Dietary plasticity in the bivalve Astarte moerchi revealed by a multimarker study in two Arctic fjords

Silvia De Cesare, Tarik Meziane, Laurent Chauvaud, Joelle Richard, Mikael K. Sejr, Julien Thébault, Gesche Winkler, Frédéric Olivier

Vol. 567: 157–172, 2017
https://doi.org/10.3354/meps12035

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published March 13

Dietary plasticity in the bivalve *Astarte moerchi* revealed by a multimarker study in two Arctic fjords

Silvia De Cesare[1], Tarik Meziane[1,*], Laurent Chauvaud[2], Joëlle Richard[2,6], Mikael K. Sejr[3,4], Julien Thébault[2], Gesche Winkler[5], Frédéric Olivier[1]

[1]Unité Mixte de Recherche Biologie des organismes et écosystèmes aquatiques (BOREA UMR 7208), Sorbonne Université, Muséum National d'Histoire Naturelle, Université Pierre et Marie Curie, Institut de Recherche pour le Développement, Université de Caen-Normandie, Université des Antilles, 75005 Paris, France

[2]Institut Universitaire Européen de la Mer, Unité Mixte de Recherche Laboratoire des sciences de l'environnement marin (LEMAR, UMR 6539), Centre National de la Recherche Scientifique, Institut de Recherche pour le Développement, Université de Bretagne Occidentale, Technopôle Brest-Iroise, 29280 Plouzané, France

[3]Arctic Research Centre, Aarhus University, Ny Munkegade bldg. 1540, 8000 Aarhus C, Denmark

[4]Department of BioScience, Aarhus University, Vejlsøvej 25, 8600 Silkeborg, Denmark

[5]Institut des Sciences de la Mer (ISMER), Université du Québec à Rimouski (UQAR), Rimouski, QC G5L 3A1, Canada

[6]*Present address:* Coastal Watershed Institute, Florida Gulf Coast University, Fort Myers, FL 33965, USA

ABSTRACT: Arctic coastal ecosystems are likely to be strongly affected by predicted environmental changes such as sea-ice decline and increase in freshwater input and turbidity. These changes are expected to impact primary production dynamics and consequently benthic consumers. The trophic relationship between primary producers and benthic primary consumers were compared in 2 Arctic fjords with different seasonal ice-cover: Young Sound (NE Greenland, a high-Arctic fjord) and Kongsfjorden (Svalbard Archipelago, a sub-Arctic fjord). For comparison, we selected the filter-feeding bivalve *Astarte moerchi* (belonging to the complex *A. borealis*), which has a broad geographical distribution in the Arctic. The bivalve digestive glands and food sources were characterized with fatty acids (FAs), bulk stable isotopes, and compound-specific stable isotopes of individual FAs. Our results suggest that diatoms of pelagic and/or benthic origin are the main contributors to the *A. moerchi* diet in Young Sound and make up a less important fraction of the diet in the Kongsfjorden population. A contribution by sympagic diatoms is clearly excluded in the sub-Arctic fjord and needs to be further assessed in the Arctic fjord. The *A. moerchi* diet in sub-Arctic Kongsfjorden is more diversified, varies with season, and has contributions from dinoflagellates and macroalgal detritus. These results, together with higher concentrations of total FAs in the Young Sound population, demonstrated and characterized the trophic plasticity of this bivalve species. Based on these results, we discuss potential effects of environmental factors (shifts in trophic resources, increase in turbidity) for *A. moerchi* populations in changing Arctic ecosystems.

KEY WORDS: Arctic benthos · Climate change · Pelagic–benthic coupling · Filter-feeding bivalves · Fatty acids · Trophic markers · Compound-specific carbon stable isotopes

INTRODUCTION

In Arctic coastal ecosystems, primary production dynamics are expected to be affected by predicted climate change (Weslawski et al. 2010, Krause-Jensen et al. 2012). The main expected changes are related to decline of sea-ice cover and accelerated melt of glacial ice, which will increase freshwater inputs and water column turbidity. In Arctic ecosystems, primary production is highly seasonal and is

*Corresponding author: meziane@mnhn.fr

limited to spring and summer periods due to light availability. The main primary producers in the Arctic are often considered to be sympagic (ice algae) and pelagic (phytoplankton): ice algae start to grow at the end of the polar night and stop when the sea ice substratum melts, while phytoplankton develops during sea-ice melting and ice-free periods (Hegseth 1998, Soreide et al. 2006, Leu et al. 2011, Kedra et al. 2015). However, for shallow water systems, recent evidence shows that the contribution of benthic producers as a carbon source should not be neglected, as microphytobenthos and macroalgae can significantly contribute to primary production in ice-free periods (Glud et al. 2002, Renaud et al. 2015a, Attard et al. 2016, Gaillard et al. 2017, this Volume). The possible effects of environmental changes on the dynamics and relative abundance of primary producers are still under debate. Sea-ice decline will decrease ice-algae production and could also modify the dynamics of stratification and light conditions, with possible cascade effects on other primary producers (Soreide et al. 2013, Kedra et al. 2015). Intensification of freshwater summer inputs could also change water column stratification and increase turbidity, which is expected to alter light conditions for phototrophic organisms. Whatever the local tendency of these impacts, it is clear that changes in primary producers will cascade to benthic primary consumers, which are strongly coupled with pelagic dynamics and dependent on organic matter availability (Sejr et al. 2009, Gaillard et al. 2015). The future of Arctic benthos is a subject of concern, given that benthic organisms are essential prey items for upper trophic levels (e.g. sea ducks, bearded seals, walruses, and gray whales; Born et al. 2003, Kedra et al. 2015, Renaud et al. 2015b).

Even though a general description of the diversity and distribution of benthic organisms on Arctic continental shelves is now available (Piepenburg et al. 2011), their trophic ecology still remains largely unexplored (Legezynska et al. 2014). The study of the diet of benthic macrofauna has proved to be useful to establish carbon flow and more particularly to study the trophic relationship between primary producers and benthic consumers. In fact, benthic macrofauna can integrate productivity signals over time, thanks to their relatively long life spans (compared to planktonic organisms) and a relative sedentary way of life (Renaud et al. 2011). Several methods can be used to assess diets in aquatic ecosystems. The use of fatty acids (FAs) as dietary markers is a reliable tool to describe aquatic food webs (Graeve et al. 1997, Dalsgaard et al. 2003, Budge et al. 2006, Iverson 2009). This technique is based on the conservative transfer of FAs from the ingested sources to the consumers. In a given environment, groups of organisms at the base of the food web (e.g. diatoms, dinoflagellates, bacteria) can be characterized by a distinct combination of FA markers, making it possible to infer the consumers' diet. For example, the ratio between specific FAs such as 16:1ω7 to 16:0 is a good indicator of diatoms (Reuss & Poulsen 2002, Dalsgaard et al. 2003). This approach can also be used for higher trophic levels, but has been shown to be a reliable means for describing the diet of primary consumers (herbivore zooplankton, filter-feeding organisms). Furthermore, trophic interactions can be quantified by coupling FA techniques with analyses of naturally occurring stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{13}N$; Post 2002, Fry 2006). More recently, compound-specific isotope analysis has been developed to disentangle food webs, using $\delta^{13}C$ values of specific FAs. In the Arctic, this method has been useful for studying carbon inputs from diatoms (Graham et al. 2014, Wang et al. 2014, 2015, 2016, Oxtoby et al. 2016). Budge et al. (2008) assessed differences in 16:4ω1 and 20:5ω3 values to determine the relative contribution of phytoplankton and sea-ice algae as food sources. One of the major advantage of these 3 methods compared to stomach content analysis is that they can indicate assimilated food sources in a more integrative way, from weeks to months depending on the studied tissue (Paulet et al. 2006, Ezgeta-Balic et al. 2012).

Within the benthic fauna, filter-feeding bivalves have been used to investigate trophic links between pelagic and benthic dynamics (Carroll et al. 2011). Filter-feeding bivalves are primary consumers and mostly sessile, thus their diet can be used as an indicator of local primary production regimes (Ezgeta-Balic et al. 2012). *Astarte borealis* (Schumacher, 1817) is a boreo-arctic burrowing bivalve of the family Astartidae, presenting a broad spatial distribution with abundant populations located throughout the Arctic Ocean (Gusev & Rudinskaya 2014). These bivalves live in soft sediments generally in shallow waters, but populations can be found at deeper depths (Zettler 2002) down to the bathyal environment (Gaillard 2016). Like other bivalves of the genus *Astarte*, *A. borealis* exhibits high polymorphism and morphological variability. In a taxonomic study based upon shell morphology, Petersen (2000) considered *A. borealis* as a species complex and described 5 different species belonging to this complex: *A. borealis*, *A. jenseni*, *A. nuuki*, *A. sericea*, and *A. moerchi.*

In this study, we sampled 2 *Astarte* populations from 2 different Arctic fjords. We confirmed that sampled individuals belong to the same species through genetic analysis, and we identified this species as *A. moerchi* following the morphological criteria of Petersen (2000). The diet of *A. moerchi* bivalves was studied with a multi-marker approach coupling FAs analysis, bulk stable isotopes, and compound-specific isotope analysis on specific FAs. Two Arctic fjords were chosen for this study: Young Sound in northeastern Greenland and Kongsfjorden in the Svalbard Archipelago. The interest of this comparison relies on the fact that the first site is a high-Arctic fjord, whereas the second is considered a sub-Arctic fjord (Dunbar 1968, Hop et al. 2002). Marine sub-Arctic areas are submitted to higher temperatures, less ice-cover, and less vertical stability than high-Arctic zones. These factors result in greater productivity in sub-Artic areas (Dunbar 1968). Our hypothesis was that, considering its wide geographical distribution, *A. moerchi* presents a trophic plasticity that allows this bivalve to cope with different environmental conditions. More specifically, we expected the diet of this species to differ between the high-Arctic Young Sound and sub-Arctic Kongsfjorden. Our main objective was to characterize and compare *A. moerchi* diet between these 2 sites, and then discuss potential consequences for populations of this bivalve in changing Arctic ecosystems.

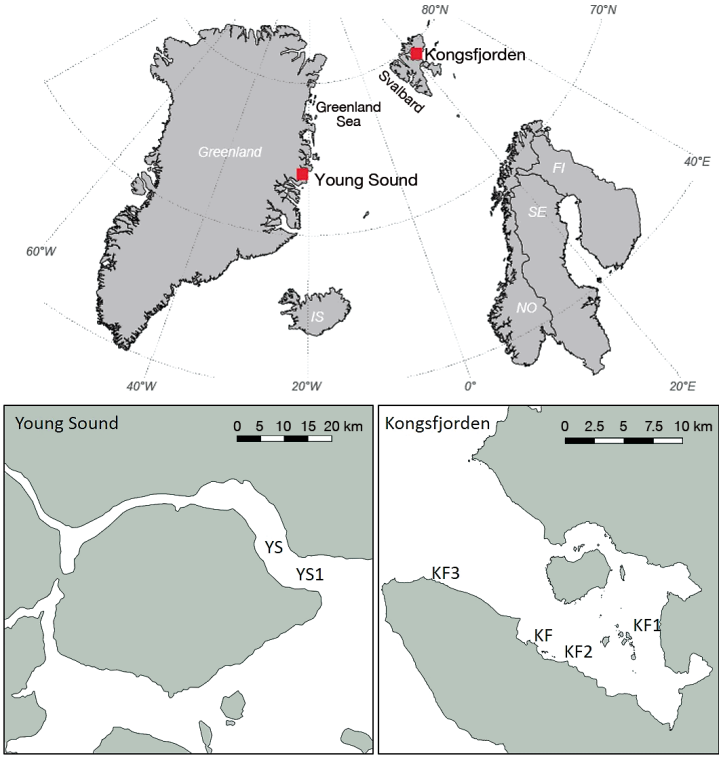

Fig. 1. Locations of sites sampled in Young Sound (NE Greenland) and Kongsfjorden (Svalbard Archipelago). See Table 1 for coordinates and sampling method

MATERIALS AND METHODS

Study sites

Samples were collected in 2 fjords: Young Sound (YS) in northeastern Greenland (74° N, 20° W) and Kongsfjorden (KF) on the western coast of the Svalbard Archipelago (79° N, 12° E; Fig. 1). YS is the outer part of a 90 km long sill fjord with a total volume of 40 km^3 and a mean depth of 100 m (Bendtsen et al. 2007). The sill at the fjord entrance has a maximum depth of 45 m, reducing exchanges with the open sea and the East Greenland Current system. This fjord system is influenced by freshwater inputs from snow and ice melting, especially during summer (Bendtsen et al. 2007), and is covered by sea ice 9 to 10 mo yr^{-1}. In the last 50 yr, sea-ice-free periods varied between 63 and 131 d, and their durations have increased over the last decade (Glud et al. 2007). Bottom water temperatures constantly remain below −1.0°C (Rysgaard et al. 1998). Annual phytoplankton production is estimated to be 10 g C m^{-2} (Rysgaard et al. 1999).

KF is a glacial open fjord approximately 30 km long and has an estimated volume of 29.4 km^3 (Svendsen et al. 2002). KF has no marked sill, and the outer part connects with the North Atlantic Ocean via a trough, the Kongsfjordrenna. It has a well-defined inner fjord area where the depth is less than 100 m, and a deeper area in the outer part of the fjord (Svendsen et al. 2002). Despite its high latitude, KF is considered sub-Arctic because it is influenced by warm Atlantic water from the West Spitsbergen Current (Hop et al. 2002). Hydrological conditions are seasonally variable and influenced by glacial input of freshwater and sediments that generate steep gradients of turbidity, nutrients, and salinity along the fjord's axis. In 2002, ice cover was estimated to be present 5 to 7 mo yr^{-1} in the inner fjord basin and only about 1 mo yr^{-1} in the central basin (Hop et al. 2002). However, ice-cover conditions changed in 2006, with increasing influx of Atlantic waters during winter (Cottier et al. 2007, Lalande et al. 2016) and a consequent increase

of water temperatures in the fjord. Since 2007, sea ice has been restricted to the inner fjord and, in 2013, a mean annual seawater temperature of 3°C was reported in the middle part of KF (Paar et al. 2015). Annual phytoplankton production is estimated to be 35 to 50 g C m^{-2} (Hop et al. 2002).

Field sampling

Bivalves and their potential food sources were sampled in 2 different seasons: the early and late productive seasons. The early season (ES) corresponds to the bloom period at both sites, which occurs sooner at KF (generally April/May; Hop et al. 2002, Hodal et al. 2012, Hegseth & Tverberg 2013, Lalande et al. 2016) than at YS (generally in July; Jensen et al. 2014). The late season (LS) corresponds to the end of summer, before the onset of winter conditions. Thus, sampling at KF was done in May and September 2013, and at YS during August and October 2014. Live specimens of *Astarte moerchi* were collected either by scuba diving (~8 m depth at KF) or by dredging (~20 m depth at YS; Fig. 1, Table 1). A total of 32 individuals were retained for trophic analyses, and shell heights were measured with a caliper (average shell height was 36.1 ± 1.8 (SD) mm at KF and 23.8 ± 3.2 mm at YS). At each site, bivalves were collected in 6 to 10 replicates and were dissected to separate digestive glands (used for trophic analysis) and adductor muscles (used for genetic analysis) from the rest of the tissues. Samples were frozen at −80°C and adductor muscles were stored in 95% ethanol in preparation for molecular analysis. Dietary sources were sampled in both seasons at KF but only during ES at YS, due to bad weather conditions during LS. The upper 1 cm of sediments were collected either by scuba diving with syringes (KF2 and KF, ~8 m depth, Fig. 1, Table 1) or using a Kayak corer (YS, ~20 m depth). Pelagic particulate organic matter (p-POM) samples were obtained from bottom water (~8 m depth at KF and ~20 m depth at YS) collected with Niskin bottles. Water samples were then filtered on pre-combusted glass fiber filters (Whatman GF/F, 47 mm diameter). To characterize the pelagic phytoplankton, 20 ml samples of seawater were fixed in Lugol's solution for identification and stored at 4°C. Brown algae were sampled either by scuba diving (KF3, Fig. 1, Table 1) or using a hook (YS). *Fucus* sp., *Desmarestia aculeata*, and *Saccharina latissima* were sampled only in ES at YS, whereas *Alaria esculenta* and *D. aculeata* were sampled in both seasons at KF. To characterize POM from ice algae (i-POM), ice cores were collected in June 2014 (Site YS1, Fig. 1, Table 1). The bottom 10 cm were taken from each core, then melted and filtered on 47 mm GF/C filters. Sympagic production was characterized with samples of i-POM collected by scuba diving in May 2013, at 1 site in the inner part of the fjord (site KF1, Fig. 1, Table 1). Dietary sources were collected with at least 3 replicates, and samples were frozen at −80°C until trophic analysis.

Sample analysis

Species identification

To confirm that the same bivalve species was sampled at both sites, a barcoding analysis of the cytochrome *c* oxidase subunit I (COI) gene of the mitochondrial DNA was done. 10 individuals from YS and 5 individuals from KF were sequenced. DNA was extracted from the adductor muscle tissue using an E.N.Z.A kit (Omega) specific for mollusks and according to the manufacturer's protocol. A 652 bp region of the COI gene (mt-DNA) was amplified with primers COIL 1490 (5′ GGT CAA CAA ATC ATA AAG ATA TTG G 3′) and COIH 2198 (5′ TAA ACT TCA GGG

Table 1. Sampling site coordinates for Kongsfjorden (KF, Svalbard) and Young Sound (YS, Greenland). i-POM (p-POM): ice-algae (pelagic) particulate organic matter. i-POM was sampled in May 2013 at site KF1 and in June 2014 at Site YS1. ES (LS): early (late) season

Site	Latitude	Longitude	Sampling
Kongsfjorden			
KF	78° 55.762′ N	11° 56.05l′ E	*Astarte moerchi* ES and LS, p-POM LS, sediment LS
KFl	78° 56.292′ N	12° 19.015′ E	i-POM
KF2	78° 54.507′ N	12° 07.204′ E	p-POM ES, sediment ES
KF3	78° 58.651′ N	11° 29.209′ E	Macroalgae ES and LS
Young Sound			
YS	74° 18.743′ N	20° 14.593′ W	*A. moerchi* ES and LS, p-POM ES sediment ES, macroalgae ES
YS1	74° 15.505′ N	20° 12.423′ W	i-POM

TGA CCA AAA AAT CA 3′; Folmer et al. 1994), using the PCR protocol described by Lee (2000). We sequenced the forward and backward branch for each individual, to ensure accuracy of the DNA sequence reads for 603 bp. Sanger sequencing was done on an ABI3730xl analyzer at the Hospital Center of Laval University in Quebec (Canada). Sequences were proofread and aligned with Mega7 software (Tamura et al. 2013). Intraspecific mean divergence, intra-population divergence for each site, and inter-population divergence between KF and YS were calculated using uncorrected p-distances (Collins & Cruickshank 2013) using the MEGA7 software (Tamura et al. 2013). All sequences have been deposited in GenBank (https://www.ncbi.nlm.nih.gov/genbank/) under accession numbers KX954354 to KX954368.

Six haplotypes were found, 2 at YS and 4 at KF. The mean intraspecific divergences of all individuals of *A. moerchi* sequenced (n = 15) was 3% (p-distance), confirming that 1 morphospecies was sampled (Blagoev et al. 2009). Genetic distance within each population was 1 and 2% at KF and YS, respectively, and the mean difference between the populations of KF and YS was 4%, suggesting a slightly higher intraspecific genetic heterogeneity between populations than within populations.

Bulk stable isotopes

Analyses of carbon and nitrogen isotopic ratios were done by the UC Davis Stable Isotope Facility (Department of Plant Sciences, University of California at Davis, Davis, CA, USA). All samples were freeze-dried before treatment and analysis. To remove inorganic carbon that could bias $\delta^{13}C$ values, some samples were treated with HCl: both the p-POM and i-POM samples were exposed to HCl vapors for 4 h (Lorrain et al. 2003), and macroalgae and sediments were treated with successive additions of 1M HCl until they stopped bubbling. Because acid wash can introduce changes in nitrogen values, $\delta^{15}N$ values were obtained from non-acidified samples and $\delta^{13}C$ data were obtained from acidified macroalgae and sediment samples. Samples were weighed in tin (non-acidified samples) or silver (acidified samples) capsules before analysis. The isotope analysis was performed with an elemental analyzer (PDZ Europa ANCA-GSL) interfaced with an isotope ratio mass spectrometer (PDZ Europa 20-20). Isotopic ratios for carbon and nitrogen were expressed using the standard δ notation according to the following equation:

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

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 N_2 for nitrogen (Peterson & Fry 1987).

FA analysis

FA analysis was performed using the method of Bligh & Dyer (1959) and modified as described by Mortillaro et al. (2011). Samples of *A. moerchi* digestive glands and potential food sources were freeze-dried and weighed. After addition of an internal standard (FA 23:0), lipids were extracted by ultrasonification with a mixture of distilled water:$CHCl_3$:MeOH (1:1:2, v:v:v), then concentrated under N_2 flux. Saponification was performed with a mixture of 2 mol NaOH:MeOH (1:2, v:v) at 90°C during 90 min, and the reaction was stopped by adding HCl (35%). Samples were incubated with BF_3-MeOH at 90°C during 10 min, in order to obtain FAs as methyl esters (Meziane & Tsuchiya 2002). These were isolated and stored frozen in chloroform, and then concentrated under N_2 flux to transfer in hexane. To separate and quantify the FAs, 1 µl aliquots were analyzed by gas chromatography (GC, Varian CP-3800 equipped with a flame ionization detector) equipped with a Supelco OMEGAWAX 320 column (30 m × 0.32 mm i.d., 0.25 µm film thickness) and using helium as a carrier gas. Each sample type (digestive gland, macroalga, sediment, p-POM, i-POM) was analyzed by gas chromatography-mass spectrometry (GC-MS Varian 450GC with Varian 220-MS) to identify peaks. FAs are designated by the nomenclature *X*:*Y*ω*Z*, where *X* is the number of carbons, *Y* is the number of double bonds, and *Z* is the position of the ultimate double bond from the methyl end. The FA concentrations (expressed in $mg_{FA}\ g_{dw}^{-1}$, where dw is dry weight, or, for filters, $mg_{FA}\ l_{fw}^{-1}$, where fw is filtered water) were calculated according to Schomburg (1987):

$$C_{FA} = \frac{A_S}{A_{IS}} \cdot \frac{C_{IS}}{W_S} \quad (2)$$

where A_S is the peak area of the FA, A_{IS} is the peak area of FA 23:0 (the internal standard), C_{IS} is the concentration of FA 23:0 (mg), and W_S is the dry weight of the sample (g) or, for filter samples, the volume of filtered water (l).

Compound-specific isotope analysis of individual FAs

All compound-specific isotope analyses of methylated FAs were done at the UC Davis Stable Isotope Facility. Methylated FAs were separated first by gas chromatography (Thermo Scientific TRACE Ultra equipped with a BPX70 column, 60 m × 0.25 mm outer diameter, 0.25 µm film thickness), coupled to an isotope-ratio mass spectrometer (Thermo Fisher Scientific Finnigan DELTA Plus Advantage). Data were corrected to account for the carbon atom added during methylation, following Gladyshev et al. (2012):

$$\delta^{13}C_{FA} = \frac{\delta^{13}C_{FAME} - (1 - x) \cdot \delta^{13}C_{MeOH}}{x} \quad (3)$$

where $\delta^{13}C_{FA}$ is the isotopic value of free FA, $\delta^{13}C_{FAME}$ is the measured isotopic value of methylated FA, x is the number of carbon atoms in the (non-methylated) FA, and $\delta^{13}C_{MeOH}$ is the $\delta^{13}C$ value of the methanol used for methylated FA preparation (–38.43‰ in our study). All $\delta^{13}C$ values are reported relative to Vienna PeeDee Belemnite using standard δ notation.

Data analysis

Data on the FA composition of *A. moerchi* digestive glands (relative FA composition, expressed in percentages) were analyzed using permutational multivariate analyses of variance (PERMANOVA, 9999 permutations), matrix of Bray-Curtis similarities (55 FAs identified) 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. Two sources of variation were tested: 'Season' fixed with 2 levels: ES (May/August) and LS (September/October), and 'Site' fixed with 2 levels: YS and KF. The number of replicates varied between 6 and 10. The FA composition of potential feeding sources were investigated via 1-factor PERMANOVAs (9999 permutations) on untransformed data (PERMDISP, $p > 0.05$) based on 21 FAs (macroalgae) to 47 FAs (sediments) with either 2 treatments for i-POM, p-POM, and *A. esculenta* (fixed with 2 levels: YS vs. KF) or 3 treatments for sediments and *D. aculeata* (fixed with 3 levels: YS, KF during ES and KF during LS). The number of replicates varied between 3 and 5. In case of significant PERMANOVA tests, post hoc tests were carried out. Pairwise multiple comparison tests were used to identify differences among levels of sources of variation. When significant, a similarity percentages (SIMPER) procedure (Clarke 1993) was performed on untransformed data to identify which FAs contribute the most to dissimilarities between different levels. Relative FA composition (expressed in percentages) was visualized using non-metric multidimensional scaling (n-MDS) ordination based on Bray-Curtis similarities between samples (R Core Team 2014). Univariate tests were performed when replicates were higher than 4. Non-parametric Wilcoxon or Kruskal-Wallis tests were used to compare differences in the 16:1ω7 to 16:0 ratio, percentages of 22:6ω3 and 18:4ω3, total FA concentrations, and stable isotope values. When a Kruskal-Wallis test was significant, a post hoc Wilcoxon test was done. For all statistical tests, the significance value was fixed at 0.05.

For bulk stable isotopes, we used a Bayesian stable isotope mixing model (SIAR; Parnell et al. 2010) to estimate probable dietary sources for *A. moerchi*. Prior to analysis with SIAR, we excluded some sources from analysis. At KF, ice algae (i-POM) were excluded because of low abundance of sympagic production in 2013 and also considering the results from compound-specific isotope FA analysis that exclude the contribution of this source. At YS, macroalgal sources were excluded based on results of FA analysis, with the exception of *Saccharina latissima*, an abundant brown alga in this fjord which, based on compound-specific isotope FA analysis, is a probable lipid source for *A. moerchi*. Although application of a trophic enrichment factor is a subject of major debate in trophic ecology, we chose to apply, prior to model generation, correction factors reported by McCutchan et al. (2003) for aquatic environments: +0.4 (± 0.17) ‰ for $\delta^{13}C$ and +2.3 (± 0.17) ‰ for $\delta^{15}N$.

RESULTS

Food-source dietary markers

p-POM

During the ES, identification and counting of microalgae at KF (site KF2) revealed a dominance of prymnesiophytes (*Phaeocystis* sp. cells, 66.2%) and diatoms (33.6%) mainly consisting of *Chaetoceros* sp., with very small percentages of dinoflagellates and cryptophyceae. During LS (KF Site), 86.3% of phytoplankton assemblages were composed of nanophytoflagellates, with dinoflagellates (4.5%), *Cryptomonas* sp. (7.8%), and few diatoms (1.4%). In con-

trast, at YS, 100% of identified phytoplankton cells during ES were diatoms, most of them belonging to the genera *Chaetoceros* and *Thalassiosira*. At KF, bulk stable isotope analyses on p-POM revealed mean $\delta^{13}C$ values of −23.1 ± 0.4‰ during ES and −25.3 ± 0.5‰ during LS (Fig. 2). Mean $\delta^{15}N$ values were 4.0 ± 0.2‰ and 6.2 ± 0.3‰ in the 2 seasons, respectively. At YS, p-POM samples during ES revealed a mean $\delta^{13}C$ signature of −25.1 ± 0.1‰ and a mean $\delta^{15}N$ signature of 6.2 ± 0.4‰. At both sites, total saturated FAs (indicators of the state of degradation of organic matter) were major components of total FAs associated with p-POM samples (>69%, see Table S1 in the Supplement at www.int-res.com/articles/suppl/m567p157_supp.pdf). All FA profiles differed among the 3 groups (PERMANOVA $p < 0.001$; pairwise tests, $p < 0.05$). At KF, seasonal variations were mostly attributable to higher values of saturated FAs during LS (16:0, 18:0, and 12:0) and lower mean proportions of 16:1ω7 (indicator of diatom biomass) during LS (0.2 ± 0.2% in LS vs 9.4 ± 3.9% in ES). $\delta^{13}C_{FA}$ of p-POM samples of KF ranged from a minimum of −27.8‰ (20:5ω3) to a maximum of −19.7‰ (16:1ω7), whereas those of YS ranged from −33.9‰ (18:3ω3) to −27.6 ‰ (18:2ω6; Fig. 3).

i-POM

Bulk stable isotopes values for i-POM differed at the 2 sites both for $\delta^{13}C$ and $\delta^{15}N$ (Fig. 2). At KF, mean values were −15.7 ± 1.4‰ for $\delta^{13}C$ and 4.8 ± 0.3‰ for $\delta^{15}N$, whereas at YS they were −28.9 ± 1.1‰ and 2.0 ± 1.7‰, respectively. The FA composition of i-POM differed significantly between sites (PERMANOVA, $p < 0.05$). The average proportions of 16:1ω7 at KF were about twice those at YS (52.0 ± 0.3% vs. 24.1 ± 3.9%, respectively) and a much higher mean percentage of 18:0 was found at YS (0.6 ± 0.0 vs. 24.8 ± 5.9, Table S1). At KF, $\delta^{13}C_{FA}$ of i-POM samples ranged from a minimum of −18.0‰ (20:5ω3) to a maximum of −14.6‰ (16:0), whereas at YS, they ranged from −33.6‰ (18:3ω3) to −26.0‰ (16:0; Fig. 3).

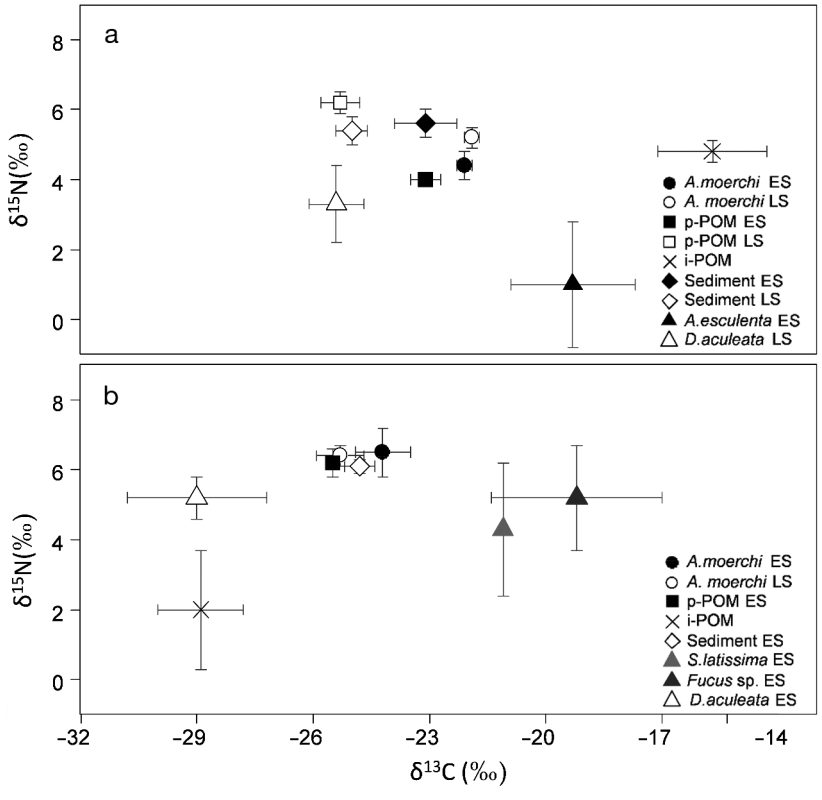

Fig. 2. Mean $\delta^{13}C$ and $\delta^{15}N$ values for (a) Kongsfjorden (KF, Svalbard) and (b) Young Sound (YS, Greenland). i-POM (p-POM): ice-algae (pelagic) particulate organic matter; ES (LS) early (late) season. Error bars are standard deviation; n = 5 for *Astarte moerchi* digestive glands, and n = 3 for sources (including the brown algae *Alaria esculenta*, *Desmarestia aculeata*, and *Saccharina latissima*)

Macroalgae

Bulk stable isotope analyses of brown algae revealed more depleted $\delta^{13}C$ values for *Desmarestia aculeata* (KF: −25.4 ± 0.7‰, YS: −29.0 ± 1.8‰) than in the other 3 species of brown algae (KF: −19.3 ± 1.6‰ for *Alaria esculenta*; YS: −21.1 ± 0.0‰ for *Saccharina latissima* and −19.2 ± 2.2‰ for *Fucus* sp.). $\delta^{15}N$ values ranged from a minimum of −1.1‰ and a maximum of 4.5‰ for the 2 brown algae sampled at KF (*D. aculeata* and *A. esculenta*) and from 2.3 to 6.6‰ for those sampled at YS (*S. latissima, Fucus* sp., and *D. aculeata*; Fig. 2). FA compositions of brown algae are shown in Table S2. The major FAs in samples from both sites were polyunsaturated C_{18} chain (18:2ω6, 18:3ω3, and 18:4ω3) and C_{20} chain (20:5ω3 and 20:4ω6). Monounsaturated FA 18:1ω9 was also abundant (Table S2). At KF, no seasonal variation in FA composition of *A. esculenta* was observed (PERMANOVA, $p > 0.05$). However, differences were evident for 2 FAs: 18:4ω3 presented higher mean percentages in ES (27.5 ± 3.7% vs. 7.7 ±

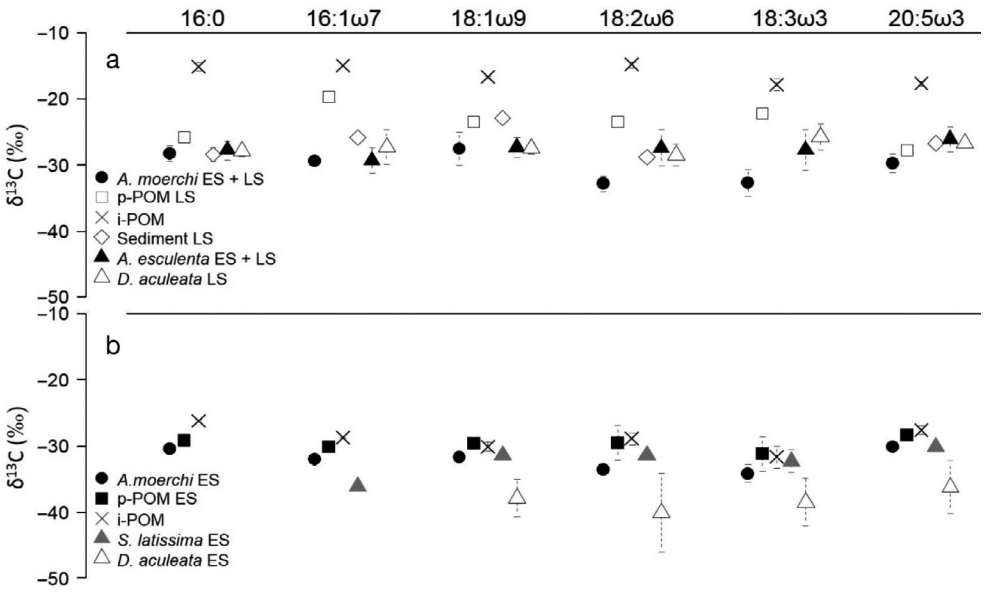

Fig. 3. Mean $\delta^{13}C$ values of individual fatty acids (FAs) for (a) Kongsfjorden (KF, Svalbard) and (b) Young Sound (YS, Greenland). i-POM (p-POM): ice-algae (pelagic) particulate organic matter; ES (LS) early (late) season. Error bars are standard deviation. Three replicates were sent for analysis, but some samples were not concentrated enough to be measurable, so replicates vary between 3 and 1. Full species names are given in Fig. 2

1.6%), and 20:4ω6 had higher mean percentages in LS (18.8 ± 2.8% vs. 6.7 ± 1.6%). For *D. aculeata* FA composition, PERMANOVA showed significant differences between YS and the ES and LS in KF ($p < 0.001$), mainly due to 16:1ω7, 16:0, and 18:4ω3. No seasonal effect was observed at KF (pairwise test, $p > 0.05$). $\delta^{13}C_{FA}$ of brown algae samples ranged from a minimum of −32.8‰ (*A. esculenta*, 18:3ω3) to a maximum of −24.3‰ (*D. aculeata*, 18:3ω3) for KF, and from −46.1‰ (*D. aculeata,* 18:2ω6) to −30.0‰ (*S. latissima,* 20:5ω3; Fig. 3) for YS. At KF, *A. esculenta* from both seasons were analyzed, and, as no seasonal effect was observed, data from ES and LS were pooled.

Sediments

For sediment samples from KF, bulk stable isotope analyses revealed mean $\delta^{13}C$ values of −23.1 ± 0.8‰ in ES and −25.0 ± 0.4‰ in LS. Mean $\delta^{15}N$ values were 5.6 ± 0.4‰ and 5.4 ± 0.4‰ in the 2 seasons, respectively (Fig. 2). At YS, sediment samples revealed a mean $\delta^{13}C$ signature of −24.8 ± 0.4‰ and a mean $\delta^{15}N$ signature of 6.1 ± 0.2‰ (Fig. 2). 16:1ω7, 16:0, and 20:5ω3 were among the most abundant FAs in sediment samples from both sites (Table S3). FA composition differed significantly between treatments (PERMANOVA, $p < 0.001$), with no seasonal effect at KF but with significant differences between ES at YS and LS at KF (pairwise tests, $p < 0.05$), mainly due to 16:1ω7, which had on average higher proportions at YS (30.9 ± 8.3%) than at KF during ES (21.8 ± 1.2%) and LS (11.3 ± 3.0%; Table S3). Values of the 16:1ω7 to 16:0 ratio (frequently used as a diatom indicator) showed the same differences, having an average higher ratio at YS (1.7 ± 0.6) than at KF during ES (1.2 ± 0.2) and LS (0.4 ± 0.2). $\delta^{13}C_{FA}$ of sediment samples from KF ranged from a minimum of −28.4‰ (16:0) to a maximum of −22.2‰ (18:1ω9; Fig. 3).

Dietary markers in *A. moerchi*

$\delta^{13}C$ values for *A. moerchi* ranged from −22.4‰ to −21.6‰ at KF, and from −26.0‰ to −23.1‰ at YS (Fig. 2). Differences between sites were significant, and a significant seasonal effect was observed at YS (Wilcoxon test, $p < 0.05$) but not at KF (Wilcoxon test, $p > 0.05$). For $\delta^{15}N$, values ranged from 3.9 to 5.6‰ at KF and from 5.9 to 7.6‰ at YS. Differences between sites were significant (Wilcoxon test, $p < 0.001$), and a significant seasonal effect was observed at KF (Wilcoxon test, $p < 0.05$) but not at YS (Wilcoxon test, $p > 0.05$). Results from the mixing model for KF and YS showing the relative contributions of sources to *A. moerchi* diet are detailed in Table 2.

A total of 55 FAs were identified in *A. moerchi* digestive glands, and mean percentages (±SD) for each FA are presented in Table S4. The 2 most abun-

Table 2. Results of mixing model, showing the contributions to *Astarte moerchi* diet of 4 sources per site. Contributions are expressed in mean percentages (±SD). Correction factors used for the model were +0.4 (± 0.17) ‰ for $\delta^{13}C$ and + 2.3 (± 0.17) ‰ for $\delta^{15}N$ (McCutchan et al. 2003). KF: Kongsfjorden, YS: Young Sound, ES (LS): early (late) season, i-POM (p-POM): ice-algae (pelagic) particulate organic matter

	Source			
	p-POM	Sediment	*Desmarestia aculeata*	*Alaria esculenta*
KF				
A. moerchi ES	24.1 ± 13.1	14.3 ± 10.6	27.8 ± 10.7	33.7 ± 7.6
A. moerchi LS	14.9 ± 10.3	20 ± 12.2	20.4 ± 11.4	44.7 ± 5.3
YS	p-POM	Sediment	i-POM	*Saccharina latissima*
A. moerchi ES	19 ± 11.3	21.9 ± 11.8	25.8 ± 6.9	33.3 ± 7.6

dant FAs were 20:5ω3 (min. average 20.5 ± 2.4%, max. average 25.9 ± 1.2%) and 16:1ω7 (min. average 5.6 ± 0.6%, max. average 24.6 ± 2.2%). FA composition of digestive glands varied significantly between seasons and sites (PERMANOVA, $p < 0.001$), with an interaction between them (PERMANOVA, $p < 0.01$). Each of the 4 groups had a specific FA composition (pairwise tests, $p < 0.01$). An n-MDS based on a Bray-Curtis similarity matrix using data from digestive glands is shown in Fig. 4. Dissimilarity percentages between FA compositions of each of the 4 groups were determined with SIMPER analysis (Table S5). Inter-site dissimilarities are mostly attributable to contrasting proportions of 16:1ω7, whose contributions are higher than 30% for both ES and LS. Proportions of 22:6ω3 and 18:4ω3 (used in this study as a dinoflagellate and a macroalgal marker, respectively) also contributed to inter-site dissimilarities, with lowest values during both seasons at YS (<3.0% and <1.5%, respectively), and the highest values at KF, where those FAs respectively reached 9.1 ± 0.8% (LS) and 6.4 ± 1.0% (ES; Fig. 5, Table S5). Other FAs contributing to inter-site dissimilarities were 18:1ω9 (highest percentages at KF of ~4%) and 20:5ω3 (highest percentage of 25.9 ± 1.2% during ES at YS). Mean values of the 16:1ω7 to 16:0 ratio (diatom indicator) in *A. moerchi* digestive glands were significantly higher at YS during ES (2.4 ± 0.2) than during LS (1.9 ± 0.4; Fig. 5). At KF, the ratio decreased significantly between ES (1.0 ± 0.2) and LS (0.5 ± 0.1, Kruskal-Wallis test, $p < 0.01$; pairwise Wilcoxon test, $p < 0.05$; Fig. 5). Branched FAs (bacterial markers)

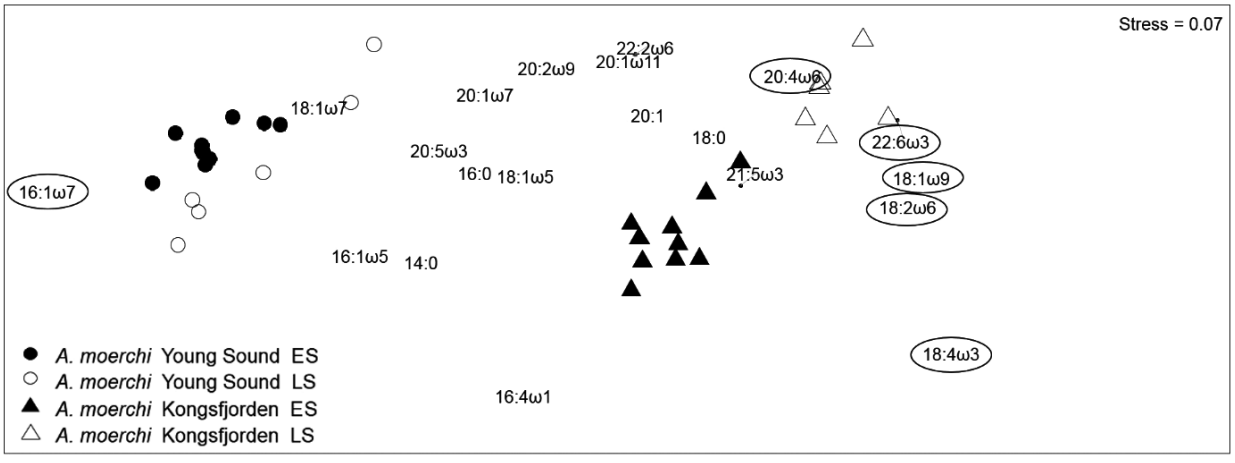

Fig. 4. Nonmetric multidimensional scaling (n-MDS) ordination based on a Bray-Curtis similarity matrix of 55 fatty acids (FAs; %) in *Astarte moerchi* digestive glands. Only FAs >1% are represented in the plot. Circles indicate Young Sound (YS, Greenland) and triangles indicate Kongsfjorden (KF, Svalbard) samples; early (ES) and late season (LS) are represented as filled and open symbols, respectively ($n_{YS\,ES} = 10$; $n_{YS\,LS} = 6$; $n_{KF\,ES} = 10$; $n_{KF\,LS} = 6$). Encircled FAs are those considered as markers in this study; 16:1ω7 (as well as the ratio 16:1ω7 to 16:0) is considered a diatom marker, 22:6ω3 is a dinoflagellate marker, and 18:4ω3, 18:1ω9, 18:2ω6, and 20:4ω6 are macroalgal markers

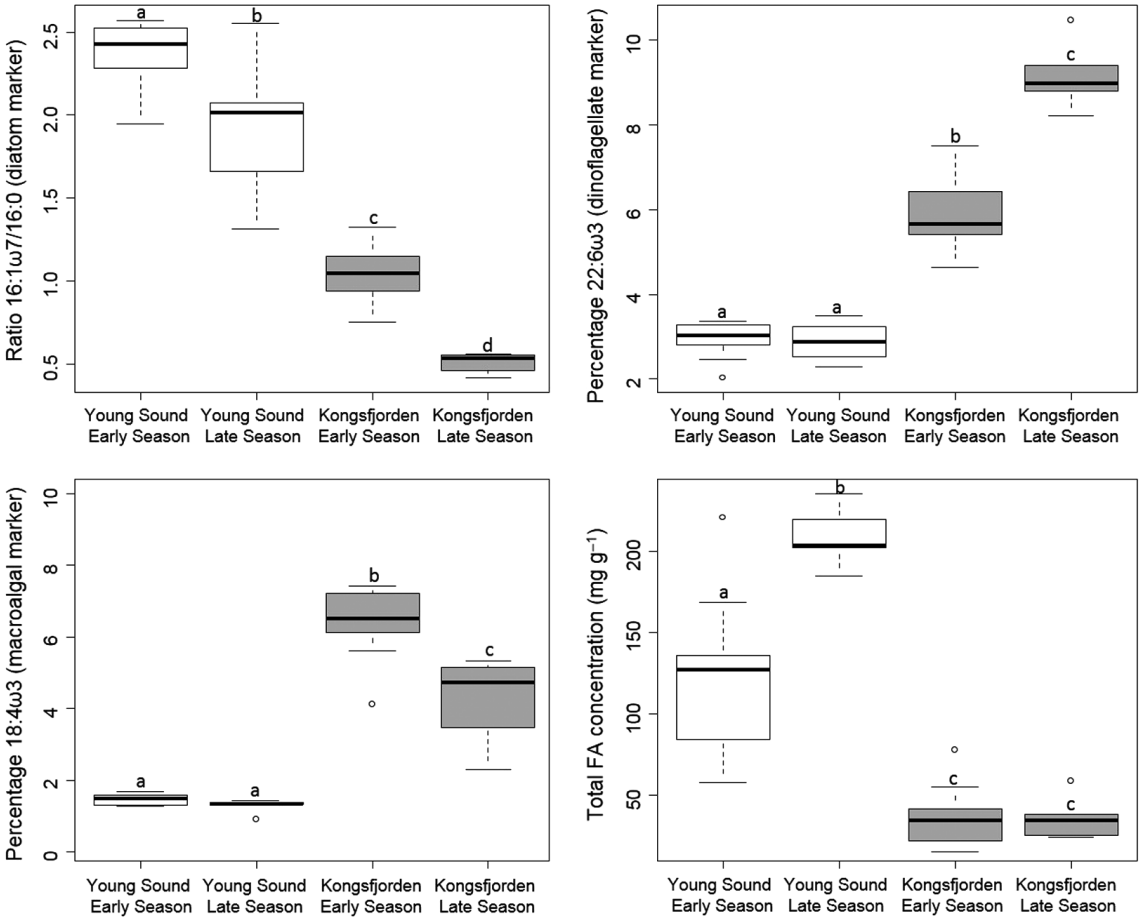

Fig. 5. Fatty acids (FAs) used as markers in this study (ratio of 16:1ω7 to 16:0, percentages of 22:6ω3 and 18:4ω3) and total FA concentrations (mg g^{-1}) in *Astarte moerchi* digestive glands in Young Sound (YS, Greenland, white bars) and Kongsfjorden (KF, Svalbard, gray bars) for 2 time periods, early (ES) and late season (LS; $n_{YS\ ES} = 10$; $n_{YS\ LS} = 6$; $n_{KF\ ES} = 10$; $n_{KF\ LS} = 6$). Differences are significant ($p < 0.05$, Kruskal-Wallis test) and letters above bars indicate differences tested by pairwise comparisons using a Wilcoxon test

were detected in low percentages (minimum 0.6 ± 0.1%, maximum 1.4 ± 0.2%) in *A. moerchi* digestive glands at both sites (Table S4). Total FA concentrations varied significantly between the 2 sites (Wilcoxon test, $p < 0.01$). At YS, concentrations were higher during LS (207.7 ± 17.2 mg g^{-1}) than during ES (123.4 ± 48.3 mg g^{-1}), whereas they were much lower at KF, where no significant seasonal difference was observed and the mean value was 36.5 mg g^{-1} (Kruskal-Wallis test, $p < 0.01$, pairwise Wilcoxon test, $p > 0.05$ for 2 seasons at KF and $p < 0.01$ for other comparisons, Fig. 5).

For *A. moerchi* digestive glands, at both sites, $\delta^{13}C_{FA}$ values ranged from −34.2 ± 1.3‰ (18:3ω3 at YS) to −27.5 ± 3.9‰ (18:1ω9 at KF; Fig. 3). At KF, digestive glands from both seasons were analyzed and, as no seasonal effect was observed, data from ES and LS were pooled.

DISCUSSION

We compared the diet of 2 populations of *Astarte moerchi* living in 2 contrasting Arctic coastal environments. At the sub-Arctic site KF, annual phytoplankton production is estimated to be roughly 3 to 5 times more elevated than at the high-Arctic site YS (35–50 g C m^{-2} vs. 10 g C m^{-2}, respectively; Rysgaard et al. 1999, Hop et al. 2002). As ice cover occurrence is much shorter at KF (<1 mo yr^{-1}) than at YS (9–10 mo yr^{-1}), the productive season is longer at the sub-Arctic site, and the peak of primary production occurs sooner during the year compared to the high-Arctic site (April/May vs. July, respectively; Hop et al. 2002, Jensen et al. 2014). Considering such contrasting trophic conditions between sites, we expected differences in the diet of these 2 populations of the filter-feeding bivalve *A. moerchi*. The

multi-marker approach used in this study revealed that diatoms represent an important fraction of the diet in both populations. However, despite the common feature of diatom contribution, several dissimilarities could be observed in *A. moerchi* diet at the 2 sites, demonstrating the trophic plasticity of this bivalve species.

Diatom contribution to *A. moerchi* diet at YS and KF

FA markers suggest diatom contribution to *A. moerchi*

High contributions of 16:1ω7 and 20:5ω3 were found in the total FA composition of *A. moerchi* digestive glands. Although 20:5ω3 can also potentially be synthesized de novo by bivalves (Monroig et al. 2013), this FA is generally used as a diatom marker (Dalsgaard et al. 2003). Concomitantly, large proportions of 16:1ω7 and a value >1 of the 16:1ω7 to 16:0 ratio are considered to be reliable indicators of a high contribution of diatoms in the environment (sediments, POM) and in invertebrate tissues (Reuss & Poulsen 2002, Dalsgaard et al. 2003). In the present study, high contributions of 20:5ω3 and 16:1ω7 measured in *A. moerchi* digestive glands from YS, as well as a ratio of 16:1ω7 to 16:0 of ~2, suggest that diatoms make up an important part of the diet of this bivalve both in ES and LS. At the sub-Arctic site KF, FA profiles and 16:1ω7 to 16:0 ratios suggest that the contribution of diatoms to the diet of *A. moerchi* is less relevant than at YS, especially during the LS. At both sites, diatoms assimilated by *A. moerchi* can have a pelagic, benthic, or sympagic origin. Relative contributions of these sources can be inferred from analyses of dietary markers in food sources: p-POM, sediments, and i-POM respectively.

Pelagic and benthic contribution

At the high-Arctic site YS, both phytoplanktonic and microphytobenthic assemblages are dominated by diatoms. The genus *Chaetoceros* is common in pelagic assemblages (Krawczyk et al. 2015), and the genera *Pinnularia*, *Nitzschia*, and *Navicula* are widespread in microalgal mats (Glud et al. 2002). It is estimated that for water depths <30 m, net benthic photosynthesis is almost 7 times higher than gross photosynthetic rates of the pelagic community (Glud et al. 2002). At the sub-Arctic site KF, diatoms dominate the pelagic compartment during spring (along with the prymnesiophyte *Phaeocystis pouchetii*; Hop et al. 2002, Hodal et al. 2012) and are abundant in microphytobenthos which, in shallow waters, has a production rate comparable to that of pelagic production (Woelfel et al. 2010).

In our study, taxonomic identification confirmed that the composition of pelagic assemblages in the year of sampling was similar to what is reported in literature. The contribution of pelagic and benthic organic matter to the diet of *A. moerchi* can be inferred from the comparison of isotopic signatures of those consumers with those of p-POM and sediments. p-POM signatures include those of living phytoplanktonic cells and detrital material (>0.7 µm) in the water column, and sediment signatures include those of living microphytobenthos and deposited detritus. Especially in p-POM samples, elevated percentages of saturated FAs and low amounts of polyunsaturated FAs are a common feature in oligotrophic waters and suggest the presence of degraded organic matter (Fileman et al. 1998). Although this decaying process of organic matter was certainly concomitant with high microbial activity, percentages of branched FAs are low in *A. moerchi* digestive glands at both sites, suggesting a low ingestion of bacterial sources.

Considering fractionation factors of +0.4‰ for $\delta^{13}C$ and +2.3‰ for $\delta^{15}N$ (McCutchan et al. 2003), our bulk isotope results indicate that at the 2 sites, both p-POM and sediment contributions are relevant to the diet of *A. moerchi*. $\delta^{13}C$ signatures of specific FAs abundant in diatoms, like 16:1ω7 and 20:5ω3, can also allow us to infer lipid sources of *A. moerchi*. For marine environments, previous literature on FA-specific stable isotope analysis showed that FAs in consumers are depleted in ^{13}C (and not enriched, as for carbon bulk isotopes) compared to FAs of their food source (Veefkind 2003, Bec et al. 2011, Gladyshev et al. 2012). This fractionation factor was estimated to be 3.17‰ by Gladyshev et al. (2014). Even if caution is exercised in applying such standard fractionations factors, which are still a subject of debate in trophic ecology (del Rio et al. 2009, Budge et al. 2011), some conclusions can be drawn from our data. At YS, p-POM appears to be a probable source of 16:1ω7 and 20:5ω3 for *A. moerchi*. At KF, the assimilated 16:1ω7 could originate from benthic organic matter and 20:5ω3 from pelagic and benthic organic matter. Globally, we can infer from our isotopic results that pelagic organic matter, as well as resuspended benthic organic matter, are probable food sources for *A. moerchi* at both sites.

We can thus suggest that organic matter from phytoplankton and microphytobenthos (dominated by diatoms at both sites) contribute to the diet of these bivalves.

Sympagic contribution

At YS, diatoms dominate sympagic production (Glud et al. 2007), which is considered to be lower than in other similar systems, possibly due to inadequate light conditions below the snow cover and/or freshwater inputs that would inhibit ice-algae production (Rysgaard & Sejr 2007). At KF, ice algae are also mainly diatoms, but as ice cover influence is low (and has been decreasing since 2006, Lalande et al. 2016), their development is limited at this site.

In our study, isotopic signatures of i-POM from KF were relatively enriched (around −15‰), both for bulk isotopes and for specific FAs. These signatures, differing from p-POM, allow the discrimination of both sources and clearly exclude i-POM contribution to the diet of *A. moerchi* at KF. By contrast, at YS, the isotopic signature is relatively depleted (around −29‰), and interpreting the data is not obvious. Bulk isotope results suggest that i-POM is a potential source for *A. moerchi*, with a contribution, as estimated by the mixing model, of 25.8 ± 6.9%. For specific FAs, values are similar for i-POM and p-POM samples: for example, 16:1ω7 and 20:5ω3 could be assimilated by bivalves both from sympagic or pelagic organic matter.

i-POM isotopic signatures differ strongly between the 2 fjords, reflecting differences in the structure and the dynamics of sympagic environments, which are highly dynamic and complex systems. As isotopic composition can be influenced by several factors like ice porosity and freshwater intrusions (Thomas et al. 2009), the isotopic values of sea-ice samples are extremely variable at a regional scale and are also related to the timing of sampling. Moreover, the rates of isotopic carbon and nitrogen assimilation by consumers may vary according to species-specific turnover rates (Weems et al. 2012). Isotopic composition of individual markers as individual FAs could allow the detection of short-term food switches more efficiently than bulk stable isotopes (McMahon et al. 2006). Further development of trophic tools, such as compound-specific stable isotope analyses, and sampling of ice algae at different times of the productive season will be essential to assess contributions of sympagic production to benthic consumers in Arctic ecosystems.

Differences in food sources and FA storage suggest dietary plasticity of *A. moerchi*

Diversified *A. moerchi* diet at KF

Whereas diatoms at both high- and sub-Arctic fjords contribute to *A. moerchi* diets, the KF population exhibited a much more diversified and seasonally variable diet, with contributions of dinoflagellates and macroalgal detritus.

Dinoflagellate contribution

At KF, during September, the phytoplanktonic pelagic biomass decreases and is dominated by heterotrophic dinoflagellates, copepods, ciliates, and nauplii (Hop et al. 2002, Bhaskar et al. 2016). Taxonomic identification confirmed a high abundance of nanophytoflagellates in the water column in September during our sampling. The seasonal variability in FA composition of *A. moerchi* sampled at KF was due to higher contributions of 22:6ω3 in the digestive glands during LS. Because 22:6ω3 is often considered a dinoflagellate marker (Dalsgaard et al. 2003, Kelly & Scheibling 2012), we hypothesize that its autumnal increase reflects higher abundances of pelagic dinoflagellates. Percentages of 22:6ω3 in *A. moerchi* digestive glands were significantly lower at YS than at KF, suggesting that dinoflagellate contribution is negligible at the high-Arctic site.

Macroalgal contribution

It is now well accepted that a large fraction of macroalgal primary production is released as POM (Buchholz & Wiencke 2016) and can thus be assimilated by filter-feeders (Wessels et al. 2004, Perez et al. 2013). Macroalgal assemblages are known to contribute to primary production both at YS and KF (Hop et al. 2002, Krause-Jensen et al. 2007, Bartsch et al. 2016). Results from FA analyses suggest that macroalgal detritus could be assimilated by *A. moerchi* especially at the sub-Arctic site KF because of higher proportions of 18:4ω3, 18:1ω9, 18:2ω6, and 20:4ω6 in the digestive glands. Those FAs are often considered as macroalgal markers (Dalsgaard et al. 2003, Kelly & Scheibling 2012) and were present in the Pheaophyceae species we analyzed. $\delta^{13}C_{FA}$ results confirm that, at KF, brown algae (both *Alaria esculenta* and *Desmarestia aculeata*) are sources of some FAs for *A. moerchi*. At YS, $\delta^{13}C_{FA}$ values

showed that only *Saccharina latissima*, and not *D. aculeata*, is a source of FAs assimilated by *A. moerchi*. Results from the mixing model on bulk stable isotopes confirmed that *S. latissima* contributes to *A. moerchi* diet at YS and also showed that the macroalgal contribution is relevant at KF, especially for *A. esculenta*.

Differences in total FA concentrations

FA concentrations in the digestive glands of *A. moerchi* were higher in the high-Arctic compared to sub-Arctic fjord, particularly during LS. For bivalves, the digestive gland plays a key role in energy storage for carbohydrates (mainly as glycogen) and lipids (Barber & Blake 1981, Napolitano & Ackman 1992, Gosling 2003). Energy reserves are generally accumulated during summer and are used for gametogenesis during autumn and winter (Gosling 2003). The observed differences in FA concentrations could originate from differences in food availability between the 2 fjords and reflect variations due to a local acclimatization in energy storage. For example, the longer ice-cover season at YS could force *A. moerchi* to accumulate more lipid reserves in its digestive gland compared to KF. Validation of such an energy storage hypothesis (to be tested by experimental work on *A. moerchi*) would confirm the plasticity of *A. moerchi* to acclimatize, through physiological responses, to different trophic conditions.

CONCLUSIONS

The comparison between the high-Arctic and sub-Arctic fjord suggest that *A. moerchi* assimilates mainly diatoms but can also adjust its diet to several other food sources, including dinoflagellates and macroalgal detritus. Moreover, inter-site differences in FA concentrations in digestive glands could be related to plastic responses of the bivalve's energy storage ability. Although trophic plasticity suggests a high potential for *A. moerchi* populations to endure future climate changes in primary production regimes, consequences to population dynamics are difficult to predict. Other ecological processes such as reproduction/recruitment dynamics or interspecific interactions (e.g. newly introduced boreal species extending their distribution area) should be studied from the perspective of investigating the impacts of climate change on Arctic biological communities. Our study also shows that benthic primary producers (macroalgae and microphytobenthos) significantly contribute as food sources for *A. moerchi*, especially in sub-Arctic areas. Environmental factors influencing the dynamics of benthic primary producers, particularly increased turbidity (limiting light availability), would have major consequences on *A. moerchi* and other filter-feeding species. In such a scenario, filter-feeders would not only have to endure increased inorganic input by adjusting filtration activity, but would also need to respond to a decreased abundance of trophic sources. The general relevance of macroalgal detritus and microphytobenthos to benthic consumers in Arctic coastal environments has recently been highlighted (Glud et al. 2002, Renaud et al. 2015a, Attard et al. 2016, Gaillard et al. 2017). In Arctic studies, much research has focused on the relative contribution of phytoplankton and ice algae to show the importance of 'pelagic–benthic coupling,' usually intended to describe the export of organic matter of pelagic primary producers to benthic consumers (Renaud et al. 2015a). For shallow-water Arctic systems, this paradigm may be less pertinent, and trophic studies should not neglect benthic sources.

Acknowledgements. We thank E. Fransen, H. Spanggaard Munch, and the staff of the AWIPEV station in Ny-Alesund for their technical support; J. M. Mortillaro and N. Thiney for their help at the Muséum National d'Histoire Naturelle (MNHN); and B. Beker for performing phytoplankton identification analysis. Funding was provided by the Fondation TOTAL and the Institut polaire français Paul Emile Victor (IPEV) through the B.B. Polar Project, the Agence Nationale de la Recherche and the IPEV as part of the Effect of Climate on the Arctic Benthos (ECOTAB) project (Ref: ANR-11-PDOC-0018), and to the French National program EC2CO2 DRIL supervised by the CNRS-INSU for the Sclerarctic project. We are grateful to the École Normale Supérieure/MNHN for providing a PhD grant to S.D.C., and to MNHN for a 3 yr visiting professorship at ISMER-UQAR to F.O. This study is a contribution to the research programs of Arctic Science Partnership and Québec-Océan. This work was performed in the framework of the International Laboratory BeBEST (LIA-INEE/UQAR) funded by the Institut des Sciences de la Mer de Rimouski (UQAR, Quebec) and the Institut Environnement Ecologie (CNRS, France). J. Coston-Guarini (EBLab) contributed to English language editing. We are grateful to 3 anonymous reviewers for fruitful comments on the first version of the manuscript.

LITERATURE CITED

Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth

Attard KM, Hancke K, Sejr MK, Glud RN (2016) Benthic primary production and mineralization in a High Arctic fjord: *in situ* assessments by aquatic eddy covariance. Mar Ecol Prog Ser 554:35–50

Barber B, Blake N (1981) Energy storage and utilization in relation to gametogenesis in *Argopecten irradians concentricus* (Say). J Exp Mar Biol Ecol 52:121–134

Bartsch I, Paar M, Fredriksen S, Schwanitz M, Daniel C, Hop H, Wiencke C (2016) Changes in kelp forest biomass and depth distribution at Kongsfjorden, Svalbard, between 1996–98 and 2012–2014 reflect Arctic warming. Polar Biol 39:2021–2036

Bec A, Perga ME, Koussoroplis A, Bardoux G, Desvilettes C, Bourdier G, Mariotti A (2011) Assessing the reliability of fatty acid-specific stable isotope analysis for trophic studies. Methods Ecol Evol 2:651–659

Bendtsen J, Gustafsson K, Rysgaard S, Vang T (2007) Physical conditions, dynamics and model simulations during the ice-free period of the Young Sound/Tyrolerfjord system. Medd Grønland Biosci 58:45–59

Bhaskar JT, Tripathy SC, Sabu P, Laluraj CM, Rajan S (2016) Variation of phytoplankton assemblages of Kongsfjorden in early autumn 2012: a microscopic and pigment ratio-based assessment. Environ Monit Assess 188:224

Blagoev GA, Hebert PDN, Adamowicz SJ, Robinson EA (2009) Prospects for using DNA barcoding to identify spiders in species-rich genera. ZooKeys 16:27–46

Bligh EG, Dyer WJ (1959) A rapid method of total lipid extraction and purification. Can J Biochem Physiol 37: 911–917

Born EW, Rysgaard S, Ehlmé G, Sejr M (2003) Underwater observations of foraging free-living Atlantic walruses (*Odobenus rosmarus rosmarus*) and estimates of their food consumption. Polar Biol 26:348–357

Buchholz CM, Wiencke C (2016) Working on a baseline for the Kongsfjorden food web: production and properties of macroalgal particulate organic matter (POM). Polar Biol 39:2053–2064

Budge SM, Iverson SJ, Koopman HN (2006) Studying trophic ecology in marine ecosystems using fatty acids: a primer on analysis and interpretation. Mar Mamm Sci 22:759–801

Budge SM, Wooller MJ, Springer AM, Iverson SJ, McRoy CP, Divoky GJ (2008) Tracing carbon flow in an Arctic marine food web using fatty acid-stable isotope analysis. Oecologia 157:117–129

Budge SM, Wang SW, Hollmén TE, Wooller MJ (2011) Carbon isotopic fractionation in eider adipose tissue varies with fatty acid structure: implications for trophic studies. J Exp Biol 214:3790–3800

Carroll ML, Ambrose WG Jr, Levin BS, Locke WLV, Henkes GA, Hop H, Renaud PE (2011) Pan-Svalbard growth rate variability and environmental regulation in the Arctic bivalve *Serripes groenlandicus*. J Mar Syst 88:239–251

Clarke KR (1993) Nonparametric multivariate analyses of changes in community structure. Aust J Ecol 18:117–143

Clarke K, Gorley R (2006) PRIMER v6: user manual/tutorial. PRIMER-E, Plymouth

Collins RA, Cruickshank RH (2013) The seven deadly sins of DNA barcoding. Mol Ecol Resour 13:969–975

Cottier FR, Nilsen F, Inall ME, Gerland S, Tverberg V, Svendsen H (2007) Wintertime warming of an Arctic shelf in response to large-scale atmospheric circulation. Geophys Res Lett 34:L10607

Dalsgaard J, St John M, Kattner G, Muller-Navarra D, Hagen W (2003) Fatty acid trophic markers in the pelagic marine environment. Adv Mar Biol 46:225–340

del Rio CM, Wolf N, Carleton SA, Gannes LZ (2009) Isotopic ecology ten years after a call for more laboratory experiments. Biol Rev Camb Philos Soc 84:91–111

Dunbar M (1968) Ecological development in polar regions. A study in evolution. Prentice-Hall, Englewood Cliffs, NJ

Ezgeta-Balic D, Najdek M, Peharda M, Blazina M (2012) Seasonal fatty acid profile analysis to trace origin of food sources of four commercially important bivalves. Aquaculture 334-337:89–100

Fileman TW, Pond DW, Barlow RG, Mantoura RFC (1998) Vertical profiles of pigments, fatty acids and amino acids: evidence for undegraded diatomaceous material sedimenting to the deep ocean in the Bellingshausen Sea, Antarctica. Deep-Sea Res I 45:333–346

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Mol Mar Biol Biotechnol 3:294–299

Fry B (2006) Stable isotope ecology. Springer, New York, NY

Gaillard B (2016) Utilisation des bivalves filtreurs pour le suivi du couplage pélago-benthique en Arctique. PhD thesis, Université de Québec à Rimouski

Gaillard B, Meziane T, Tremblay R, Archambault P, Layton KKS, Martel AL, Olivier F (2015) Dietary tracers in *Bathyarca glacialis* from contrasting trophic regions in the Canadian Arctic. Mar Ecol Prog Ser 536:175–186

Gaillard B, Meziane T, Tremblay R, Archambault P and others (2017) Food resources of the bivalve *Astarte elliptica* in a sub-Arctic fjord: a multi-biomarker approach. Mar Ecol Prog Ser 567:139–156

Gladyshev MI, Sushchik NN, Kalachova GS, Makhutova ON (2012) Stable isotope composition of fatty acids in organisms of different trophic levels in the Yenisei River. PLOS ONE 7:e34059

Gladyshev MI, Sushchik NN, Makhutova ON, Kalachova GS (2014) Trophic fractionation of isotope composition of polyunsaturated fatty acids in the trophic chain of a river ecosystem. Dokl Biochem Biophys 454:4–5

Glud RN, Kühl M, Wenzhöfer F, Rysgaard S (2002) Benthic diatoms of a high Arctic fjord (Young Sound, NE Greenland): importance for ecosystem primary production. Mar Ecol Prog Ser 238:15–29

Glud RN, Rysgaard S, Kühl M, Hansen JW (2007) The sea ice in Young Sound: implications for carbon cycling. Medd Grønland Biosci 58:62–85

Gosling E (2003) Bivalve molluscs. Biology, ecology and culture. Fishing News Books, Blackwell Publishing, Oxford

Graeve M, Kattner G, Piepenburg D (1997) Lipids in Arctic benthos: Does the fatty acid and alcohol composition reflect feeding and trophic interactions? Polar Biol 18: 53–61

Graham C, Oxtoby L, Wang SW, Budge SM, Wooller MJ (2014) Sourcing fatty acids to juvenile polar cod (*Boreogadus saida*) in the Beaufort Sea using compound-specific stable carbon isotope analyses. Polar Biol 37: 697–705

Gusev AA, Rudinskaya LV (2014) Shell form, growth, and production of *Astarte borealis* (Schumacher, 1817) (Astartidae, Bivalvia) in the southeastern Baltic Sea. Oceanology 54:458–464

Hegseth EN (1998) Primary production of the northern Barents Sea. Polar Res 17:113–123

Hegseth EN, Tverberg V (2013) Effect of Atlantic water inflow on timing of the phytoplankton spring bloom in a high Arctic fjord (Kongsfjorden, Svalbard). J Mar Syst 113-114:94–105

Hodal H, Falk-Petersen S, Hop H, Kristiansen S, Reigstad M (2012) Spring bloom dynamics in Kongsfjorden, Svalbard: nutrients, phytoplankton, protozoans and primary production. Polar Biol 35:191–203

Hop H, Pearson T, Hegseth EN, Kovacs KM and others (2002) The marine ecosystem of Kongsfjorden, Svalbard. Polar Res 21:167–208

Iverson SJ (2009) Tracing aquatic food webs using fatty acids: from qualitative indicators to quantitative determination. In: Arts MT, Brett MT, Kainz M (eds) Lipids in aquatic ecosystems. Springer, New York, NY, p 281–308

Jensen L, Christensen T, Schmidt NM (2014) Zackenberg Ecological Research Operations, 19th Annual Report 2013. Aarhus University, DCE – Danish Centre for Environment and Energy, Roskilde

Kedra M, Moritz C, Choy ES, David C and others (2015) Status and trends in the structure of Arctic benthic food webs. Polar Res 34:23775

Kelly JR, Scheibling RE (2012) Fatty acids as dietary tracers in benthic food webs. Mar Ecol Prog Ser 446:1–22

Krause-Jensen D, Kühl M, Christensen P, Borum J (2007) Benthic primary production in Young Sound, Northeast Greenland. Medd Grønland Biosci 58:160–173

Krause-Jensen D, Marba N, Olesen B, Sejr MK and others (2012) Seasonal sea ice cover as principal driver of spatial and temporal variation in depth extension and annual production of kelp in Greenland. Glob Change Biol 18:2981–2994

Krawczyk DW, Arendt KE, Juul-Pedersen T, Sejr MK, Blicher ME, Jakobsen HH (2015) Spatial and temporal distribution of planktonic protists in the East Greenland fjord and offshore waters. Mar Ecol Prog Ser 538:99–116

Lalande C, Moriceau B, Leynaert A, Morata N (2016) Spatial and temporal variability in export fluxes of biogenic matter in Kongsfjorden. Polar Biol 39:1725–1738

Lee CE (2000) Global phylogeography of a cryptic copepod species complex and reproductive isolation between genetically proximate 'populations'. Evolution 54:2014–2027

Legezynska J, Kedra M, Walkusz W (2014) Identifying trophic relationships within the high Arctic benthic community: How much can fatty acids tell? Mar Biol 161: 821–836

Leu E, Soreide JE, Hessen DO, Falk-Petersen S, Berge J (2011) Consequences of changing sea-ice cover for primary and secondary producers in the European Arctic shelf seas: timing, quantity, and quality. Prog Oceanogr 90:18–32

Lorrain A, Savoye N, Chauvaud L, Paulet YM, Naulet N (2003) Decarbonation and preservation method for the analysis of organic C and N contents and stable isotope ratios of low-carbonated suspended particulate material. Anal Chim Acta 491:125–133

McCutchan JH, Lewis WM, Kendall C, McGrath CC (2003) Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102:378–390

McMahon KW, Ambrose WG Jr, Johnson BJ, Sun MY, Lopez GR, Clough LM, Carroll ML (2006) Benthic community response to ice algae and phytoplankton in Ny Ålesund, Svalbard. Mar Ecol Prog Ser 310:1–14

Meziane T, Tsuchiya M (2002) Organic matter in a subtropical mangrove-estuary subjected to wastewater discharge: origin and utilisation by two macrozoobenthic species. J Sea Res 47:1–11

Monroig O, Tocher DR, Navarro JC (2013) Biosynthesis of polyunsaturated fatty acids in marine invertebrates: recent advances in molecular mechanisms. Mar Drugs 11:3998–4018

Mortillaro JM, Abril G, Moreira-Turcq P, Sobrinho RL, Perez M, Meziane T (2011) Fatty acid and stable isotope ($\delta^{13}C$, $\delta^{15}N$) signatures of particulate organic matter in the lower Amazon River: seasonal contrasts and connectivity between floodplain lakes and the mainstem. Org Geochem 42:1159–1168

Napolitano GE, Ackman RG (1992) Anatomical distributions and temporal variations of lipid classes in sea scallops *Placopecten magellanicus* (Gmelin) from Georges Bank (Nova Scotia). Comp Biochem Physiol B Biochem Mol Biol 103:645–650

Oxtoby LE, Budge SM, Iken K, O'Brien DM, Wooller MJ (2016) Feeding ecologies of key bivalve and polychaete species in the Bering Sea as elucidated by fatty acid and compound-specific stable isotope analyses. Mar Ecol Prog Ser 557:161–175

Paar M, Voronkov A, Hop H, Brey T and others (2016) Temporal shift in biomass and production of macrozoobenthos in the macroalgal belt at Hansneset, Kongsfjorden, after 15 years. Polar Biol 39:2065–2076

Parnell AC, Inger R, Bearhop S, Jackson AL (2010) Source partitioning using stable isotopes: coping with too much variation. PLOS ONE 5:e9672

Paulet YM, Lorrain A, Richard J, Pouvreau S (2006) Experimental shift in diet $\delta^{13}C$: a potential tool for ecophysiological studies in marine bivalves. Org Geochem 37: 1359–1370

Perez V, Olivier F, Tremblay R, Neumeier U, Thebault J, Chauvaud L, Meziane T (2013) Trophic resources of the bivalve, *Venus verrucosa*, in the Chausey archipelago (Normandy, France) determined by stable isotopes and fatty acids. Aquat Living Resour 26:229–239

Petersen GH (2000) Studies on some Arctic and Baltic *Astarte* species (Bivalvia, Mollusca). Medd Grønland Biosci 52:1–71

Peterson B, Fry B (1987) Stable isotopes in ecosystem studies. Annu Rev Ecol Syst 18:293–320

Piepenburg D, Archambault P, Ambrose WG Jr, Blanchard AL and others (2011) Towards a pan-Arctic inventory of the species diversity of the macro- and megabenthic fauna of the Arctic shelf seas. Mar Biodivers 41:51–70

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703–718

R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Renaud PE, Tessmann M, Evenset A, Christensen GN (2011) Benthic food-web structure of an Arctic fjord (Kongsfjorden, Svalbard). Mar Biol Res 7:13–26

Renaud PE, Løkken TS, Jørgensen LL, Berge J, Johnson BJ (2015a) Macroalgal detritus and food-web subsidies along an Arctic fjord depth-gradient. Front Mar Sci 2:1–15

Renaud PE, Sejr MK, Bluhm BA, Sirenko B, Ellingsen IH (2015b) The future of Arctic benthos: expansion, invasion, and biodiversity. Prog Oceanogr 139:244–257

Reuss N, Poulsen LK (2002) Evaluation of fatty acids as biomarkers for a natural plankton community. A field study of a spring bloom and a post-bloom period off West Greenland. Mar Biol 141:423–434

Rysgaard S, Sejr MK (2007) Vertical flux of particulate organic matter in a High Arctic fjord: relative importance

of terrestrial and marine sources. Medd Grønland Biosci 58:110–119

Rysgaard S, Thamdrup B, Risgaard-Petersen N, Fossing H, Berg P, Christensen PB, Dalsgaard T (1998) Seasonal carbon and nutrient mineralization in a high-Arctic coastal marine sediment, Young Sound, Northeast Greenland. Mar Ecol Prog Ser 175:261–276

Rysgaard S, Nielsen TG, Hansen BW (1999) Seasonal variation in nutrients, pelagic primary production and grazing in a high-Arctic coastal marine ecosystem, Young Sound, Northeast Greenland. Mar Ecol Prog Ser 179:13–25

Schomburg G (1987) Gaschromatographie Grundlagen, Praxis und Kapillartechnik, 2nd edn. Wiley, VCH, Weinheim

Sejr MK, Blicher ME, Rysgaard S (2009) Sea ice cover affects inter-annual and geographic variation in growth of the Arctic cockle *Clinocardium ciliatum* (Bivalvia) in Greenland. Mar Ecol Prog Ser 389:149–158

Soreide JE, Hop H, Carroll ML, Falk-Petersen S, Hegseth EN (2006) Seasonal food web structures and sympagic-pelagic coupling in the European Arctic revealed by stable isotopes and a two-source food web model. Prog Oceanogr 71:59–87

Soreide JE, Carroll ML, Hop H, Ambrose WG, Hegseth EN, Falk-Petersen S (2013) Sympagic-pelagic-benthic coupling in Arctic and Atlantic waters around Svalbard revealed by stable isotopic and fatty acid tracers. Mar Biol Res 9:831–850

Svendsen H, Beszczynska-Moller A, Hagen JO, Lefauconnier B and others (2002) The physical environment of Kongsfjorden-Krossfjorden, an Arctic fjord system in Svalbard. Polar Res 21:133–166

Tamura K, Stecher G, Peterson D, Filipski A, Kumar S (2013) MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. Mol Biol Evol 30:2725–2729

Thomas D, Papadimitriou S, Michel C (2009) Biogeochemistry of sea ice. In: Thomas D, Dieckmann G (eds) Sea ice. Wiley, Hoboken, NJ, p 425–467

Veefkind RJ (2003) Carbon isotope ratios and composition of fatty acids: tags and trophic markers of pelagic organisms. PhD thesis, University of Victoria

Wang SW, Budge SM, Gradinger RR, Iken K, Wooller MJ (2014) Fatty acid and stable isotope characteristics of sea ice and pelagic particulate organic matter in the Bering Sea: tools for estimating sea ice algal contribution to Arctic food web production. Oecologia 174:699–712

Wang SW, Budge SM, Iken K, Gradinger RR, Springer AM, Wooller MJ (2015) Importance of sympagic production to Bering Sea zooplankton as revealed from fatty acid-carbon stable isotope analyses. Mar Ecol Prog Ser 518: 31–50

Wang SW, Springer AM, Budge SM, Horstmann L, Quakenbush LT, Wooller MJ (2016) Carbon sources and trophic relationships of ice seals during recent environmental shifts in the Bering Sea. Ecol Appl 26:830–845

Weems J, Iken K, Gradinger R, Wooller MJ (2012) Carbon and nitrogen assimilation in the Bering Sea clams *Nuculana radiata* and *Macoma moesta*. J Exp Mar Biol Ecol 430-431:32–42

Weslawski JM, Wiktor J, Kotwicki L (2010) Increase in biodiversity in the Arctic rocky littoral, Sorlappland, Svalbard, after 20 years of climate warming. Mar Biodivers 40:123–130

Wessels H, Hagen W, Wiencke C, Karsten U (2004) Trophic interactions between macroalgae and herbivores from Kongsfjorden (Svalbard) In: Wiencke C (ed) The coastal ecosystem of Kongsfjorden, Svalbard. Synopsis of biological research performed at the Koldewey Station in the years 1991–2003. Ber Polar-Meeresforsch 492: 63–72

Woelfel J, Schumann R, Peine F, Flohr A and others (2010) Microphytobenthos of Arctic Kongsfjorden (Svalbard, Norway): biomass and potential primary production along the shore line. Polar Biol 33:1239–1253

Zettler ML (2002) Ecological and morphological features of the bivalve *Astarte borealis* (Schumacher, 1817) in the Baltic Sea near its geographical range. J Shellfish Res 21: 33–40

Editorial responsibility: James McClintock, Birmingham, Alabama, USA

Submitted: May 30, 2016; Accepted: December 22, 2016
Proofs received from author(s): February 23, 2017