Seasonal trophic linkages in Arctic marine invertebrates assessed via fatty acids and compound-specific stable isotopes

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Abstract. Climate change is having profound impacts on Arctic ecosystems with important implications for coastal productivity and food web dynamics. We investigated seasonal variations in resource use of 16 invertebrate taxa in lagoon ecosystems along the Alaska Beaufort Sea coast using a combination of fatty acid (FA) biomarkers, bulk stable carbon isotope measurements of whole animals, and compound-specific stable carbon isotope measurements of total lipid extracts and individual FAs. Invertebrates were collected during full-ice cover (April), ice breakup (June), and open water (August) periods. Amphipods (Onisimus glacialis) had higher proportions of 18:2n-6 and 18:3n-3 FAs in April than in the other months. These elevated markers were accompanied by relatively low bulk and 18:2n-6 δ13C values, indicating proportionally higher contributions from terrestrial/freshwater sources in April. A wider range of invertebrates examined during June and August showed increases in algae-specific markers and higher proportions of essential FAs (e.g., 22:6n-3 [docosahexaenoic acid] and 20:5n-3 [eicosapentaenoic acid]) later in the summer. There were also marked differences in FA characteristics among invertebrates that highlighted differential feeding modes. For example, proportions of bacterial FAs were generally higher in deposit-feeding invertebrates than in suspension feeders. These results highlight the current role of diverse carbon sources to Arctic coastal food webs, which may change with future warming.

Key words: Alaska; Arctic; Beaufort Sea; fatty acids; seasonal; Special Feature: Biomarkers in Trophic Ecology; stable isotopes; zooplankton.

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INTRODUCTION

Current observations in the Arctic show that seasonal patterns in the environment, including seasonality of terrestrial runoff and ocean ice cover, are shifting due to climate change (Carmack et al. 2006, White et al. 2007). These changes may lead to shifts in carbon cycling and ecosystem productivity. It was originally thought that terrestrial organic carbon (tOC) is mostly refractory and not an important food source for marine consumers in the Arctic (e.g., Schell 1983, Dittmar and Kattner 2003). However, new evidence has shown that the tOC delivered by Arctic rivers during the spring freshet is a relatively labile carbon source that may be important for microbial and metazoan communities within coastal waters (Holmes et al. 2008,Letscher et al. 2011, Alling et al. 2012).
Coastal lagoons and estuaries in the Beaufort Sea are vital habitats for many organisms including many species of migratory birds (Brown 2006) and fishes (Arctic cisco and Arctic cod), which feed primarily on epibenthic fauna (polychaetes, mysids, amphipods) that flourish in coastal waters (Dunton et al. 2006). Using stable isotope (SI) analysis, previous work by Dunton et al. (2012) demonstrated the importance of terrestrial carbon inputs as summer food resources for coastal metazoan communities in the Alaskan Beaufort Sea. Specifically, stable carbon and nitrogen isotope ratios of benthic and epibenthic fauna indicate a food web dominated by a variety of omnivorous consumers that are highly influenced by terrestrial carbon sources (Dunton et al. 2012). However, much information is still unknown about seasonal variation of carbon sources, including terrestrial and non-terrestrial carbon sources, such as in situ production (i.e., diatom, dinoflagellate, green algae), bacterial inputs, primary consumers (i.e., copepods), and the nutritional quality (i.e., omega-3s) of fauna as prey items for higher trophic levels.

Fatty acid (FA) biomarkers are used in trophic studies to understand the linkages between primary producers and secondary production, as they help elucidate food sources and provide longer-term dietary information than gut- and fecal-content analysis (Dalsgaard et al. 2003, Kelly and Scheibling 2012). Connelly et al. (2015) applied FA, SI, and photosynthetic pigment analyses to particulate organic matter (POM) collected from lagoons along the Alaskan Beaufort Sea coast during winter (April), spring freshet (June), and open water (August) and found strong seasonal variability in the sources of FAs in POM. In general, April POM was comprised of relatively refractory FAs (e.g., saturated FAs [SFAs] and bacterial FAs) and animal detritus products (e.g., 18:1n-9), with little evidence of autochthonous production (see Connelly et al. 2015 for more detail). June POM contained relatively high amounts of diatom FA markers (Σ16:1/16:0), monounsaturated FAs (MUFAs), and bulk δ13C values of ~28‰, indicating that diatom production and terrestrial inputs were important sources of POM at that time. In August, POM was characterized by high proportions of polyunsaturated FAs (PUFAs), dinoflagellate markers (e.g., 22:6n-3/20:5n-3; C18 PUFA/ C16 PUFA), and copepod markers, with average bulk δ13C values of ~29‰.

Collectively, results from Connelly et al. (2015) suggest that POM from Beaufort Sea lagoons was highly terrestrial (δ13C ≤ ~25‰) throughout the year, but contains seasonally distinct, highly nutritious essential FAs (EFAs; e.g., 22:6n-3 [docosahexaenoic acid, DHA] and 20:5n-3 [eicosapentaenoic acid, EPA]) that may contribute to consumer food resources. However, the assimilation of these FAs by invertebrate consumers is yet to be tested. To date, lipid and FA profiles of invertebrates from the Beaufort Sea are scarce (with the exception of Connelly et al. 2014, 2016, Wold et al. 2011). Further, comparatively little is known about FA profiles of benthic-associated fauna across the Arctic from any season (Graeve et al. 1997, Connelly et al. 2014, Legeżyńska et al. 2014) compared to the better studied pelagic zooplankton (Mayzaud and Boutoute 2015).

In this study, we investigated the diets of benthic and epibenthic invertebrates collected in Beaufort Sea lagoons and nearshore sites in April, June, and August. We used a combination of FA profiles, FA-stable isotopes (FA-SI), and total lipid-SI to (1) determine the dominant primary producers influencing consumer diets across seasons and (2) identify taxa with high EFA content as nutritious prey items for higher trophic levels. We hypothesized that the FAs present in consumer tissues would reflect feeding habits and would coincide with the POM findings of Connelly et al. (2015). However, POM measurements represent a snapshot of ambient conditions (on the order of days), whereas FA dynamics in tissues can change on the order of weeks to months, depending on food availability and tissue type (Huenerlage et al. 2015, Mohan et al. 2016). Therefore, we anticipated that there could be significant lags associated with the timing of primary production in POM and the accumulation of tracer signals within consumers.

Materials and Methods

Sample collection

Invertebrates were collected in April, June, and August from sites within lagoons (n = 6) and outside lagoons (referred to as nearshore, n = 4) along the eastern Alaskan Beaufort Sea coast (Fig. 1). Sampling began in August 2011 and ended in
August 2013. Six samples of the amphipod *Onisimus glacialis* containing one to six individuals between 10 and 12 cm in length (see next paragraph for explanation of composite samples) were collected in April. All other samples, including additional *O. glacialis* and 15 other taxa, were collected in June and August (Table 1). Despite low sample sizes in some instances, data from the less abundant taxa are valuable because published information (beyond taxonomic classification) on these organisms is scarce, and FA and SI studies of these organisms are even rarer.

Infaunal and epibenthic invertebrates were collected using Ponar grabs (April, June, and August) and small beam trawls (June and August), then sorted, and washed over a 1-mm sieve. The copepod *Calanus hyperboreus* was collected using a 335-μm plankton net. Individuals were identified to species level (except for two genera of amphipods), measured for length, and frozen at −20°C in Kaktovik, Alaska, USA. Individuals of the same taxa and from the same sampling site were pooled into a single sample (Table 1). Samples were kept frozen and transported back to the laboratory at the University of Texas Marine Science Institute (UTMSI) in coolers, usually within 10 d of sample collection. Immediately upon arrival in Texas, samples were placed in glass centrifuge tubes (15 mL), covered with chloroform (2 mL), and stored in N₂ gas at −20°C until lipid extraction. Fatty acids were determined from a total of 96 samples from 16 taxa. *Onisimus glacialis* samples were collected for bulk SI analysis from the same field program in April (n = 4), June (n = 2), and August (n = 8) (Appendix S1).

**Lipid extraction and fatty acid analysis**

Total lipids were extracted from samples in a 2:1:0.5 ratio of chloroform:methanol:water following Parrish (1999), modified from Folch et al. (1957). The animals were ground and homogenized using a Teflon-capped metal rod, sonicated, and centrifuged in the chloroform: methanol: water mixture. Lipid extractions were repeated for a total of three times per sample and resuspended in 2 mL of chloroform. Of the
Table 1. Species information and sites where animals were collected from nearshore locations and lagoons of the Alaskan Beaufort Sea coast.

| Taxon       | Species                  | Site          | June | August | June | August |
|-------------|--------------------------|---------------|------|--------|------|--------|
|             |                          |               | n    | n      | Individual/Sample | Length (mm) | n    | n      | Individual/Sample | Length (mm) | TL | TG | Type |
| Annelida    | Spionida Marenzellaria wireni | AN | 2 | 5,7 | 17–22 | 2 | 2,5 | 16–17 | 1.7 | De | Po |
|             | Terrebellida Terebellides stroemii | KA | – | – | – | 2 | 2,5 | 16–17 | 1.7 | De | Po |
| Arthropoda  | Amphipoda Atylus carinatus | JA, KA | – | – | – | 3 | 1–4 | 14–20 | 1.6 | Om | Am |
|             | Amphipoda Gammarus spp.† | AN, NU, TA | 2 | 2 | 14,15 | 3 | 1 | 14–21 | 1.5 | Om | Am |
|             | Amphipoda Monoculodes sp. | BE, JA | – | – | – | 2 | 3,6 | 9–10 | – | Om | Am |
|             | Amphipoda Monoporeia affinis‡ | JA, NU, TA | – | – | – | 3 | 1–16 | 8–11 | 1.6 | De | Am |
|             | Amphipoda Onisimus glacialis† ‡ § | AN, BE, BPDL, DE, DP, HU, JA, KA, NA, TA | 3 | 1–6 | 9–10 | 7 | 1–27 | 7–14 | 1.8 | Om | Am |
|             | Amphipoda Pontoporeia fenorata† | KA, NU, TA | 1 | 5 | 10 | 4 | 1–8 | 6–9 | 1.5 | De | Am |
|             | Cumacea Diastylis goodsiri | KA | – | – | – | 1 | 25 | 9 | 2.4 | Om | Cu |
|             | Isopoda Saduria entomon† ‡ | AN, JA, KA, NU | 8 | 1–5 | 8–25 | 1 | 1 | 15 | 2.3 | Om | I |
|             | Mysidacea Mysis relicta† ‡ | AN, BE, BPDL, DE, DP, HU, JA, KA, NA, TA | 3 | 2–8 | 19–25 | 30 | 1–25 | 10–50 | 1.6 | Om | M |
|             | Copepoda Calanus hyperboreus‡ | BE, JA | – | – | – | 2 | 6–11 | 3–4 | 2 | Su | Co |
|             | Bryozoa Ctenostomata Alcyonidium disciforme | JA | – | – | – | 3 | 1–2 | 25–39 | 1.8 | Su | B |
|             | Cephalorhyncha Priapulida Halicriptus spinulosus | AN | – | – | – | 1 | 3 | 12 | 2.3 | De | Pr |
|             | Priapulida Priapus caudatus† | BE, JA | 2 | 2–6 | 8–20 | 1 | 4 | 23 | 2.4 | De | Pr |
|             | Chordata Stolidobranchia Rhizomolgula globularis | KA, TA | – | – | – | 6 | 1–2 | 15–22 | – | Su | As |

Notes: Lagoons sites include the following: Angun (An), Demarcation Bay (DE), Jago (JA), Kaktovik (KA), Nuvagapak (NU), and Tapkaurak (TA). Nearshore sites include the following; Bernard Spit (BE), Bernard Point (BP), Demarcation Point (DP), and the Hulahula Delta (HU). “n” is the number of samples per species for each month. Individual/sample is the range in the number of individuals pooled in each sample. Mean length (mm) is the range in the lengths of individuals in each sample. Trophic level (TL) is reported where available, as determined by Harris (2015) from species collected in August from four lagoons (KA, JA, AN, and NU). Trophic guild (TG) denotes feeding mode (De = deposit, Om = omnivore, Su = suspension). Taxa types are noted as follows: amphipod (Am), ascidian (As), bryozoan (B), copepod (Co), cumacean (Cu), isopod (I), mysid (M), polychaete (Po), priapulid (Pr).

† ‡ § Species collected in both June and August. Table excludes O. glacialis amphipods collected in April; see methods for details.

† Taxa measured for lipid-stable isotopes (SI).
‡ Taxa measured for fatty acid-specific SIs. Fatty acid profiles were analyzed for all samples and taxa.
resulting total lipid extract, 600 μL was blown dry with N2 gas, and FAs were transformed to FA methyl esters (FAMEs) by derivatizing samples with BF3-methanol. Fatty acid methyl esters were run on a Shimadzu GC-FID with a ZB-WAX plus column (Phenomenex; 30 m, 0.53 mm id, 1.0 μm film thickness). Fatty acid peaks of commercial standards (Supelco COMP 37, BAME, PUFA 1, PUFA 3) were used to identify FA peaks within samples. An internal standard (23:0) was added to each sample to quantify peaks. Fatty acids are expressed proportionally as a percentage of total identified FAs. Full FA profiles are available in Data S1: Tables S1–S3.

**Dietary fatty acid biomarkers**

Established FA biomarkers were used to identify dietary source, feeding mode, and nutritional quality of invertebrates (e.g., Dalsgaard et al. 2003). While we realize that a number of the biomarkers used in this study were established for POM samples, we apply the markers to invertebrates as a starting point to investigate source contributions. When available, results from species-specific feeding studies are helpful for interpreting FA biomarker data from the field. However, no such data exist for the organisms listed here, and it was not practical to conduct feeding experiments on the multiple species collected in this study. The diatom FA marker used herein is the sum of C16 monounsaturates divided by C16 saturates (Σ16:1/16:0), when found in ratios > 1 in POM (Claustre et al. 1988). Notably, 14:0, 16:3n-4, 16:4n-1, and 20:5n-3 are also potential diatom markers (Lévêillé et al. 1997). In contrast, a ratio of 22:6n-3/20:5n-3 > 1 can indicate greater contributions of dinoflagellates compared to diatoms in POM. The FAs 18:2n-6 and 18:3n-3 are broadly produced by macrophytes, chlorophytes, cryptophytes, cyanobacteria, freshwater phytoplankton, and terrestrial plants (Budge and Parrish 1998, Dunstan et al. 1992, Galloway et al. 2012, Taipale et al. 2013, Galloway and Winder 2015). Although 18:2n-6 + 18:3n-3 has been used to identify terrestrial sources in some studies (Parrish et al. 2000), we do not apply 18:2n-6 + 18:3n-3 as a terrestrial-specific marker in this study to avoid potential misinterpretation of results due to 18:2n-6 and 18:3n-3 contributions from other known sources. We have, however, included 18:2n-6 + 18:3n-3 in our analyses as it was an important component in some consumers and was useful for elucidating terrestrial/freshwater sources in combination with SI data in some instances.

Bacterial markers (Σodd-carbon-numbered and branched-chain FAs; Graeve et al. 1997) are generally associated with deposit-feeding organisms that consume reworked organic matter and detrital food sources (Legeżyńska et al. 2014). The copepod marker is the sum of 22:1 + 20:1 MUFAs (Falk-Petersen et al. 1987). Carnivory can be inferred from high levels of 18:1n-9, as it is a major storage of FA in most marine animals (Graeve et al. 1997, Dalsgaard et al. 2003). The ratio of 18:1n-9/18:1n-7 > 1 can also distinguish carnivores vs. herbivores. Yet, this ratio should be used with caution, as it may also change due to starvation and fluctuating lipid content (Stübing and Hagen 2003). Nutritional quality of invertebrates as prey items can be inferred from higher levels of PUFA, 20:5n-3, 22:6n-3, and n-3/ω-6.

Although the sources of single FAs or markers in invertebrate tissues cannot be unequivocally identified, the advantage of this approach is that multiple FAs and markers can be evaluated simultaneously to give greater accuracy. In our interpretations, we have used multiple markers as the basis of our conclusions. When the source of a marker is not supported by additional markers, we discuss alternative interpretations. Further, we use FA-SI to refine our source attributions.

**Stable isotope analysis**

Stable carbon isotope values of total lipids were measured from remaining total lipid extracts (1400 μL) from a subset of crustaceans, which included August samples: *C. hyperboreus* (n = 2), *Gammarus* spp. (n = 3), *Monoporeia affinis* (n = 2), *Mysis relicta* (n = 3), *O. glacialis* (n = 7), *Pontoporeia femorata* (n = 3); June samples: *O. glacialis* (n = 3), *Saduria entomon* (n = 3); and April samples: *O. glacialis* (n = 6). Lipid extracts were blown dry with N2 gas and resuspended in 100–300 μL of chloroform. From the chloroform–lipid extract, 50 μL was transferred to a preweighed tin capsule containing a small piece of precombusted glass fiber filter. The extract was absorbed onto the filter and kept under the fume hood for at least five hours to allow the excess chloroform to evaporate. Prepared samples were analyzed using a Finnigan MAT Delta Plus SI mass spectrometer coupled to a Carlo Erba.
1500 elemental analyzer (CE Instruments, Wigan, UK, NC 2500) at the UTMSI. Lipid-SI values are reported in relation to conventional standards (114859) and USGS Isotopic Reference Material Standard 20192 L-Glutamic Acid with a standard deviation of approximately 0.08‰.

Compound-specific isotope analysis (CSIA) was performed using the same aliquot of previously derivatized FAMEs. The FAMEs dissolved in hexane were measured with a GC/combustion/isotope ratio mass spectrometer (GC/IRMS) with a BPX70 column (60 m, 0.25 mm O.D., 0.25-μm film; constant flow 1.5 mL/min) at the UC Davis SI Facility (University of California, Davis, California, USA). Fatty acid methyl esters were corrected for the addition of the methyl group by measuring the δ13C value of the BF3-methanol (~51.5‰) used in the derivatization process. The fractional contribution of the methyl group in a FAME depends on its chain length, where \( x \) is the fractional carbon contribution of the free FA to the ester. For example, 18:2n-6 has an \( x \) of 18/19. The corrected δ13C value of each FA was calculated with the equation (Abrajano et al. 1994):

\[
\delta^{13}\text{C}_{\text{FA}} = \frac{(\delta^{13}\text{C}_{\text{FAME}} - (1-x) \times \delta^{13}\text{C}_{\text{CH}_3\text{OH}})}{x}
\]

Compound-specific isotope analysis values were reported in relation to an internal standard (12:0), precision ranging from ±0.0‰ to 0.9‰. Stable isotope ratios for lipid-SI and FA-SI are calculated using δ notation (Eq. 2) relative to the international standard for carbon, Vienna Pee Dee Belemnite (VPDB) (13C/12C = 0.0112372).

\[
\delta^{13}\text{C}(‰) = \left( \frac{13\text{C}_{\text{Sample}}}{12\text{C}_{\text{Sample}}} - \frac{13\text{C}_{\text{VPDB}}}{12\text{C}_{\text{VPDB}}} \right) \times 1000
\]

Statistical analysis
To test for generalized (i.e., non-taxon-specific) differences between June and August, mean values of major FAs (>5% in more than one taxon) were calculated for each taxon. The seasonal difference (\( D \)) was then calculated by taking the mean \%FA_{JUN} - mean \%FA_{AUG} for each taxon. The \( D \) values for five peracarida crustaceans available for both seasons (denoted by †; Table 2) were pooled together to calculate a mean \( D \) for all five species. The mean \( D \) was tested against zero using a one-sample \( t \) test. This test was performed for all five major FAs (Table 2).

Principal component analysis (PCA) was used on FA biomarker data and individual FAs were not included in biomarker calculations from August and June. Only individual FAs >1% in all samples were included in the analysis. The same factors were used in August and June PCAs, except for the addition of 16:2n-4 in August and 18:1n-11 in June, due to the proportions (>1%) in each data set. Before the analysis, FA data were transformed to meet the assumptions of normality using the centered log-ratio “robCompositions” package in R Statistical Software (Templ et al. 2011; R version 3.1.1). Taxonomic attributions (color coding and labeling) in the PCA plots were performed ad hoc.

One-way analysis of variance (ANOVA) was used to test for differences among seasons in \( O. \text{ glacialis} \) for (1) individual FAs (mean >3% total FA [TFA]), (2) FA biomarkers, (3) FA-SI values, and (4) lipid-SI values. Post hoc pairwise comparisons were used to test for significant differences among seasons. Bulk SI values for \( O. \text{ glacialis} \) were tested for seasonal differences between two months (April and June), using a Welch's \( t \) test (Appendix S1).

Spatial variation in the FA profiles of taxa was not assessed due to sampling limitations. There could be important spatial drivers (i.e., variation of freshwater inflow) influencing the ecology of these taxa that influences their FA profiles (Guest et al. 2010). However, results from FAs in the suspended POM pool (Connelly et al. 2015) suggest that spatial variability is relatively low among lagoons compared to seasonal variability.

RESULTS

Fatty acids
Across all seasons, the most abundant FAs for all taxa were 16:0, 16:1n-7, 18:1n-9, 18:1n-7, 20:5n-3, and 22:6n-3 (Table 2). In addition, 14:0 (Marenzellaria wireni in June), 16:3n-4 (\( P. \text{ femorata} \) in August), 18:0 (\( P. \text{ caudatus caudatus} \) in June), or 18:2n-6 (\( O. \text{ glacialis} \) in April) were >10% of total FAs in some taxa.

August
In August, ratios of \( \sum 16:1/16:0 \) (diatom FA markers) were greater than one for seven taxa including the following: \( P. \text{ caudatus}, \text{Terebellides stroemii}, \text{M. relicta}, \text{Alycyonium disciforine}, \) and the amphipods \( O. \text{ glacialis}, A. \text{ caudatus, and} \)

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Table 2. Major fatty acids (FAs) (% of total FAs; >5% in more than one taxon) for species collected in August and June from nearshore sites and lagoons of the Alaskan Beaufort Sea coast.

| Taxon       | Species               | n  | 16:0         | 16:1n-7       | 18:1n-9       | 18:1n-7       | 20:5n-3       | 22:6n-3       |
|-------------|-----------------------|----|--------------|---------------|---------------|---------------|---------------|---------------|
| August      | Annelida              |    |              |               |               |               |               |               |
|             | Terebellida           | 2  | 20.2 ± 0.0   | 20.4 ± 0.4    | 3.1 ± 0.0     | 10.6 ± 0.8    | 13.1 ± 0.1    | 1.9 ± 0.0     |
|             | Terebellides stroemi |    |              |               |               |               |               |               |
| Arthropoda  | Amphipoda             |    |              |               |               |               |               |               |
|             | Atylus carinatus      | 3  | 21.1 ± 2.5   | 20.2 ± 2.3    | 14.6 ± 0.7    | 5.3 ± 0.4     | 12.2 ± 3.7    | 3.7 ± 0.9     |
|             | Gammarus spp.         | 3  | 27.5 ± 4.6   | 21.2 ± 14.8   | 15.5 ± 5.5    | 4.2 ± 0.5     | 6.6 ± 2.3     | 2.0 ± 1.1     |
|             | Monoculodes sp.       | 2  | 25.0 ± 0.4   | 10.7 ± 2.9    | 10.5 ± 0.8    | 8.9 ± 0.4     | 14.0 ± 1.9    | 7.1 ± 3.4     |
|             | Monoporeia affinis    | 2  | 27.3 ± 3.2   | 15.9 ± 3.3    | 15.6 ± 7.7    | 3.6 ± 1.1     | 5.4 ± 2.7     | 1.9 ± 0.6     |
|             | Onisimus glacialis†   | 7  | 21.6 ± 5.8   | 25.0 ± 7.6    | 14.0 ± 2.8    | 4.4 ± 0.9     | 10.4 ± 4.2    | 2.1 ± 1.1     |
|             | Pontoporeia femorata† | 4  | 24.0 ± 4.2   | 23.4 ± 6.2    | 10.8 ± 1.2    | 4.0 ± 2.1     | 4.0 ± 1.6     | 0.7 ± 0.4     |
|             | Cumacea               |    |              |               |               |               |               |               |
|             | Diastylis goodsi†     | 1  | 19.1         | 11.8          | 6.6           | 14.4          | 21.5          | 2.9           |
|             | Isopoda               |    |              |               |               |               |               |               |
|             | Saduria entomon       | 1  | 28.0         | 10.5          | 6.9           | 6.0           | 2.2           | 9.3           |
|             | Mysis relicta†        | 30 | 23.2 ± 3.8   | 21.1 ± 7.2    | 11.9 ± 1.9    | 4.3 ± 1.0     | 14.3 ± 4.4    | 6.8 ± 3.7     |
|             | Copepoda              |    |              |               |               |               |               |               |
|             | Calanus hyperboreus   | 2  | 17.1 ± 1.2   | 15.0 ± 0.3    | 3.7 ± 0.8     | 1.7 ± 0.4     | 8.2 ± 1.6     | 4.7 ± 0.8     |
|             | Bryozoa               |    |              |               |               |               |               |               |
|             | Ctenostomata          | 3  | 12.5 ± 1.7   | 11.9 ± 4.8    | 3.6 ± 0.7     | 1.9 ± 0.3     | 11.6 ± 1.4    | 15.7 ± 2.8    |
|             | Alcyonidium disciforme|    |              |               |               |               |               |               |
|             | Cephalorhyncha        |    |              |               |               |               |               |               |
|             | Priapulida            | 1  | 16.0         | 7.0           | 4.9           | 13.3          | 9.4           | 1.4           |
|             | Halicriptus spinolesus|    |              |               |               |               |               |               |
|             | Priapulida            | 1  | 13.0         | 21.5          | 2.1           | 16.3          | 21.9          | 1.2           |
|             | Mysidacea             |    |              |               |               |               |               |               |
|             | Myisis relicta†       | 3  | 23.2 ± 3.8   | 21.1 ± 7.2    | 11.9 ± 1.9    | 4.3 ± 1.0     | 14.3 ± 4.4    | 6.8 ± 3.7     |
|             | Copepoda              |    |              |               |               |               |               |               |
|             | Calanus hyperboreus   | 2  | 17.1 ± 1.2   | 15.0 ± 0.3    | 3.7 ± 0.8     | 1.7 ± 0.4     | 8.2 ± 1.6     | 4.7 ± 0.8     |
|             | Chordata              |    |              |               |               |               |               |               |
|             | Stolidobranchia       | 6  | 25.1 ± 6.6   | 12.6 ± 4.2    | 3.6 ± 0.7     | 8.5 ± 0.9     | 8.3 ± 4.8     | 5.7 ± 1.7     |
|             | Rhizomogula globularis|    |              |               |               |               |               |               |
|             | Bryozoa               |    |              |               |               |               |               |               |
|             | Ctenostomata          | 3  | 12.5 ± 1.7   | 11.9 ± 4.8    | 3.6 ± 0.7     | 1.9 ± 0.3     | 11.6 ± 1.4    | 15.7 ± 2.8    |
|             | Alcyonidium disciforme|    |              |               |               |               |               |               |
|             | Cephalorhyncha        |    |              |               |               |               |               |               |
|             | Priapulida            | 1  | 16.0         | 7.0           | 4.9           | 13.3          | 9.4           | 1.4           |
|             | Halicriptus spinolesus|    |              |               |               |               |               |               |
|             | Priapulida            | 1  | 13.0         | 21.5          | 2.1           | 16.3          | 21.9          | 1.2           |
|             | Mysidacea             |    |              |               |               |               |               |               |
|             | Myisis relicta†       | 3  | 23.2 ± 3.8   | 21.1 ± 7.2    | 11.9 ± 1.9    | 4.3 ± 1.0     | 14.3 ± 4.4    | 6.8 ± 3.7     |
|             | Copepoda              |    |              |               |               |               |               |               |
|             | Calanus hyperboreus   | 2  | 17.1 ± 1.2   | 15.0 ± 0.3    | 3.7 ± 0.8     | 1.7 ± 0.4     | 8.2 ± 1.6     | 4.7 ± 0.8     |
|             | Chordata              |    |              |               |               |               |               |               |
|             | Stolidobranchia       | 6  | 25.1 ± 6.6   | 12.6 ± 4.2    | 3.6 ± 0.7     | 8.5 ± 0.9     | 8.3 ± 4.8     | 5.7 ± 1.7     |
|             | Rhizomogula globularis|    |              |               |               |               |               |               |

**Notes:** Standard deviation is reported for n ≥ 3; except when n = 2, the half range is reported. Nomenclature is reported to the closest taxonomic level. “n” is the number of samples analyzed for FA proportions.† Taxa collected in both June and August.
**P. femorata** (Data S1: Table S1). The sum of odd-carbon-numbered and branched-chain FAs (bacterial FA marker) ranged from 2.5% for mysids to 18.6% for the isopod *S. entomon*, with the majority of taxa containing > 5%. $\Sigma C_{20}$ and $C_{22}$ MUFA (Calanus copepod markers) were relatively low among taxa, except for the priapulid worm *Halicryptus spinulosus*, the bryozoan *A. disciforme*, and the native taxa, *C. hyperboreus*, which exceeded 5%. The ratio of 22:6n-3/20:5n-3 was > 1 in the suspension feeders *A. disciforme* and *Rhizomolgula globularis* and in the isopod *S. entomon*. 18:2n-6 + 18:3n-3 (two terrestrial markers) were relatively low among taxa, except for *C. hyperboreus* and *R. globularis* (Data S1: Table S1). In general, %PUFA was quite variable, ranging from 14.8% in the amphipod *M. affinis* to 41.6% in the bryozoan *A. disciforme*. The n-3/n-6 ratios were highest for cumaceans, mysids, *P. caudatus*, isopods, and the amphipods *Monoculodes* sp.

The PCA revealed that the first principle component (PC1) accounted for 26% of the variability in biomarker composition (Fig. 2), while the second principle component (PC2) accounted for 20% (Fig. 2c). Despite large variation among taxa, PC1 separated invertebrates by taxa type, with suspension feeders (e.g., ascidians, bryozoans, and copepods) having negative scores, and omnvores (e.g., mysids and most amphipods) generally having positive scores. Factors important for negative scores in PC1 were 18:0, copepod markers, 18:2n-6 + 18:3n-3, bacterial FAs, and 18:1n-7. Factors influencing positive scores were predominantly the diatom marker, 16:1n-7, 16:2n-4, and 18:4n-3. For PC2, negative scores were driven predominantly by 18:4n-3, 20:5n-3, 22:6n-3, and copepod markers. Invertebrates on the negative axis of PC2 included predominantly mysids, copepods, bryozoans, and ascidians. Invertebrates on the positive axis included mostly amphipods and polychaetes, which was largely driven by 16:0, bacterial FAs, 18:1n-9, 16:1n-7, and 18:0. Amphipods were highly variable across PC1 and PC2, possibly due to high taxonomic diversity with a variety of feeding modes. Interestingly, the priapulid worms *H. spinulosus* and *P. caudatus* were found on opposite sides of PC1.

**June**

In June, diatom markers were relatively low, with the majority of samples having a ratio value < 1 (Data S1: Table S2). Bacterial markers were high (means > 5%) for all taxa measured. Overall, bacterial FAs ranged from 5.5% in mysids to 14.7% in the polychaete *M. wireni*. Copepod markers varied across taxa, but were > 5% for isopods and *P. caudatus* worms. The 22:6n-3/20:5n-3 ratio was less than one for all taxa. Higher levels of 18:2n-6 + 18:3n-3 were observed for *Gammarus* amphipods, isopods (7.8%), and the worms *P. caudatus* (3.5%) and *M. wireni* (3.5%) (Data S1: Table S2). Proportions of PUFA were relatively similar among taxa collected in June compared to August, ranging from 15% in *P. femorata* to 26.5% in mysids. Levels of n-3/n-6 were lower in June compared to August too, ranging from 1.0 in *Gammarus* amphipods to 5.7 in mysids (Data S1: Table S2).

Of the June PCA, the PCI accounted for 47% of the variability in biomarker composition (Fig. 3b), and PC2 accounted for 17% (Fig. 3c). PCI separated invertebrates by taxa, with worms *P. caudatus* and *M. wireni* on the negative side and mysids and amphipods *Gammarus* spp., *O. glacialis*, and *P. femorata* on the positive side. The factors important for negative scores in PCI were 18:0, 18:4n-3, copepod markers, and bacterial FAs. Factors influencing positive scores were 18:1n-9, 22:6n-3, 20:4n-6, 20:5n-3, and 16:1n-7. For PC2, positive scores were driven by 16:0, 14:0, 16:1n-7, and bacterial FAs. Invertebrates on the positive axis of PC2 include *M. wireni* and all amphipod species. Invertebrates on the negative axis included higher trophic level organisms (e.g., *P. caudatus*, mysids, and isopods), which were largely driven by 20:4n-6, 18:1n-7, 20:5n-3, copepod markers, and 22:6n-3.

**Seasonal shifts**

Despite low sample sizes for some taxa, seasonal differences between June and August were observed for major FAs. Notably, proportions of 18:1n-9 decreased significantly from June to August in peracarida crustaceans (Table 2). General trends in biomarker compositions were observed between invertebrates collected in both seasons. For instance, n-3/n-6 levels increased from June to August for all taxa, and diatom markers either increased or stayed the same for most species.

Seasonal shifts between April, June, and August were observed for certain FAs and biomarkers.
Fig. 2. Scores (a) from the August principle component analysis (PCA) for fatty acid (FA) biomarkers in invertebrates collected from nearshore and lagoon sites along the Alaskan Beaufort Sea, and loadings of variables on PC1 (b) and PC2 (c). Taxa are colored based on taxonomic type. Taxa names (a) are labeled as follows: *Alcyonidium disciforme* (Al), *Atylus carinatus* (At), *Calanus hyperboreus* (C), *Diastylis goodsiri* (D), *Gammarus* spp. (G), *Halicypris spinulosus* (H), *Monoculodes* sp. (Mo), *Monoporeia affinis* (Mp), *Mysis relicta* (My), *Onisimus glacialis* (O), *Pontoporeia femorata* (Po), *Priapulus caudatus* (Pr), *Rhizomolgula globularis* (R), *Saduria entomon* (S), *Terebellides stroemii* (T). Biomarkers include the following: diatom markers ($\sum 16:1/16:0$), ($18:2n-6 + 18:3n-3$), bacterial markers ($\sum$odd-branched-FAs), and copepod markers ($\sum 20:1 + 22:1$).
Fig. 3. Scores (a) from the June principle component analysis (PCA) for fatty acid (FA) biomarkers in invertebrates collected from nearshore and lagoon sites along the Alaskan Beaufort Sea, and loadings of variables on PC1 (b) and PC2 (c). Taxa are colored based on taxonomic type. Taxa names (a) are labeled as follows: *Gammarus* spp. (G), *Marenzellaria wireni* (Ma), *Mysis relicta* (My), *Onisimus glacialis* (O), *Pontoporeia femorata* (Po), *Priapulus caudatus* (Pr), *Saduria entomon* (S). Biomarkers include the following: diatom markers (∑16:1/16:0), (18:2n-6 + 18:3n-3), bacterial markers (∑odd-branched-FAs), and copepod markers (∑20:1 + 22:1).
for the amphipod *O. glacialis* (Figs. 4 and 5). Specifically, proportions of 18:2n-6 were significantly higher in April (8.9% ± 6.3%) compared to June (1.1% ± 0.4%) and August (1.2% ± 0.5%), and proportions of 18:1n-9 were significantly higher in April (21.8% ± 1.9%) compared to August (14.2% ± 3.0%). Likewise, 22:6n-3/20:5n-3 was significantly higher in April (0.4 ± 0.1) than in August (0.2 ± 0.1). The lower 22:6n-3/20:5n-3 values in August were due to increasing proportions of 20:5n-3 from April to August, as proportions of 22:6n-3 did not change. Further, n-3/n-6 values were significantly lower in April (1.6 ± 1.4) compared to August (4.8 ± 2.4). Copepod markers were highest in June, and diatom markers were highest in August (Fig. 5).

**Stable isotopes**

Fatty acid-stable isotopes for *O. glacialis* showed general patterns of relatively 13C-depleted values in April, enriched values in June, and either enriched or intermediate values in August (Fig. 6). Significant differences in δ13C values among seasons were found for 18:0 and 18:2n-6, which were lower in April (−29.8‰ and −36.5‰, respectively) compared to June (−23.2‰ and −30.3‰) and August (−24.4‰ and −32.5‰), and for 18:1n-9 and the mean of all FAs measured (ΣFA), which were lower in April (−31.1‰ and −30.1‰) compared to June (−25.9‰ and −26.1‰), but similar to August (−28.6‰ and −28.1‰). These results agree with bulk isotope values that were relatively depleted in April (−21.4‰), enriched in June (−18.5‰), and intermediate in August (−19.9‰).

Mean SI values of total lipid extracts from *O. glacialis* did not change significantly between the three seasons, but the overall range of values for this species was > 10‰ (Fig. 7). Likewise, total lipid-SI values varied widely among crustaceans, ranging from −30.4‰ in *C. hyperboreus* to −17.1‰ in *O. glacialis*. While error bars surrounding mean values for individual taxa are large, *C. hyperboreus* stands out as having more depleted isotope values (−30.4‰) than the other species.

**Discussion**

**Seasonal shifts in fatty acids**

Fatty acid profiles and biomarkers were studied in a range of Arctic invertebrate taxa to identify dietary source, feeding mode, and nutritional quality. Despite low sample sizes for some of the taxa collected, the work presented herein provides valuable dietary information about rarely studied species in the Arctic. We encourage future studies to expand upon our work and to use these data as a starting point for larger scale sampling efforts. The majority of samples were collected in June (spring) and August (summer) and reveal seasonal shifts in available food sources. The June–August transition was characterized by an increase in fresh algal food sources, predominantly from diatoms, and an increase in nutritionally important EFAs. Fatty acid-SI values for *Onisimus* amphipods showed enhanced importance of terrestrial/freshwater-derived organic matter in April compared to June and August.

**June**

While terrestrial inputs of organic matter (McClelland et al. 2014) and diatom contributions (Connelly et al. 2015) to nearshore waters both peak in the spring, our FA results for consumers suggest that detritivory and carnivory are the dominant feeding modes during June. This is particularly true for benthic worms, amphipods, and isopods (Data S1: Table S2). Alternatively, given that incorporation of FAs from diet to tissues occurs with an associated lag-time (e.g., Huenerlage et al. 2015), elevated Σ16:1/16:0 and 20:5n-3 from diatom production during June may not have been fully incorporated in invertebrates collected at the same time period. Rather, the FA profiles in June most likely reflect food sources consumed in late April, and May, before the onset of snow and sea ice melt. It is possible that ice algae are present in these lagoons in months leading up to June, but there was no evidence of ice algae in April or June in either 2012 or 2013 at our study sites. The lack of diatom markers in FA profiles suggests that ice algae, and even benthic diatoms, were not important components of consumer diets in June. Mysids collected in June had higher levels of 22:6n-3 and 20:5n-3, compared to other taxa. A laboratory study by Schlechtriem et al. (2008) investigated the influence of starvation on the FA profiles of *M. relicta* and found that proportions of 22:6n-3 increased after 3–6 weeks of fasting. Given the high proportions of 22:6n-3, and low levels of diatom, copepod, and bacterial markers in *M. relicta* in this study, we conclude that mysids are removed...
Fig. 4. Fatty acid profiles of *Onisimus glacialis* collected in April (*n* = 6), June (*n* = 3), and August (*n* = 7) from lagoons and nearshore sites along the Beaufort Sea coast. Box and whisker plots show the median (black vertical line), and 25th and 75th percentile (left and right of box). The horizontal line is 1.5 times the interquartile range of data. Seasonal values that were statistically similar or dissimilar are noted (a, b, ab), based on one-way ANOVA and pairwise comparison with an adjusted *P*-value.
Fig. 5. Proportions of fatty acids (FAs) (% of total FAs, %TFA) and biomarkers of *Onisimus glacialis* collected in April (n = 6), June (n = 3), and August (n = 7) in lagoons and nearshore sites of the Beaufort Sea. See Fig. 4 for definitions of box and whiskers. Months that were statistically similar or dissimilar are noted (a, b, ab), based on a pairwise comparison with an adjusted P-value. Biomarkers include the following: docosahexaenoic acid/eicosapentaenoic acid (22:6n-3/20:5n-3), diatom markers (∑16:1/16:0), omega-3/omega-6 (n-3/n-6), 18:2n-6 + 18:3n-3, bacterial markers (∑odd-branched-FAs), copepod markers (∑20:1 + 22:1), sum of saturated FAs (SFA), sum of monounsaturated FAs (MUFA), and the sum of polyunsaturated FAs (PUFA).
from autochthonous food sources and may be experiencing a period of fasting in months leading up to June.

**August**

In contrast with June, diatoms were an important dietary component of most taxa in August, including priapulid worms, amphipods, mysids, and polychaetes. Connelly et al. (2015) reported an increase in dinoflagellate markers relative to diatom markers in POM in the lagoons between June and August. This was not evident in our consumer data, once again suggesting a lag between available food sources and incorporation by consumers. It is likely that August FA profiles reflect feeding in June and July. Legeżyńskiego et al. (2014) also documented high amounts of diatom FAs in benthic invertebrates collected in summer fjords. In our study, a few taxa (A. disciforme, S. entomon, and R. globularis) had 22:6n-3/20:5n-3 ratios >1, which might indicate a dominance of dinoflagellates in the diet. However, 22:6n-3 is also known to increase with trophic level for epibenthic invertebrates in the Beaufort Sea (Connelly et al. 2014), as also seen elsewhere (Carreón-Palau et al. 2013), which is probably the case of the isopod S. entomon. The bryozoan and ascidian are both suspension feeders and likely have a stronger link to pelagic production (i.e., dinoflagellates) than benthic production (i.e., benthic microalgae). Little is known about the feeding ecology of the suspension feeder A. disciforme, the only free-living Arctic bryozoan (Kukliski and Porter 2004), and FA profiles from this study may provide the first look into their dietary sources. The high amount of FA biomarkers indicative of copepods, dinoflagellates, and bacteria suggests that A. disciforme employ a polytrophic feeding strategy.

Bacteria make important contributions in microbial food webs, especially in coastal lagoons (Pomeroy 1974, Cushing 1989). Bacterial FAs found at high levels during August in the amphipods P. femorata and M. affinis, and the polychaete...
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_Terebellides stroemii_ are consistent with their deposit-feeding behavior (Legeżyńska et al. 2014). The isopod _S. entomon_ is a scavenger and predator, known to feed selectively on the amphipod _M. affinis_ (syn. _Pontoporeia affinis_, e.g., Baltic Sea; Ejdung and Elmgren 2001, Leonardsson 1991). Thus, it is possible that high bacterial FAs in _S. entomon_ are due to predation on deposit-feeding amphipods and not directly on detrital material.

Overall, our results suggest a strong linkage between the microbial loop and invertebrate consumers in this nearshore Arctic system. The bacteria represent an important pathway between cycling of dissolved organic carbon (DOC) and incorporation into food webs. Whether the predominant DOC source supporting this linkage is of terrestrial or marine origin is yet to be defined and should be investigated in the future.

Percentages of 18:2n-6 + 18:3n-3 were generally low during August, except for the suspension feeders _R. globularis_ (ascidian) and _C. hyperbo-reus_ (copepod), with proportions >5%. Elevated 18:2n-6 + 18:3n-3 in these two species is consistent with elevated 18:2n-6 + 18:3n-3 in suspended POM during August (Connelly et al. 2015). Connelly et al. (2015) also reports relatively negative bulk δ13C values (~29‰) of POM in August and a significant negative relationship between δ13C and 18:2n-6 + 18:3n-3 of POM among seasons. The elevated percentage of 18:2n-6 + 18:3n-3 in _R. globularis_ and _C. hyperbo-reus_ in August may reflect an increased proportional contribution of terrestrial/freshwater food sources. However, it is known that 18:2n-6 and 18:3n-3 are produced by a wide variety of primary producers (e.g., terrestrial plants, freshwater phytoplankton, macrophytes, chlorophytes, cryptophytes, cyanobacteria), including some in the marine environment, and so the exact source cannot be determined with FA profiles alone (Galloway et al. 2012, Galloway et al. 2015). _Rhizomolgula globularis_ is a non-selective filter feeder (Hobson et al. 2002), and thus, dietary contributions from terrestrial/freshwater sourced material could come via a wide variety of pathways. _Calanus hyperbo-reus_, on the other hand, is primarily an herbivore (Stevens et al. 2004), and it is more likely that this species is consuming sources of in situ production. In any case, it is clear that these two suspension feeders are utilizing dietary resources high in 18:2n-6 and 18:3n-3 (particularly during August) that are not being used by the benthic omnivores or deposit feeders analyzed in this study.

April

Of the invertebrate taxa included in this study, the amphipod _O. glacialis_ was the only taxa collected from all three seasons. In these coastal lagoons, complete darkness and cold winter conditions persist from late November to January, with snow-covered sea ice remaining until May or June (Nicolau et al. 2013). As little sunlight can reach the waters below, primary production is limited, and new food sources are likely unavailable for consumers. Enhanced levels of 18:2n-6, 18:3n-3, and 18:1n-9 in _O. glacialis_ in April relative to the other two months suggest that this amphipod subsists on material other than fresh autochthonous production during the winter, such as detrital material, with tendencies toward carnivory. _Onisimus_ spp. are scavengers, known to consume detritus, carcasses, and plant material (Arndt and Beuchel 2006). Stomach content

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**Fig. 7.** Carbon stable isotope values of total lipid extracts from a subset of invertebrates collected from nearshore and lagoons sites along the Beaufort Sea in April, June, and August. See Fig. 4 for definitions of box and whiskers. Sample sizes are as follows: _Calanus hyperbo-reus_ (n = 2), _Gammarus_ spp. (n = 3), _Monoporeia affinis_ (n = 2), _Mysis relicta_ (n = 3), _Onisimus glacialis_ (April, n = 6; June, n = 3; August, n = 7), _Pontoporeia femorata_ (n = 3), _Saduria entomon_ (n = 3). All taxa, except _C. hyperbo-reus_, are peracarida crustaceans.
analysis of a congeneric species, *Onisimus littoralis*, collected from the Beaufort Sea in April revealed low concentrations of diatom cells and high prevalence of crustacean parts in guts (Carey and Boudrias 1987, Gradinger and Bluhm 2010). It was not until late May and June that ice algae (pennate diatoms) were found in the guts of *O. littoralis* (Gradinger and Bluhm 2010). Likewise, diatom FA markers were low in *O. glacialis* (this study) and in POM samples (Connelly et al. 2015) collected in April.

The high levels of 22:6n-3/20:5n-3 in *O. glacialis* in April likely reflect catabolism of 20:5n-3, not enhanced inputs of 22:6n-3, which did not change seasonally in the amphipods’ tissues. Studies have demonstrated that 22:6n-3 is more conserved than 20:5n-3 through marine food webs (Carreón-Palau et al. 2013), including epibenthic food webs of the Beaufort Sea (Connelly et al. 2014), likely because 20:5n-3 is generally more metabolically active (e.g., involved in enzymatic reactions resulting in eicosanoids, catabolism, or modification into other FAs) than 22:6n-3, which is retained (e.g., an important component in structural nervous tissue; Tocher 2010). We hypothesize that FA profiles in winter were more strongly influenced by catabolism of FAs rather than direct dietary sources. As more metabolically active PUFA were catabolized (e.g., 20:5n-3), the less active PUFA (e.g., 18:2n-6) were retained and remained at higher proportions.

**Fatty acid-stable isotopes**

FA-δ13C measurements for *O. glacialis* revealed shifts from relatively depleted values in April to more enriched values in June and August. Goh et al. (2005) measured the FA-δ13C values of organic carbon in suspended sediments and surface sediments from the Mackenzie River and shelf in the eastern Beaufort Sea. River suspended sediments contained FAs with highly depleted δ13C values (~36‰ to ~40‰), indicative of C3 vascular plants and/or other freshwater primary producers. Shelf sediments contained FAs with more enriched values (~26‰ to ~30‰). Given these sources, *O. glacialis* FA-δ13C values in April displayed a mixture of marine and terrestrial/freshwater sources, ranging from ~25‰ (15:0) to ~38‰ (18:3n-3), with June and August having stronger influence from marine production.

Possible sources of 18:2n-6 and 18:3n-3 in the Arctic may be macrophytes, chlorophytes, cryptophytes, freshwater phytoplankton, and terrestrial plants. Field studies have shown that chlorophytes and cryptophytes can be found in high amounts in Arctic waters (Jeffrey 1976, Suzuki et al. 2002, Morata et al. 2008, Wilce and Dunton 2014), but were only significant contributors in August in these lagoons (C. T. E. Kellogg, unpublished manuscript). Although cyanobacteria can be important contributors of these FAs in lower latitudes, marine cyanobacteria are rare in this lagoon system (C. T. E. Kellogg, unpublished manuscript). Compound-specific isotope data of chlorophytes and cryptophytes FAs in the Arctic are scarce, but studies from other cold water environments may be useful for distinguishing between terrestrial and algal sources. Field measurements of primary producers in Trinity Bay, Newfoundland, found that the terrestrial plant *Equisetum* sp. had 18:2n-6 and 18:3n-3 values at approximately −33‰ (Budge et al. 2001), whereas marine green algae (i.e., chlorophyte) had 18:3n-3 values of approximately −26‰ in the North Sea (e.g., Scheldt estuary, Boschker et al. 2005). In *O. glacialis*, significant changes from lower 18:2n-6 δ13C values in April (~37‰) to higher δ13C 18:2n-6 values in June and August (~30‰ and ~33‰, respectively) suggest a shift from a predominantly terrestrial/freshwater source in April, to a mixture that includes an increased proportion of marine-derived material in later months. Although 18:3n-3 was not detected in some June and August *O. glacialis* samples, values for all three months were less than ~33‰ where measurable. Overall, the FA-SI trends in *O. glacialis* of lower δ13C in April for several individual FAs and for total FAs suggest that terrestrial/freshwater-derived carbon sources are proportionally most important during late winter, while in situ marine production becomes increasingly important during spring and summer for this species.

Recent studies have characterized the FA-SI values of ice algae and pelagic phytoplankton using common diatom markers such as 20:5n-3. Ice algae collected near Barrow, Alaska, USA, have been reported to have higher 20:5n-3 δ13C values (~18‰) compared to pelagic algae (~27‰) (e.g., Budge et al. 2008). Likewise, ice algae in the Bering Sea had higher 20:5n-3 δ13C values (~27‰) compared to pelagic algae below the ice (~30‰; Wang et al. 2014). While absolute FA-SI signatures are not possible to obtain due
to environmental variation, these studies have shown a carbon enrichment in ice algae relative to pelagic phytoplankton, most likely due to the dissolved inorganic carbon-limited, semi-enclosed ice environment in which they grow. *Onisimus glacialis* 20:5n-3 values in our study were not significantly different across seasons, although moderate increases were observed in June (−26‰) compared to August and April (−28‰). It is likely that 20:5n-3 came from the same source across seasons, but this source cannot be identified with the available data. Future field studies that quantify ice algae vs. pelagic phytoplankton contributions to diets should make FA-SI measurements of pOM a priority.

**Total lipid-stable isotopes**

We provide the first bulk lipid-SI data for Arctic crustaceans. Variation in δ13C among and within taxa suggests that total lipid isotopes could be used to track the flow of lipids within a food web, given distinct endmember sources. While this is not possible with our current sample size, some interesting trends were found. The most negative values (−30‰) were observed in *C. hyperboreus*, which may be the result of endogenous lipid production. Herbivorous copepods (e.g., *C. hyperboreus*) contain up to 85% lipids per total body mass (Vogedes et al. 2010) and synthesize high levels of wax esters, particularly in the form of long-chain MUFAs (20:1n-9 and 22:1n-11) (Graeve et al. 2005). At least half of the wax ester pool (comprising 85–95% of lipids in *C. hyperboreus* on the Beaufort Sea shelf; Connelly et al. 2015) are not derived from dietary lipids, but are produced de novo from protein and carbohydrate precursors (Falk-Petersen et al. 2009). We speculate that the high amount of endogenous production may result in depleted lipid isotope values. Our finding that none of the other crustaceans have values similar to *C. hyperboreus* suggests that the lipid stores of the other crustaceans were not derived from copepod lipids. This agrees with the biomarker data for peracarida crustaceans which all had copepod markers <5%. Interestingly, Von Biela et al. (2012) observed high amounts of copepods in the guts of young-of-year Arctic cisco (*Coregonus autumnalis*), with unusually negative bulk carbon SI values (−26‰), thought to be attributed to terrestrial carbon sources. We speculate that the depleted isotope values may have resulted from a *Calanus*-rich diet with high proportions of lipids.

It is well known that high amounts of lipids, which are 13C depleted, can alter the bulk carbon isotope value of an organism, and equations have been created to mathematically normalize for this “lipid bias” (Post et al. 2007). Based on our total lipid-SI results, however, it is clear that lipids can possess significant variability in their isotopic composition (e.g., Matthews and Mazumder 2005). Equations that “correct” for a lipid fraction are based on the assumption that lipids are defined by a constant δ13C value, related to the carbon-to-nitrogen (C:N) ratio (Post et al. 2007), when in fact their lipid δ13C values are taxon-specific. Consequently, application of such generalized models that alter the isotopic signatures of consumers may in fact introduce unnecessary error in trophic studies by their significant and unpredictable “downstream” effects on consumer isotopic values. In the absence of species-specific information, generic adjustments for lipid content seem unjustified. In polar regions especially, the flux of energy within food webs is lipid-driven (Møller 2006). By removing or “correcting” for lipids, valuable information about trophic sources is likely compromised.

**Nutritional content of prey for higher consumers**

Invertebrates with high 20:5n-3 (EPA), 22:6n-3 (DHA), and n-3/n-6 ratios are essential prey items for fish, birds, and mammals because these EFAs are required for growth, reproduction, survival, and pigmentation (Sargent et al. 1999, Parrish 2009). In general, specimens collected in August had higher proportions of EFAs and n-3 PUFAs than those collected in June. Regardless of season, mysids, isopods, and some amphipod species (*O. glacialis, A. carinatus, Monoculodes* sp.) were the most nutritious in this regard. These particular prey species (mysids and amphipods) are also known to be the principal prey items found in stomachs of demersal fish, like Arctic cod (*Boreogadus saida*) collected in nearshore waters (Craig et al. 1982). Arctic cod represent a critical trophic link between lower trophic levels and top predators such as whales, seals, and seabirds, and their dietary sources change seasonally (Bradstreet et al. 1986, Hobson et al. 2002). Arctic
cod have been shown to consume amphipods and copepods during ice-covered periods, while copepods and mysids are their primary food source during warmer ice-free seasons (Bradstreet and Cross 1982, Benoit et al. 2010). Our study suggests that a variety of dietary sources are important for sustaining invertebrate communities throughout the year. In winter, when autochthonous sources are scarce, detritus, bacteria, and terrestrial/freshwater-derived organic matter are important dietary sources for amphipods. Therefore, not only does the nutritional content of prey (e.g., EFA content) affect Arctic cod feeding, but non-algal sources are indirectly important as subsistence sources for prey. Our results may also provide insight into the dietary influences of other important Arctic species such as bowhead whales (*Balaena mysticetus*), which are known to feed heavily on copepods and mysids (Lowry and Burns 1980, Pomerleau et al. 2010).

**Conclusions**

High seasonal variability of organic matter sources in the Arctic often leads to rapid diet changes that cannot be observed by sampling in one season (Kaufman et al. 2008). Our data for *O. glacialis* provides an example of a consumer that shifted from a subsistence/carnivorous diet in April to a more herbivorous diet during the summer, predominately driven by diatom blooms. The depleted FA-specific δ¹³C values of *O. glacialis* in April relative to June and August highlight the importance of terrestrial/freshwater-derived sources of organic matter for sustenance throughout winter, whereas inputs from primary producers rich in EFAs during the growing season are crucial for rapidly accumulating energy stores for a variety of physiological uses. Fatty acid data from a much wider range of invertebrate consumers collected in June and August also show the increasing influence of fresh algal sources as the summer progresses. In addition, bacterial sources of FAs stand out as important resources to consumers throughout the year. The results presented herein provide a baseline understanding of seasonal trophic linkages in Beaufort Sea lagoons, and we encourage future work to expand upon our research through larger field-based programs and through controlled feeding experiments. As the advancement of climate change and coastal development in the Arctic progresses, it is becoming increasingly important to compare past and current physical, chemical, and biological drivers to anticipate future changes.

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Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1429/supinfo

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