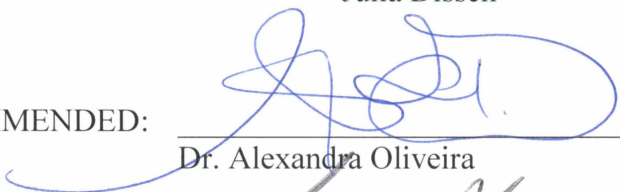# FATTY ACID PROFILES OF ALASKAN ARCTIC FORAGE FISHES:

EVIDENCE OF REGIONAL AND TEMPORAL VARIATION

By

Julia Dissen

RECOMMENDED: _____

Dr. Alexandra Oliveira

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Dr. Lara Horstmann-Dehn
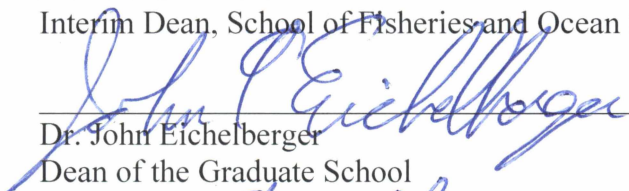
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Dr. Sarah Hardy
Advisory Committee Chair

_____

Dr. Katrin Iken
Program Head, Marine Sciences and Limnology

APPROVED: _____

Dr. Joan Braddock
Interim Dean, School of Fisheries and Ocean Sciences

_____

Dr. John Eichelberger
Dean of the Graduate School

_____

12 August 2015
Date

FATTY ACID PROFILES OF ALASKAN ARCTIC FORAGE FISHES:

EVIDENCE OF REGIONAL AND TEMPORAL VARIATION

A

THESIS

Presented to the Faculty

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Julia Dissen, B.S.

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ABSTRACT

Fatty acids, the main components of lipids, are crucial for energy storage and other physiological functions in animals and plants. Dietary fatty acids are incorporated and conserved in consumer tissues in predictable patterns and can be analyzed in animal tissues to determine the composition of an individual's diet. This study measured the variation in fatty acid profiles of three abundant Arctic forage fish species, Arctic Cod (*Boreogadus saida*), Canadian Eelpout (*Lycodes polaris*), and Longear Eelpout (*Lycodes seminudus*) across multiple years (2010–2013) and geographic locations (Beaufort and Chukchi seas). These fishes are important prey items of marine mammals, sea birds, and predatory fishes, and as such they serve as a critical trophic step connecting lower trophic-level production to higher level predators. Analyzing forage fish fatty acid profiles across multiple years and geographic locations can provide insight into system-level trends in lipid transfer through the Arctic ecosystem. Fatty acid profiles differed among species, with Arctic Cod having higher concentrations of pelagic zooplankton indicator fatty acids, and Eelpout species containing higher concentrations of indicators for benthic prey. While the two Eelpout species displayed major overlap in fatty acid profiles, differences in individual fatty acids may represent niche separation between Canadian and Longear Eelpout in the Beaufort Sea. In addition to variation between species, fatty acid profiles also differed in Arctic Cod between the Beaufort and Chukchi seas, and among collection years. High lipid content and energy-rich fatty acid classes observed in Chukchi Sea Arctic Cod relative to the Beaufort Sea Arctic Cod may indicate favorable feeding conditions in this region over the years sampled, and high energy density of Arctic Cod as prey. Despite the within-species variation observed, the results of this study suggest that Alaskan Arctic forage fish with different foraging ecology can be distinguished based on fatty acid profile, which could be useful in studies that use fatty acid data to characterize diets of top predators.

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INTRODUCTION

Arctic Cod and Eelpout species are among the most widespread and abundant fishes throughout the Alaskan Arctic (Lowry & Frost 1981, Logerwell et al. 2011, Mecklenburg et al. 2011, Rand & Logerwell 2011, Christiansen et al. 2012). These forage fishes make up a critical trophic step in the Arctic food web, linking primary and secondary production to higher trophic-level predators such as sea birds and marine mammals (Bradstreet & Cross 1982, Finley & Evans 1983, Weslawski et al. 1994, Dehn et al. 2007). However, in addition to predation pressure from higher trophic levels, forage fishes are subject to bottom-up controls by environmental conditions that affect primary production (Cury & Roy 1989, Bouchard & Fortier 2011, Crawford et al. 2012). In the Arctic, where temperatures are rising at as much as twice the rate of other regions (ACIA 2004), annual mean sea ice extent has been declining by about 4% per decade (IPCC 2013). Changes in thickness and timing/extent of seasonal ice retreat are expected to alter patterns of primary production (Harley et al. 2006, Grebmeier 2012), which could affect the quality and quantity of available food sources for forage fishes (Cury et al. 2000, Chavez et al. 2011). Changes in food resources are likely to be reflected in biochemical composition of fish tissues (Parrish et al. 2015), which may have cascading effects for their predators. This study examined inter- and intraspecific variation in lipid content and fatty acid profiles of Arctic Cod (*Boreogadus saida*), Canadian Eelpout (*Lycodes polaris*), and Longear Eelpout (*Lycodes seminudus*) across multiple years in the Beaufort and Chukchi seas, to explore how existing spatial and temporal differences in trophic conditions are manifested in forage fishes.

Fatty acids are components of dietary lipids and are essential for energy storage, structural components of cell walls, thermoregulation, and other important physiological processes (Parrish 2013). Fatty acids found in marine fishes consist of carbon chains, normally

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10 to 24 carbons long, with a methyl group at one end and an acid (carboxyl) terminus at the other (Budge et al. 2006). Those with carbon chains containing no double bonds (e.g., 16:0 and 18:0) are termed saturated fatty acids (SFA), while monounsaturated fatty acids (MUFA) contain one double bond. Those with two or more double bonds are called polyunsaturated fatty acids (PUFA), which include the important omega-3 fatty acids essential in the diet of many animals (Parrish 2013). The distinctive structures of fatty acid molecules, and the apparent transfer of unaltered fatty acids from prey to predator, make them useful in identifying key trophic linkages (Graeve et al. 1997, Dalsgaard et al. 2003, Budge et al. 2006, Parrish 2013).

Fatty acid profiles (i.e., the identities and amounts of specific fatty acids present in an individual organism or tissue) are like fingerprints that can be used to examine inter- or intraspecific differences in diet (Budge et al. 2002, Iverson et al. 2002, Pethybridge et al. 2014, Richoux et al. 2014,). Diet studies are often conducted using stomach content analysis, but this method is invasive, only identifies very recently ingested items, and is biased against easily digested or assimilated prey (Baker et al. 2014). Alternatively, biochemical methods can estimate assimilated diet items on a longer time-integrated scale (Budge et al. 2006). Consequently, fatty acids and other chemical tracers, such as stable isotopes, are now widely used in tracking organic matter pathways through the marine food web (e.g., Budge et al. 2006, El-Sabaawi et al. 2009, Revill et al. 2009). Lipid and fatty acid analysis (quantification of lipid classes and fatty acid profiles) can provide information about forage fish feeding habits as well as the quality of the fish as prey items, and may thus indicate the lipids available for transfer to higher trophic levels and how that could affect the physiological condition of predators (Falk-Petersen et al. 2009, Stowasser et al. 2012). Furthermore, if patterns of fatty acids in forage fish and other prey are characterized in an ecosystem they can be used to investigate diets of higher trophic level

predators (Iverson, et al. 2004, Budge et al. 2006). However, the ability to estimate predator diets using fatty acid analysis will depend on the degree of differentiation between fatty acid profiles of prey species (Nordstrom et al. 2008).

The relative amounts of specific fatty acids in tissues can vary among individuals of the same species due to a variety of factors including reproductive status, diet, or environmental

Figure 1. Fatty Acid Transfer Through Food Webs. Fatty acids produced by open water phytoplankton or ice algae are deposited into consumer tissues. Animals have limited ability to alter certain ingested fatty acids. This allows for specific fatty acids (e.g., 20:1ω9 and 22:1ω11) to be used as chemical tracers of diet sources.

conditions (St. John & Lund 1996, Kirsch et al. 1998, Budge et al. 2002). For example, differences in temperature have the potential to directly affect fatty acid composition of the lipid bilayer of cell membranes, which require a specific composition to maintain proper fluidity (Hazel 1984, Parrish 2013). Increased membrane rigidity at low temperatures can result in lowered cell permeability and impairment of enzymatic functions (Dey et al. 1993, Masuda 2003). Poikilotherms such as teleost fishes may increase the amounts of MUFAs (i.e., 18:1) and PUFAs (i.e., 20:5 and 22:6) in cell membranes to maintain membrane functions at low Arctic temperatures (Hazel 1984, Bell et al. 1986, Dey et al. 1993). Fatty acids present in fishes and other consumers also reflect their feeding habits, and can sometimes indicate whether specific

prey items were consumed (Dalsgaard et al. 2003, Nordstrom et al. 2008, Kelly & Scheibling 2012) (Figure 1). Similarly, differences in the fatty acid composition of lower trophic-level organisms may be reflected in the composition of their consumers (Rosen & Trites 2005, Jeanniard du Dot et al. 2008).

Fatty acid profiles differ among phytoplankton species, or between open water phytoplankton and sea ice algae (Ackman et al. 1968, Viso & Marty 1993; Figure 1), and can also differ within species depending on growth conditions, including light intensity, temperature, nutrient availability, and turbulence (Shifrin & Chisholm 1981, Richardson 1985, Fraser et al. 1989, Reitan et al. 1994). Thus, inputs of fatty acids to the Arctic food web may vary in space and time due to environmental factors that impact phytoplankton species composition and their growth. Large-scale differences in fatty acid inputs to the food web are investigated here by comparing fatty acid profiles of Arctic Cod from the Chukchi and Beaufort seas. These two regions differ in the magnitude of primary production as well as in a number of environmental controls on phytoplankton growth (Carmack & Wassmann 2006) that can in turn influence fatty acid composition of primary producers (Skerratt et al. 1995, St. John & Lund 1996, Skerratt et al. 1998, Leu et al. 2010).

Large-scale water and geological characteristics occur between the Beaufort and Chukchi seas such as the broad, shallow Chukchi Sea shelf that encompasses an area nearly three times that of the Beaufort Sea shelf (Carmack & Wassmann 2006). Nutrient-rich Pacific waters travel north through the Bering Strait into the Chukchi Sea (Weingartner et al. 2005, Carmack & Wassmann 2006), supporting high production of phytoplankton (Gradinger 2009), which are producers of the nutritionally important PUFAs (Falk-Petersen et al. 1998). In contrast to the rich Pacific-influenced waters of the Chukchi Sea, the Beaufort Sea is characterized by greater

riverine inputs (Carmack & Wassmann 2006, Dunton et al. 2006). In the Eastern Beaufort Sea in particular, the Mackenzie River is responsible for high influx of sediments, terrestrial matter, and fresh water (Omstedt et al. 1994, Macdonald et al. 1998). In addition, the narrow Beaufort Sea shelf drops steeply after the shelf break, creating strong depth gradients (Carmack & Wassmann 2006) that could impact food availability or quality, such that fish lipid composition varies with depth down the slope (Christensen 2000).

In addition to spatial variation in physical geography and oceanographic features, sea ice cover and differences in ice formation and thaw timing between regions could affect lipid manufacture of primary producers (Leu et al. 2011). Currently, the Beaufort Sea experiences an open water period of about two to three months, which is approximately one month shorter than observed in the Chukchi Sea (Wang & Overland 2015). However, in the next thirty years, both of these regions could experience an additional 1–3 months of open water during the summer (Wang & Overland 2015). Nutrient-rich Pacific waters support large ice-edge phytoplankton blooms in the Chukchi Sea as seasonal ice retreats northward (Wang & Overland 2015). Because community structure of primary producers is related to water-column irradiance and nutrient concentration (Hill et al. 2005), these large scale differences in sea ice dynamics create distinct production regimes between the Chukchi and Beaufort seas, which could also be creating distinct lipid dynamics between the two regions.

High irradiance and temperature, such as that created from thin and early sea ice retreat, can have detrimental effects on lipid and PUFA production in primary producers, decreasing the nutritional quality of sea ice algae (Smith et al. 1989, Leu et al. 2010). For this reason, sea ice thickness, extent, and snow cover can influence PUFA production and trophic transport at the base of the food web with consequences for secondary consumers (Leu et al. 2011). Animals

have limited ability to synthesize PUFAs and must obtain them from primary producers (Budge et al. 2006). These essential nutrients are necessary for reproductive success, growth, and development in zooplankton grazers (Falk-Petersen et al. 2009, Søreide et al. 2010), and for the forage fishes that feed on them (Olsen et al. 1991, March 1993, Copeman & Laurel 2010). Growth and fatty acid profiles of forage fish, particularly the ice-associated Arctic Cod (Bradstreet & Cross 1982, Lønne & Gulliksen 1989), could thus be tightly coupled to changing ice conditions, affecting the available prey source for Arctic sea birds and mammals.

Stomach content analysis of Arctic Cod and Eelpout has demonstrated that these forage fishes have distinct but overlapping diets that include zooplankton (McAllister et al. 1981, Walkusz et al. 2011). Arctic Cod are considered generalist pelagic feeders, but they reproduce under ice, and their larvae feed on the eggs and nauplii of crustaceans that rely on ice-associated primary production (Bradstreet & Cross 1982). Thus, reproductive success and PUFA acquisition of early Arctic Cod life stages is tightly linked to sea ice cover. In open water, Arctic Cod can be found throughout the water column feeding largely on copepods (Lowry & Frost 1981, Bradstreet & Cross 1982, Ajiad & Gjøsæter 1990). Arctic Cod also occur near the seafloor, where they feed on copepods, amphipods, mysids, and euphausiids (Walkusz et al. 2013, Rand et al. 2013). In addition to variation in diet throughout the water column, Arctic Cod exhibit ontogenetic shifts in size and diversity of prey consumed (Walkusz et al. 2013). In contrast, Eelpout are primarily demersal species, and are normally found on soft muddy bottoms feeding on epibenthic prey, such as shrimp, polychaetes, and mysids (Aydin et al. 2007, Wienerroither et al. 2011). While Eelpout do not rely on sea ice for reproduction and larval development like Arctic Cod, their benthic prey items will depend on export of organic matter

from the water column to the seafloor, which is closely tied to timing and extent of sea ice advance and retreat (Grebmeier & Barry 1991).

Investigating variations in fatty acid concentrations among taxa may compliment other diet studies and allow for better characterization of foraging ecology of fish species. Lipid content and presence of specific fatty acids in forage fish tissues can indicate overall feeding conditions and specific diet items (Pethybridge et al. 2014). Comparing Arctic Cod to Eelpout species can indicate how ecological differences (i.e., commonly feeding in pelagic versus demersal realms) affect fatty acid concentrations and nutritional value. Fatty acids were also compared between Canadian Eelpout and Longear Eelpout to investigate differences between two closely related species. These Eelpout

Figure 2. Study Species. *(a)* Arctic Cod (*Boreogadus saida*), *(b)* Canadian Eelpout (*Lycodes polaris*), and *(c)* Longear Eelpout (*Lycodes seminudus*). Numbers on the image are maximum lengths obtained from fishbase.org.

species are predicted to have diets dominated by epibenthic species based on previous Eelpout stomach content diet analyses (Aydin et al. 2007); however, the extent of niche separation between species is unknown. Additionally, interannual and regional differences in fatty acid composition within forage fish will provide insights into variations in the food sources and nutritional quality of these taxa. In this study, fatty acids were quantified in three Arctic forage fishes (Arctic Cod, Canadian Eelpout, and Longear Eelpout; Figure 2) collected during multiple years in the Beaufort and Chukchi seas to characterize variability in fatty acid profiles across

time and space. Specific objectives were to: (i) examine differences in fatty acid concentrations among species and determine if these species can be distinguished based on fatty acid profile regardless of within-species variations, (ii) compare fatty acid profiles of Arctic Cod from the Beaufort and Chukchi seas collected within the same years to examine spatial variability, and (iii) analyze interannual variations in fatty acid composition of all three species in samples collected from 2010–2013.

MATERIALS & METHODS

Sample collection

Arctic Cod, Canadian Eelpout, and Longear Eelpout were acquired from a series of expeditions in the Chukchi and Beaufort seas (Figure 3) between 2010 and 2013 (n = 177, Table 1). Chukchi Sea samples were collected as part of the 2012 Russian-American Long-Term Census of the Arctic (RUSALCA) and 2010 and 2011 Alaska Monitoring and Assessment Program (AKMAP) cruises using plumb-staff beam and otter trawls. Stations in the Chukchi Sea ranged from 22 to 109 m depth. Beaufort Sea samples were collected on the 2011 Central Beaufort Sea Fish Monitoring (Beaufish) and the 2012 and 2013 U.S.-Canada Transboundary Fish and Lower Trophic Communities projects using otter and beam trawls. Beaufort Sea samples used in this study were taken from stations ranging from 13 to 500 m depth. All samples were collected in late summer (August 14–September 30). Trawl nets had 7 mm mesh in body and 4 mm mesh in the cod-end liner. Samples were collected according to the protocols outlined by Norcross et al. (2010) and fishes euthanized according to the UAF International Care and Use Committee protocol 134765 by submerging fish in a solution of 130 mg/ liter solution of tricane
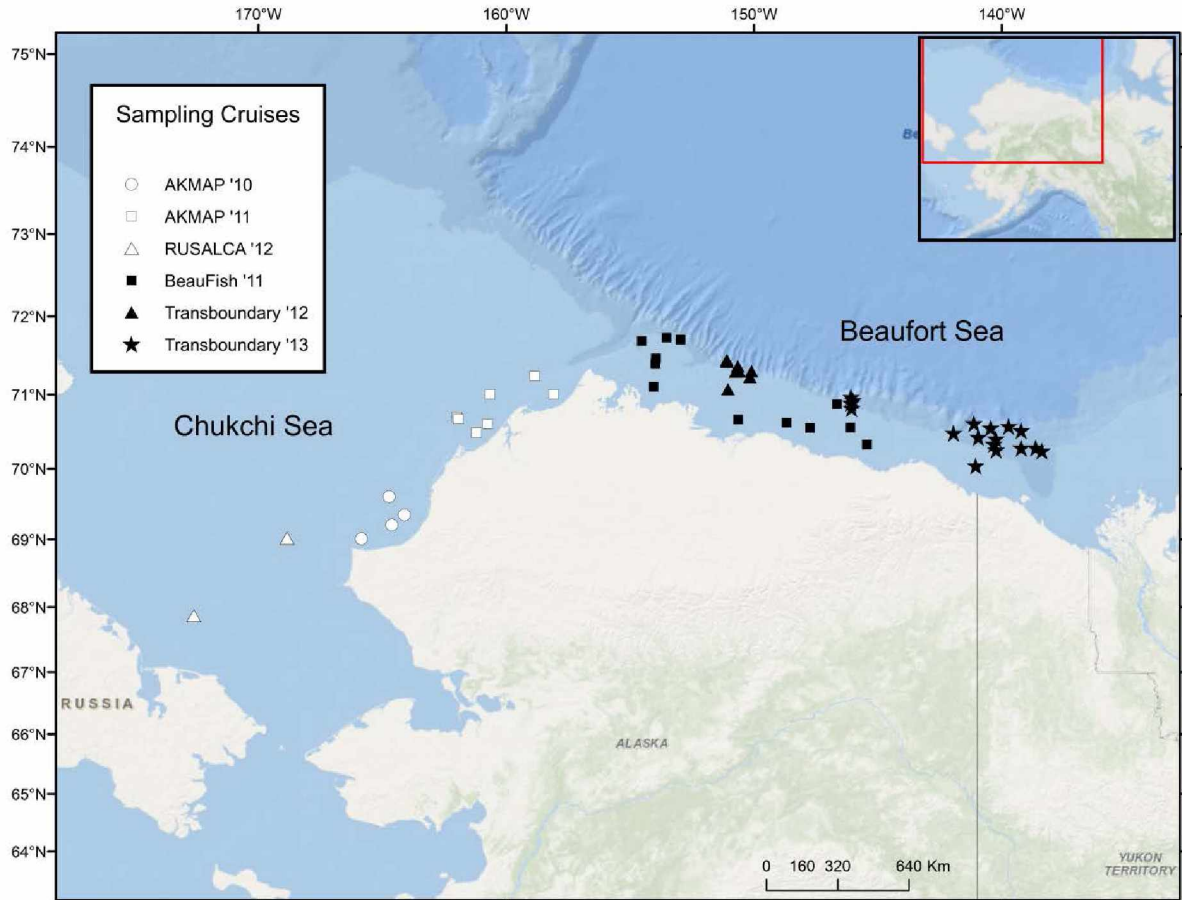
Figure 3. Sample Stations in the Beaufort and Chukchi seas. Samples were taken during the Alaska Monitoring and Assessment Program 2010 (AKMAP '10) and 2011 (AKMAP '11), Central Beaufort Sea Fish Monitoring 2011 (BeauFish '11), Russian-American Long-Term Census of the Arctic 2012 (RUSALCA '12), and U.S. Transboundary 2012 (Transboundary '12) and 2013 (Transboundary '13).

methanesulfonate (MS-222) in seawater. Trawls were sorted on deck and individual fishes were frozen in plastic bags. Samples were stored at -20 °C in the field, and then stored frozen at -80 °C prior to analysis. In the lab, fishes were weighed wet (to the nearest 0.0001 g) and measured for total length (from the most forward point of the head, with the mouth closed, to the farthest tip of the tail, to the nearest 1 mm).

Table 1. Fish Sample Size by Species, Region, and Year. Numbers of individual fish analyzed from each species (Arctic Cod, Canadian Eelpout, and Longear Eelpout) by region (Beaufort and Chukchi seas) and year (2010–2013).

		Arctic Cod	Canadian Eelpout	Longear Eelpout
Beaufort Sea	2011	20	19	-
	2012	19	6	22
	2013	22	-	23
Chukchi Sea	2010	11	-	-
	2011	15	-	-
	2012	20	-	-
Total		107	25	45

Lipid extraction and fatty acid transesterification

Lipids were extracted from whole-body homogenates using a modified Folch extraction (Folch et al. 1957) at the Marine Mammal lab in Fairbanks, Alaska. Frozen fish samples were homogenized using a heavy-duty stainless steel blender (Waring Commercial, New Hartford, CT, U.S.A.). Homogenates were sub-sampled into 1.5 g aliquots and lipids were extracted using 30 ml of 2:1 chloroform ($CHCl_3$, VWR, West Chester, PA, U.S.A.) and methanol (CH_4O, VWR, West Chester, PA, U.S.A.) with 0.01% butylated hydroxytoluene (v/w) (BHT, 2,6-Di-tert-butyl-p-cresol, Spectrum Chemical, Gardena, CA, U.S.A.), where BHT was added to prevent lipid oxidation. Vials were flushed with nitrogen and lipids were allowed to extract in this solution overnight at 4 °C. Solids were separated from the solution using glass funnels lined with grade 202 creped filter paper (VWR, West Chester, PA, U.S.A.) and rinsed with the chloroform:methanol mixture. A 0.88% sodium chloride (NaCl, ACS grade, VWR International, LLC) solution was added to the filtrate and centrifuged to create a biphasic system, such that lipids were retained in one layer and non-lipids in another. The top layer containing methanol, water, and non-lipid compounds was discarded, and the lower layer containing chloroform and lipids was filtered a second time through anhydrous sodium sulfate (Na_2SO_4, EMD Chemicals

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Inc., Gibbstown, NJ, U.S.A.) to fully dehydrate the solution, because water will prevent the acid-catalyzed transesterification. Chloroform was then evaporated off the filtered lipids under nitrogen, and the resulting concentrated lipid was weighed to the nearest 0.0001 g.

Extracted fatty acids were converted to fatty acid methyl esters (FAME) as described by Budge et al. (2006). Lipid extracts were transesterified with Hilditch reagent (Iverson et al. 2004). A maximum of 0.1 g of the lipid extract was dissolved in 3.0 ml Hilditch reagent [0.5 N sulfuric acid (H_2SO_4, Fischer Scientific, Fair Lawn, NJ, U.S.A.) in methanol] and 1.5 ml methylene chloride ($MeCl_2$, VWR, West Chester, PA, U.S.A.) containing 0.01% BHT and 1 mg of 25:0 internal standard (Cayman Chemical, Ann Arbor, MI, U.S.A.). The working stock of internal standard was prepared using 10 mg of 25:0 in 1 ml of methylene chloride containing 0.01% BHT. Samples were capped with nitrogen and reaction was carried out at 100 °C for 1 h using a digital 2 block heater 120 (VWR, West Chester, PA, U.S.A) to keep temperature constant. Hexane (C_6H_{14}, VWR, West Chester, PA, U.S.A.) and water were added after the completion of the reaction, and samples were centrifuged to separate the solvent layer containing FAMEs from the aqueous layer. The solvent layer was removed and saved, and the hexane-water wash was repeated with the aqueous layer twice. The recovered FAME in solvent was dehydrated with anhydrous sodium sulfate, and then the solvent was evaporated under a stream of nitrogen. The FAME was weighed and solubilized in hexane to a concentration of 50 mg/ ml, flushed with nitrogen, capped, and stored at -80 °C until fatty acid analysis.

Fatty acid quantification and identification

Fatty acid analyses were conducted at the University of Alaska Fairbanks' Kodiak Seafood and Marine Science Center. Fatty acids were quantified on a gas chromatogram (GC)

model 6850N Series II (Agilent Technologies, Wilmington, DE, U.S.A.) coupled to a flame

ionization detector (FID; Agilent Technologies) and fitted with a DB-23 (60 m × 0.25 mm i.d.,

0.25 μm film) capillary column (Agilent Technologies) according to Bechtel & Oliveira (2006).

The GC ChemStation program (Rev.A.08.03 [847]; Agilent Technologies 1990–2000,

Wilmington, DE) was used with the enhanced integrator program to integrate chromatogram

peaks. An autosampler model 6850 (Agilent Technologies) injected standards and samples into

the GC. Each sample was injected in split mode with a 1-μl volume at a ratio of 75:1 with the

injector held at 250 °C. The carrier gas was hydrogen (Airgas USA, LLC, Nor Pac region) at

linear constant flow of 0.9 ml/ min and average velocity of 28 ml/ sec. The detector (FID) was

held at 275 °C, and constant makeup flows of hydrogen, air, and nitrogen (Airgas USA, LLC,

Nor Pac region) were maintained at 40, 450, and 35 ml/ min, respectively. Oven programming

started from an initial temperature of 140 °C and rose at 2 °C/ min to 180 °C, then 0.50 °C/ min

to 200 °C, and then 1 °C/ min to 215 °C for a final run time of 75 min. If samples appeared too

concentrated to accurately integrate chromatogram peaks, as observed by tailing of predominant

peaks in a given sample, the sample was diluted to a ratio of 1:10 sample to hexane and rerun

under the same column conditions outlined above. The rate of dilution was applied to peak areas

from diluted samples to standardize results to the concentration of 50 mg FAME/ ml hexane

before conducting statistical data analyses. Peaks were compared to retention times of

commercial FAME standards, including FAME Mix C4-C24 Unsaturates (Sigma-Aldrich Co.

LLC), Bacterial Acid Methyl Esters Mix (Sigma-Aldrich Co. LLC), PUFA No. 1 (marine source,

Sigma-Aldrich Co. LLC), PUFA No. 2 (animal source, Sigma-Aldrich Co. LLC), PUFA No. 3

(Menhaden oil, Sigma-Aldrich Co. LLC), 22:3ω3 (docosatrienoic acid, Nu-Check-Prep, Inc.,

Elysian, MN, U.S.A.), 22:4ω6 (adrenic acid, Nu-Check-Prep, Inc.), and 22:5ω6 (osbond acid,

Nu-Check-Prep, Inc.). Concentrations of individual fatty acids were quantified to mg fatty acid/ g lipids using the relationship of internal standard peak area to its known concentration (25:0; 1mg). Concentrations of individual fatty acids (μg) in 1 g of wet tissue were calculated using the lipid content of the sample. Trends within and across species were reported using μg fatty acid/ g wet tissue. This allows us to examine how these fishes serve as prey items over temporal and regional scales. Additionally, comparisons were investigated in mg fatty acid/ g lipid and % of total fatty acids to determine if similar or different patterns are apparent through other forms of data expression commonly used in fatty acid analysis. Comparing data types, μg fatty acid/ g wet tissue versus mg fatty acid/ g lipid, will infer whether trends in fatty acid concentration are differences between sample group fatty acids or simply a function of changes in total lipid.

To identify fatty acids not present in commercial standards a subset of individuals from each species and sampling expedition was further analyzed using a gas chromatograph GC 6890N coupled to a mass spectrometer MS5973 (Agilent Technologies) fitted with a DB-23 (60 m × 0.25 mm i.d., 0.25 μm film) capillary column (Agilent Technologies) following Chantarachoti et al. (2007). An autosampler model 6850 (Agilent Technologies) was used for injections of standards and samples at a split ratio of 100:1. The carrier gas used was helium (Airgas USA, LLC, Nor Pac region) at a constant flow of 1.0 ml/ min, and an average velocity of 26 cm/ sec. Inlet temperature was held at 250 °C. Oven programming started from an initial temperature of 140 °C and rose at 2 °C/ min to 180 °C, then 0.50 °C/ min to 200 °C, then 1 °C/ min to 203 °C, and then 20 °C/ min to 220 for a final run time of 65.30 min. The mass spectrometer was operated in electron impact mode at 70eV, and the mass range scanned was 41–440 amu at a rate of 3.42 scans/ sec. Data acquisition started after a 4.50 min solvent delay.

Transfer line, quadrupole, and source temperatures were 280, 150, and 230 °C, respectively. Data were collected and analyzed using the MSD ChemStation (Rev. E.02.02.1431, Agilent Technologies). Mass spectra of FAMEs were compared to the NIST/EPA/NIH Mass Spectral Library (NIST 05 v.2.0, National Institute of Standards and Technology, Gaithersburg, MD, U.S.A.). All standards were rerun on the MS for comparison with sample fatty acids. Seventy-two fatty acids were identified and quantified for each sample (Table 2).

A five-point calibration curve was generated using FAME Mix C4-C24 Unsaturates to determine the response factors (Rf) for 35 fatty acids. The Rf were calculated in relation to 18:0 as proposed by Ackman & Sipos (1964). The Rf were used as multipliers for measured peak areas of these fatty acids, as they were identified in the samples. For fatty acids not present in FAME Mix C4-C24 Unsaturates standard, Rf's were "borrowed" from fatty acids with a similar number of double bonds and carbon chain length. Unidentified and non-fatty acid peaks were removed from analysis. Fatty acids were named according to the shorthand notation of A:BωX, where A is the number of carbon atoms, B is the number of double bonds, and X is the positon of the first double bond with respect to the terminal methyl group (Budge et al. 2006).

Table 2. Fatty Acids Quantified in Fish Samples. Fatty acids identified and measured in whole-body homogenates of Arctic Cod, Canadian Eelpout, and Longear Eelpout from the Chukchi and Beaufort seas.

Fatty Acid	Fatty Acid Common Name
10:0	decanoic acid
11:0	undecanoic acid
12:0	lauric acid
13:0	tridecanoic acid
iso 14:0	13-methyl-tetradecanoic acid
14:0	myristic acid
14:1ω9	physeteric acid
14:1ω7	*cis*-7-tetradecenoic acid
14:1ω5	myristoleic acid
iso 15:0	14-methyl-pentadecanoic acid
anteiso 15:0	13-methyl-pentadecanoic acid
15:0	pentadecanoic acid
15:1	pentadecenoic acid
iso 16:0	15-methyl-hexadecanoic acid
anteiso 16:0	14-methyl-hexadecanoic acid
16:0	palmitic acid
16:1ω11	*cis*-5-hexadecenoic acid
16:1ω9	hypogeic acid
16:1ω7	palmitoleic acid
16:1ω5	*cis*-11-hexadecenoic acid
iso 17:0	16-methyl-heptadecanoic acid
16:1ω1	*cis*-15-hexadecenoic acid
16:2ω6	7,10-hexadecadienoic acid
anteiso 17:0	15-methyl-heptadecanoic acid
16:2ω4	*cis*-9,12-hexadecadienoic acid
17:0	margaric acid
16:3ω4	*cis*-6,9,12-hexadecatrienoic acid
17:1ω9	*cis*-8-heptadecenoic acid
18:0	stearic acid
18:1ω13	*cis*-5-octadecenoic acid
18:1ω9 *trans*	oleic acid
18:1ω11	*cis*-7-octadecenoic acid
18:1ω9 *cis*	oleic acid
18:1ω7	vaccenic acid
18:1ω5	*cis*-13-octadecenoic acid

Table 2. Continued.

Fatty Acid	Fatty Acid Common Name
18:2ω6 *cis*	linoleic acid
18:2ω4	*cis*-11,14-octadecadienoic acid
18:3ω6	gamolenic acid
18:3ω3	alpha-linolenic acid
18:4ω3	stearidonic acid
18:4ω1	*cis*-8,11,14,17-octadecatetraenoic acid
20:0	arachidic acid
20:1ω13	*cis*-7-eicosenoic acid
20:1ω11	gadoleic acid
20:1ω9	gondoic acid
20:1ω7	paullinic acid
22:2Δ5,11	C_{22} non-methylene-interrupted
22:2Δ5,13	C_{22} non-methylene-interrupted
20:1ω5	*cis*-15-eicosenoic acid
20:2ω9	*cis*-8,11-eicosadienoic acid
20:2ω6	eicosadienoic acid
21:0	heneicosanoic acid
20:3ω6	*cis*-8,11,14-eicosatrienoic acid
20:4ω6	arachidonic acid
20:3ω3	*cis*-11,14,17-eicosatrienoic acid
20:4ω3	*cis*-8,11,14,17-eicsoatetraenoic acid
20:5ω3	eicosapentaenoic acid
22:0	behenic acid
22:1ω11	cetoleic acid
22:1ω9	erucic acid
22:1ω7	*cis*-15-docosenoic acid
22:2Δ7,13	C_{22} non-methylene-interrupted
22:2Δ7,15	C_{22} non-methylene-interrupted
21:5ω3	*cis*-6,9,12,15,18-heneicosapentaenoic
22:4ω6	adrenic acid
22:5ω6	osbond acid
22:5ω3	docosapentaenoic acid
24:0	lignoceric acid
22:6ω3	docosahexaenoic acid
24:1ω11	*cis*-13-tetracosenoic acid
24:1ω9	nervonic acid
24:1ω7	*cis*-17-tetracosenoic acid

Statistical Analysis

To analyze profiles while conferring equal weight to all fatty acid variables, data were left untransformed for all analyses. To examine the potential effect of down-weighting the more abundant fatty acids, tests were repeated after taking the square root and the log(x+1) of the data. Statistical outcome and interpretation were not affected by either square root or a more severe log(x+1) transformation (Appendix A). For all tests performed, $P \leq 0.05$ was considered significant.

Differences in fish wet weight (g) and total lipid content (g lipid/ g wet tissue) between regions and years were analyzed using Analysis of Variance (ANOVA) and Tukey HSD tests for pairwise comparisons across all sample groups (i.e., 2011, 2012, and 2013 Chukchi Sea Arctic Cod; 2010, 2011, and 2012 Beaufort Sea Arctic Cod; 2011 and 2012 Canadian Eelpout; 2012 and 2013 Longear Eelpout) using R statistical software (R Core Team 2013). ANOVA, Tukey HSD, and Welch two-sample t-tests were used to compare mean concentrations of specific fatty acids, fatty acid classes, and fatty acid trophic markers (i.e., summed concentrations or ratios of individual or summed fatty acids) in R. Multivariate analyses were conducted using the software package PRIMER v6 (PRIMER-E Ltd, Plymouth, UK). The 72 fatty acids measured were converted from peak area to μg fatty acid/ g wet tissue by relation to known quantities of an internal standard (25:0) as described above. Fatty acid concentrations were also quantified as mg fatty acid/ g lipid to determine whether patterns in fatty acid profiles were influenced by differences in total lipid among individuals.

Fatty acids were grouped into classes based on the number of double bonds: saturated fatty acids (SFA), monounsaturated fatty acids (MUFA), and polyunsaturated fatty acids (PUFA). In addition to fatty acid classes, fatty acid trophic markers were examined to investigate

potential food habits and food web conditions. Fatty acid trophic markers measured included the sum of $20:1\omega9$ and $22:1\omega11$, a marker for calanoid copepods (Graeve et al. 1997, Auel et al. 2002, Falk-Petersen et al. 2002), the ratio of $18:1\omega9/18:1\omega7$ as a marker for carnivory (Graeve et al. 1997, Auel et al. 2002, Falk-Petersen et al. 2009), and the ratio of $\omega7/\omega9$ fatty acids as a marker for benthic feeding (Budge et al. 2007). The relative proportion of diatoms to flagellates in the fish diet was investigated using the diatom marker $16:1\omega7/16:0$ (Viso & Marty 1993, St. John & Lund 1996, Falk-Petersen et al. 2002) and the diatom versus dinoflagellate marker $20:5\omega3/22:6\omega3$ (Falk-Petersen et al. 2002, Dalsgaard et al. 2003).

Concentration data (in µg fatty acid/ g wet tissue and mg fatty acid/ g lipid) for the full suite of 72 fatty acids were used to test the null hypotheses of no difference in fatty acid profiles of Arctic forage fishes among species, years, or between regions. Analysis of Similarity (ANOSIM) and Permutational Analysis of Variance (PERMANOVA) were used for hypothesis-testing based on Bray-Curtis similarity matrices (Bray & Curtis 1957). PERMANOVA was used to determine whether fatty acid profiles differed among species, or within species among regions and years. Fish weight and sampling depth were also included in PERMANOVA tests as covariates to determine whether fatty acid profiles varied with fish weight, or across the depths at which they were sampled. Covariates were fit first into the model, and then, given the effect of these factors, the individual terms of interest (i.e., species, region, and year) were fit into the model in the order they appear in Tables 3 and 4 from top to bottom. With few outliers, fish weight was correlated to length (Figure 4). Consequently, weight and length had similar effects on fatty acid profile and were thus considered as analogous variables for fish size. For simplicity, all results presented here used total fish wet weight (g) as a proxy for fish size. For tests that showed significant differences between sample groups, Similarity Percentages (SIMPER) tests

were used to investigate the contribution of specific fatty acids to differences among species, regions, and years. Only fatty acids that contributed to 90% of the cumulative dissimilarity among sample sets were reported. Differences in fish fatty acid profiles were visualized using Non-Metric Multidimensional Scaling (nMDS) based on the Bray-Curtis similarity matrix.

Table 3. PERMANOVA of Fatty Acid Profiles and Covariates Corrected to Total Tissue Mass. Results of PERMANOVA tests for all fish sample fatty acid profiles in µg fatty acids/ g wet tissue to test the effect of species (Arctic Cod, Canadian Eelpout, and Longear Eelpout), region (Beaufort and Chukchi seas), and years (2010–2013). Fish wet weight and station depth were included in the model as covariates. Summary includes degrees of freedom (df), sum of squares (SS), mean square (MS), pseudo-F statistic (Pseudo-F), P-values, and number of unique permutations (Unique perms). Significant P-values (P < 0.05) are given in bold.

	Df	SS	MS	Pseudo-F	P-value	Unique perms
All Fishes						
Weight	1	3806	3806	4.241	**0.011**	998
Depth	1	26460	26460	29.486	**0.001**	998
Species	2	47510	23755	26.471	**0.001**	998
Region	1	12463	12463	13.888	**0.001**	998
Year	3	29111	9703.8	10.813	**0.001**	998
Residuals	168	150760	897.39			
Total	176	270110				

Table 4. PERMANOVA of Fatty Acid Profiles and Covariates Corrected to Total Lipid. Results of PERMANOVA tests for all fish fatty acid profiles in mg fatty acids/ g lipid to test the effect of species (Arctic Cod, Canadian Eelpout, and Longear Eelpout), region (Beaufort and Chukchi seas), and year (2010–2013). Fish wet weight and station depth were included in the model as covariates. Summary includes degrees of freedom (df), sum of squares (SS), mean square (MS), pseudo-F statistic (Pseudo-F), P-values, and number of unique permutations (Unique perms). Significant P-values (P < 0.05) are given in bold.

	Df	SS	MS	Pseudo-F	P-value	Unique perms
All Fishes						
Weight	1	8340.7	8340.7	11.982	**0.001**	999
Depth	1	13324	13324	19.142	**0.001**	999
Species	2	24469	12234	17.576	**0.001**	999
Region	1	3127.4	3127.4	4.493	**0.005**	998
Year	3	12438	4145.8	5.956	**0.001**	998
Residuals	168	116940	696.08			
Total	176	178640				
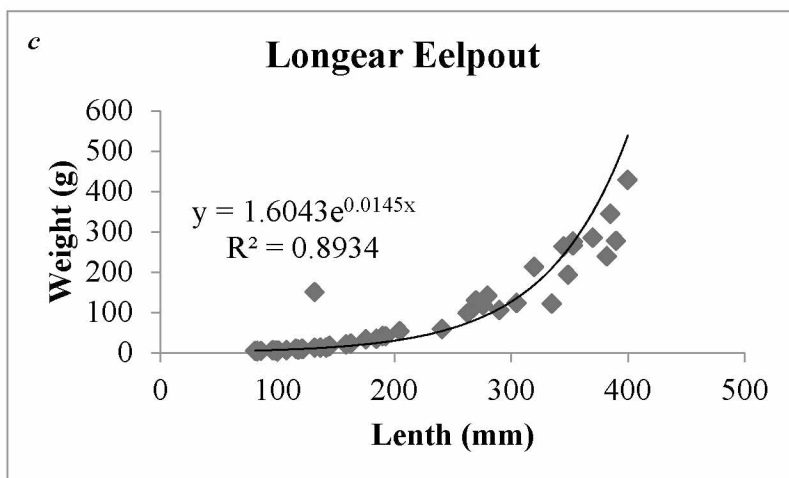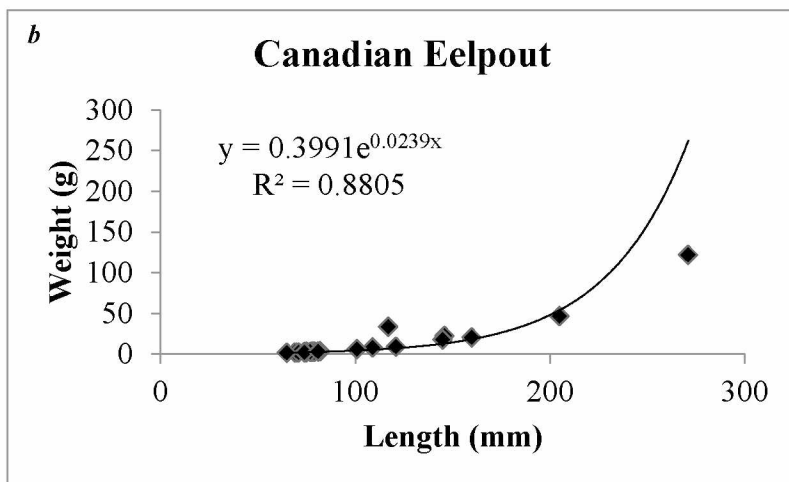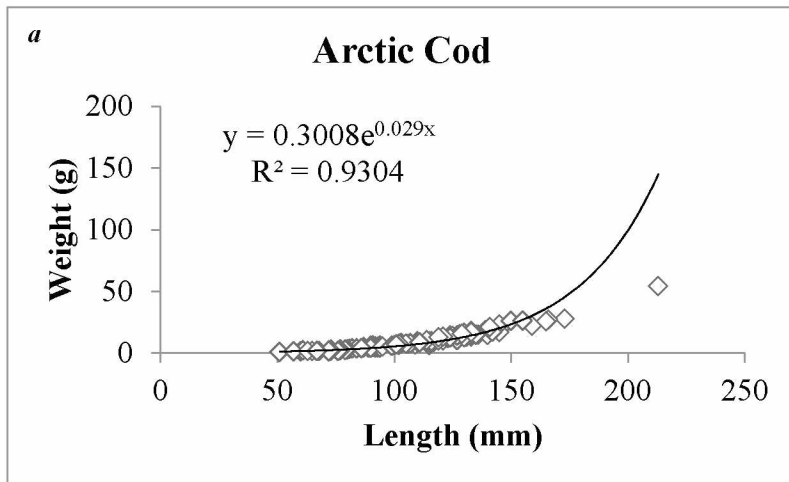
Figure 4. Length to Weight Correlation of Forage Fishes. Fish wet weight (g) vs fish length (mm) for (*a*) Arctic Cod, (*b*) Canadian Eelpout, and (*c*) Longear Eelpout.

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RESULTS

Interspecific variation

Mean fish weights, lengths, and total lipid content by species, region, and year are summarized in Table 5. Total lipid content was highest for Arctic Cod pooled for all collection years and regions at a mean of 0.04 ± 0.02 g lipid/ g wet tissue. Although, when pooled for all collection years, Longear Eelpout were significantly heavier (95.57 g ± 111.75) than Arctic Cod
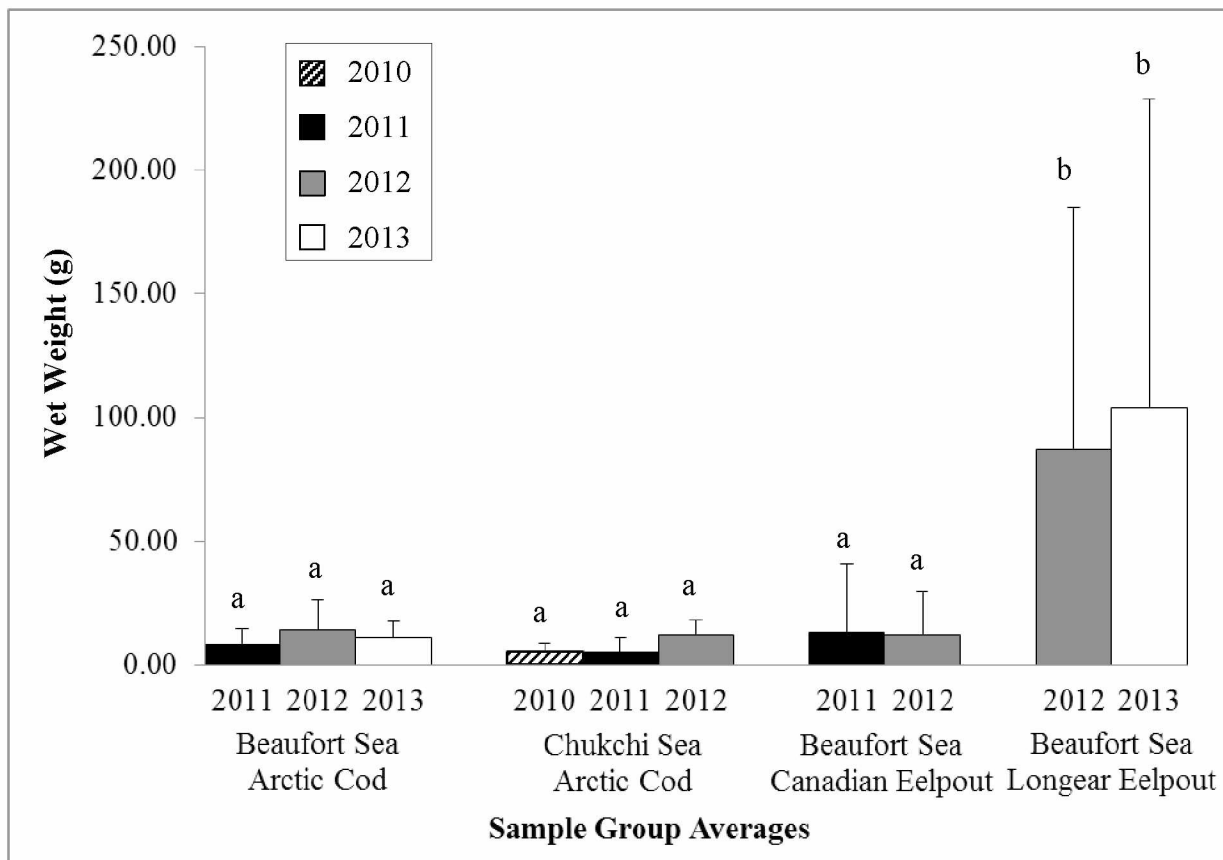
Figure 5. Mean Fish Sample Wet Weight. Mean wet weight (g) for sample sets: for: 2011–2012 Beaufort Sea Arctic Cod, 2010–2012 Chukchi Sea Arctic Cod, 2011–2012 Beaufort Sea Canadian Eelpout, 2012–2013 Beaufort Sea Canadian Eelpout. Error bars represent 1 standard deviation, and lower-case letters above bars represent significant differences among sample sets (i.e., 2010, 2011, and 2012 Beaufort Sea Arctic Cod; 2011, 2012, and 2013 Chukchi Sea Arctic Cod; 2011 and 2012 Canadian Eelpout; 2012 and 2013 Longear Eelpout; P < 0.05); same letter means no difference. Bars are shaded according to year.

(9.73 g ± 0.01; P = 0.001) and Canadian Eelpout (12.66 g ± 25.25; P = 0.001; Figure 5), both

Eelpout species had significantly less total lipid than Arctic Cod (P = 0.001 for both

comparisons; Table 5, Figure 6). Total lipid content did not differ significantly between the two

Eelpout species when all years were pooled (P = 0.350). Classification of species using statistical

analysis of fatty acid profiles can be improved by taking into account size or age classes of

species (Iverson et al. 2002). In this study, weight (which was positively correlated to fish length

for all three study species) had a significant effect on fatty acid profile; however, when included
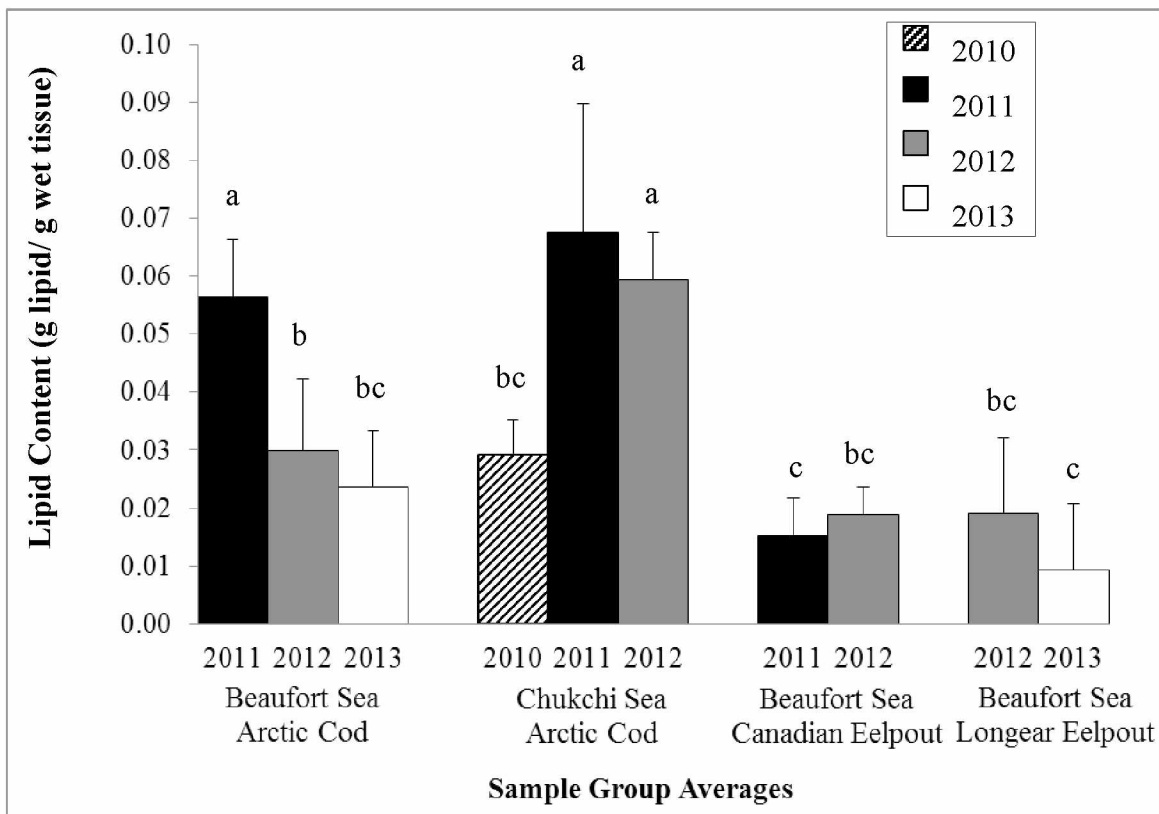
Figure 6. Mean Fish Lipid Content. Mean total lipid content (g lipid/ g wet tissue) for:
2011–2012 Beaufort Sea Arctic Cod, 2010–2012 Chukchi Sea Arctic Cod, 2011–2012
Beaufort Sea Canadian Eelpout, 2012–2013 Beaufort Sea Canadian Eelpout. Error bars
represent 1 standard deviation, and lower-case letters above bars represent significant
differences among sample sets (i.e., 2010, 2011, and 2012 Beaufort Sea Arctic Cod; 2011,
2012, and 2013 Chukchi Sea Arctic Cod; 2011 and 2012 Canadian Eelpout; 2012 and 2013
Longear Eelpout; P < 0.05); same letter means no difference. Bars are shaded according to
year.

Table 5. Length, Weight, and Lipid Content of Arctic Cod, Canadian Eelpout, and Longear Eelpout. Mean length (mm), weight (g), and total lipid content (g lipid/ g wet tissue) of Arctic Cod by region (Beaufort and Chukchi seas) and year (2010–2013), Canadian Eelpout by year (2011–2012), and Longear Eelpout by year (2012–2013). Values are reported as mean ± 1 standard deviation.

Beaufort Sea Arctic Cod			
	2011	**2012**	**2013**
Length (mm)	98.95 ± 26.84	126.74 ± 32.71	117.36 ± 26.38
Weight (g)	7.86 ± 6.46	14.13 ± 12.06	10.99 ± 6.53
Lipid Content (g lipid/ g wet tissue)	0.06 ± 0.01	0.03 ± 0.01	0.02 ± 0.01

Chukchi Sea Arctic Cod			
	2010	**2011**	**2012**
Length (mm)	89.64 ± 21.37	84.67 ± 24.73	118.30 ± 17.37
Weight (g)	5.39 ± 3.10	4.81 ± 6.26	12.13 ± 6.01
Lipid Content (g lipid/ g wet tissue)	0.03 ± 0.01	0.07 ± 0.02	0.06 ± 0.01

Beaufort Sea Canadian Eelpout		
	2011	**2012**
Length (mm)	101.53 ± 48.99	106.83 ± 56.34
Weight (g)	12.89 ± 27.69	11.96 ± 17.96
Lipid Content (g lipid/ g wet tissue)	0.02 ± 0.01	0.02 ± 0.00

Beaufort Sea Longear Eelpout		
	2012	**2013**
Length (mm)	214.41 ± 114.30	211.83 ± 99.23
Weight (g)	87.18 ± 98.06	103.60 ± 125.14
Lipid Content (g lipid/ g wet tissue)	0.02 ± 0.01	0.01 ± 0.01

in the PERMANOVA model, other factors (i.e., species, region, year) affected fatty acid profile beyond the observed differences based on weight alone (Tables 3 – 4).

Seventy-two fatty acids were identified and quantified for each sample, which accounted for an average of 90.1% of the total peak area measured (the remaining 9.9% included unidentified fatty acids and non-fatty acid molecules). Mean concentrations of fatty acids, fatty acid classes, and trophic markers by species, regions, and years are summarized in Appendix B Tables 11 – 16. When all samples were pooled across regions and years, fish species had a significant effect on fatty acid profile when fatty acids were expressed as μg fatty acid/ g wet tissue and mg fatty acid/ g lipid (P = 0.001; Tables 3 – 4). Most noticeably, Arctic Cod had a significantly different profile than those of both Eelpout species, in both tests with all samples pooled and comparisons with only 2012 samples from the Beaufort Sea (Tables 6 and 7, Figure 7a). The two Eelpout species, Canadian Eelpout and Longear Eelpout, did not demonstrate significantly different fatty acid profiles expressed in μg fatty acid/ g wet tissue when all sample years were pooled (P = 0.062; Table 6, Figure 7a). However, when data were converted to units of mg fatty acid/ g lipid, fatty acid profiles of Canadian Eelpout and Longear Eelpout did differ significantly (P = 0.001; Table 7).

Mean concentrations of individual fatty acids, fatty acid classes, and fatty acid trophic markers for Arctic Cod, Canadian Eelpout and Longear Eelpout are summarized in Appendix B Tables 11–16 as μg fatty acid/ g wet tissue and mg fatty acid/ g lipid. With all sample years pooled, Arctic Cod had higher concentrations of total MUFAs/ g wet tissue and as % of total fatty acids than Canadian and Longear Eelpout (P = 0.001 for both comparisons; Figure 8a and c). However, as total MUFAs/ g lipid, Longear Eelpout had the highest mean concentration of total MUFAs, followed by Arctic Cod and then Canadian Eelpout, with Longear and Canadian

Eelpout total MUFAs differing significantly (P = 0.042; Figure 8b). Arctic Cod and Longear

Eelpout also differed significantly in total SFA/ g wet tissue (P = 0.002), but all three species had

similar amounts of total PUFA (P = 0.926; Figure 8a). When converted to total SFAs/ g lipid and

PUFAs/ g lipid, mean concentrations of total SFAs and PUFAs were highest in Longear Eelpout,

followed by Canadian Eelpout, with Arctic Cod displaying the lowest mean concentrations of

both fatty acid classes and differing significantly from Longear Eelpout (SFA: P = 0.003, PUFA:

P = 0.001; Figure 8b).

Six fatty acids, 16:1ω7, 20:1ω9, 16:0, 22:1ω11, 22:6ω3, and 18:1ω9 *cis*, in order of

decreasing contribution, accounted for 64.5% of the dissimilarities in fatty acid profiles among

Arctic Cod and Eelpout species (Table 8 a–b; Figure 9). When concentration data were examined

in units of μg fatty acid/ g wet tissue, these six fatty acids had higher mean concentrations in

Arctic Cod than both Eelpout species. However, when data were expressed as mg fatty acid/ g

total lipid, 16:0, 22:6ω3, and 18:1ω9 *cis* displayed higher mean concentrations in Eelpout species

compared with Arctic Cod, and the mean concentration of 16:1ω7 was highest in Longear

Eelpout, followed by Arctic Cod and Canadian Eelpout. Mean concentrations of the long-chain

MUFAs 20:1ω9 and 22:1ω11 were significantly higher in Arctic Cod than both Eelpout species

(relative to both wet tissue weight and total lipid; P = 0.001 for both data types, fatty acids, and

species). Mean concentrations of non-methylene-interrupted fatty acids (NMIs), an indicator of

benthic food sources (Budge et al. 2007, Cooper et al. 2009), were highest in Longear Eelpout,

followed by Canadian Eelpout (Figure 10). NMIs 22:2Δ7,13 and 22:2Δ7,15 were significantly

higher in Longear Eelpout than Canadian Eelpout (P = 0.01 and 0.03, respectively). NMIs were

not identified in any Arctic Cod samples. The ratio of total ω7/ ω9 fatty acids for species group

means was also used as an indicator of benthic feeding (Budge et al. 2007). Canadian Eelpout

and Longear Eelpout displayed significantly higher ratios of ω7/ ω9 fatty acids compared with

Arctic Cod (P = 0.001; Figure 11).

Table 6. ANOSIM Tests for Differences in Fatty Acid Profiles Between Sample Sets Corrected to Total Tissue Mass. Results of ANOSIM test of fatty acid profiles (μg fatty acids/ g wet tissue) for differences among species (all samples pooled), test for among-species differences in Beaufort Sea fish (all years pooled), test for among-species differences in 2012 Beaufort Sea fish, test for regional and interannual differences in pooled Beaufort and Chukchi Sea Arctic Cod from 2011 and 2012, and tests for interannual differences in Beaufort Sea Arctic Cod (2011–2013), Chukchi Sea Arctic Cod (2010–2012), Canadian Eelpout (Beaufort Sea, 2011–2012), and Longear Eelpout (Beaufort Sea, 2012–2013). Significant P-values (P < 0.05) are given in bold.

Groups	R Statistic	P-value
All fishes		
Global Test	0.375	**0.001**
Arctic Cod vs. Canadian Eelpout	0.470	**0.001**
Arctic Cod vs. Longear Eelpout	0.400	**0.001**
Canadian Eelpout vs. Longear Eelpout	0.074	0.062
Beaufort Sea		
Global Test	0.258	**0.001**
Arctic Cod vs. Canadian Eelpout	0.352	**0.001**
Arctic Cod vs. Longear Eelpout	0.291	**0.001**
Canadian Eelpout vs. Longear Eelpout	0.074	0.061
Beaufort Sea 2012		
Global Test	0.198	**0.003**
Arctic Cod vs. Canadian Eelpout	0.231	**0.045**
Arctic Cod vs. Longear Eelpout	0.246	**0.001**
Canadian Eelpout vs. Longear Eelpout	0.044	0.302
Arctic Cod 2011 & 2012		
Beaufort Sea vs. Chukchi Sea	0.297	**0.001**
2011 vs. 2012	0.315	**0.001**
Arctic Cod Beaufort Sea		
Global Test	0.339	**0.001**
2011 vs. 2012	0.439	**0.001**
2011 vs. 2013	0.532	**0.001**
2012 vs. 2013	0.047	0.097

Table 6. Continued

Groups	R Statistic	P-value
Arctic Cod Chukchi Sea		
Global Test	0.386	**0.001**
2010 vs. 2011	0.627	**0.001**
2010 vs. 2012	0.513	**0.001**
2011 vs. 2012	0.166	**0.009**
Canadian Eelpout		
2011 vs. 2012	0.062	0.296
Longear Eelpout		
2012 vs. 2013	0.036	0.099

Figure 7. Multivariate Representation of Fatty Acid Profiles of Species, Regions, and Years. Non-metric multidimensional scaling (nMDS) plots of fatty acid profiles based on Bray-Curtis similarity matrices for *(a)* all samples, *(b)* 2011 and 2012 Arctic Cod from the Chukchi and Beaufort seas, *(c)* Beaufort Sea Arctic Cod, *(d)* Chukchi Sea Arctic Cod, *(e)* Beaufort Sea Canadian Eelpout, and *(f)* Beaufort Sea Longear Eelpout. Each data point represents the fatty acid profile of one individual fish.

Table 7. ANOSIM Tests for Differences in Fatty Acid Profiles Between Sample Sets Corrected to Total Lipid. Results of ANOSIM test of fatty acid profiles (mg fatty acids/ g lipid) for differences among species (all samples pooled), test for among-species differences in Beaufort Sea fish (all years pooled), test for among-species differences in 2012 Beaufort Sea fish, test for regional and interannual differences in pooled Beaufort and Chukchi Sea Arctic Cod from 2011 and 2012, and tests for interannual differences in Beaufort Sea Arctic Cod (2011–2013), Chukchi Sea Arctic Cod (2010–2012), Canadian Eelpout (Beaufort Sea, 2011–2012), and Longear Eelpout (Beaufort Sea, 2012–2013). Significant P-values (P < 0.05) are given in bold.

Groups	R Statistic	P-value
All fishes		
Global Test	0.466	**0.001**
Arctic Cod vs. Canadian Eelpout	0.528	**0.001**
Arctic Cod vs. Longear Eelpout	0.483	**0.001**
Canadian Eelpout vs. Longear Eelpout	0.222	**0.001**
Beaufort Sea		
Global Test	0.384	**0.001**
Arctic Cod vs. Canadian Eelpout	0.448	**0.001**
Arctic Cod vs. Longear Eelpout	0.424	**0.001**
Canadian Eelpout vs. Longear Eelpout	0.222	**0.001**
Beaufort Sea 2012		
Global Test	0.345	**0.001**
Arctic Cod vs. Canadian Eelpout	0.538	**0.003**
Arctic Cod vs. Longear Eelpout	0.377	**0.001**
Canadian Eelpout vs. Longear Eelpout	0.127	0.153
Arctic Cod 2011 & 2012		
Beaufort Sea vs. Chukchi Sea	0.197	**0.001**
2011 vs. 2012	0.302	**0.001**
Arctic Cod Beaufort Sea		
Global Test	0.217	**0.001**
2011 vs. 2012	0.360	**0.001**
2011 vs. 2013	0.291	**0.001**
2012 vs. 2013	0.025	0.193
Arctic Cod Chukchi Sea		
Global Test	0.337	**0.001**
2010 vs. 2011	0.712	**0.001**
2010 vs. 2012	0.231	**0.009**
2011 vs. 2012	0.231	**0.001**

Table 7. Continued.

Groups	R Statistic	Significance Level (P-value)
Canadian Eelpout		
2011 vs. 2012	-0.001	0.448
Longear Eelpout		
2012 vs. 2013	0.237	**0.001**
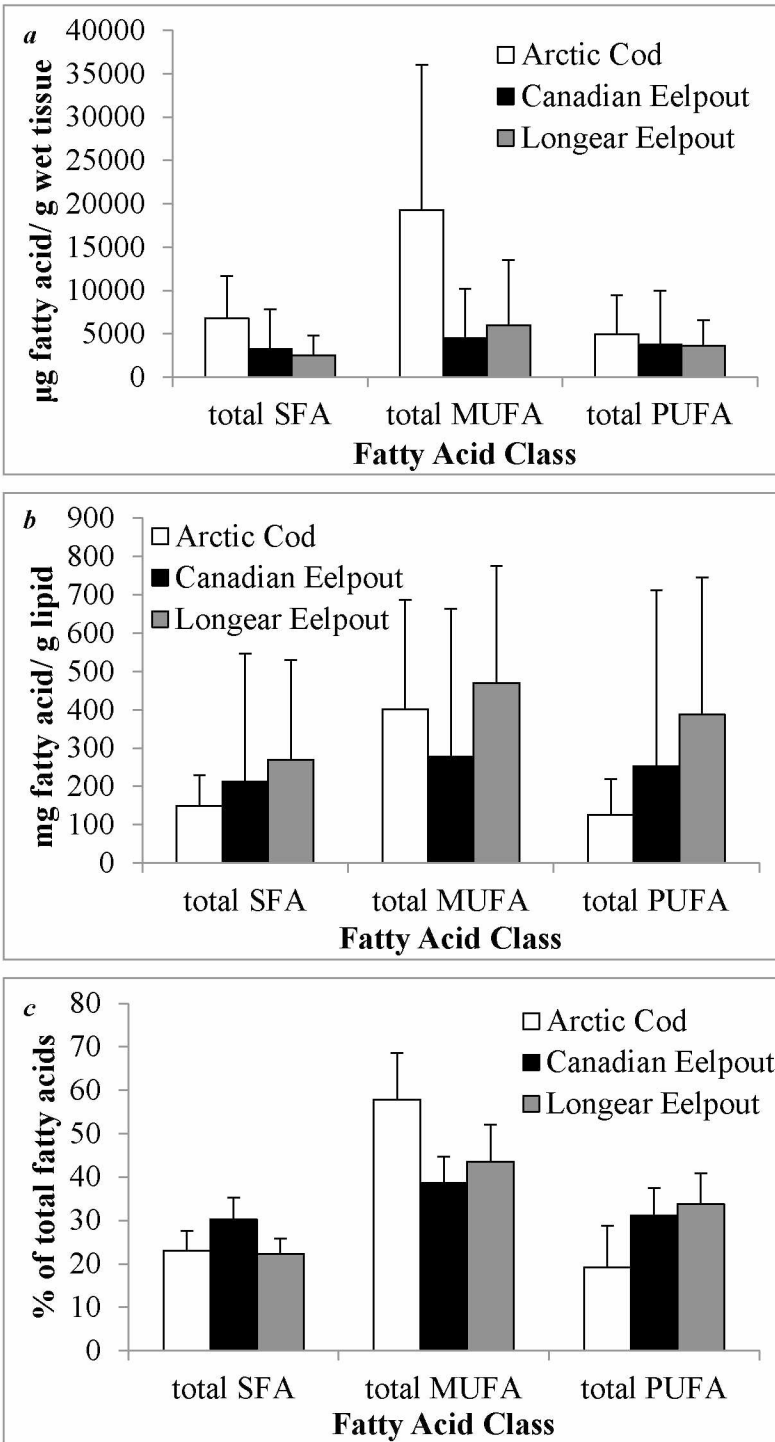
Figure 8. Variation in Major Fatty Acid Classes Among Arctic Cod and Eelpout Species. Mean concentration of fatty acids by class expressed as *(a)* μg fatty acid/ g wet tissue, *(b)* mg fatty acid/ g lipid, and *(c)* % of total fatty acids for saturated fatty acids (SFA), monounsaturated fatty acids (MUFA), and polyunsaturated fatty acids (PUFA). Bars are shaded according to species. Error bars represent 1 standard deviation.

Table 8. Individual Fatty Acids Contributing to Differences in Fatty Acid Profiles Between Sample Sets, Corrected to Total Tissue Mass. Average dissimilarity (Av. Diss) between sample sets and percent contribution of individual fatty acids to the dissimilarity between species, region, and year. Only fatty acids contributing up to 90% of cumulative dissimilarity among sample sets were reported. Dashes represent fatty acids that did not contribute up to the 90% cumulative dissimilarity among sample sets. Comparison between groups *(a)* Arctic Cod and Canadian Eelpout (Beaufort Sea 2012), *(b)* Arctic Cod and Longear Eelpout (Beaufort Sea 2012), *(c)* Chukchi and Beaufort seas Arctic Cod (2011 & 2012), *(d)* 2011 and 2012 Beaufort Sea Arctic Cod, *(e)* 2011 and 2013 Beaufort Sea Arctic Cod, *(f)* 2010 and 2011 Chukchi Sea Arctic Cod, *(g)* 2010 and 2012 Chukchi Sea Arctic Cod, and *(h)* 2011 and 2012 Chukchi Sea Arctic Cod. Comparisons were only reported for those that displayed significant differences based on ANOSIM (Table 6).

Comparison	*a*	*b*	*c*	*d*	*e*	*f*	*g*	*h*
Av. Diss.	57.38	53.16	41.83	48.83	54.65	40.75	46.83	33.92
14:0	3.91	4.17	5.58	5.17	5.55	7.39	6.47	4.44
16:0	10.82	10.44	10.35	9.35	10.98	9.46	8.55	8.18
16:1ω7	15.22	16.39	13.25	17.36	17.30	8.97	14.35	12.64
16:2ω4	-	-	-	-	-	-	-	0.84
17:0	-	-	-	-	-	-	1.08	1.16
18:0	1.85	1.40	1.46	1.14	1.31	-	1.15	1.27
18:1ω11	1.71	1.68	1.43	1.58	1.52	1.77	1.10	1.34
18:1ω9 *cis*	6.60	6.85	6.93	6.79	6.75	4.06	6.16	6.52
18:1ω7	4.10	3.99	3.61	3.44	3.46	1.61	3.55	3.99
18:1ω5	0.99	1.00	-	-	-	-	-	-
18:4ω3	-	-	0.95	-	-	-	1.34	1.43
20:1ω11	1.20	1.22	4.27	1.73	1.67	4.62	3.96	4.65
20:1ω9	14.07	13.90	16.94	17.48	17.79	26.09	18.09	15.48
20:1ω7	1.59	1.88	1.27	2.62	2.43	-	-	-
20:4ω6	1.71	2.45	-	-	-	-	-	-
20:5ω3	5.84	5.80	5.88	3.30	2.87	1.98	8.21	9.96
22:1ω11	10.42	10.49	11.86	12.38	11.74	18.82	10.75	11.02
22:1ω9	2.45	2.43	1.96	3.25	3.14	2.78	1.58	1.45
22:6ω3	8.14	6.28	4.35	4.67	3.50	2.64	4.21	5.67

Intraspecific variation

Regional differences in Arctic Cod

Within-species differences among regions were only examined for Arctic Cod as Eelpout were not collected in the Chukchi Sea. When pooled across years, mean Arctic Cod size did not significantly differ between the Chukchi and Beaufort seas ($P = 0.061$; Figure 5). Mean lipid content of Arctic Cod was higher in the Chukchi Sea than in the Beaufort Sea in 2011 and 2012 (Figure 6), but the difference was only significant in 2012 ($P = 0.001$). When data from all years were pooled, Arctic Cod had higher lipid content in the Chukchi Sea than in the Beaufort Sea ($P = 0.001$).
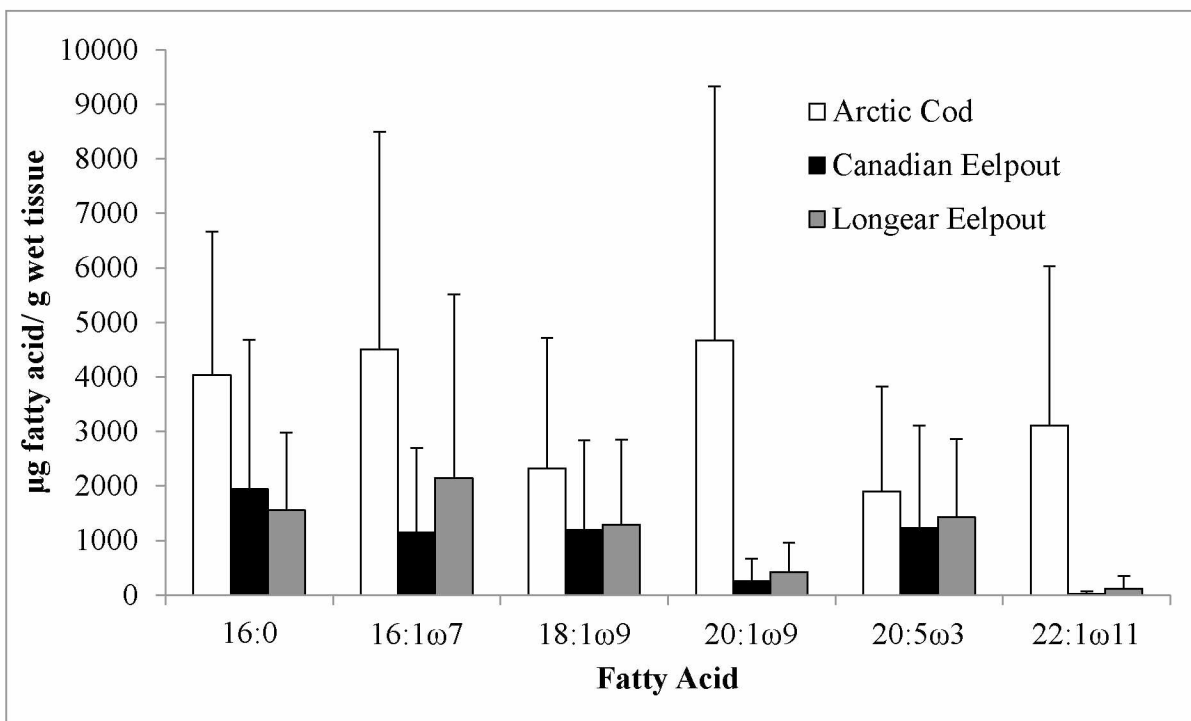
Figure 9. Mean Concentration of Individual Fatty Acids Contributing to Differences Among Arctic Cod and Eelpout Species. Fatty acids (μg fatty acid/ g wet tissue) that contribute the most to dissimilarity among species based on similarity percentages test (SIMPER). Error bars represent 1 standard deviation.

Fatty acid profiles of Arctic Cod also differed between the Chukchi and Beaufort seas (P = 0.001; Table 6, Figure 7b). However, when the variation explained by sampling depth was removed from the PERMANOVA model, region no longer had an effect on the fatty acid profile when expressed in relation to total lipid (P = 0.141), suggesting that apparent regional differences in fatty acid profiles may actually reflect differences in sampling depth (mean Beaufort Sea sampling depth was 236 m compared with 49 m in the Chukchi Sea). When fatty acid concentrations were expressed as μg fatty acid/ g wet tissue, region had a significant effect on fatty acid profile (P = 0.032) even when removing the effect of depth in the PERMANOVA model. However, when variation explained by fish weight was also removed, the regional effect disappeared (P = 0.066). This could suggest that sample depth and fish weight were better predictors of within-species variation in fatty acid profile than region alone.

The six fatty acids 20:1ω9, 16:1ω7, 22:1ω11, 16:0, 18:1ω9 *cis*, and 20:5ω3 (in order of decreasing contribution) contributed to 65.2% of the difference in Arctic Cod fatty acid

Figure 10. Non-Methylene-Interrupted Fatty Acids (NMI) in Eelpout Species. Mean concentrations of NMIs (μg fatty acid/ g wet tissue) for Canadian Eelpout and Longear Eelpout. Error bars represent 1 standard deviation.

profiles between regions with all years pooled (Table 8c, Figure 12). Concentrations of long-chain MUFAs exhibited some of the greatest differences between regions, such as 20:1ω9 (P = 0.001) and 22:1ω11 (P = 0.001). Essential fatty acid 20:5ω3 (EPA; μg/ g wet tissue) was significantly higher in Chukchi Sea Arctic Cod (P = 0.004; Figure 13a), but did not differ significantly from Beaufort Sea fish when expressed as mg/ g lipid or % of total fatty acid (P = 0.433 and 0.242, respectively; Figure 13b and c). The mean concentration of 22:6ω3 (DHA; μg/ g wet tissue) was slightly higher in Chukchi Sea Arctic Cod than in the Beaufort Sea, though not significantly different (P = 0.156; Figure 13a); however, when expressed as mg/ g lipid and % of total fatty acid, mean concentration of 22:6ω3 was significantly lower in Chukchi Sea fish (P = 0.028 and 0.001, respectively; Figure 13b and c).

Total SFA (P = 0.001), MUFA (P = 0.004), and PUFA (P = 0.012) per g wet tissue were higher in the Chukchi Sea than the Beaufort Sea (Figure 14a); however, when expressed on a total lipid basis, only total SFA were higher in the Chukchi Sea than the Beaufort Sea (P = 0.003), while total MUFA and PUFA were not significantly different (Figure 14b; P = 0.274 and 0.824, respectively) and

Figure 11. Comparison of ω7/ ω9 Fatty Acids among Forage Fish Species. Mean ratios of total ω7 to ω9 fatty acids for Arctic Cod, Canadian Eelpout, and Longear Eelpout. Error bars represent 1 standard deviation.

when expressed as % of total fatty acids total PUFA were lower in the Chukchi Sea than the Beaufort Sea (P = 0.018) and total SFA and MUFA did not change (P = 0.061 and 0.212, respectively; Figure 14c).

Interannual differences

In the Beaufort Sea, mean Arctic Cod weight did not differ between years (P = 0.084; Figure 5). However, lipid content (g lipid/ g wet tissue) in Beaufort Sea Arctic Cod was significantly higher in 2011 than 2012 and 2013 (P = 0.001; Figure 6). In Chukchi Sea Arctic Cod, both mean body weight and lipid content varied significantly with year (P = 0.001 and 0.001, respectively). Fish from 2012 in the Chukchi Sea had significantly higher mean weight than 2010 and 2011 (P = 0.001; Figure 5), while 2010 had significantly lower lipid content than 2011 and 2012 (P = 0.001; Figure 6).

When fatty acid profiles of Arctic Cod were examined within each region, they differed among years in almost all pairwise comparisons (Table 6, Figure 7c–d). In the Beaufort Sea, profiles differed significantly between 2011 and 2012 (P = 0.001) and 2011 and 2013 (P = 0.001), but not between 2012 and 2013 (P = 0.097; Table 6, Figure 7c). In the Chukchi Sea, profiles differed significantly among all three sampling years (2010–2011, P = 0.001; 2010–2012, P = 0.001; 2011–2012, P = 0.009; Table 6, Figure 7d).

In Beaufort Sea Arctic Cod, total SFA and MUFA decreased from 2011 to 2013 when data were expressed as μg fatty acid/ g wet tissue (P = 0.001 and 0.001, respectively ; Figure 15a). When expressed as mg fatty acid/g lipid total PUFA decreased from 2011 to 2013 (P = 0.001; Figure 15b), and when expressed as % of total fatty acid PUFA increased from 2011 to 2013 (P = 0.001; Figure 15c). The same fatty acids (14:0, 16:0, 16:1ω7, 18:1ω9 *cis*, 20:1ω9,
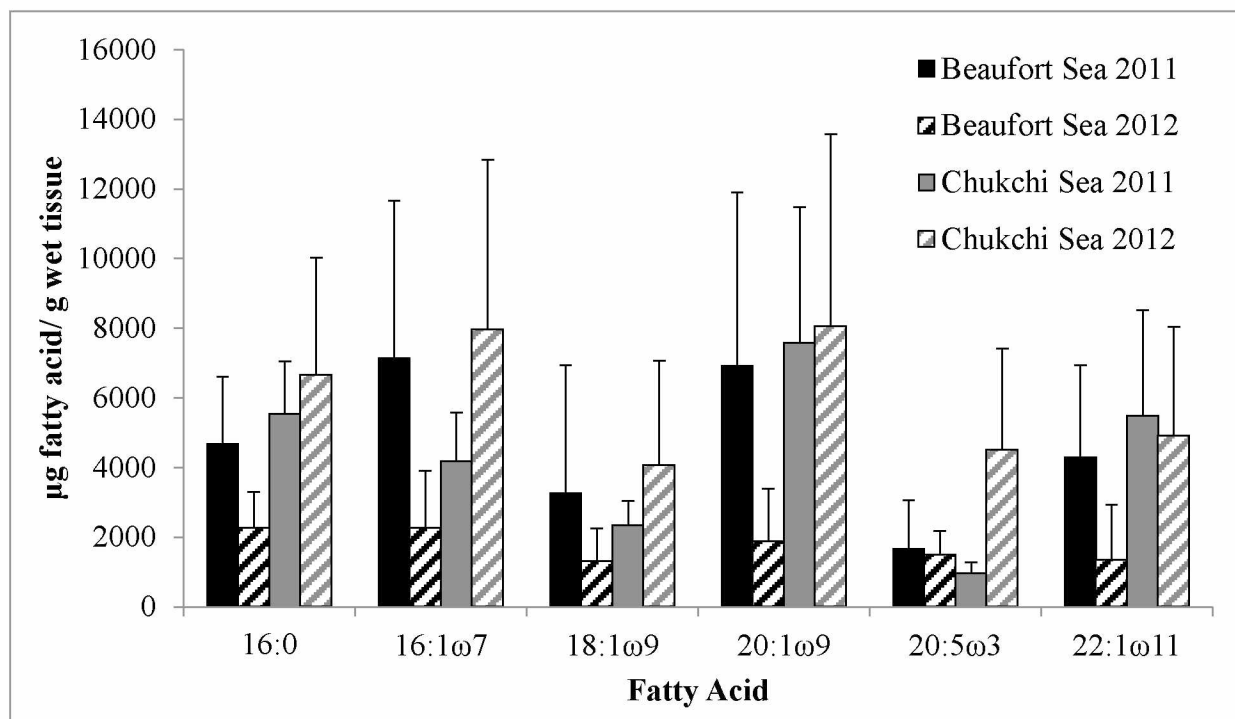
Figure 12. Mean Concentration of Individual Fatty Acids in Arctic Cod Contributing to Differences Among Regions and Years. Fatty acids (μg fatty acid/ g wet tissue) in Arctic Cod that contribute to the most dissimilarity among regions (Beaufort and Chukchi seas) and years (2011 and 2012) based on similarity percentages test (SIMPER). Error bars represent 1 standard deviation.

20:5ω3, 22:1ω11, 22:6ω3) contributed to the majority of differences among years in the Beaufort Sea as well as the Chukchi Sea Arctic Cod (Table 8d-e). However, while concentrations (μg fatty acid/ g wet tissue and mg fatty acid/ g lipid) of most of these eight fatty acids increased or did not change during the study period in the Chukchi Sea, they decreased in the Beaufort Sea (Figure 12). Two exceptions were 20:5ω3 and 22:6ω3, which increased significantly from 2011 to 2012 in the Beaufort Sea when fatty acid concentration was corrected to total lipid (P = 0.001 and 0.001, respectively).

When data were expressed as μg fatty acid/ g wet tissue, total SFA, MUFA, and PUFA increased from 2010 to 2012 in Chukchi Sea Arctic Cod (P = 0.001, 0.001, and 0.001; Figure 16a). Trends were similar when data were expressed as mg fatty acid/ g lipid (Figure 16b).

However, when data were expressed as % of total fatty acids total SFA decreased significantly from 2010 to 2011 (P = 0.001), total MUFA increased from 2010 to 2011 (P = 0.001) then decreased in 2012 (P = 0.001), and total PUFA was significantly lower in 2011 (P = 0.001; Figure 16c). When comparing all three sample years (2010–2012) for Chukchi Sea Arctic Cod, the fatty acid 20:1ω9, which has been used as an ice-algal marker (North et al. 2014), contributed to the most dissimilarity among years (Table 8f-h). The fatty acids 16:0 and 16:1ω7 showed a similar pattern of increase from 2010 to 2012 (P = 0.003 and 0.001, respectively), and mean concentrations of 20:1ω9 and 22:1ω11 increased from 2010 to 2011 (P = 0.001 and 0.001, respectively), but did not change significantly from 2011 to 2012 (P = 0.947 and 0.812, respectively; Figure 12).

Eelpout were only sampled in the Beaufort Sea, and each species was only sampled in two years. Canadian Eelpout were sampled in 2011 and 2012, and Longear Eelpout were sampled in 2012 and 2013. While no significant difference was found in fatty acid profiles between years for Canadian Eelpout when data were corrected to total wet tissue or lipid weight (2011 and 2012; P = 0.296 and 0.448, respectively), Longear Eelpout fatty acid profiles showed significant differences between years (2012 and 2013) when data were expressed as mg fatty acid/ g lipid (P = 0.001), but not when data were expressed as μg fatty acid/ g wet tissue (P = 0.099; Tables 5 and 6, Figure 7e–f). In order of decreasing contribution, fatty acids 16:0, 16:1ω7, 22:6ω3, 18:1ω9, 20:5ω3, and 18:1ω7 contributed to 65.1% of the difference between fatty acid profiles of Longear Eelpout from the two sampling years (Table 9, column m).
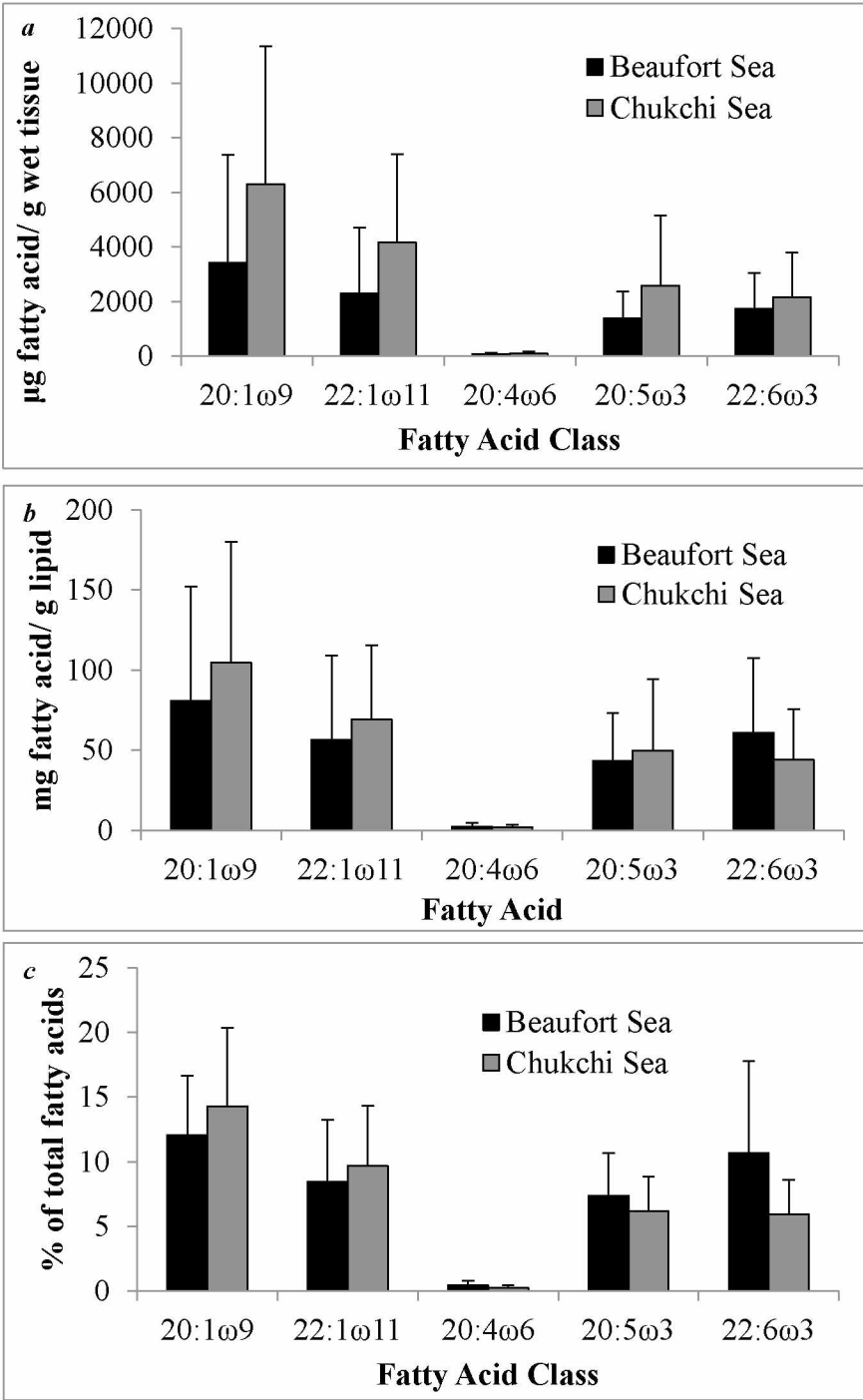
Figure 13. Fatty Acids in Beaufort and Chukchi sea Arctic Cod. Mean of *(a)* μg fatty acid/ g wet tissue, *(b)* mg fatty acid/ g lipid, and *(c)* % of total fatty acids for long chain MUFAs and PUFAs in Arctic Cod from the Beaufort and Chukchi seas. Bars are colored according to region. Error bars represent 1 standard deviation.
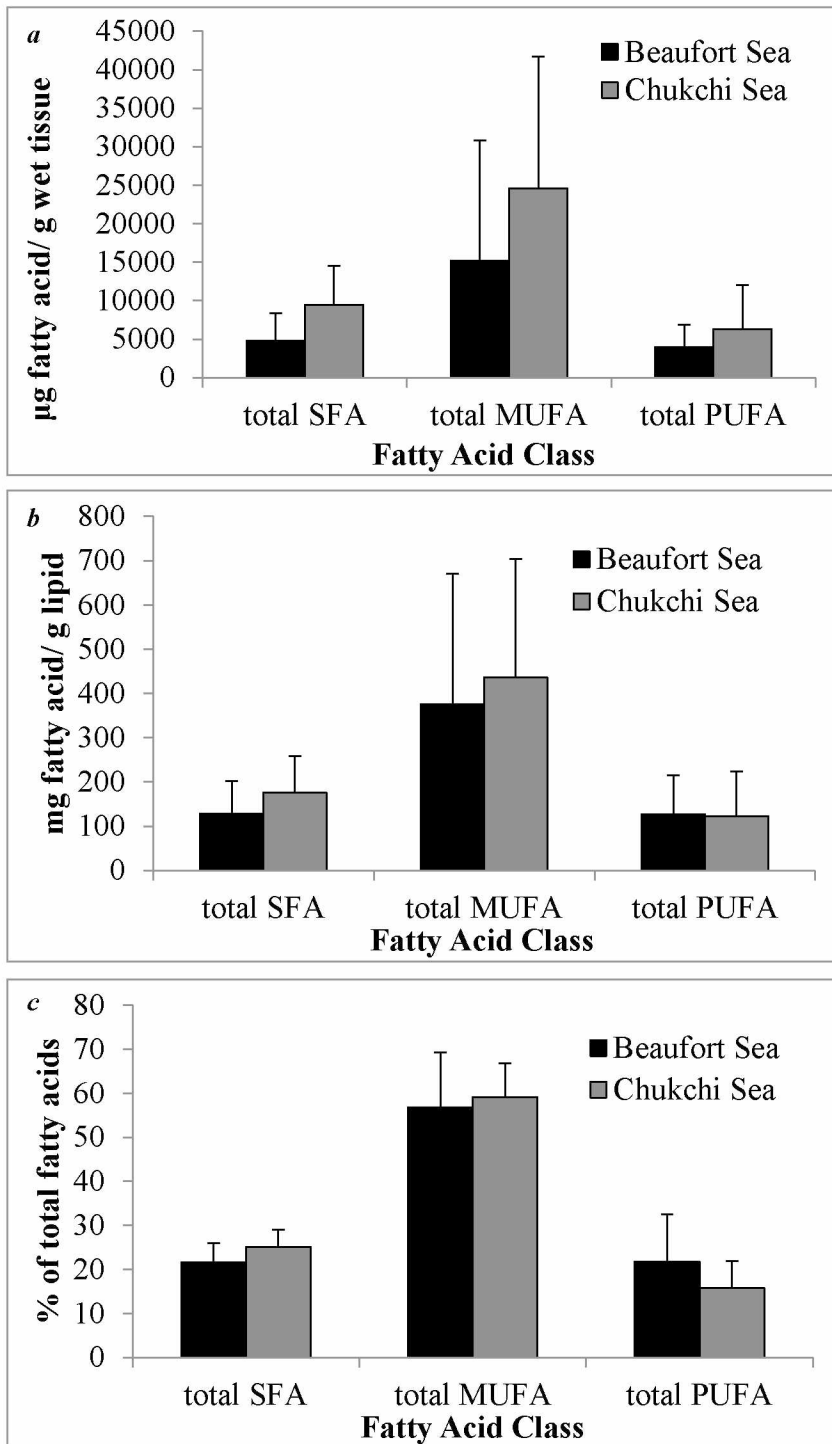
Figure 14. Regional Variation in Major Fatty Acid Classes for Arctic Cod. Mean concentrations of total fatty acids in each class expressed as *(a)* µg fatty acid/ g wet tissue, *(b)* mg fatty acid/ g lipid, and *(c)* % of total fatty acids for saturated fatty acids (SFA), monounsaturated fatty acids (MUFA), and polyunsaturated fatty acids (PUFA) for Beaufort and Chukchi seas Arctic Cod. Bars are colored according to region. Error bars represent 1 standard deviation.
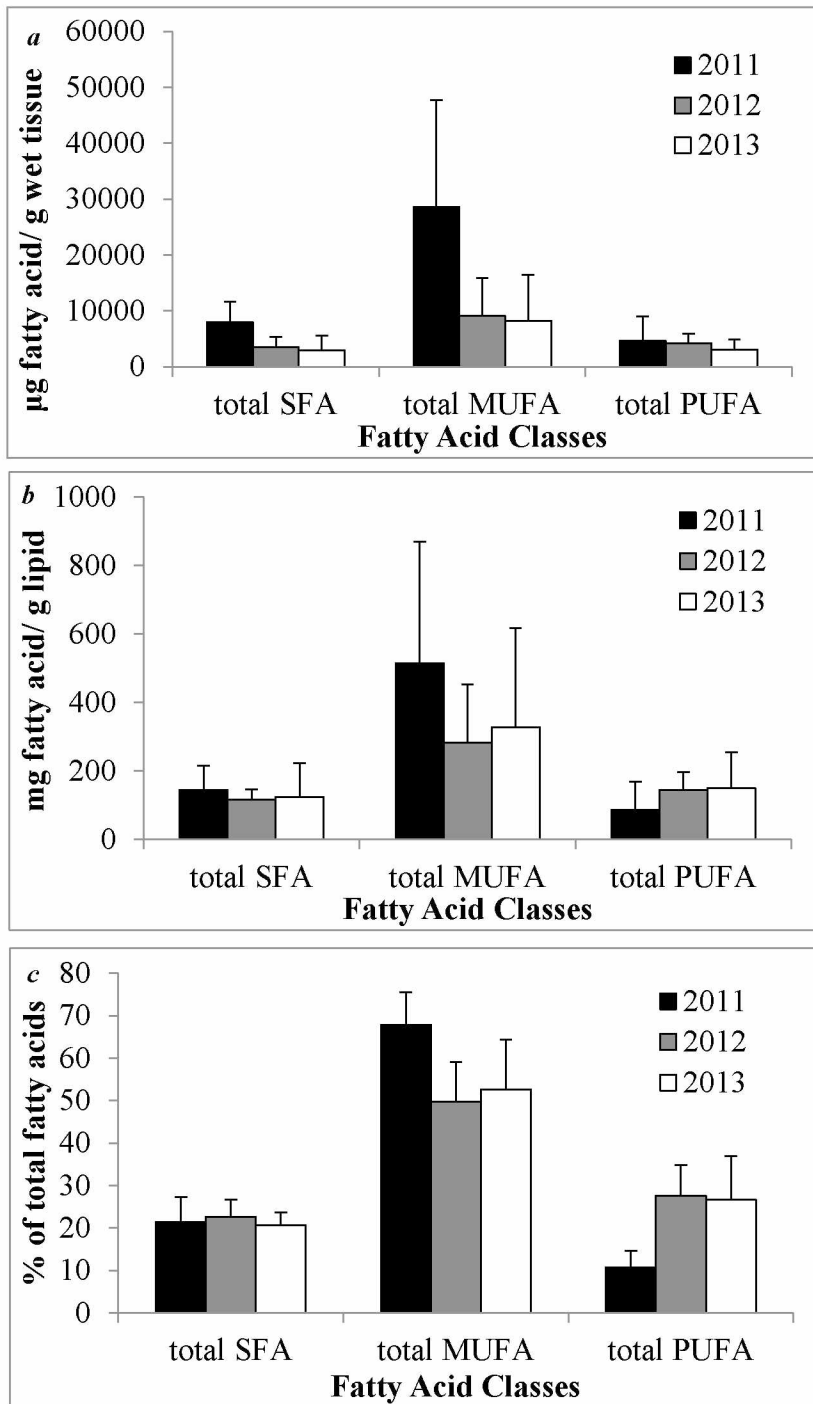
Figure 15. Temporal Variation in Major Fatty Acid Classes for Beaufort Sea Arctic Cod. Mean concentrations of total fatty acids in each class expressed as *(a)* μg fatty acid/ g wet tissue, *(b)* mg fatty acid/ g lipid, and *(c)* % of total fatty acids for saturated fatty acids (SFA), monounsaturated fatty acids (MUFA), and polyunsaturated fatty acids (PUFA) for Beaufort Sea Arctic Cod from 2011–2013. Bars are colored according to year. Error bars represent 1 standard deviation.
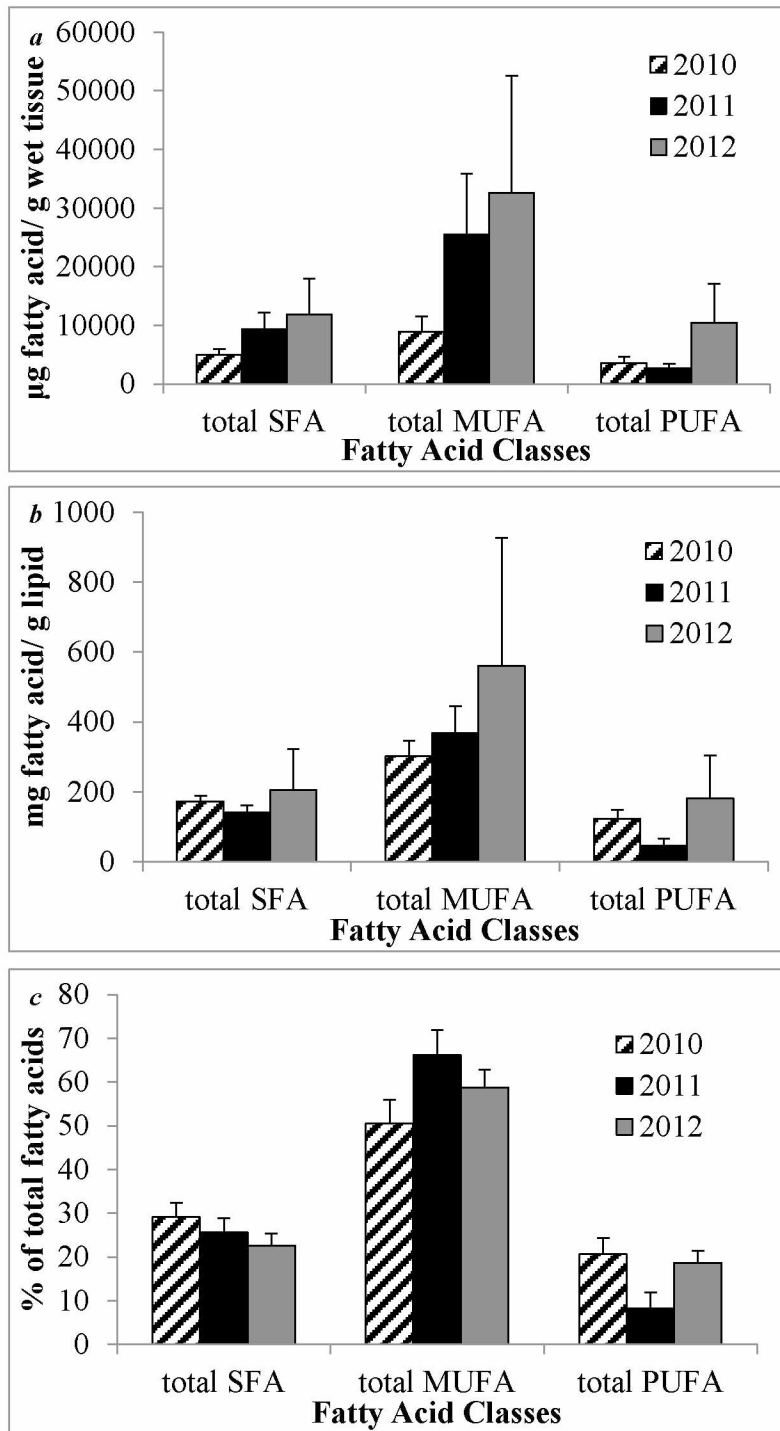
Figure 16. Temporal Variation in Major Fatty Acid Classes for Chukchi Sea Arctic Cod. Mean concentrations of total fatty acids in each class expressed as *(a)* µg fatty acid/ g wet tissue, *(b)* mg fatty acid/ g lipid, and *(c)* % of total fatty acids for saturated fatty acids (SFA), monounsaturated fatty acids (MUFA), and polyunsaturated fatty acids (PUFA) for Chukchi Sea Arctic Cod from 2010–2012. Bars are colored according to year. Error bars represent 1 standard deviation.

Table 9. Individual Fatty Acids Contributing to Differences in Fatty Acid Profiles Between Sample Sets, Corrected to Total Lipid. Average dissimilarity (Av. Diss) between sample sets and percent contribution of individual fatty acids to the dissimilarity between species, region, and year. Only fatty acids contributing up to 90% of cumulative dissimilarity among sample sets were reported. Dashes represent fatty acids that did not contribute up to the 90% cumulative dissimilarity among sample sets. Comparison between groups *(a)* Arctic Cod and Canadian Eelpout (Beaufort Sea 2012), *(b)* Arctic Cod and Longear Eelpout (Beaufort Sea 2012), *(c)* Canadian Eelpout and Longear Eelpout (Beaufort Sea 2012), *(d)* Chukchi and Beaufort seas Arctic Cod (2011 & 2012), *(e)* 2011 and 2012 Beaufort Sea Arctic Cod, *(f)* 2011 and 2013 Beaufort Sea Arctic Cod, *(g)* 2010 and 2011 Chukchi Sea Arctic Cod, *(h)* 2010 and 2012 Chukchi Sea Arctic Cod, *(k)* 2011 and 2012 Chukchi Sea Arctic Cod, and *(m)* 2012 and 2013 Longear Eelpout. Comparisons were only reported for those that displayed significant differences based on ANOSIM (Table 7).

Comparison	*a*	*b*	*c*	*d*	*e*	*f*	*g*	*h*	*k*	*m*
Av. Diss.	47.75	46.59	47.84	32.16	36.03	38.34	31.10	32.72	31.69	41.83
14:0	3.02	2.03	1.94	4.80	3.87	4.72	3.58	4.98	3.97	1.60
16:0	9.07	9.57	12.34	7.34	5.10	6.66	8.78	9.34	8.08	14.58
16:1ω7	12.41	11.77	13.64	14.98	14.99	15.42	6.30	11.70	13.65	13.21
16:1ω5	-	-	0.63	-	1.00	-	-	-	-	-
16:2ω4	-	-	-	-	-	-	-	-	0.96	-
17:0	-	-	-	-	-	-	-	-	1.31	-
18:0	2.99	3.71	3.88	1.43	1.49	1.46	3.86	2.81	1.49	5.17
18:1ω11	1.59	1.03	0.79	1.52	1.60	1.52	-	1.30	1.30	0.94
18:1ω9 *cis*	6.67	8.15	9.16	7.30	6.95	7.00	5.82	6.97	7.10	9.92
18:1ω7	5.73	7.21	7.26	3.97	3.30	3.25	4.95	4.48	4.48	6.78
18:1ω5	0.83	0.67	0.87	0.87	-	1.08	-	-	-	-
18:2ω6 *cis*	-	-	0.65	-	-	-	-	-	-	0.62
18:4ω3	-	-	-	1.02	-	-	-	1.21	1.61	-
20:1ω11	1.11	0.94	1.13	4.60	1.62	1.45	4.74	4.46	4.79	1.00
20:1ω9	12.56	7.47	3.82	14.83	14.58	15.21	18.31	16.62	13.15	4.08
20:1ω7	1.48	1.72	1.83	1.58	2.51	2.32	-	-	-	1.48
20:4ω6	3.12	6.06	5.33	-	-	-	-	-	-	6.13
20:5ω3	6.71	9.60	11.04	6.21	6.84	5.45	7.59	7.10	11.26	8.17

Table 9. Continued.

Comparison	a	B	c	d	e	f	g	h	k	m
22:1ω11	9.82	6.66	0.94	10.89	11.95	10.77	13.86	10.41	8.93	1.20
22:1ω9	2.22	1.36		1.95	3.02	2.67	1.89	1.35	1.16	-
22:5ω6	-	-	-	-	-	-	-	-	-	0.61
22:5ω3	0.78	1.42	1.54	-	-	-	-	-	0.74	1.27
22:6ω3	10.04	10.42	12.55	7.07	11.51	11.51	10.83	6.20	6.67	12.45
24:1ω9	-	0.74	0.87	-	-	-	-	-	-	1.18

DISCUSSION

This study investigated inter- and intra-species variations in fatty acid profiles, lipid content, and fatty acid trophic markers of Alaskan Arctic forage fish. Differing patterns in fatty acid classes, thus indicating variations in energy storage, suggest variable feeding conditions and fluctuations in forage fish quality as prey in the Alaskan Arctic. Regional and interannual variations in fatty acid profiles were observed in Arctic Cod from the Beaufort and Chukchi seas, potentially signifying that the Chukchi Sea supports a more energy-dense Arctic Cod than the Beaufort Sea. Variations in climate and ice conditions affecting food sources for forage fishes may cause interannual fluctuations in the fatty acid profile of this important prey base for higher trophic levels in either region. In addition to regional variation within Arctic Cod, this study measured significant differences in fatty acid profiles among different forage fish species in the Beaufort Sea. Differences in lipid content, fatty acid classes, and fatty acid trophic markers among Arctic Cod and Eelpout species are consistent with previous findings of Arctic Cod feeding on mainly pelagic prey (Lowry & Frost 1981, Bradstreet & Cross 1982, Ajiad & Gjøsæter 1990), and Eelpout feeding on mainly benthic prey (Aydin et al. 2007, Wienerroither et al. 2011). While there was some overlap in fatty acid profiles among species, these differences support differential habitat use between these three taxa in the Alaskan Arctic.

Species-specific variation in feeding preferences

This study demonstrated significant differences in fatty acid profiles between Arctic Cod and the two Eelpout species, confirming niche separation in foraging habits of these fishes. Previous studies have found that fish and invertebrates with similar foraging ecologies have similar fatty acid profiles, such that groups of similar species could be clustered through fatty

acid mixing models (Iverson et al. 2002). However, the utility of fatty acid tracers in food web studies is limited without accurate data on how their composition varies between species, and across regional and temporal scales. Furthermore, the interpretation of fatty acid data may change depending on how fatty acids are quantified.

In this study, differentiation of Eelpout species by fatty acid profile was dependent on data type and sampling year. Canadian Eelpout and Longear Eelpout could not be differentiated based on fatty acid profiles when concentrations were corrected to total wet tissue mass. In contrast, profiles of the two Eelpout species were distinguishable when data were corrected to total lipid. Subtle differences in diet may yield small differences in the composition and concentrations of fatty acids as a part of the total lipid pool in each species, but their nutritional value as prey items (as indicated by concentration of fatty acids per g of tissue mass) is likely similar. Interestingly, profiles were more similar between species in some years than in others, particularly when expressed as mg fatty acid/ g lipid. In 2012, the only year in which both Eelpout species were sampled, Canadian Eelpout did not differ significantly from Longear Eelpout for either form of data expression. Thus, inter-species differences observed when data are pooled across years could actually reflect interannual differences rather than real differences in foraging ecology between species. Based on fatty acid concentration relative to total tissue mass, Canadian Eelpout did not differ from 2011 to 2012, but Longear Eelpout did differ from 2012 to 2013. Longear Eelpout were also larger and had higher total lipid content in 2013, yet fatty acid concentrations (relative to total lipid content) of the top six fatty acids that contributed the most to differences between years (16:0, 16:1ω7, 22:6ω3, 18:1ω9 *cis*, 20:5ω3, and 18:1ω7) were higher in 2012 samples. Because Canadian Eelpout were not measured for 2013, the interannual differences observed in Longear Eelpout could be responsible for the differences in

fatty acid profiles of total pooled Eelpout species rather than true differences between the species.

Fatty acid trophic markers measured here confirm feeding differences between Arctic Cod and Eelpout species. Data on specific diets of Canadian Eelpout and Longear Eelpout have not been reported previously for the Beaufort Sea region, but Eelpout in the Bering Sea have shown a predominance of epibenthic feeding on invertebrates, such as shrimp, polychaetes, and mysids (Aydin et al. 2007). Not surprisingly, the ratio of $\omega7/\omega9$ fatty acids, a marker for benthic feeding (Budge et al. 2007), was higher in Eelpout than Arctic Cod. Additionally, NMIs, which indicate feeding on benthic gastropods and bivalves (Joseph 1982, Cooper et al. 2009), were only found in Eelpout species and were not present in any Arctic Cod samples. Some NMIs previously identified as benthic mollusk markers (22:2Δ7,13 and 22:2Δ7,15; Budge et al. 2007, Thiemann et al. 2007) were significantly higher in Longear Eelpout than Canadian Eelpout. As suggested by Budge et al. (2007) for marine mammals, the difference in NMIs may suggest that while both species are feeding on benthic prey, Canadian Eelpout and Longear Eelpout focus their feeding on different prey items.

Similar to what is reported here, Arctic Cod have previously been identified as having high levels of 20:1ω9 and 22:1ω11 indicative of pelagic feeding on calanoid copepods (Dahl et al. 2000). While SFAs and shorter chain MUFAs are abundant in marine food webs and can be synthesized by zooplankton and fishes (Ackman et al. 1980), marine fishes commonly lack the enzymes necessary to elongate short-chain to long-chain fatty acids, and must obtain these higher molecular weight MUFAs through diet (Bell et al. 1986). However, long-chain MUFAs such as 20:1ω9 and 22:1ω11 can be synthesized *de novo* by calanoid copepods, and their abundance in fish tissues has been taken to indicate consumption of large herbivorous copepods (Graeve et al.

1997, Scott et al. 2002). The relatively high levels of long-chain MUFAs we observed here suggest Arctic Cod is feeding on calanoid copepods. Alternatively, Arctic Cod could be feeding on predators of *Calanus* spp., such as carnivorous amphipods, which can have similar fatty acid signatures (Auel et al. 2002). While many studies indicate that Arctic Cod diet is made up of mainly copepods and other zooplankton species (Lowry & Frost 1981, Craig et al. 1982, Walkusz et al. 2013), Rand et al. (2013) focused on demersal Arctic Cod and reported a diet dominated by fishes. However, although samples used in this study were also collected in benthic trawls, the absence of NMIs and low levels of other markers indicative of benthic feeding suggest that Arctic Cod relied little on benthic prey. Rather, these results are consistent with stomach content analyses that indicate Beaufort and Chukchi sea Arctic Cod were feeding primarily on pelagic prey (Lowry & Frost 1981).

Recent work using compound-specific stable carbon isotope analyses of individual fatty acids has suggested that Beaufort Sea Arctic Cod are not ultimately dependent on sea ice-derived particulate organic matter for their fatty acids (Graham et al. 2014), although earlier studies indicated feeding on ice-associated calanoid copepods, which consume under-ice algae (Bradstreet & Cross 1982). Ice algal communities are commonly made up largely of diatoms, whereas open water phytoplankton commonly has relatively greater proportions of flagellates (Falk-Petersen et al. 1998, Von Quillfeldt et al. 2003). In Arctic systems, $16:1\omega7$ and $20:5\omega3$ have been used as indicators of diatoms in the food web, and these diatoms could be sea ice algae (Kirsch et al. 1998, Wang et al. 2014). High levels of diatom fatty acids ($16:1\omega7$ and $20:5\omega3$) and calanoid copepod fatty acids ($20:1\omega9$ and $22:1\omega11$) observed in Arctic Cod may suggest that they are dependent on copepods that feed on ice-associated algae. $20:1\omega9$ has also

been used as a marker of ice algae (North et al. 2014), so its high abundance in Arctic Cod further supports the link to sea ice-derived primary production.

The differences in fatty acid profiles across forage fishes suggest species-specific diets, yet physiological differences between species could also be contributing to the differences observed here. Differences in rates of organic matter assimilation can cause the chemical makeup of tissues to represent differing timescales (Weems et al. 2012). All fish were sampled in August and September, and are assumed to be exhibiting fatty acid profiles reflective of diet from similar time frames, but this assumption may be invalid if forage fishes have differing metabolic rates. For example, metabolic rates can be relatively high in visual predators, whereas deep-sea fishes, which are less likely to actively pursue prey, may have lower selective pressure for high metabolic rates (Seibel & Drazen 2007). Similarly, Arctic Cod feeding pelagically may have higher metabolic rates than the demersal (and presumably more sedentary) Eelpout species. While controlled diet studies have not been performed on the species here, new fatty acids from a change in diet may show up in fish lipid composition in as little as a few weeks (Skonberg et al. 1994, Kirsch et al. 1998). Because metabolic rates will affect the rate of incorporation of fatty acids into tissues (Tocher 2003), metabolic effects could be contributing to the inter-species differences observed here. Thus, if Arctic Cod metabolize lipids faster than Eelpout, their fatty acid profile will be representative of more recent seasonal feeding than Eelpout, which will display signatures from earlier in the season. The seasonal progression of phytoplankton communities coincides with a succession of lipid production that is then incorporated into zooplankton and on up the food web (Fraser et al. 1989, Pethybridge et al. 2014, Mayzaud & Boutoute 2015). Therefore, even if these fishes feed on similar diets, their fatty acid profiles may

reflect different timeframes, making interspecies studies using fatty acid profiles difficult to accurately interpret without experimental feeding studies or stomach content analysis.

Temporal and regional variations in feeding of Arctic Cod

The spatial variation observed in Arctic Cod fatty acid profiles may be influenced by large-scale regional differences in primary production and environmental characteristics in the Beaufort and Chukchi seas. Although Arctic Cod have a broad distribution throughout diverse habitats in both regions, (Lowry & Frost 1981, Carmack & Wassmann 2006, Crawford et al. 2012), concentrations of certain fatty acids such as 20:5ω3 were higher in the Chukchi Sea. The fatty acid 20:5ω3 is often interpreted as an indicator of the presence of diatoms or sea ice-derived particulate organic matter (Pethybridge et al. 2014, Wang et al. 2014). When combined with higher total lipid, SFA, and MUFA content, high 20:5ω3 concentration may also indicate a superior feeding environment of higher available lipid quality and/or quantity prey (Stowasser et al. 2012) in the Chukchi Sea relative to the Beaufort Sea. Due to processes required for biochemical breakdown, each double bond present in a fatty acid reduces the number of ATPs that can be derived in energy production, making SFAs the most energy dense fatty acid class followed by MUFAs (Trumble & Kanatous 2012). High concentrations of MUFAs in Chukchi Sea fish tissues may represent an energetic advantage, because MUFAs can be catabolized to generate metabolic energy more readily than PUFAs (Sargent et al. 1999). Higher total lipid content in Chukchi Sea Arctic Cod relative to the Beaufort Sea fish could make them better prey for higher trophic levels, although overall they were not higher in PUFAs, which are especially important to many physiological functions in fishes and their predators (Parrish 2013).

Regional differences in Arctic Cod were most apparent in 2012, which was a low-ice year that resulted in high primary productivity across the Arctic, especially in the Chukchi Sea (Dolan et al. 2014). Variation in lipid content and fatty acids have been tied to year-to-year variations in primary and secondary production in other regions as well (Pethybridge et al. 2014). While average PUFA content was similar in both regions, Chukchi Sea Arctic Cod did have elevated levels of PUFAs in 2012 over Beaufort Arctic Cod, providing further evidence of better feeding conditions in that year. Interestingly, the essential fatty acids 20:5ω3 and 22:6 ω3, generally thought to be indicators of fish health and nutritional quality (Sargent et al. 1999), were also high in 2012 Chukchi Sea Arctic Cod, although total lipid content was slightly lower. Although Arctic Cod use sea ice for feeding and protection against predators (Bradstreet & Cross 1982, Gradinger & Bluhm 2004), the high nutritional density of Arctic Cod during a low ice year could suggest that this species encounters favorable feeding conditions under this environmental regime. Consequently, Arctic Cod may continue to be a desirable food source under decreased sea ice levels. However, without controlled feeding experiments to measure the turnover rates of fatty acids in Arctic Cod, correlating fatty acid data to interannual or seasonal conditions is only speculative.

Similar to trends in the Chukchi Sea, when looking at concentration of fatty acids corrected to total lipid, Beaufort Sea Arctic Cod displayed an increase in the PUFAs 20:5ω3 and 22:6ω3 from 2011 to 2012. Alternatively, the significantly higher total SFA and MUFA in 2011 than 2012 in Beaufort Sea Arctic Cod suggests that periods of favorable feeding conditions in the Beaufort and Chukchi seas do not always coincide. Long chain MUFAs 20:1ω9 and 22:1ω11 decreased significantly from 2011 to 2012 in Beaufort Sea Arctic Cod, whereas there was no significant difference in in these fatty acids in Chukchi Sea Arctic Cod over the same time frame.

These results support differences in Arctic Cod fatty acid trends between the Chukchi and Beaufort seas and encourage the use of fatty acids in monitoring regional variations in ecosystem dynamics. However, in this study fish weight and collection depth were found to be significant covariates with fatty acid profile. Similarly, size-related shifts in prey items have been observed in Arctic Cod (Matley et al. 2013), and lipids change with length in sardine (Caponio et al. 2004). Differences in sampling depth between regions, or differences in the sizes of fish available for this study could be responsible for the differences in fatty acids observed between the Chukchi and Beaufort seas. Further analysis of Alaskan Arctic fish fatty acids over a greater size and depth range is needed to fully investigate the differences in Arctic Cod between the two Arctic regions.

Future directions

This study demonstrated the utility of fatty acid profiles for investigating within- and among-species variation in Arctic forage fishes. The total lipid content and specific fatty acid composition, essentially the quality of forage fish, are connected to the health and physiological condition of higher trophic level predators (Rosen & Trites 2005, Jeanniard du Dot et al. 2008). However, because this was a single trophic level study with no analysis of prey, lipid turnover, or other physiological measures, results cannot be definitively matched to specific diet items. While fatty acid trophic markers have been identified as useful indicators of prey items or food web trends (Graeve et al. 1994, St. John & Lund 1996, Falk-Petersen et al. 1998), the same fatty acids can be derived or vary from different sources, making it difficult to accurately delineate food sources. Future studies should attempt to mitigate this complication by incorporating fatty acid analysis of phytoplankton and zooplankton matched to region and year of study, as well as

utilizing other diet analysis techniques, such as stomach content and compound-specific stable isotopes to verify the trends observed in fatty acids.

As the Arctic is a region especially vulnerable to climate change in the coming years, tools for annual monitoring of key species are needed to assess ecosystem change. Significant variation was observed in fatty acid profiles of fish collected from different years. This suggests that fatty acids could be a useful tool in interannual monitoring, such that the nutritional content of these fish can indicate the energy transfer and nutritional quality of the food chain they are feeding on and how these fish vary in quality for higher trophic level predators. Other studies have shown fatty acid profiles to be useful in temporal studies of forage fishes (Pethybridge et al. 2014). In addition to monitoring species themselves, fatty acid profiles could be used as a tool to identify ecosystem variability (Iverson et al. 2007, Parrish et al. 2014, Pethybridge et al. 2015) and changes associated with high and low ice years.

Despite significant within-species variation based on sampling year and region, fatty acid profiles of Arctic Cod were significantly different than those of Eelpout in all forms of data expression. Conversely, the two Eelpout species were not reliably differentiated based on fatty acid profiles. These results are consistent with previous studies that found fatty acids profiles to be distinguished based on species groups of different foraging ecologies, though more difficult to discriminate between closely related species (Budge et al. 2002, Iverson et al. 2002). Where prey species or groups such as forage fish and invertebrates in the Alaskan Arctic can be defined by fatty acid profile regardless of regional or temporal variations, fatty acid analysis could be reliably used to estimate predator diets (Iverson,et al. 2004, Nordstrom et al. 2008, Wang et al. 2010).

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CONCLUSIONS

In summary, fatty acid profiles were consistent with previous diet studies of Alaskan Arctic forage fishes, supporting the use of fatty acids as tools for diet analysis along with traditional methods. Significant regional and interannual variation was also revealed, suggesting fluctuations in lipid transport through the food web. Vital nutrients, such as fatty acids, are transferred through the food web via forage species, and it is critical to assess spatial and temporal patterns in forage fish fatty acids to understand how their variability may influence regional food webs and higher trophic level consumers. A number of studies have demonstrated the utility of fatty acid profiles in diet analysis of Arctic top predators (Budge et al. 2008, Tucker et al. 2009, Loseto et al. 2009, Bromaghin et al. 2013), yet, all such studies depend on construction of a library of fatty acid data for relevant prey taxa. While this study documented significant within-species variation across regions and years, there was also evidence that regardless of sampling variables (region, year, depth, and weight), Arctic Cod and Eelpout can be distinguished based on fatty acid profile. This was consistent with other quantitative fatty acid studies that were able to classify prey to species groups based on fatty acid profiles despite regional, temporal, and body size variations (Iverson et al. 1997, 2002, Pethybridge et al. 2014). The information gained from this study can inform future food web modeling by indicating necessary levels of temporal and regional differences required to be included in prey libraries to capture natural lipid variability in forage fish species. However, it is important to note that inferences based on fatty acid profiles will depend on the form of data used (i.e., µg fatty acid/ g wet tissue versus mg fatty acid/ g lipid). When investigating the nutritional value of forage fish as prey, it is practical to use concentration of fatty acids in relation to total tissue mass because that is applicable to how they will be consumed by predators. Alternatively, when attempting to

use fatty acids as trophic markers or tracers of food web sources, it may be more effective to use

concentration of fatty acids in relation to total lipid. As demonstrated here, expressing fatty acids

as mg fatty acid/ g lipid may reveal similarities or differences in fatty acids when comparing fish

of differing lipid content that are not apparent in % of total fatty acids (a common approach in

food web studies) or μg fatty acid/ g wet tissue. In addition to providing information on the prey

base of higher trophic level predators in the Alaskan Arctic, the investigation of forage fish fatty

acids furthers our understanding of their diet habits and processes affecting the base of the food

web.

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Analysis of the Effect of Transformations on Data Interpretation

Select analyses were compared under multiple data transformations: square root, log(x+1), and untransformed data. Transformations were not found to differ in statistical significance of the main quantitative hypotheses tests from the original untransformed data (Table 9) or the visualization of data (Figure 17–19). Due to the lack of effect from transformation, all analyses were conducted and reported on untransformed data.

Table 10. Analysis of Transformations. Comparison of main statistical tests used to analyze differences in fatty acid profiles among species, regions, and years under no transformation, square root transformation, and log (x+1) transformation of sample data. Significant P-values (P < 0.05) are given in bold.

	No Transformation	Square Root	Log (x+1)
All fishes: PERMANOVA			
Weight	**0.004**	**0.003**	**0.009**
Depth	**0.001**	**0.001**	**0.001**
Species	**0.001**	**0.001**	**0.001**
Region	**0.001**	**0.001**	**0.001**
Year	**0.001**	**0.001**	**0.001**
Beaufort Sea 2012: ANOSIM			
Global Test	**0.002**	**0.001**	**0.001**
Arctic Cod vs. Canadian Eelpout	**0.041**	**0.002**	**0.014**
Arctic Cod vs. Longear Eelpout	**0.003**	**0.002**	**0.001**
Canadian Eelpout vs. Longear Eelpout	0.306	0.227	0.293
Arctic Cod 2011 & 2012: ANOSIM			
Beaufort Sea vs. Chukchi Sea	**0.001**	**0.001**	**0.001**
2011 vs. 2012	**0.001**	**0.001**	**0.001**
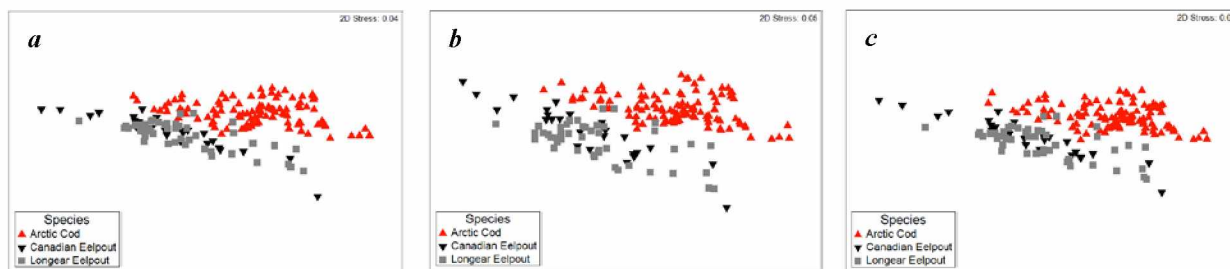
Figure 17. Effect of Transformations to all Fish Fatty Acid Profiles by Species. Non-metric multidimensional scaling (nMDS) plots of fatty acid profiles based on Bray-Curtis similarity matrices for all fish samples by species (Arctic Cod, Canadian Eelpout, and Longear Eelpout) with *(a)* no transformation, *(b)* square root, and *(c)* log(x+1) transformations.
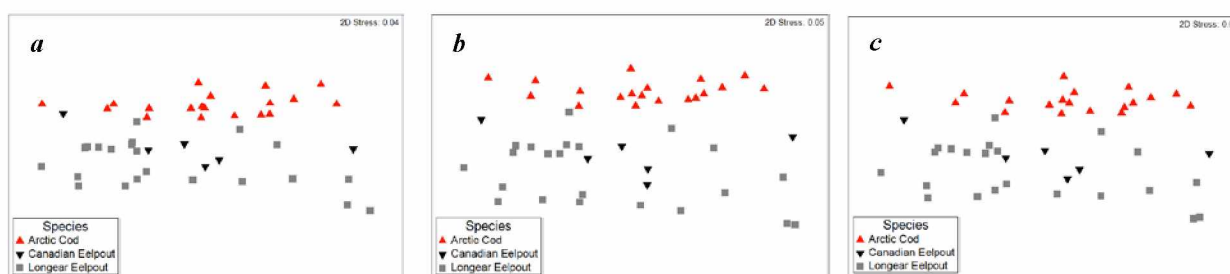
Figure 18. Effect of Transformations to Beaufort Sea Fish Fatty Acid Profiles by Species. Non-metric multidimensional scaling (nMDS) plots of fatty acid profiles based on Bray-Curtis similarity matrices for Beaufort Sea 2012 fish samples by species (Arctic Cod, Canadian Eelpout, and Longear Eelpout) with *(a)* no transformation, *(b)* square root, and *(c)* log(x+1) transformations.
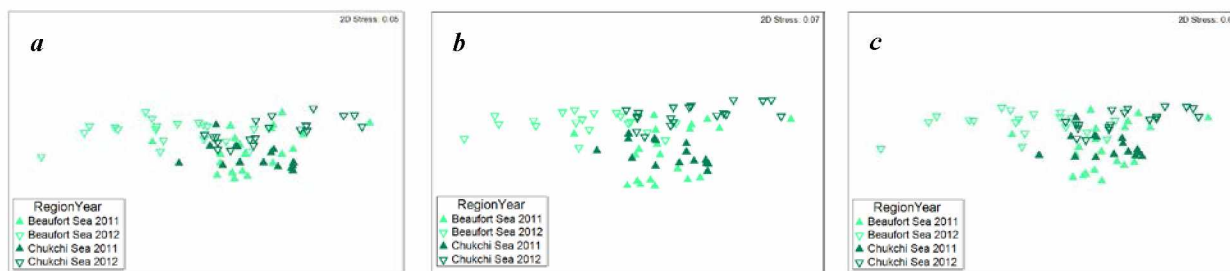
Figure 19. Effect of Transformations to Arctic Cod Fatty Acid Profiles by Region and Year. Non-metric multidimensional scaling (nMDS) plots of fatty acid profiles based on Bray-Curtis similarity matrices for 2011 and 2012 Arctic Cod from Beaufort and Chukchi seas with *(a)* no transformation, *(b)* square root, and *(c)* log(x+1) transformations.

Mean Concentrations of Fatty Acids, Fatty Acid Classes, and Trophic Markers by Species, Region, and Year.

Table 11. Fatty Acid Concentrations of Beaufort Sea Arctic Cod Corrected to Total Tissue Mass. Fatty acid concentrations in μg fatty acid/ g wet tissue of Beaufort Sea Arctic Cod by year (2011–2013). Values are reported as mean ± 1 standard deviation. (a) Calanoid copepod marker (Graeve et al. 1997, Auel et al. 2002, Falk-Petersen et al. 2002), (b) Carnivory marker (Graeve et al. 1997, Auel et al. 2002, Falk-Petersen et al. 2009), (c) Benthic feeding marker (Budge et al. 2007), (d) Diatom marker (Viso & Marty 1993, St. John & Lund 1996, Falk-Petersen et al. 2002), (e) Diatom versus dinoflagellate dominated system marker (Falk-Petersen et al. 2002, Dalsgaard et al. 2003).

	Arctic Cod - Beaufort Sea							
	2011			2012			2013		
Fatty Acids (μg fatty acid/ g wet tissue)								
10:0	24.70	±	36.54	28.68	±	10.11	0.17	±	0.38
11:0	25.79	±	23.34	2.18	±	4.92	0.00	±	0.00
12:0	75.81	±	36.45	15.47	±	12.09	8.80	±	8.29
13:0	17.15	±	12.48	2.67	±	3.62	1.86	±	4.43
iso 14:0	9.85	±	13.18	2.62	±	3.17	1.41	±	4.07
14:0	1957.33	±	881.67	575.05	±	400.80	573.12	±	875.76
14:1ω9	101.37	±	71.14	34.36	±	23.40	37.54	±	55.25
14:1ω7	11.62	±	15.51	5.37	±	4.41	1.71	±	3.94
14:1ω5	47.24	±	35.57	13.12	±	12.81	14.29	±	20.91
iso 15:0	121.31	±	130.31	37.48	±	24.83	21.17	±	27.29
anteiso 15:0	27.88	±	39.27	7.68	±	6.02	6.13	±	9.78
15:0	152.42	±	88.88	69.93	±	44.35	47.37	±	49.59
15:1	17.72	±	14.94	4.95	±	4.14	5.62	±	8.16
iso 16:0	31.39	±	39.90	18.30	±	8.31	3.05	±	5.15
anteiso 16:0	0.84	±	2.70	0.00	±	0.00	0.00	±	0.00
16:0	4686.27	±	1919.01	2275.49	±	1022.89	1879.52	±	1487.14

Table 11. Continued.

	Arctic Cod - Beaufort Sea							
	2011			2012			2013		
16:1ω11	193.32	±	155.55	66.06	±	44.15	49.61	±	46.61
16:1ω9	100.94	±	112.01	47.70	±	28.60	33.84	±	27.83
16:1ω7	7140.26	±	4516.04	2269.08	±	1642.10	2267.90	±	2441.11
16:1ω5	346.16	±	364.98	126.37	±	72.53	65.87	±	60.93
iso 17:0	47.06	±	48.42	28.75	±	16.92	21.84	±	19.57
16:1ω1	47.68	±	41.69	14.87	±	11.51	5.88	±	8.34
16:2ω6	9.48	±	9.37	7.01	±	5.89	0.00	±	0.00
anteiso 17:0	46.41	±	59.73	23.72	±	17.77	8.13	±	8.95
16:2ω4	136.68	±	87.01	63.25	±	43.44	52.01	±	52.63
17:0	117.26	±	115.82	59.28	±	36.48	30.47	±	36.11
16:3ω4	128.19	±	98.82	23.20	±	17.30	17.52	±	27.20
17:1ω9	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
18:0	628.33	±	429.51	409.36	±	176.92	284.36	±	180.84
18:1ω13	47.75	±	67.34	1.74	±	5.24	1.24	±	5.80
18:1ω9 *trans*	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
18:1ω11	714.66	±	725.98	293.92	±	241.36	226.22	±	187.80
18:1ω9 *cis*	3263.65	±	3669.08	1310.03	±	950.76	1073.69	±	943.92
18:1ω7	1664.59	±	1449.82	677.35	±	396.99	578.38	±	425.32
18:1ω5	527.73	±	581.24	188.33	±	121.06	107.49	±	109.31
18:2ω6 *cis*	215.57	±	247.92	98.55	±	79.49	91.33	±	74.12
18:2ω4	45.13	±	31.66	17.05	±	10.92	14.68	±	15.92
18:3ω6	5.84	±	14.37	17.98	±	15.22	3.04	±	4.49
18:3ω3	97.36	±	139.32	55.83	±	46.57	35.69	±	35.84
18:4ω3	197.55	±	221.15	117.47	±	102.53	68.08	±	82.07
18:4ω1	3.02	±	9.64	0.82	±	3.59	2.83	±	6.25

Table 11. Continued.

	Arctic Cod - Beaufort Sea								
	2011			2012			2013		
20:0	9.79	±	16.87	0.00	±	0.00	0.00	±	0.00
20:1ω13	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
20:1ω11	629.04	±	468.56	164.08	±	158.80	132.78	±	113.11
16:1ω5	346.16	±	364.98	126.37	±	72.53	65.87	±	60.93
iso 17:0	47.06	±	48.42	28.75	±	16.92	21.84	±	19.57
16:1ω1	47.68	±	41.69	14.87	±	11.51	5.88	±	8.34
16:2ω6	9.48	±	9.37	7.01	±	5.89	0.00	±	0.00
anteiso 17:0	46.41	±	59.73	23.72	±	17.77	8.13	±	8.95
16:2ω4	136.68	±	87.01	63.25	±	43.44	52.01	±	52.63
17:0	117.26	±	115.82	59.28	±	36.48	30.47	±	36.11
16:3ω4	128.19	±	98.82	23.20	±	17.30	17.52	±	27.20
17:1ω9	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
18:0	628.33	±	429.51	409.36	±	176.92	284.36	±	180.84
18:1ω13	47.75	±	67.34	1.74	±	5.24	1.24	±	5.80
18:1ω9 *trans*	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
18:1ω11	714.66	±	725.98	293.92	±	241.36	226.22	±	187.80
18:1ω9 *cis*	3263.65	±	3669.08	1310.03	±	950.76	1073.69	±	943.92
18:1ω7	1664.59	±	1449.82	677.35	±	396.99	578.38	±	425.32
18:1ω5	527.73	±	581.24	188.33	±	121.06	107.49	±	109.31
18:2ω6 *cis*	215.57	±	247.92	98.55	±	79.49	91.33	±	74.12
18:2ω4	45.13	±	31.66	17.05	±	10.92	14.68	±	15.92
18:3ω6	5.84	±	14.37	17.98	±	15.22	3.04	±	4.49
18:3ω3	97.36	±	139.32	55.83	±	46.57	35.69	±	35.84
18:4ω3	197.55	±	221.15	117.47	±	102.53	68.08	±	82.07

Table 11. Continued.

	Arctic Cod - Beaufort Sea							
	2011			2012			2013		
18:4ω1	3.02	±	9.64	0.82	±	3.59	2.83	±	6.25
20:0	9.79	±	16.87	0.00	±	0.00	0.00	±	0.00
20:1ω13	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
20:1ω11	629.04	±	468.56	164.08	±	158.80	132.78	±	113.11
20:1ω9	6921.81	±	4974.98	1883.35	±	1505.06	1600.67	±	1677.11
20:1ω7	821.12	±	605.09	144.87	±	151.01	220.71	±	309.65
22:2Δ5,11	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
22:2Δ5,13	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
20:1ω5	57.80	±	56.19	22.39	±	22.66	12.73	±	23.41
20:2ω9	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
20:2ω6	50.07	±	83.77	32.48	±	24.95	27.17	±	21.16
21:0	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
20:3ω6	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
20:4ω6	59.46	±	89.76	75.27	±	39.74	68.82	±	41.38
20:3ω3	8.46	±	37.83	0.00	±	0.00	0.00	±	0.00
20:4ω3	90.48	±	192.56	48.90	±	33.81	30.89	±	25.05
20:5ω3	1663.07	±	1390.17	1500.90	±	676.76	1028.05	±	651.51
22:0	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
22:1ω11	4294.41	±	2642.34	1358.39	±	1580.20	1315.25	±	1523.89
22:1ω9	1130.84	±	662.91	306.98	±	316.86	275.65	±	289.22
22:1ω7	291.67	±	208.85	58.66	±	65.54	81.85	±	105.11
22:2Δ7,13	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
22:2Δ7,15	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
21:5ω3	0.00	±	0.00	20.44	±	19.97	4.49	±	8.18
22:4ω6	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00

Table 11. Continued.

	Arctic Cod - Beaufort Sea					
	2011		2012		2013	
22:5ω6	0.00 ±	0.00	0.72 ±	2.25	1.56 ±	4.14
22:5ω3	149.49 ±	96.48	139.65 ±	83.67	96.23 ±	58.71
24:0	0.00 ±	0.00	0.92 ±	2.87	0.00 ±	0.00
22:6ω3	1752.73 ±	1975.22	1969.12 ±	714.94	1547.89 ±	863.52
24:1ω11	19.28 ±	30.56	1.39 ±	6.06	0.00 ±	0.00
24:1ω9	210.13 ±	129.20	129.73 ±	59.31	117.76 ±	103.78
24:1ω7	0.00 ±	0.00	0.00 ±	0.00	0.00 ±	0.00
Fatty Acid Classes (µg fatty acid/ g wet tissue)						
ΣSFA	7979.58 ±	3700.66	3557.58 ±	1734.44	2887.38 ±	2648.99
ΣMUFA	28600.79 ±	19172.82	9123.08 ±	6767.26	8226.68 ±	8234.08
ΣPUFA	4612.58 ±	4354.53	4188.63 ±	1747.01	3090.28 ±	1855.72
Fatty Acid Trophic Markers						
µg fatty acid/ g wet tissue						
20:1ω9 + 22:1ω11[a]	11216.22 ±	7102.32	3241.74 ±	2938.32	2915.92 ±	3180.53
Ratio						
18:1ω9/ 18:1ω7[b]	1.82 ±	0.46	1.89 ±	0.31	1.84 ±	0.45
ω7/ ω9 fatty acids[c]	0.87 ±	0.23	0.85 ±	0.26	0.95 ±	0.22
16:1ω7/ 16:0[d]	1.50 ±	0.75	0.87 ±	0.34	1.03 ±	0.49
20:5ω3/ 22:6ω3[e]	1.17 ±	0.57	0.75 ±	0.17	0.68 ±	0.25

Table 12. Fatty Acid Concentrations of Chukchi Sea Arctic Cod Corrected to Total Tissue Mass. Fatty acid concentrations in µg fatty acid/ g wet tissue of Chukchi Sea Arctic Cod by year (2010–2012). Values are reported as mean ± 1 standard deviation. (a) Calanoid copepod marker (Graeve et al. 1997, Auel et al. 2002, Falk-Petersen et al. 2002), (b) Carnivory marker (Graeve et al. 1997, Auel et al. 2002, Falk-Petersen et al. 2009), (c) Benthic feeding marker (Budge et al. 2007), (d) Diatom marker (Viso & Marty 1993, St. John & Lund 1996, Falk-Petersen et al. 2002), (e) Diatom versus dinoflagellate dominated system marker (Falk-Petersen et al. 2002, Dalsgaard et al. 2003).

Fatty Acids (µg fatty acid/ g wet tissue)	Arctic Cod - Chukchi Sea		
	2010	2011	2012
10:0	0.00 ± 0.00	2.36 ± 5.94	63.87 ± 39.58
11:0	0.00 ± 0.00	6.61 ± 5.71	28.00 ± 19.25
12:0	14.49 ± 3.77	50.05 ± 17.44	76.11 ± 51.15
13:0	6.27 ± 2.84	28.31 ± 14.51	13.39 ± 8.16
iso 14:0	1.11 ± 1.99	13.12 ± 6.02	14.16 ± 11.43
14:0	646.23 ± 155.94	2413.02 ± 1037.76	3006.58 ± 1559.26
14:1ω9	24.81 ± 14.93	84.50 ± 41.51	121.27 ± 79.97
14:1ω7	7.69 ± 3.86	12.38 ± 5.79	6.09 ± 9.06
14:1ω5	12.88 ± 3.43	45.05 ± 16.90	69.40 ± 48.19
iso 15:0	36.65 ± 12.54	130.61 ± 57.44	137.56 ± 96.07
anteiso 15:0	8.19 ± 3.16	36.68 ± 18.37	34.51 ± 28.38
15:0	97.58 ± 25.77	202.90 ± 76.78	190.22 ± 97.19
15:1	7.88 ± 7.55	17.51 ± 11.80	19.99 ± 20.05
iso 16:0	5.76 ± 8.44	36.57 ± 22.00	42.93 ± 28.49
anteiso 16:0	0.00 ± 0.00	0.00 ± 0.00	7.84 ± 14.20
16:0	3320.89 ± 634.00	5539.67 ± 1507.83	6671.24 ± 3350.78
16:1ω11	77.23 ± 22.54	239.20 ± 103.84	223.25 ± 146.54
16:1ω9	56.64 ± 13.64	88.75 ± 29.73	110.00 ± 73.49
16:1ω7	2250.49 ± 570.32	4178.27 ± 1404.52	7960.54 ± 4885.42

Table 12. Continued.

	2010			2011			2012		
Arctic Cod - Chukchi Sea									
16:1ω5	146.13	±	53.77	335.60	±	168.36	349.59	±	222.99
iso 17:0	69.75	±	23.93	101.94	±	33.21	67.46	±	34.88
16:1ω1	9.88	±	2.67	16.43	±	6.23	45.06	±	39.76
16:2ω6	0.00	±	0.00	0.00	±	0.00	46.81	±	29.64
anteiso 17:0	23.61	±	8.19	38.25	±	13.38	72.00	±	48.69
16:2ω4	59.52	±	15.61	86.21	±	30.84	379.29	±	235.03
17:0	53.15	±	17.00	65.07	±	21.09	476.44	±	432.32
16:3ω4	24.93	±	7.79	8.54	±	15.60	224.08	±	152.41
17:1ω9	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
18:0	718.02	±	200.99	705.67	±	194.47	962.74	±	555.09
18:1ω13	4.92	±	12.28	2.77	±	10.73	102.41	±	185.16
18:1ω9 *trans*	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
18:1ω11	255.11	±	159.41	648.69	±	261.49	532.05	±	400.85
18:1ω9 *cis*	1599.61	±	418.15	2350.33	±	699.33	4065.66	±	3002.59
18:1ω7	980.94	±	253.64	1103.33	±	295.86	2380.15	±	1778.10
18:1ω5	249.29	±	105.06	406.89	±	158.81	433.72	±	275.78
18:2ω6 *cis*	122.66	±	38.29	163.20	±	44.33	313.31	±	199.73
18:2ω4	25.53	±	5.27	30.78	±	15.03	73.04	±	46.35
18:3ω6	0.99	±	3.28	0.00	±	0.00	69.96	±	47.21
18:3ω3	54.77	±	21.48	60.63	±	19.74	184.69	±	137.24
18:4ω3	124.58	±	70.09	132.46	±	44.49	646.12	±	468.18
18:4ω1	0.00	±	0.00	0.00	±	0.00	58.06	±	45.18
20:0	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
20:1ω13	0.00	±	0.00	34.57	±	133.88	0.00	±	0.00
20:1ω11	533.67	±	469.52	1354.10	±	1394.57	1808.48	±	1406.06

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Table 12. Continued.

	2010			2011			2012		
				Arctic Cod - Chukchi Sea					
20:1ω9	1341.29	±	911.71	7589.57	±	3886.20	8054.56	±	5513.29
20:1ω7	83.75	±	18.58	231.38	±	68.62	286.89	±	192.73
22:2Δ5,11	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
22:2Δ5,13	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
20:1ω5	26.60	±	19.17	73.16	±	47.14	13.34	±	19.59
20:2ω9	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
20:2ω6	32.45	±	10.15	18.38	±	25.46	66.75	±	60.28
21:0	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
20:3ω6	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
20:4ω6	80.92	±	20.08	32.10	±	38.60	136.60	±	117.00
20:3ω3	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
20:4ω3	39.86	±	23.19	28.33	±	34.96	144.09	±	95.93
20:5ω3	1248.80	±	371.81	974.15	±	296.57	4517.68	±	2903.54
22:0	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
22:1ω11	971.30	±	790.96	5495.48	±	3023.13	4921.47	±	3123.96
22:1ω9	135.78	±	65.26	799.66	±	374.03	722.54	±	469.21
22:1ω7	16.16	±	18.78	127.91	±	76.81	110.05	±	70.93
22:2Δ7,13	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
22:2Δ7,15	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
21:5ω3	9.09	±	20.22	0.00	±	0.00	129.67	±	94.10
22:4ω6	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
22:5ω6	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
22:5ω3	81.89	±	31.16	47.70	±	48.21	283.40	±	171.99
24:0	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
22:6ω3	1669.79	±	492.05	1153.69	±	296.90	3196.11	±	2015.44

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Table 12. Continued.

	Arctic Cod - Chukchi Sea					
	2010		2011		2012	
24:1ω11	0.00 ±	0.00	0.00 ±	0.00	0.00 ±	0.00
24:1ω9	118.97 ±	36.17	250.82 ±	117.25	233.17 ±	122.15
24:1ω7	0.00 ±	0.00	1.37 ±	5.30	0.00 ±	0.00
Fatty Acid Classes (μg fatty acid/ g wet tissue)						
ΣSFA	5001.69 ±	998.36	9370.85 ±	2815.43	11865.07 ±	6135.08
ΣMUFA	8911.00 ±	2631.56	25487.71 ±	10364.24	32569.69 ±	19950.04
ΣPUFA	3575.79 ±	1084.61	2736.17 ±	758.56	10469.66 ±	6585.14
Fatty Acid Trophic Markers						
μg fatty acid/ g wet tissue						
20:1ω9 + 22:1ω11[a]	2312.60 ±	1636.83	13085.05 ±	6717.68	12976.03 ±	8549.38
Ratio						
18:1ω9/ 18:1ω7[b]	1.66 ±	0.28	2.14 ±	0.27	1.73 ±	0.18
ω7/ ω9 fatty acids[c]	1.13 ±	0.41	0.56 ±	0.19	0.82 ±	0.17
16:1ω7/ 16:0[d]	0.68 ±	0.10	0.75 ±	0.17	1.14 ±	0.28
20:5ω3/ 22:6ω3[e]	0.75 ±	0.07	0.85 ±	0.14	1.39 ±	0.19

Table 13. Fatty Acid Concentrations of Beaufort Sea Arctic Cod Corrected to Total Lipid.
Fatty acid concentrations in mg fatty acid/ g lipid of Beaufort Sea Arctic Cod by year (2011–2013). Values are reported as mean ± 1 standard deviation. (a) Calanoid copepod marker (Graeve et al. 1997, Auel et al. 2002, Falk-Petersen et al. 2002), (b) Carnivory marker (Graeve et al. 1997, Auel et al. 2002, Falk-Petersen et al. 2009), (c) Benthic feeding marker (Budge et al. 2007), (d) Diatom marker (Viso & Marty 1993, St. John & Lund 1996, Falk-Petersen et al. 2002), (e) Diatom versus dinoflagellate dominated system marker (Falk-Petersen et al. 2002, Dalsgaard et al. 2003).

Arctic Cod - Beaufort Sea								
	2011			2012			2013	
Fatty Acids (mg fatty acid/ g lipid)								
10:0	0.44	±	0.68	1.05	±	0.44	0.01	±	0.03
11:0	0.46	±	0.43	0.05	±	0.11	0.00	±	0.00
12:0	1.40	±	0.71	0.48	±	0.29	0.39	±	0.33
13:0	0.31	±	0.23	0.07	±	0.08	0.06	±	0.15
iso 14:0	0.18	±	0.24	0.07	±	0.07	0.05	±	0.14
14:0	35.23	±	16.28	17.51	±	7.25	22.05	±	30.34
14:1ω9	1.83	±	1.31	1.12	±	0.62	1.45	±	1.95
14:1ω7	0.22	±	0.28	0.16	±	0.11	0.06	±	0.14
14:1ω5	0.85	±	0.65	0.36	±	0.25	0.53	±	0.72
iso 15:0	2.23	±	2.41	1.16	±	0.44	0.82	±	0.93
anteiso 15:0	0.52	±	0.72	0.23	±	0.11	0.23	±	0.34
15:0	2.77	±	1.65	2.20	±	0.70	1.96	±	1.75
15:1	0.32	±	0.27	0.14	±	0.11	0.18	±	0.26
iso 16:0	0.59	±	0.74	0.62	±	0.19	0.11	±	0.18
anteiso 16:0	0.02	±	0.08	0.00	±	0.00	0.00	±	0.00
16:0	85.30	±	36.63	75.83	±	18.02	82.72	±	59.76
16:1ω11	3.54	±	2.89	2.05	±	0.78	2.11	±	1.68
16:1ω9	1.87	±	2.08	1.58	±	0.78	1.47	±	0.99
16:1ω7	127.92	±	82.34	68.31	±	35.77	88.52	±	88.34
16:1ω5	6.37	±	6.82	4.08	±	1.51	2.72	±	2.10
iso 17:0	0.88	±	0.91	0.92	±	0.27	0.92	±	0.68
16:1ω1	0.86	±	0.76	0.46	±	0.28	0.22	±	0.30
16:2ω6	0.18	±	0.17	0.20	±	0.14	0.00	±	0.00
anteiso 17:0	0.88	±	1.12	0.71	±	0.32	0.33	±	0.29
16:2ω4	2.46	±	1.57	1.98	±	1.19	1.98	±	1.75
17:0	2.10	±	2.10	1.97	±	0.97	1.32	±	1.51
16:3ω4	2.29	±	1.81	0.69	±	0.40	0.64	±	0.90
17:1ω9	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00

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Table 13. Continued.

	Arctic Cod - Beaufort Sea								
	2011			2012			2013		
18:0	11.62	±	8.18	13.83	±	3.37	13.36	±	9.18
18:1ω13	0.82	±	1.23	0.04	±	0.11	0.10	±	0.47
18:1ω9 *trans*	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
18:1ω11	13.11	±	13.47	9.24	±	6.67	9.67	±	8.28
18:1ω9 *cis*	60.12	±	68.36	40.95	±	16.40	46.02	±	32.12
18:1ω7	30.48	±	26.98	21.87	±	8.55	25.07	±	17.12
18:1ω5	9.66	±	10.90	5.93	±	2.33	4.38	±	3.79
18:2ω6 *cis*	3.99	±	4.63	3.07	±	1.51	3.99	±	2.97
18:2ω4	0.82	±	0.58	0.54	±	0.28	0.58	±	0.60
18:3ω6	0.11	±	0.28	0.52	±	0.36	0.13	±	0.17
18:3ω3	1.82	±	2.57	1.67	±	0.82	1.52	±	1.31
18:4ω3	3.63	±	4.08	3.47	±	1.93	2.91	±	3.20
18:4ω1	0.05	±	0.16	0.02	±	0.09	0.08	±	0.18
20:0	0.16	±	0.27	0.00	±	0.00	0.00	±	0.00
20:1ω13	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
20:1ω11	11.60	±	8.95	5.15	±	4.47	5.48	±	4.39
20:1ω9	124.57	±	91.94	57.14	±	33.75	61.19	±	56.16
20:1ω7	14.26	±	10.45	4.57	±	4.82	8.63	±	11.17
22:2Δ5,11	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
22:2Δ5,13	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
20:1ω5	1.02	±	1.04	0.65	±	0.55	0.45	±	0.82
20:2ω9	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
20:2ω6	0.95	±	1.56	0.99	±	0.49	1.19	±	0.92
21:0	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
20:3ω6	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
20:4ω6	1.17	±	1.71	2.71	±	1.36	3.52	±	2.46
20:3ω3	0.14	±	0.61	0.00	±	0.00	0.00	±	0.00
20:4ω3	1.68	±	3.47	1.52	±	0.68	1.39	±	1.26
20:5ω3	30.83	±	26.27	51.16	±	19.41	48.61	±	36.57
22:0	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
22:1ω11	76.39	±	46.55	42.95	±	53.70	50.75	±	53.29
22:1ω9	19.86	±	11.45	10.03	±	10.88	10.78	±	10.01
22:1ω7	5.05	±	3.57	1.90	±	2.29	3.22	±	3.86
22:2Δ7,13	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
22:2Δ7,15	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
21:5ω3	0.00	±	0.00	0.61	±	0.52	0.21	±	0.33
22:4ω6	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00

Table 13. Continued.

	Arctic Cod - Beaufort Sea								
	2011			2012			2013		
22:5ω6	0.00	±	0.00	0.04	±	0.11	0.11	±	0.29
22:5ω3	2.74	±	1.79	4.87	±	2.93	4.58	±	3.47
24:0	0.00	±	0.00	0.05	±	0.16	0.00	±	0.00
22:6ω3	33.29	±	37.54	70.48	±	28.88	77.96	±	55.37
24:1ω11	0.31	±	0.50	0.06	±	0.25	0.00	±	0.00
24:1ω9	3.82	±	2.42	4.49	±	1.79	5.15	±	3.80
24:1ω7	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
Fatty Acid Classes (mg fatty acid/ g lipid)									
ΣSFA	145.11	±	69.87	116.76	±	28.76	124.33	±	99.00
ΣMUFA	514.85	±	354.45	283.22	±	169.13	328.12	±	288.64
ΣPUFA	86.15	±	82.34	144.55	±	52.06	149.40	±	105.83
Fatty Acid Trophic Markers									
mg fatty acid/ g lipid									
20:1ω9 + 22:1ω11[a]	200.96	±	130.21	100.09	±	85.29	111.93	±	108.74
Ratio									
18:1ω9/ 18:1ω7[b]	1.82	±	0.46	1.89	±	0.31	1.84	±	0.45
ω7/ ω9 fatty acids[c]	0.87	±	0.23	0.85	±	0.26	0.95	±	0.22
16:1ω7/ 16:0[d]	1.50	±	0.75	0.87	±	0.34	1.03	±	0.49
20:5ω3/ 22:6ω3[e]	1.17	±	0.57	0.75	±	0.17	0.68	±	0.25

Table 14. Fatty Acid Concentrations of Chukchi Sea Arctic Cod Corrected to Total Lipid.
Fatty acid concentrations in mg fatty acid/ g lipid of Chukchi Sea Arctic Cod by year (2010–2012). Values are reported as mean ± 1 standard deviation. (a) Calanoid copepod marker (Graeve et al. 1997, Auel et al. 2002, Falk-Petersen et al. 2002), (b) Carnivory marker (Graeve et al. 1997, Auel et al. 2002, Falk-Petersen et al. 2009), (c) Benthic feeding marker (Budge et al. 2007), (d) Diatom marker (Viso & Marty 1993, St. John & Lund 1996, Falk-Petersen et al. 2002), (e) Diatom versus dinoflagellate dominated system marker (Falk-Petersen et al. 2002, Dalsgaard et al. 2003).

Arctic Cod - Chukchi Sea								
	2010			2011			2012	
Fatty Acids (mg fatty acid/ g lipid)								
10:0	0.00	±	0.00	0.03	±	0.07	1.11	±	0.78
11:0	0.00	±	0.00	0.08	±	0.06	0.47	±	0.33
12:0	0.51	±	0.18	0.75	±	0.16	1.29	±	0.89
13:0	0.22	±	0.08	0.40	±	0.12	0.23	±	0.14
iso 14:0	0.03	±	0.06	0.19	±	0.05	0.24	±	0.20
14:0	22.12	±	3.14	34.95	±	7.48	51.85	±	29.65
14:1ω9	0.82	±	0.44	1.21	±	0.37	2.05	±	1.38
14:1ω7	0.26	±	0.13	0.19	±	0.07	0.10	±	0.16
14:1ω5	0.45	±	0.13	0.67	±	0.18	1.19	±	0.88
iso 15:0	1.23	±	0.23	1.89	±	0.47	2.35	±	1.70
anteiso 15:0	0.27	±	0.06	0.52	±	0.16	0.59	±	0.50
15:0	3.35	±	0.69	2.99	±	0.61	3.26	±	1.77
15:1	0.25	±	0.22	0.26	±	0.17	0.33	±	0.34
iso 16:0	0.20	±	0.28	0.51	±	0.23	0.74	±	0.50
anteiso 16:0	0.00	±	0.00	0.00	±	0.00	0.14	±	0.28
16:0	114.38	±	11.73	84.24	±	13.96	114.89	±	64.50
16:1ω11	2.62	±	0.40	3.47	±	0.79	3.85	±	2.70
16:1ω9	1.94	±	0.33	1.34	±	0.36	1.91	±	1.40
16:1ω7	77.96	±	17.38	62.61	±	15.87	137.41	±	93.35
16:1ω5	4.88	±	0.93	4.77	±	1.22	6.00	±	4.02
iso 17:0	2.37	±	0.60	1.53	±	0.31	1.16	±	0.63
16:1ω1	0.34	±	0.06	0.26	±	0.09	0.78	±	0.74
16:2ω6	0.00	±	0.00	0.00	±	0.00	0.80	±	0.54
anteiso 17:0	0.80	±	0.19	0.58	±	0.18	1.23	±	0.87
16:2ω4	2.05	±	0.39	1.34	±	0.48	6.55	±	4.40
17:0	1.81	±	0.44	1.00	±	0.30	8.43	±	8.61
16:3ω4	0.86	±	0.25	0.18	±	0.33	3.84	±	2.70
17:1ω9	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00

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Table 14. Continued.

	Arctic Cod - Chukchi Sea								
	2010			**2011**			**2012**		
18:0	24.59	±	5.03	11.31	±	4.86	16.55	±	10.11
18:1ω13	0.21	±	0.54	0.06	±	0.24	1.77	±	3.18
18:1ω9 *trans*	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
18:1ω11	8.21	±	4.23	9.54	±	2.50	9.20	±	7.23
18:1ω9 *cis*	54.74	±	9.12	36.64	±	12.27	70.51	±	56.37
18:1ω7	34.21	±	9.16	17.43	±	6.45	41.57	±	34.89
18:1ω5	8.22	±	2.18	5.97	±	1.41	7.45	±	4.95
18:2ω6 *cis*	4.16	±	0.68	2.55	±	0.78	5.38	±	3.59
18:2ω4	0.88	±	0.14	0.49	±	0.23	1.27	±	0.87
18:3ω6	0.04	±	0.14	0.00	±	0.00	1.20	±	0.88
18:3ω3	1.87	±	0.55	0.96	±	0.38	3.16	±	2.42
18:4ω3	4.17	±	1.72	2.19	±	1.07	10.98	±	7.97
18:4ω1	0.00	±	0.00	0.00	±	0.00	1.01	±	0.82
20:0	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
20:1ω13	0.00	±	0.00	0.71	±	2.77	0.00	±	0.00
20:1ω11	17.47	±	14.93	19.12	±	16.88	31.75	±	25.82
20:1ω9	43.11	±	24.89	107.37	±	37.05	136.27	±	94.39
20:1ω7	2.91	±	0.56	3.54	±	1.14	4.96	±	3.64
22:2Δ5,11	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
22:2Δ5,13	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
20:1ω5	0.87	±	0.57	1.00	±	0.49	0.22	±	0.33
20:2ω9	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
20:2ω6	1.11	±	0.23	0.37	±	0.48	1.15	±	1.10
21:0	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
20:3ω6	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
20:4ω6	2.85	±	0.85	0.65	±	0.75	2.40	±	2.26
20:3ω3	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
20:4ω3	1.32	±	0.62	0.57	±	0.66	2.47	±	1.69
20:5ω3	43.16	±	10.33	16.30	±	8.17	78.12	±	54.13
22:0	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
22:1ω11	32.07	±	27.42	76.15	±	26.18	84.20	±	55.53
22:1ω9	4.53	±	1.84	11.31	±	2.54	12.29	±	8.18
22:1ω7	0.51	±	0.59	1.76	±	0.69	1.91	±	1.30
22:2Δ7,13	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
22:2Δ7,15	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
21:5ω3	0.25	±	0.57	0.00	±	0.00	2.24	±	1.75
22:4ω6	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00

Table 14. Continued.

	Arctic Cod - Chukchi Sea								
	2010			**2011**			**2012**		
22:5ω6	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
22:5ω3	2.78	±	0.70	0.94	±	0.93	4.90	±	3.17
24:0	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
22:6ω3	57.41	±	11.47	18.83	±	7.53	55.75	±	38.89
24:1ω11	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
24:1ω9	4.05	±	0.79	3.59	±	0.94	4.01	±	2.20
24:1ω7	0.00	±	0.00	0.04	±	0.15	0.00	±	0.00
Fatty Acid Classes (mg fatty acid/ g lipid)									
ΣSFA	171.88	±	16.50	140.96	±	21.00	204.53	±	117.91
ΣMUFA	300.66	±	44.79	369.02	±	76.49	559.75	±	367.01
ΣPUFA	122.92	±	26.33	45.37	±	20.48	181.22	±	123.31
Fatty Acid Trophic Markers									
mg fatty acid/ g lipid									
20:1ω9 + 22:1ω11[a]	75.18	±	50.34	183.52	±	59.62	220.47	±	148.44
Ratio									
18:1ω9/ 18:1ω7[b]	1.66	±	0.28	2.14	±	0.27	1.73	±	0.18
ω7/ ω9 fatty acids[c]	1.13	±	0.41	0.56	±	0.19	0.82	±	0.17
16:1ω7/ 16:0[d]	0.68	±	0.10	0.75	±	0.17	1.14	±	0.28
20:5ω3/ 22:6ω3[e]	0.75	±	0.07	0.85	±	0.14	1.39	±	0.19

Table 15. Fatty Acid Concentrations of Beaufort Sea Eelpout Species Corrected to Total Tissue Mass. Fatty acid concentrations in μg fatty acid/ g wet tissue of Eelpout by species (Canadian Eelpout and Longear Eelpout) and year (2011–2013). Values are reported as mean ± 1 standard deviation. (a) Calanoid copepod marker (Graeve et al. 1997, Auel et al. 2002, Falk-Petersen et al. 2002), (b) Carnivory marker (Graeve et al. 1997, Auel et al. 2002, Falk-Petersen et al. 2009), (c) Benthic feeding marker (Budge et al. 2007), (d) Diatom marker (Viso & Marty 1993, St. John & Lund 1996, Falk-Petersen et al. 2002), (e) Diatom versus dinoflagellate dominated system marker (Falk-Petersen et al. 2002, Dalsgaard et al. 2003).

	Canadian Eelpout - Beaufort Sea		Longear Eelpout - Beaufort Sea	
	2011	2012	2012	2013
Fatty Acids (μg fatty acid/ g wet tissue)				
10:0	63.53 ± 108.97	123.88 ± 125.52	5.49 ± 5.65	2.34 ± 1.56
11:0	0.84 ± 3.03	0.19 ± 0.46	0.02 ± 0.10	0.00 ± 0.00
12:0	21.50 ± 27.89	37.29 ± 50.68	13.04 ± 9.94	10.47 ± 14.84
13:0	1.07 ± 2.53	4.49 ± 6.13	4.49 ± 7.04	1.04 ± 2.61
iso 14:0	0.58 ± 1.03	2.71 ± 4.55	2.87 ± 4.57	0.64 ± 2.21
14:0	258.09 ± 341.29	428.34 ± 407.09	444.94 ± 542.44	207.20 ± 313.30
14:1ω9	2.53 ± 3.98	9.10 ± 10.87	5.36 ± 5.09	5.29 ± 10.41
14:1ω7	3.60 ± 5.32	11.64 ± 9.11	13.47 ± 18.91	7.18 ± 12.80
14:1ω5	4.20 ± 6.09	14.31 ± 14.44	41.59 ± 83.72	12.62 ± 27.47
iso 15:0	19.22 ± 28.70	38.69 ± 39.55	38.57 ± 46.09	15.48 ± 18.71
anteiso 15:0	4.78 ± 6.80	10.39 ± 10.19	9.62 ± 10.17	4.13 ± 4.94
15:0	50.80 ± 82.70	100.96 ± 85.41	67.19 ± 64.68	28.01 ± 25.61
15:1	0.54 ± 2.37	1.21 ± 2.03	6.28 ± 6.64	8.14 ± 5.48
iso 16:0	23.55 ± 46.49	37.43 ± 33.39	42.37 ± 57.44	10.02 ± 15.56
anteiso 16:0	5.43 ± 9.12	44.20 ± 64.33	1.14 ± 5.33	0.22 ± 0.53
16:0	1775.32 ± 2949.61	2469.23 ± 2073.17	1765.99 ± 1668.46	1354.53 ± 1135.42
16:1ω11	42.89 ± 59.46	101.63 ± 99.66	61.22 ± 50.36	48.66 ± 40.86
16:1ω9	39.41 ± 58.93	73.46 ± 74.76	70.44 ± 69.90	47.69 ± 43.90

Table 15. Continued.

	Canadian Eelpout - Beaufort Sea				Longear Eelpout - Beaufort Sea			
	2011		2012		2012		2013	
16:1ω7	963.81 ±	1540.60	1732.06 ±	1554.11	2599.17 ±	3845.66	1706.06 ±	2856.36
16:1ω5	52.33 ±	93.55	141.26 ±	180.27	125.93 ±	112.86	39.73 ±	39.46
iso 17:0	48.56 ±	88.29	73.95 ±	62.76	49.83 ±	46.65	29.41 ±	21.68
16:1ω1	0.00 ±	0.00	0.00 ±	0.00	15.02 ±	38.78	5.78 ±	14.11
16:2ω6	1.10 ±	3.48	8.33 ±	11.52	1.38 ±	4.78	0.87 ±	4.16
anteiso 17:0	29.04 ±	50.06	49.43 ±	38.84	48.16 ±	54.10	21.50 ±	15.97
16:2ω4	18.39 ±	24.95	36.63 ±	39.44	28.66 ±	29.33	24.14 ±	47.44
17:0	91.92 ±	167.05	108.94 ±	82.03	41.57 ±	29.43	23.05 ±	11.82
16:3ω4	13.72 ±	17.94	22.34 ±	21.06	9.62 ±	10.73	6.45 ±	17.15
17:1ω9	3.71 ±	9.31	2.03 ±	3.30	0.00 ±	0.00	0.00 ±	0.00
18:0	567.14 ±	1020.96	600.77 ±	456.22	389.70 ±	256.31	355.12 ±	215.15
18:1ω13	20.71 ±	34.29	44.14 ±	36.04	67.92 ±	76.91	31.55 ±	22.62
18:1ω9 *trans*	0.25 ±	1.11	0.00 ±	0.00	0.00 ±	0.00	0.00 ±	0.00
18:1ω11	23.89 ±	29.86	92.80 ±	109.18	59.20 ±	81.73	108.18 ±	186.86
18:1ω9 *cis*	1032.65 ±	1651.71	1695.69 ±	1689.61	1427.28 ±	1674.26	1148.06 ±	1474.37
18:1ω7	1047.10 ±	1898.96	1242.60 ±	1041.88	1276.64 ±	1400.35	700.52 ±	649.55
18:1ω5	71.36 ±	127.31	193.72 ±	256.00	185.81 ±	183.97	56.10 ±	64.83
18:2ω6 *cis*	77.12 ±	141.47	116.83 ±	113.30	101.44 ±	106.51	67.63 ±	80.14
18:2ω4	13.94 ±	23.04	19.35 ±	17.21	23.69 ±	29.79	7.09 ±	14.15
18:3ω6	22.64 ±	39.74	32.85 ±	26.06	8.74 ±	12.81	11.82 ±	19.73
18:3ω3	19.40 ±	36.85	155.96 ±	243.28	27.44 ±	30.59	17.12 ±	32.48
18:4ω3	30.55 ±	44.84	78.35 ±	114.60	39.74 ±	38.03	39.14 ±	86.03
18:4ω1	0.51 ±	2.24	0.00 ±	0.00	5.86 ±	12.56	0.00 ±	0.00
20:0	1.07 ±	1.90	0.00 ±	0.00	0.00 ±	0.00	0.21 ±	1.02

Table 15. Continued.

	Canadian Eelpout - Beaufort Sea				Longear Eelpout - Beaufort Sea			
	2011		2012		2012		2013	
20:1ω13	0.67 ± 2.38		0.00 ± 0.00		0.00 ± 0.00		0.00 ± 0.00	
20:1ω11	48.69 ± 73.05		117.31 ± 102.52		188.67 ± 255.17		96.65 ± 100.47	
20:1ω9	155.88 ± 202.39		565.57 ± 708.44		377.75 ± 384.23		456.59 ± 665.65	
20:1ω7	117.31 ± 159.37		251.11 ± 202.67		422.13 ± 550.12		118.84 ± 120.04	
22:2Δ5,11	0.00 ± 0.00		5.16 ± 12.64		7.96 ± 29.83		9.09 ± 23.45	
22:2Δ5,13	1.48 ± 4.90		3.87 ± 9.48		13.81 ± 27.65		1.02 ± 3.65	
20:1ω5	0.00 ± 0.00		20.64 ± 31.35		11.26 ± 14.65		2.04 ± 7.31	
20:2ω9	1.69 ± 7.36		4.30 ± 10.53		18.27 ± 31.09		1.16 ± 3.26	
20:2ω6	26.55 ± 50.42		49.04 ± 37.51		54.64 ± 71.76		31.51 ± 22.47	
21:0	0.00 ± 0.00		0.00 ± 0.00		9.42 ± 17.81		16.62 ± 15.77	
20:3ω6	3.55 ± 7.49		6.20 ± 15.18		0.00 ± 0.00		0.00 ± 0.00	
20:4ω6	407.76 ± 898.05		626.60 ± 529.86		563.07 ± 597.35		366.09 ± 295.28	
20:3ω3	0.00 ± 0.00		0.00 ± 0.00		7.48 ± 19.00		0.00 ± 0.00	
20:4ω3	2.82 ± 7.47		9.21 ± 16.57		27.91 ± 42.49		13.53 ± 34.39	
20:5ω3	1074.43 ± 2019.00		1727.67 ± 1369.67		1896.81 ± 1714.55		980.64 ± 938.62	
22:0	1.19 ± 5.21		0.00 ± 0.00		14.78 ± 18.91		9.52 ± 11.86	
22:1ω11	9.51 ± 15.40		70.50 ± 89.32		77.10 ± 130.14		147.41 ± 309.96	
22:1ω9	21.51 ± 29.03		55.34 ± 64.22		58.44 ± 57.16		58.20 ± 91.67	
22:1ω7	24.30 ± 37.03		24.00 ± 21.43		4.37 ± 15.51		0.94 ± 4.52	
22:2Δ7,13	2.64 ± 11.49		9.11 ± 22.33		24.98 ± 56.22		23.94 ± 43.05	
22:2Δ7,15	2.94 ± 11.06		5.93 ± 14.52		69.84 ± 135.48		5.15 ± 14.21	
21:5ω3	3.92 ± 9.54		7.09 ± 11.01		19.43 ± 31.76		8.19 ± 23.03	
22:4ω6	17.04 ± 48.48		35.93 ± 47.53		45.41 ± 55.73		25.56 ± 18.59	
22:5ω6	42.95 ± 94.90		73.41 ± 64.50		56.54 ± 46.56		29.75 ± 27.25	

Table 15. Continued.

	Canadian Eelpout - Beaufort Sea				Longear Eelpout - Beaufort Sea			
	2011		2012		2012		2013	
22:5ω3	104.47 ±	187.48	193.52 ±	129.70	217.60 ±	184.47	120.87 ±	90.45
24:0	19.38 ±	42.61	5.58 ±	9.28	0.00 ±	0.00	0.00 ±	0.00
22:6ω3	1431.69 ±	3121.17	2074.63 ±	1898.80	1338.65 ±	706.92	1075.47 ±	807.11
24:1ω11	0.00 ±	0.00	0.00 ±	0.00	0.00 ±	0.00	0.00 ±	0.00
24:1ω9	80.53 ±	128.10	144.68 ±	154.81	64.68 ±	44.36	68.09 ±	45.44
24:1ω7	22.81 ±	49.65	15.46 ±	20.25	9.93 ±	26.49	6.58 ±	10.74
Fatty Acid Classes (µg fatty acid/ g wet tissue)								
ΣSFA	2983.01 ±	4910.92	4136.46 ±	3523.55	2949.19 ±	2739.76	2089.53 ±	1710.02
ΣMUFA	3790.18 ±	5523.26	6620.24 ±	6206.59	7169.66 ±	8302.21	4880.91 ±	6608.03
ΣPUFA	3314.26 ±	6702.27	5278.24 ±	4495.87	4492.38 ±	3361.67	2827.02 ±	2269.94
Fatty Acid Trophic Markers								
µg fatty acid/ g wet tissue								
20:1ω9 + 22:1ω11[a]	165.39 ±	204.90	636.07 ±	796.76	454.85 ±	510.40	604.00 ±	972.48
Ratio								
18:1ω9/ 18:1ω7[b]	1.07 ±	0.31	1.29 ±	0.26	1.18 ±	0.47	1.42 ±	0.37
ω7/ ω9 fatty acids[c]	1.60 ±	0.76	1.45 ±	0.30	1.91 ±	0.95	1.42 ±	0.50
16:1ω7/ 16:0[d]	0.52 ±	0.43	0.68 ±	0.28	1.07 ±	0.58	0.97 ±	0.63
20:5ω3/ 22:6ω3[e]	0.87 ±	0.35	0.89 ±	0.23	1.32 ±	0.79	0.89 ±	0.28

Table 16. Fatty Acid Concentrations of Beaufort Sea Eelpout Species Corrected to Total Lipid. Fatty acid concentrations in mg fatty acid/ g lipid of Eelpout by species (Canadian Eelpout and Longear Eelpout) and year (2011–2013). Values are reported as mean ± 1 standard deviation. (a) Calanoid copepod marker (Graeve et al. 1997, Auel et al. 2002, Falk-Petersen et al. 2002), (b) Carnivory marker (Graeve et al. 1997, Auel et al. 2002, Falk-Petersen et al. 2009), (c) Benthic feeding marker (Budge et al. 2007), (d) Diatom marker (Viso & Marty 1993, St. John & Lund 1996, Falk-Petersen et al. 2002), (e) Diatom versus dinoflagellate dominated system marker (Falk-Petersen et al. 2002, Dalsgaard et al. 2003).

	Canadian Eelpout - Beaufort Sea		Longear Eelpout - Beaufort Sea	
	2011	2012	2012	2013
Fatty Acids (mg fatty acid/ g lipid)				
10:0	4.43 ± 8.26	7.13 ± 7.04	0.29 ± 0.32	0.68 ± 0.67
11:0	0.03 ± 0.08	0.01 ± 0.02	0.00 ± 0.01	0.00 ± 0.00
12:0	1.49 ± 2.11	2.08 ± 2.78	0.72 ± 0.44	1.55 ± 1.13
13:0	0.06 ± 0.16	0.26 ± 0.34	0.16 ± 0.16	0.15 ± 0.30
iso 14:0	0.04 ± 0.08	0.15 ± 0.25	0.10 ± 0.12	0.02 ± 0.07
14:0	16.23 ± 21.68	23.41 ± 22.46	18.59 ± 11.73	24.09 ± 13.54
14:1ω9	0.14 ± 0.20	0.50 ± 0.60	0.34 ± 0.37	0.41 ± 0.47
14:1ω7	0.20 ± 0.23	0.61 ± 0.49	0.51 ± 0.41	0.71 ± 0.50
14:1ω5	0.25 ± 0.34	0.69 ± 0.62	1.30 ± 1.63	0.84 ± 0.76
iso 15:0	1.35 ± 2.19	2.11 ± 2.19	1.68 ± 1.09	2.43 ± 1.93
anteiso 15:0	0.35 ± 0.53	0.56 ± 0.57	0.44 ± 0.31	0.70 ± 0.70
15:0	3.59 ± 6.31	5.45 ± 4.70	3.20 ± 1.72	4.93 ± 3.82
15:1	0.01 ± 0.06	0.05 ± 0.09	0.31 ± 0.30	1.90 ± 1.74
iso 16:0	1.74 ± 3.56	2.03 ± 1.85	1.82 ± 1.65	1.49 ± 2.36
anteiso 16:0	0.39 ± 0.70	2.40 ± 3.54	0.02 ± 0.11	0.08 ± 0.20
16:0	123.26 ± 223.44	135.83 ± 115.44	86.24 ± 43.49	249.29 ± 201.51
16:1ω11	2.97 ± 4.53	5.43 ± 5.49	3.15 ± 1.78	7.74 ± 5.09
16:1ω9	2.79 ± 4.52	3.92 ± 4.12	3.26 ± 1.58	7.60 ± 5.13

Table 16. Continued.

	Canadian Eelpout - Beaufort Sea				Longear Eelpout - Beaufort Sea			
	2011			2012			2012		2013

	2011			2012			2012			2013		
16:1ω7	53.25	±	63.21	91.63	±	84.94	97.84	±	75.71	177.05	±	94.80
16:1ω5	3.70	±	7.14	7.71	±	9.93	6.41	±	4.27	6.64	±	4.71
iso 17:0	3.53	±	6.77	4.05	±	3.52	2.42	±	1.35	5.16	±	3.91
16:1ω1	0.00	±	0.00	0.00	±	0.00	0.42	±	0.74	0.26	±	0.39
16:2ω6	0.04	±	0.11	0.42	±	0.62	0.04	±	0.12	0.02	±	0.09
anteiso 17:0	2.13	±	3.86	2.65	±	2.16	2.19	±	1.65	4.69	±	4.42
16:2ω4	1.09	±	1.36	1.97	±	2.18	1.36	±	0.92	1.94	±	1.47
17:0	6.38	±	12.58	5.90	±	4.53	2.29	±	1.36	5.43	±	4.65
16:3ω4	0.81	±	1.02	1.19	±	1.15	0.44	±	0.35	0.26	±	0.51
17:1ω9	0.28	±	0.71	0.09	±	0.14	0.00	±	0.00	0.00	±	0.00
18:0	40.64	±	78.04	33.32	±	25.82	22.09	±	12.75	81.33	±	75.16
18:1ω13	1.54	±	2.68	2.20	±	1.48	2.99	±	2.04	7.34	±	6.83
18:1ω9 trans	0.01	±	0.05	0.00	±	0.00	0.00	±	0.00	0.00	±	0.00
18:1ω11	1.57	±	2.11	4.98	±	6.02	3.45	±	4.04	10.46	±	5.81
18:1ω9 cis	72.28	±	125.89	91.10	±	93.61	62.25	±	33.58	157.33	±	91.53
18:1ω7	74.54	±	144.98	67.76	±	59.59	58.78	±	40.27	117.74	±	77.55
18:1ω5	5.03	±	9.71	10.55	±	14.11	8.95	±	4.85	8.25	±	5.10
18:2ω6 cis	5.56	±	10.83	6.34	±	6.35	4.73	±	2.41	10.44	±	6.53
18:2ω4	0.97	±	1.75	1.06	±	0.97	0.99	±	0.65	0.48	±	0.57
18:3ω6	1.61	±	3.04	1.82	±	1.47	0.46	±	0.50	1.92	±	2.14
18:3ω3	1.40	±	2.79	7.95	±	13.10	1.20	±	0.79	1.54	±	1.36
18:4ω3	2.03	±	3.34	4.23	±	6.30	2.00	±	1.41	2.54	±	2.14
18:4ω1	0.03	±	0.11	0.00	±	0.00	0.23	±	0.47	0.00	±	0.00
20:0	0.09	±	0.18	0.00	±	0.00	0.00	±	0.00	0.29	±	1.38

Table 16. Continued

	Canadian Eelpout - Beaufort Sea				Longear Eelpout - Beaufort Sea			
	2011		2012		2012		2013	
20:1ω13	0.05	± 0.15	0.00	± 0.00	0.00	± 0.00	0.00	± 0.00
20:1ω11	3.56	± 5.97	5.90	± 5.23	7.55	± 6.21	13.78	± 8.01
20:1ω9	10.81	± 15.40	30.45	± 39.05	20.86	± 17.40	53.08	± 31.15
20:1ω7	8.25	± 12.37	12.62	± 8.95	18.13	± 17.36	16.78	± 7.99
22:2Δ5,11	0.00	± 0.00	0.21	± 0.52	0.36	± 1.15	1.58	± 3.20
22:2Δ5,13	0.12	± 0.41	0.16	± 0.39	0.40	± 0.68	0.09	± 0.33
20:1ω5	0.00	± 0.00	1.10	± 1.72	0.76	± 0.91	0.27	± 0.96
20:2ω9	0.14	± 0.62	0.18	± 0.43	0.70	± 1.07	0.19	± 0.58
20:2ω6	1.99	± 3.85	2.58	± 2.04	2.32	± 1.72	6.29	± 5.36
21:0	0.00	± 0.00	0.00	± 0.00	0.39	± 0.67	4.83	± 4.97
20:3ω6	0.25	± 0.49	0.50	± 1.23	0.00	± 0.00	0.00	± 0.00
20:4ω6	30.39	± 68.52	34.82	± 31.41	31.74	± 24.74	92.70	± 99.94
20:3ω3	0.00	± 0.00	0.00	± 0.00	0.22	± 0.49	0.00	± 0.00
20:4ω3	0.16	± 0.40	0.42	± 0.74	1.02	± 1.17	0.50	± 0.94
20:5ω3	77.21	± 154.72	92.52	± 77.39	94.13	± 60.77	157.23	± 109.78
22:0	0.10	± 0.43	0.00	± 0.00	1.05	± 1.22	2.70	± 3.46
22:1ω11	0.56	± 0.92	3.70	± 4.91	4.21	± 6.68	9.34	± 9.49
22:1ω9	1.48	± 2.18	2.93	± 3.60	2.87	± 2.03	6.45	± 3.97
22:1ω7	1.67	± 2.68	1.50	± 1.61	0.14	± 0.45	0.08	± 0.37
22:2Δ7,13	0.22	± 0.96	0.37	± 0.91	0.69	± 1.41	2.72	± 4.70
22:2Δ7,15	0.24	± 0.92	0.24	± 0.59	2.39	± 3.64	0.42	± 1.19
21:5ω3	0.29	± 0.76	0.31	± 0.48	0.74	± 0.97	0.24	± 0.64
22:4ω6	1.33	± 3.74	1.81	± 2.33	2.17	± 2.76	6.73	± 5.57
22:5ω6	3.25	± 7.22	4.00	± 3.69	3.23	± 2.20	8.60	± 8.91

Table 16. Continued.

	Canadian Eelpout - Beaufort Sea				Longear Eelpout - Beaufort Sea			
	2011		2012		2012		2013	
22:5ω3	7.69 ± 14.45		10.26 ± 7.30		11.22 ± 8.03		21.84 ± 15.68	
24:0	1.47 ± 3.24		0.39 ± 0.72		0.00 ± 0.00		0.00 ± 0.00	
22:6ω3	105.04 ± 238.31		112.64 ± 107.07		82.00 ± 47.70		214.53 ± 199.35	
24:1ω11	0.00 ± 0.00		0.00 ± 0.00		0.00 ± 0.00		0.00 ± 0.00	
24:1ω9	5.73 ± 9.80		7.97 ± 8.50		4.34 ± 2.94		17.07 ± 15.52	
24:1ω7	1.70 ± 3.77		1.10 ± 1.60		0.74 ± 1.95		2.91 ± 5.72	
Fatty Acid Classes (mg fatty acid/ g lipid)								
ΣSFA	207.30 ± 371.99		227.74 ± 196.15		143.70 ± 72.49		389.85 ± 314.57	
ΣMUFA	252.39 ± 403.27		354.49 ± 343.51		309.56 ± 182.48		624.02 ± 320.85	
ΣPUFA	241.26 ± 512.91		285.02 ± 254.55		240.94 ± 139.66		527.98 ± 440.45	
Fatty Acid Trophic Markers								
mg fatty acid/ g lipid								
20:1ω9 + 22:1ω11[a]	11.37 ± 15.47		34.15 ± 43.92		25.07 ± 23.86		62.41 ± 36.79	
Ratio								
18:1ω9/ 18:1ω7[b]	1.07 ± 0.31		1.29 ± 0.26		1.18 ± 0.47		1.42 ± 0.37	
ω7/ ω9 fatty acids[c]	1.60 ± 0.76		1.45 ± 0.30		1.91 ± 0.95		1.42 ± 0.50	
16:1ω7/ 16:0[d]	0.52 ± 0.43		0.68 ± 0.28		1.07 ± 0.58		0.97 ± 0.63	
20:5ω3/ 22:6ω3[e]	0.87 ± 0.35		0.89 ± 0.23		1.32 ± 0.79		0.89 ± 0.28	