, Beaufort Sea shelf; Stn 3 = 312, Victoria Strait; Stn 4 = 323, Lancaster Sound; Stn 5 = 111, northern Baffin Bay

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.

Table 1. Collection information of bivalves *Bathyarca glacialis* with station ID for this study (official designations as in Fig. 1), 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	52
2	71° 01′ N	132° 41′ W	17/09/2011	66
3	69° 10′ N	100° 45′ W	09/08/2011	69
4	74° 12′ N	79° 44′ W	14/10/2010	780
5	76° 17′ N	73° 17′ W	16/10/2010	568

MATERIALS AND METHODS

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 (Fig. 1, Table 1) using an Agassiz trawl deployed from the CCGS 'Amundsen'. Table 1 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.

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.

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).

Statistical analysis

Multivariate analyses on total FA composition of each fraction (neutral and polar lipids), including *a posteriori* pairwise 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 2 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.

Table 2. 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

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.

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 S1 in the Supplement at www.int-res.com/articles/suppl/m536p175_supp.pdf.

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 3, Fig. 2). Within coastal populations, Stns 2 and 3 were similar (Fig. 2; pairwise test, p(perm) = 0.05, Table S2) and both differed from

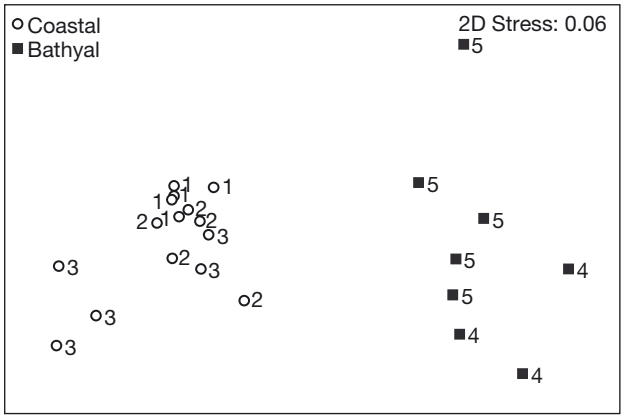

Fig. 2. Non-metric multidimensional scaling (n-MDS) plot based on Bray-Curtis dissimilarities matrix calculated on fourth-root transformed data for the total fatty acid composition of neutral lipids in coastal (Stns. 1, 2 and 3) and bathyal (Stns. 4 and 5) *Bathyarca glacialis* populations

Stn 1 (Fig. 2; pairwise test, p(perm) < 0.01, Table S2). FA profiles for the 2 bathyal populations (Stns 4 and 5) were similar (Fig. 2; pairwise test, p(perm) = 0.12, Table S2). SIMPER analysis showed that the average of the Bray-Curtis dissimilarities between coastal and bathyal stations was 14.08 (Table S3). 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 S3). Differences between 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 Stn 1 compared to *B. glacialis* from Stns 2 and 3 (Table S3).

Table 3. 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 df	MS	Pseudo-*F*	p(perm)	Polar lipids df	MS	Pseudo-*F*	p(perm)
Z	1	787.05	**13.32**	<0.01	1	1838.00	**78.63**	<0.01
Stn(Z)	3	63.00	**3.13**	<0.01	3	23.99	**4.03**	<0.01
Residual	18	20.15			19	5.95		

In regards to specific trophic markers, the 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, $p < 0.01$; Fig. 3). 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; Fig. 3). 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, $p < 0.001$; Fig. 3). Analysis on DHA (marker of dinoflagellates) showed a significant difference among Stations within Depths (2-way nested ANOVA, $p < 0.001$; Fig. 3). Proportion of DHA in *B. glacialis* from the costal 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; Fig. 3). Furthermore, bathyal Stns 4 and 5 showed significant levels of FA markers of zooplankton (2-way nested ANOVA, $p < 0.01$; Fig. 3). 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; Fig. 3). 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.

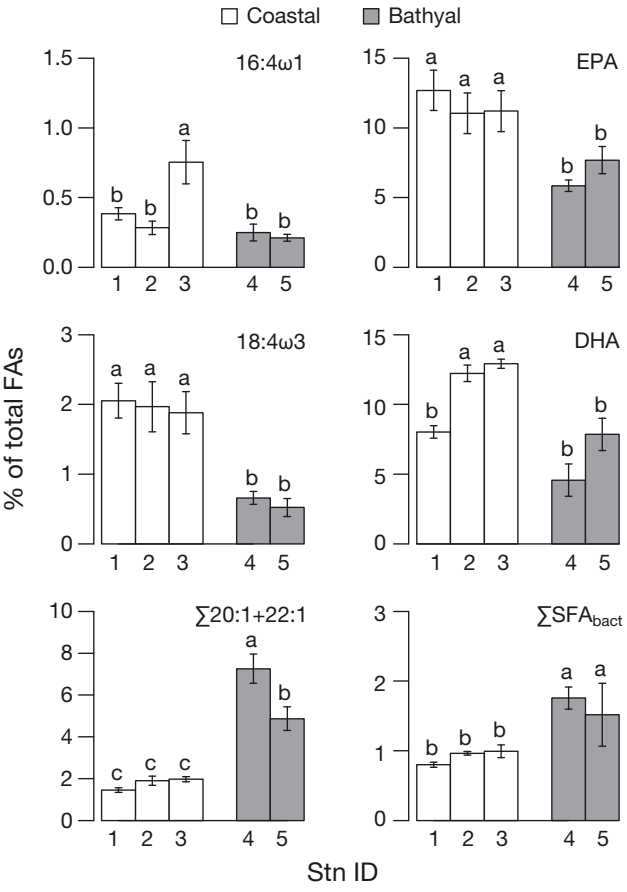

Fig. 3. Fatty acid trophic markers (mean ± SE) (see Table 2) in the neutral lipids of *Bathyarca glacialis* from coastal (Stns 1, 2 and 3; white bars) and bathyal (Stns 4 and 5; grey bars) populations. Different letters above bars indicate significant differences (see Table S4 in the Supplement for test results)

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 3). Within coastal populations, FA composition in PL of *B. glacialis* from Stns 2 and 3 were similar (pairwise test, p(perm) = 0.09; Table S2) and significantly differed from that of *B. glacialis* from Stn 1 (pairwise test, p(perm) < 0.05; Table S2). The 2 bathyal populations showed significant differences in FA composition (pairwise test, p(perm) < 0.05; Table S2). SIMPER analysis indicated that the average of the Bray-Curtis dissimilarities between coastal and bathyal stations is 18.62 (Table S3). 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, $p < 0.01$; Fig. 4). Additionally, no significant difference was found in the sum of SFAs between the depths or among populations (2-way nested ANOVA, $p > 0.05$; Fig. 4). 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 $p < 0.001$; Fig. 4). MUFAs showed the highest variability, with significant differences between Depths and among Stations nested within Depth (2-way nested ANOVA, $p < 0.05$; Fig. 4). 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; Fig. 4).

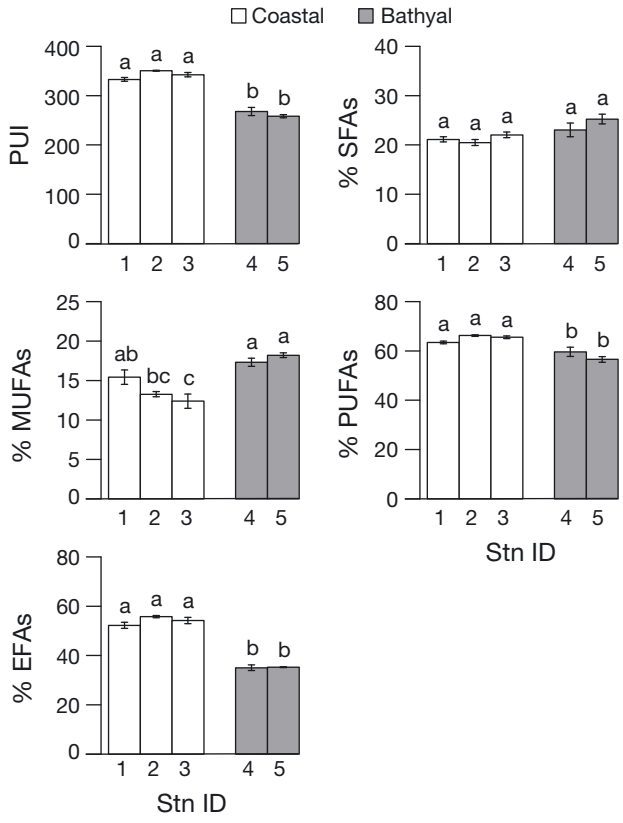

Fig. 4. Unsaturation index (PUI), sum of saturated fatty acids (SFAs), monounsaturated fatty acids (MUFAs), polyunsaturated fatty acids (PUFAs) and essential fatty acids (EFAs) in the polar lipids of *Bathyarca glacialis* from coastal (Stns 1, 2 and 3; white bars) and bathyal (Stns 4 and 5; grey bars) populations (mean ± SE). Different letters above bars indicate significant differences (see Table S5 in the Supplement for test results)

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. 2004, 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 provides 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 dependent 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 dinoflagellates (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 reduces 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 Stn 1 differed from *B. glacialis* from 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 m^3 yr^{-1} of freshwater (Holmes et al. 2012) and 125 × 10^6 t yr^{-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 produce high amounts of 20:1ω9 and 22:1ω11 (Sargent & Falk-Petersen 1988, Dalsgaard et al. 2003). Major biomass production 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 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 multimethod 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 FA 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.

Acknowledgements. We thank the CCGS 'Amundsen' officers and crew, scientists and technicians for their support on board. Special thanks go to V. Roy, A. Fontaine, K. Chalut, M. Bouchard Marmen, J. Nephin, L. de Montety, and C. Grant for assistance with sample collection in the field. We kindly acknowledge I. Redjah for fatty acids extraction; N. Thiney and M. Babin for fatty acids analysis; P. Hebert and staff at the Canadian Centre for DNA Barcoding for aid in sequence acquisition; and P. Guillot for sharing environmental data. We also thank 3 anonymous reviewers for constructive comments. This study was financially supported by ArcticNet and Canadian Healthy Oceans Networks (CHONe) to P.A., Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant 299100 to R.T., Québec-Océan, and by MNHN via a 3-yr visiting professorship at ISMER-UQAR to F.O. Sequence analysis was enabled by funding from the government of Canada through Genome Canada and the Ontario Genomics Institute in support of the International Barcode of Life Project. Data collected in 2011

on the Beaufort Sea shelf area were gathered through research collaborations among the CCGS Amundsen program, ArcticNet, BP Exploration Operating Company Limited, ExxonMobil and Imperial Oil. This study is part of the project B.B. Polar (resp. L. Chauvaud) financially supported by the Fondation Total and the Institut polaire français Paul Emile Victor.

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Editorial responsibility: James McClintock, Birmingham, Alabama, USA

Submitted: March 16, 2015; Accepted: July 14, 2015
Proofs received from author(s): September 15, 2015