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ORIGINAL PAPER

Ontogenetic and spatial variability in trophic biomarkers of juvenile saffron cod (*Eleginus gracilis*) from the Beaufort, Chukchi and Bering Seas

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Abstract Climate models indicate the Arctic will undergo dramatic environmental change with forecasted increases in temperature and river runoff. Saffron cod (*Eleginus gracilis*) is abundant in nearshore waters and appears in the diet of many Arctic sea birds and marine mammals; however, little is known about its early ecology and consequently how they might be affected by environmental changes. We aimed to characterize the mechanisms of spatial and ontogenetic variation in trophic biomarkers (lipid classes, fatty acids and bulk C and N stable isotopes) of saffron cod from the Western Arctic, Chukchi and Bering Seas. Size-standardized analyses showed a significant difference in lipid condition metrics and trophic biomarkers as a function of survey location. Both ontogeny and sampling location played an important role in determining lipid stores with elevated levels in both small offshore juveniles (<55 mm) and larger inshore juveniles (>75 mm). Higher lipid storage in Arctic juveniles was associated with elevated levels of diatom fatty acid markers, but not with nearshore carbon input. Increased lipids were found in age-1 juveniles from Prudhoe Bay in the Western Beaufort that were feeding at a lower trophic level than similarly sized age-0 juveniles from surface trawls in the Bering Sea. The use of otolith annuli revealed two discrete patterns of growth that help explain the trade-offs between energy storage and rapid growth that diverge between the Arctic and Bering Sea. Laboratory temperature-growth experiments confirmed that saffron cod have a eurythermal growth response and are able to store excess lipids at temperatures as high as 20 °C.

Keywords Saffron cod · Arctic · Ontogeny · Fatty acids · Lipids · Nutrition

Introduction

Prey quality of forage fish is an important component of cold ocean marine ecosystems that has been linked to broadscale ecosystem changes. In fish populations, shifts in

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prey quality can impact fisheries productivity (Heintz et al. 2013; Siddon et al. 2013b) and distribution (Anderson and Piatt 1999), which in turn can catalyze and sustain regime shifts in commercially harvested species (Litzow et al. 2008). Reduced prey quality can negatively impact breeding success in seabirds (Hipfner et al. 2000; Suryan et al. 2002), and adult recruitment in marine mammals (Merrick et al. 1997). Collectively, such differences in prey quality have broad impacts on foraging habits (spatial–temporal, prey switching, etc.) and subsequent fitness of piscivorous marine predators.

Schooling fish of the family Gadidae are an important prey group for high-latitude marine organisms, including mammals, seabirds and larger demersal fish (Bluhm and Gradinger 2008; Erikstad et al. 2013; Harter et al. 2013; Hop and Gjosaeter 2013). Although the energetic value of gadids is typically lower than that of pelagic schooling fish species (e.g., Ammodytidae, Cluepeidae and Osmeridae), the inter- and intraspecific body composition of gadids can be highly variable (Anthony et al. 2000) to the point that generalizations of their qualitative energetic value are too imprecise for trophic models (Anthony et al. 2000). Juvenile gadids (30–100 mm TL) can vary by more than four times their lipid density (mg/g) over the course of a season (Copeman et al. 2008). While gadids tend to gain energy density in their early ontogeny, both direct environmental conditions (namely temperature) and indirect food web variability can impact energy storage (Anthony et al. 2000; Heintz et al. 2013; Siddon et al. 2013a). Unfavorable temperatures can reduce their physiological ability to store lipids by increasing metabolic activity associated with high-temperature environments (Jobling et al. 1998). Further, higher temperatures may lead to unfavorable prey fields, as previously described for juvenile pollock in the Bering Sea (Heintz et al. 2013). Such plasticity in the energetic composition of individuals has implications for both their predators as well as fish overwintering survival (Sogard and Olla 2000; Hurst 2007) and reproductive success.

The Arctic is typified by food chains where Arctic cod (*Boreogadus saida*) is a major forage species, playing a key role in the marine ecosystem, by transferring up to 75 % of the zooplankton production to marine vertebrate predators (Hobson and Welch 1992; Welch et al. 1992; Matley et al. 2012; Benoit et al. 2014). However, spatial changes in Arctic cod, likely due to increased warming from climate change, are altering the availability of this species to a number of predators. Direct catches of Arctic cod in commercial fisheries are declining in Russia (Zeller et al. 2011), and Arctic cod is less represented in the diets of piscivorous predators relative to levels in the past (Marcoux et al. 2012). New attention has been focused on the ecological role of another gadid in the Arctic, saffron cod (*Eleginus gracilis*), as it is also abundant and occurs with a high frequency in the diets of many fish, birds and mammals (Schmutz and Hobson 1998; Quakenbush et al. 2010; Thedinga et al. 2013). Given their limited commercial importance, relatively little is known about the ecological role and energetic value of saffron cod compared to other Alaskan gadids [e.g., walleye pollock (*Gadus chalcogrammus*) and Pacific cod (*Gadus macrocephalus*)]. Juvenile saffron cod regionally co-occur with gadid species of similar size (30–130 mm TL), and recent increases in saffron cod abundance in Prince William Sound and around Kodiak Island have made them a species of interest as far south as the Gulf of Alaska (Laurel et al. 2007; Johnson et al. 2009).

In Western Arctic waters, saffron cod are typically the most abundant gadid in the nearshore (Griffiths et al. 1998), but generally have a high co-occurrence with Arctic cod in offshore regions as well. However, saffron cod have a broad latitudinal range (Laurel et al. 2009), and tolerance to temperature (Laurel et al. this issue) and salinity (Loseto et al. 2008; Wong et al. 2013), suggesting saffron cod have physiology more resilient to forecasted warming and freshening in the polar seas compared to Arctic cod (Gradinger and Bluhm 2004).

In this study, we used both lipid/fatty acid and isotope biomarkers to understand the early energetics and feeding of juvenile saffron cod. Lipid trophic biomarkers are compounds that provide signatures of a species, groups of organisms or environmental processes (Dalsgaard et al. 2003; Budge et al. 2006). Fatty acid (FA) biomarkers are normally synthesized at low trophic levels and correlate with various sources of primary production such as diatoms, bacteria, dinoflagellates and terrestrial runoff (Budge and Parrish 1998; Dalsgaard et al. 2003). These biomarkers are conservatively transferred throughout the food web and indicate dietary sources in both invertebrates and fish (St John and Lund 1996; Budge and Parrish 1999; Copeman et al. 2009; Kelly and Scheibling 2012). Bulk stable carbon and nitrogen isotopes are widely used in food web studies to determine sources of dietary primary production and differences in trophic levels of consumers (Fry and Sherr 1983). When used together, these biomarker approaches provide the energetic status of the fish in addition to recent time-integrated (weeks for fatty acids and months for isotopes) individual feeding histories.

The goal of this study was to characterize and explore the mechanisms of spatial and ontogenetic changes in lipid storage and trophic dynamics of juvenile saffron cod in the North Pacific and Western Arctic. We examine differences between surface and demersal fish as well as nearshore and offshore regions, with the goal of understanding implications of prey quality for piscivorous predators foraging in such regions. Finally, we experimentally measure the role of temperature on lipid storage in saffron cod, both to

provide a mechanistic understanding of spatial differences presently observed in the field and under scenarios of future warming in the region.

Methods

Field fish sampling and tissue collections

One hundred and fifty-six juvenile fish (age-0 and age-1) from four different research efforts were included in this study (Fig. 1). Saffron cod were collected during the summer of 2012 using three different vessels spanning 17.5° of latitude (55°N–72.5°N; Fig. 1) on the Arctic Ecosystem Integrated Survey (Arctic EIS). Saffron cod (<100 mm) were sampled using a 198-m-long surface trawl towed behind 54.9-m chartered fishing vessel between August 8–September 21, 2012. The trawl had hexagonal mesh on the wings and body, 1.2-cm mesh cod end liner, 50 m × 25 m mouth (horizontal × vertical). Each tow lasted for 30 min at approximately 8.3 km/h at stations within a 103 km^2 grid along the Western Alaskan coast between 72.5°N and 60°N.

Nearshore juvenile saffron cod were also collected in 2012 from the Arctic Costal Ecosystem Survey (ACES) from beach seine locations within 20 km of Barrow, AK (71.3°N–156.8°W). The seine was 37 m long with variable mesh sizes (10 m of 32-mm outer panels, 4 m of 6-mm middle panels and 9 m of 3.2-mm blunt panel). Each set was round-haul style, paid out of a 7-m skiff following methods used by Johnson et al. (2010). All collections occurred during daylight hours. Juvenile saffron cod

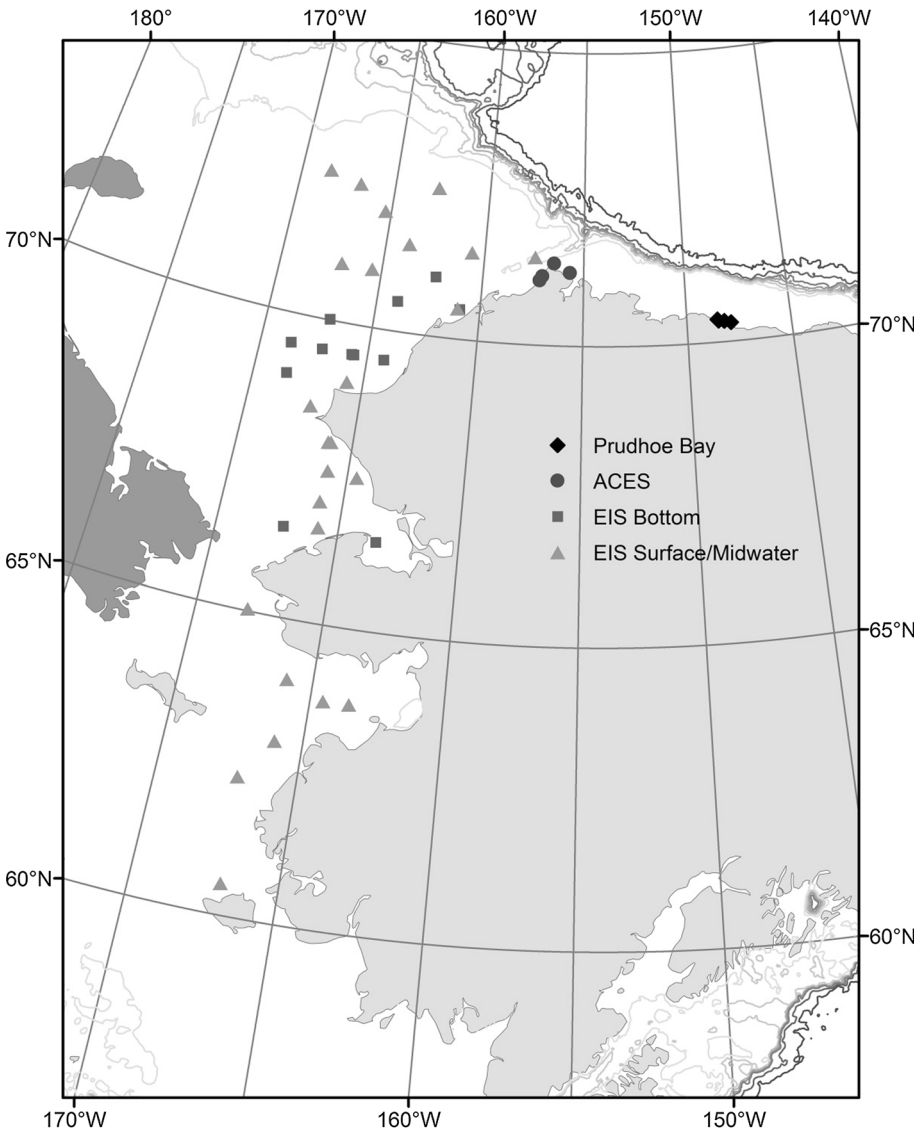

Fig. 1 Sampling locations for saffron cod (*Eleginus gracilis*) within four different survey efforts in 2012 and 2013

(75–105 mm) were also collected by fyke net in Prudhoe Bay, AK, in early August of 2013 (See Laurel et al. this issue).

Cod from all surveys were placed immediately on ice after capture and were then frozen in a −20 or −80 °C freezer prior to shipping. Samples were shipped frozen overnight from Alaska to the Hatfield Marine Science Center in Newport, OR, USA. Upon returning to the laboratory, fork length (FL, ±0.1 mm) and wet weight (±0.0001 g) were recorded. Fish intestinal tracts were removed, fish were washed with filtered seawater and blotted dry, and heads were removed for later otolith analysis (Helser et al. in revision). Fish were bisected along a dorsal ventral plane, and half of the tissues were frozen for later bulk isotope analyses. One half of the body tissues were placed in chloroform under nitrogen until extraction, within 2 months of sampling.

Lipid extraction and analysis

Tissues were homogenized in chloroform/methanol, and total lipids were extracted according to Parrish (1987) using a modified Folch procedure (Folch et al. 1956). Lipid classes were determined using thin layer chromatography with flame ionization detection (TLC/FID) with a MARK V Iatroscan (Iatron Labratories, Tokyo, Japan) as described by Lu et al. (2008). Extracts were spotted on duplicate silica-gel-coated Chromarods, and a three-stage development system was used to separate lipid classes (lipid classes quantified were: wax esters, triacylglycerols, free fatty acids, sterols and polar lipids). Within, we refer to neutral lipids as the sum of wax esters, triacylglycerols, free fatty acids and sterols, while polar lipids are mostly comprised of phospholipids with minor amounts of other acetone mobile polar lipids. The first rod development was in a chloroform/methanol/water solution (5:4:1 by volume) until the leading edge of the solvent phase reached 1 cm above the spotting origin. The rods were then developed in a hexane/diethyl ether/formic acid solution (99:1:0.05) for 48 min, and finally rods were developed in a hexane/diethyl ether/formic acid solution (80:20:0.1) for 38 min. After each solvent development, rods were dried (5 min) and conditioned (5 min) in a constant humidity chamber. Following the last development, rods were scanned using Peak Simple software (ver. 3.67, SRI Inc.) and the signal detected in millivolts was quantified using lipid standards (Sigma, St Louis, MO, USA). A specific triacylglycerol standard was purified from walleye pollock liver using column chromatography following the methods of (Miller et al. 1998) with the addition of a final elution of 15 ml of hexane/diethyl ether/formic acid solution (80:20:0.1). Lipid classes were expressed both in relative (% of total lipids) and in absolute amounts (lipid per wet weight (WW) mg/g).

Lipid extracts were derivatized through acid transesterification using H_2SO_4 in MeOH as described in Budge et al. (2006). Resulting fatty acid methyl esters (FAMEs) were analyzed on an HP 7890 GC FID equipped with an autosampler and a DB wax + GC column (Agilent Technologies, Inc., USA). The column was 30 m in length, with an internal diameter of 0.25 μm. The column temperature began at 65 °C and held this temperature for 0.5 min. Temperature was increased to 195 °C (40 °C/min), held for 15 min and then increased again (2 °C/min) to a final temperature of 220 °C. Final temperature was held for 1 min. The carrier gas was hydrogen, flowing at a rate of 2 ml/min. Injector temperature was set at 250 °C, and the detector temperature was constant at 250 °C. Peaks were identified using retention times based upon standards purchased from Supelco (37 component FAME, BAME, PUFA 1, PUFA 3). Nu-Check Prep GLC 487 quantitative FA mixed standard was used to develop correction factors for individual FAs. Chromatograms were integrated using Chem Station (version A.01.02, Agilent).

Bulk stable isotope analysis

A subset ($n = 124$) of saffron cod tissue samples were analyzed at the Southeast Environmental Research Center Stable Isotope Laboratory at Florida International University. Approximately 5 mg of epaxial muscle tissue was excised from individual saffron cod and dried at 60 °C until a constant mass was achieved and subsequently homogenized with a cleaned mortar and pestle. Carbon (% C) and nitrogen (% N) content and stable isotope ratios ($^{13}C/^{12}C$, $^{15}N/^{14}N$) were estimated using an elemental analysis–isotope ratio mass spectrometry (EA-IRMS), with a NA1500 NC (EA) connected to a Delta C (IRMS). Stable isotope values are reported using δ notation and relative to the standard atmospheric N_2 for $\delta^{15}N$ and Vienna PeeDee belemnite for $\delta^{13}C$ following δ sample (‰) = $(R_{sample}/R_{standard} - 1) \times 1000$ where R represents $^{15}N/^{14}N$ and $^{13}C/^{12}C$ ratio, respectively. We analyzed ratios of $\delta^{15}N$ and $\delta^{13}C$ in consumers as $\delta^{15}N$ reveals shifts in trophic transfer and therefore trophic position within the food web and $\delta^{13}C$ offers inference into the role of dietary sources of carbon and exhibits little change with trophic transfers (Layman et al. 2012). Given that C/N ratios of measured samples were near the threshold (3.32–4.88) for which lipid concentrations might influence $\delta^{13}C$, we normalized $\delta^{13}C$ values following Post et al. (2007), yielding an average adjustment of only 0.47 ‰. Error based on internal glycine standards ranged 0.07–0.17 ‰ for $\delta^{15}N$ and 0.12–0.15 ‰ for $\delta^{13}C$.

Laboratory experiment: temperature effects on lipid allocation

The effect of temperature on lipid allocation in saffron cod was conducted on fish exposed to a range of temperatures in the laboratory. The full experimental design and methodology is detailed in Laurel et al. (this issue) where temperature-dependent growth was characterized for saffron cod and other gadids. Briefly, saffron cod (70–85 mm SL) were collected by fyke net and live-transported from Prudhoe Bay, AK, to the Alaska Fisheries Science Center laboratory at the Hatfield Marine Science Center in Newport, OR, USA. Groups of fish ($n = 3$) were acclimated and reared at 0°, 5°, 9°, 16° and 20 °C in duplicate tanks for each temperature treatment for a 6-week exposure period (see Laurel et al. this issue). Fish were fed to satiation every day using a combination of thawed krill and a gelatinized combination of squid, krill, herring, commercial fish food, amino acid supplements and vitamins ('gel food'). At the end of the temperature exposure, saffron cod from each temperature treatment ($n = 6$ per temperature) were frozen (−80 °C) for subsequent lipid analyses. All lipid sampling was done within 3 months of the end of the laboratory experiment.

Fish were rinsed, patted dry and measured for whole body WW (g ± 0.001) and FL (mm ± 0.1). Fish were then dissected on ice, and the liver was removed and weighed. Muscle tissue was taken by first removing the skin above the anus up to the dorsal margin and then dissecting a 300-mg portion of tissue along the dorsal margin. A hepatosomatic index was calculated using the following equation HSI = (H/M) × 100 where H = liver mass (H, 0.1 mg) and M = total mass (M, 0.1 mg). A 100-mg sample of the liver and a 300-mg portion of muscle were removed and placed in chloroform under nitrogen at −20 °C for lipid class analyses within 2 months of sampling.

Statistics

The relationship between log length and log weight as well as lipid content (mg/g) was analyzed separately for small (<55 mm) and large (>75 mm) juvenile fish using linear regressions (Sigma Plot version 12.0). Residuals from the linear models were normally distributed and were tested for significant differences between survey groups using a one-way ANOVA with Tukey's pairwise comparisons (Minitab version 16.0). Total lipids (mg/g) and the proportion of neutral and polar lipids were log-transformed and then investigated separately for small and large fish to look at differences between survey collections (one-way ANOVA).

Fatty acids present at >0.5 % in all samples were included in multivariate analyses using PRIMER *v*6 (Primer-E Ltd). Qualitative fatty acid data (% total FA) were log ($x + 1$) transformed prior to analyses and were then used to calculate a triangular matrix of similarities (Bray-Curtis similarity) between each pair of samples. Non-metric multidimensional scaling (nMDS), an iterative process that uses ranks of similarities, was utilized to explore spatial and size variation associated with the FA composition of saffron cod samples. Cluster analyses based on Bray–Curtis similarity matrices were used to group samples in nMDS plots.

Size-specific (small <55 mm or large >75 mm) ANOSIM (analysis of similarity) procedures were performed to determine whether fish within a given size class differed significantly in their FA profiles as a function of survey collection. The ANOSIM test statistic, R, is a measure of similarity between groups on a scale of 0–1. Values between 0.5 and 0.75 indicate that groups are different, but have some degree of overlap, while $R > 0.75$ indicates well-separated groups (Jaschinski et al. 2011; Kelly and Scheibling 2012). Similarity percentage routines (SIMPER) were used to determine the FA variables that accounted for the largest portion of the variance between similar-sized saffron cod from different sampling regions.

Isotopic composition of tissues was examined among regions and fish size (<55 or >75 mm) using generalized linear models (SAS 9.3) with both $\delta^{13}C$ and $\delta^{15}N$ modeled separately as independent variables. Pairwise comparisons were computed with Tukey's HSD post hoc tests, and marginal means were examined for significant patterns of carbon and nitrogen by size class within each survey region. The ontogenetic heterogeneity in diet preferences [i.e., niche width; (Layman 2007)] in saffron cod was explored by computing the convex hull area [CHA; Matlab, Mathworks; Simonsen et al. (2015)] of $\delta^{13}C$ and $\delta^{15}N$ for small and large saffron cod among study regions.

Data from the temperature-experiment were analyzed by linear regression to look for the significance of tank temperature on liver lipid storage (mg/g) (Sigma Plot version 12.0).

Results

Sample collection

All fish were collected in August and September of 2012 except for Prudhoe Bay fish that were collected in August of 2013. There was a wide range in sample location from both surface and bottom waters, and fish size ranged from 20 to 110 mm in FL. Collections varied between nearshore and offshore locations with collection temperatures that ranged from a low of 3.5 °C in bottom trawls to a high of 11.7 °C in beach seines. Further, salinity was relatively

constant in offshore surveys (~30.8 psu), but variable in nearshore surveys and ranged from 0 to 18 psu in Prudhoe Bay to 25 psu in the ACES survey around Elson Lagoon (Table 1, Fig. 1). Otolith analyses revealed that all small fish (<55 mm) were age-0, while large fish (>75 mm) were a mixture of age-0 and age-1 depending on sampling region. Large fish from the EIS surface trawl were all age-0, while the same-sized fish from EIS bottom surveys and Prudhoe Bay were age-1 (Helser et al. in revision).

Length–weight relationships showed an overlap of three surveys both in the small fish range (<55 mm) and in the larger fish range (>75 mm, Fig. 2). There were not many fish between 55 to 75 mm in FL, supporting the notion that small and large fish largely represent age-0 and age-1 fish, respectively (Helser et al. in revision). For this reason, fish between 55 and 75 mm were excluded from comparisons of condition as well as lipid or isotopic biomarkers. This is with

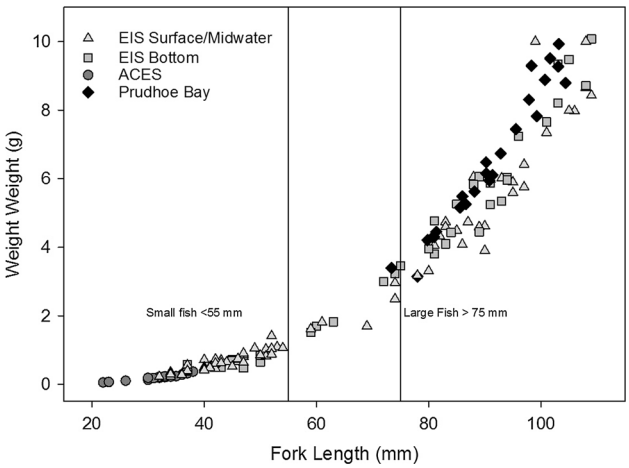

Fig. 2 Fork length (FL, mm) to wet weight (g) relationship for juvenile saffron cod (*Eleginus gracilis*) collected on four different research surveys during 2012–2013 ($n = 156$)

Table 1 Lipid and bulk isotope composition of small (<55 mm) and large (>75 mm) juvenile saffron cod (*Eleginus gracilis*) from four surveys ($n = 140$, means with standard errors in brackets)

	Small fish, fork length <55 mm			Large fish, fork length >75 mm		
	ACES $n = 19$	EIS bottom $n = 8$	EIS surface $n = 41$	Prudhoe Bay $n = 22$	EIS bottom $n = 27$	EIS surface $n = 23$
Otolith (age)	0	0	0	1	1	0
Salinity (psu)	25.0	31.5	30.1	0–18	31.5	30.1
Temperature (°C)	11.7	3.9	8.4	11.0	3.5	7.4
Total lipid (mg/g)	10.1 (0.5)[a]	10.9 (1.6)[a]	19.3 (1.3)[b]	20.8 (2.8)[a]	16.3 (1.8)[ab]	11.5 (1.0)[b]
% Neutral lipids	41.2 (2.0)	38.3 (1.8)	37.3 (1.4)	71.1 (1.5)[a]	50.0 (2.7)[b]	42.3 (3.1)[b]
% Polar lipids	41.0 (1.8)[a]	49.1 (1.7)[ab]	49.4 (1.4)[b]	22.7 (1.1)[a]	40.4 (2.5)[b]	44.4 (2.6)[b]
% 14:0	1.5 (0.1)	1.9 (0.2)	3.0 (0.2)	2.5 (0.1)	2.4 (0.1)	1.6 (0.2)
% 16:0	19.9 (0.3)	17.9 (1.0)	17.8 (0.3)	14.7 (0.7)	15.1 (0.3)	15.6 (0.3)
% 18:0	6.3 (0.3)	4.8 (0.6)	4.0 (0.2)	2.6 (0.1)	2.8 (0.2)	3.5 (0.1)
% $\sum$SFA[1]	29.7 (0.6)	26.9 (1.7)	27.0 (0.4)	20.7 (0.7)	21.2 (0.4)	21.8 (0.4)
% 16:1 n-7	4.5 (0.5)	4.6 (0.3)	5.4 (0.3)	19.2 (0.8)	11.0 (0.7)	7.3 (1.1)
% 18:1 n-9	9.5 (0.2)	9.1 (0.4)	9.2 (0.2)	12.2 (0.3)	10.0 (0.4)	8.8 (0.4)
% 18:1 n-7	3.9 (0.2)	4.0 (0.3)	3.3 (0.1)	6.0 (0.3)	7.1 (0.3)	5.2 (0.3)
% 20:1 n-9	4.2 (0.3)	6.7 (0.6)	5.4 (0.4)	1.2 (0.1)	3.8 (0.5)	3.5 (0.6)
% 22:1 n-11	0.2 (0.1)	1.4 (0.1)	1.3 (0.2)	ND	1.2 (0.3)	1.1 (0.3)
% $\sum$MUFA[2]	25.6 (0.8)	30.1 (1.2)	29.1 (0.9)	41.2 (1.1)	36.6 (1.4)	29.2 (1.6)
% 18:4 n-3	1.1 (0.1)	1.3 (0.2)	2.3 (0.2)	1.0 (0.0)	1.0 (0.1)	1.0 (0.1)
% 20:5 n-3	11.9 (0.5)	11.9 (0.9)	13.3 (0.3)	17.8 (0.3)	14.6 (0.6)	14.9 (0.5)
% 22:6 n-3	25.2 (0.6)	22.9 (1.7)	21.4 (0.6	11.2 (0.5)	18.0 (1.2)	24.3 (1.4)
% $\sum$PUFA[3]	43.5 (0.8)	42.0 (2.5)	42.9 (0.7)	37.5 (0.7)	41.3 (1.5)	48.1 (1.6)
δ^{13}C	−21.0 (0.1)	−19.9 (0.2)	−20.9 (0.1)	−20.4 (0.1)	−18.4 (0.4)	−20.5 (0.2)
δ^{15}N	13.7 (0.2)	14.9 (0.3)	13.1 (0.1)	13.1 (0.2)	16.2 (0.6)	15.5 (0.2)

Surveys included: *ACES* Arctic Costal Ecosystem Survey, *EIS* Arctic Ecosystem Integrated Survey and Prudhoe Bay collections

[a,b] Different letters are statistically different values within small or large saffron cod lipid class parameters

[1] Also contains <2 % of i-15:0, ai-15:0, 15:0, i16:0, ai16:0, i17:0, ai17:0, 17:0, 20:0, 22:0, 24:0

[2] Also contains <2 % of 14:1, 15:1, 16:1n-11, 16:1 n-9, 16:1 n-5, 17:1, 18:1 n-11, 18:1 n-6, 18:1 n-5, 20:1 n-9, 20:1 n-11, 20:1 n-7, 22:1 n-9, 22:1 n-7, 24:1

[3] Also contains <2 % 16:3n-4, 16:4n-3, 16:4n-1, 18:2n-4, 18:2n-6, 18:3n-6, 18:3n-4, 18:3n-3, 18:4n-1, 18:5n-3, 20:2a, 20:2b, 20:2n-6, 20:3n-6, 20:3n-3, 20:4n-3, 22:4n-6, 22:4n-3

the exception of Bering Sea fish that were all age-0 up to 110 mm in FL. Therefore, analyses on the small and large size classes were conducted separately to look at differences in energetics between fish from different surveys.

Morphometric data

The log-transformed length–weight relationship was well described ($r^2 = 0.98$, $p < 0.0001$, Fig. 3a) by the linear regression equation, log (WW) $= -5.37 + 3.13$ [log (length)]. Examination of the residuals from the length–weight relationship shows a significantly higher condition index in Prudhoe Bay fish compared to ACES fish (ANOVA, $F_{3,147} = 5.87$, $p = 0.001$, Fig. 3b). Patterns in lipid per WW showed that fish increased in lipid density with size up until ~60 mm in FL and after that showed no further increase in lipid density with length (Fig. 4a).

Within the small age-0 fish (<55 mm), there was a significant relationship between FL and the amount of lipid per WW [linear regression $r^2 = 0.36$, $p < 0.0001$, total

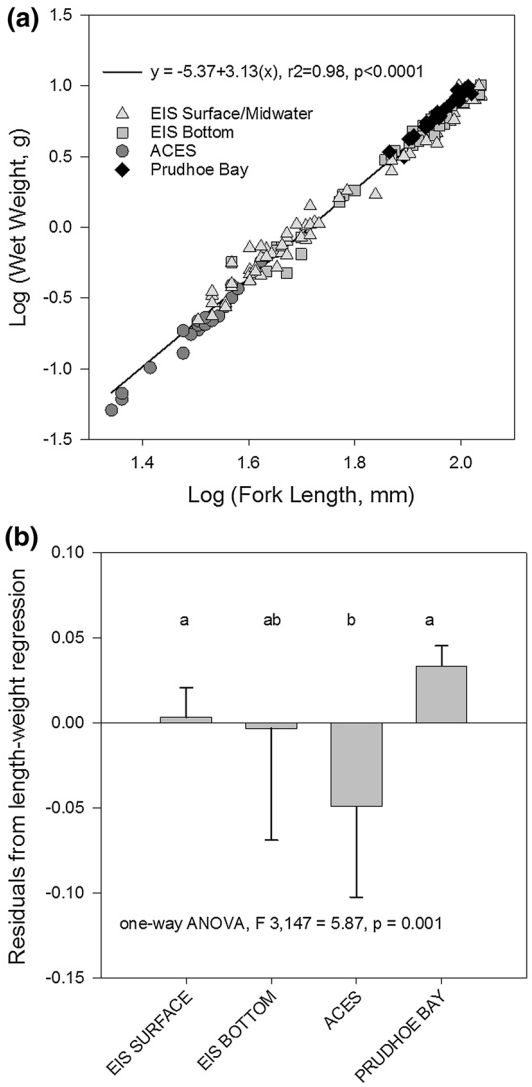

Fig. 3 **a** Linear relationship between log length (FL, mm) to log wet weight (g) for juvenile saffron cod (*Eleginus gracilis*) from four different research surveys ($n = 156$). Log WW (g) $= -5.37 + 3.13$ [Log (length, mm)], $r^2 = 0.98$, $p < 0.0001$. **b** Residuals of linear log length and log WW relationship for saffron cod from four different research surveys. Differences in length–weight residuals between surveys were analyzed using a one-way ANOVA with Tukey's multiple comparison tests, $\alpha = 0.05$

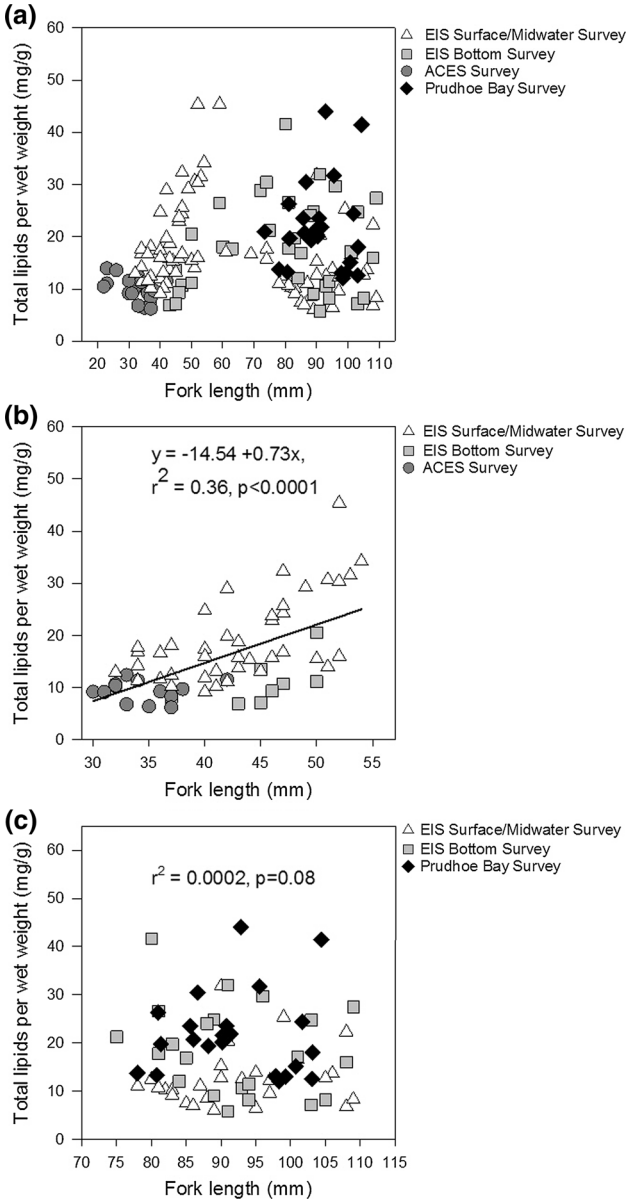

Fig. 4 Relationship between length and total lipids per WW (mg/g) in **a** all juveniles (*Eleginus gracilis*) from four research surveys, $n = 154$. Linear regression between FL (mm) and total lipids per WW (mg/g) for **b** smaller fish (<55 mm, $n = 65$) from three research surveys and **c** larger fish (>75 mm, $n = 73$) from three research surveys

lipids = −14.5 + 0.73 (FL)]. Saffron cod showed a wide range in lipid per WW, with the smallest fish (35 mm) from ACES surveys around Barrow, AK, having a low lipid density of ~6 mg/g and larger age-0 fish (55 mm) from the EIS survey having a high density of ~45 mg/g (Fig. 4b). There was no relationship between total lipids per WW and FL in the larger size category (>75 mm, $r^2 = 0.0002$, $p = 0.08$, Fig. 4c) which had on average 18 mg/g lipid per WW (Fig. 4).

Analysis of the residuals from the linear regression of length and total lipids showed significant differences in the lipid density of small fish when de-trended for size (Fig. 5a). Saffron cod collected on the EIS surface/mid-water survey had significantly higher lipids per WW than small fish that were collected on the EIS bottom trawl survey (ANOVA, $F_{2,61} = 11.22$, $p < 0.001$). There was no significant relationship between length and total lipids in large fish (Fig. 4c); however, this size class showed significant differences in lipids per WW between collection sites. Cod from Prudhoe Bay had higher levels than EIS surface/mid-water fish (ANOVA, $F_{2,69} = 5.99$, $p = 0.004$). Generally, large fish had higher proportion of neutral lipids (>75 mm, 53.9 ± 2.1) than small fish (<55 mm, 38.5 ± 1.2). However, within large fish there was high variability demonstrated by Prudhoe Bay fish having very high proportions of neutral lipids, ~71 % (Table 1). The proportion of polar lipids ranged from a low of 23 % in large Prudhoe Bay fish to a high of 49 % in small EIS fish (Table 2).

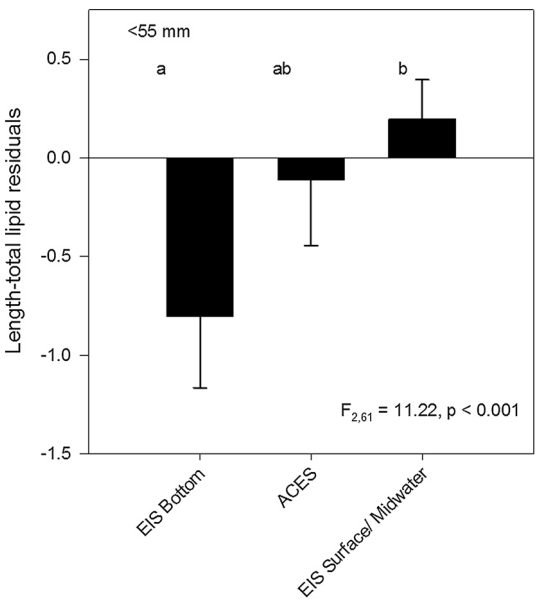

Fig. 5 Residuals of length–total lipid regression analyses for small juvenile saffron cod (*Eleginus gracilis*, FL <55 mm, $n = 65$) from three different research surveys. Differences in length–total lipid residuals between surveys were analyzed using a one-way ANOVA with Tukey's multiple comparison tests, $\alpha = 0.05$

Lipid composition of field-collected saffron cod

A total of 56 FAs were identified in juvenile saffron cod fish tissues. The three most abundant saturated FAs (SFAs) in all juvenile saffron cod were 14:0, 16:0 and 18:0. In large and small fish, 16:0 was the most abundant and comprised on average 15.2 ± 0.3 % in large fish and 18.4 ± 0.3 % in small fish. The proportion of ∑SFA was higher in small fish (27.7 ± 0.4) than in large fish (21.3 ± 0.3, Table 1).

The most abundant monounsaturated FAs (MUFAs) were 16:1n-7, 18:1n-9 and 18:1n-7 which were present on average at high levels in all size classes of fish at levels of 8.8, 9.9 and 4.9 %, respectively. The ∑MUFA were significantly higher in large fish (35.3 %) compared to smaller fish (28.2 %). Large Prudhoe Bay cod had elevated proportions of 16:1n-7 compared to all other fish from other surveys and size classes (Table 1).

The two most abundant polyunsaturated FAs (PUFAs) were DHA (docosahexaenoic acid, 22:6n-3) and EPA (eicosapentaenoic acid, 20:5n-3). Averaged over all fish, 22:6n-3 was 20.1 ± 0.5 %, while 20:5n-3 was 14.1 ± 0.2 %. The ∑PUFA was on average 43.4 ± 0.5 % over all fish sampled. The ratio of DHA/EPA averaged 1.50 ± 0.04, and the sum of n-3 PUFA was 38 .0 ± 0.54 %. The ratio of MUFA to PUFA was on average 0.8 ± 0.3 in all saffron cod. Further, large fish had higher ratios of MUFA/PUFA than small fish at 0.88:1 and 0.68:1, respectively (Table 1).

Variability in juvenile saffron cod FA profiles was seen to trend both with survey collection and with size class (nMDS plots, Fig. 6a). Saffron cod that were <55 mm in FL and were collected on the ACES survey in the nearshore were the most dissimilar to >75 mm saffron cod collected in nearshore Prudhoe Bay. Fish that were >75 mm in FL were generally located on the left side of the nMDS plot and were associated with high proportions of the diatom indicator FAs 16:1n-7 and 20:5n-3, while smaller fish were located on the right and had higher relative proportions of 22:6n-3 (Fig. 6a).

Size-class-specific ANOSIM analyses demonstrated more dissimilarity among large saffron cod collected in different surveys than within small saffron cod from different regions (Table 2, large fish $R = 0.502$, $p = 0.001$, small fish $R = 0.394$, $p = 0.001$). Smaller saffron cod showed a lot of homogeneity among collection surveys, and EIS bottom and EIS surface fish showed no significant differences ($R = 0.128$, $p = 0.136$) in FA trophic markers. ACES fish were more dissimilar from EIS fish collections on both surface ($R = 0.487$, $p = 0.001$) and bottom surveys ($R = 0.517$, $p = 0.001$, see Fig. 6b, Table 2). SIMPER analyses demonstrated that the top 5 FAs explained on

Table 2 Size-specific ANOSIM results of the FA composition of saffron cod (*Eleginus gracilis*) from different surveys

Small fish, <55 mm FL					
ANOSIM with pairwise comparisons			SIMPER		
Global test statistic $R = 0.394$, $p < 0.0001$	R		Dissimilarity	Top 5 FA	Cum %
$ACES_{(90\%\ group\ similarity)}$ versus $EIS\ bottom_{(87\%\ group\ similarity)}$	0.517	$p = 0.001$	13.7	22:6 n-3	56
				16:0	
				20:1 n-9	
				20:5 n-3	
				18:0	
$ACES_{(90\%\ group\ similarity)}$ versus $EIS\ surface/mid\text{-}water_{(87\%\ group\ similarity)}$	0.487	$p = 0.001$	15.23	22:6 n-3	50
				20:5 n-3	
				20:1 n-9	
				16:0	
				18:0	
$EIS\ bottom_{(87\%\ group\ similarity)}$ versus $EIS\ surface/mid\text{-}water_{(87\%\ group\ similarity)}$	0.128	$p = 0.136$	14.15	22:6 n-3	52
				20:1 n-9	
				16:0	
				20:5 n-3	
				16:1 n-7	
Large fish, >75 mm FL					
ANOSIM with pairwise comparisons			SIMPER		
Global test statistic $R = 0.502$, $p < 0.0001$	R		Dissimilarity	Top 5 FA	Cum %
$EIS\ bottom_{(86\%\ within\ group\ similarity)}$ versus $EIS\ surface/mid\text{-}water_{(82\%\ group\ similarity)}$	0.183	$p = 0.002$	18.5	22:6 n-3	65
				16:1 n-7	
				20:5 n-3	
				20:1 n-9	
				18:1 n-7	
$EIS\ bottom_{(86\%\ group\ similarity)}$ versus $Prudhoe\ Bay_{(91\%\ group\ similarity)}$	0.709	$p = 0.001$	18.3	16:1 n-7	70
				22:6 n-3	
				20:5 n-3	
				20:1 n-9	
				18:1 n-9	
$EIS\ surface/mid\text{-}water_{(82\%\ group\ similarity)}$ vs $Prudhoe\ Bay_{(91\%\ group\ similarity)}$	0.647	$p = 0.001$	24.3	22:6 n-3	74
				16:1 n-7	
				18:1 n-9	
				20:5 n-3	
				20:1 n-9	

Global R statistics and significance values from one-way ANOSIM are shown as well as pairwise comparisons between cruises. SIMPER shows FAs that are responsible for pairwise dissimilarity between fish collected on different cruises. Finally, the cumulative percent contribution of the top 5 FAs to differences among groups is shown

average 53 % of the dissimilarity between small fish groups (Table 2).

Within the larger size class of fish, there was the most dissimilarity between Prudhoe Bay and EIS bottom-collected saffron cod ($R = 0.709$, $p < 0.001$, Fig. 6c). SIMPER analyses of differences between fish from different surveys showed that 16:1n-7 and 22:6n-3 explained most of the dissimilarity (Table 2). The top 5 FAs explained on average 72 % of the differences between Prudhoe Bay fish and the EIS fish. Prudhoe Bay fish had higher proportions of 16:1n-7 and lower proportions of 22:6n-3 when compared to EIS fish.

There was a significant relationship between the ratio of 16:1n-7/16:0 (diatom marker) and the density of lipid in saffron cod tissues (lipid per WW in mg/g). Small and large fish from four different cruises showed this significant

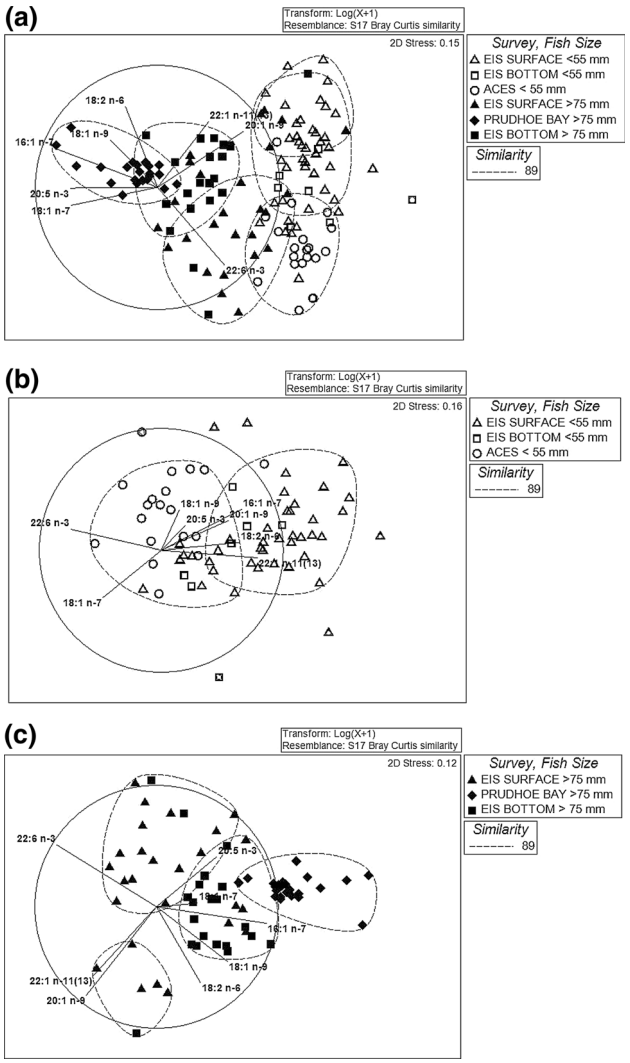

Fig. 6 Juvenile saffron cod (*Eleginus gracilis*) nMDS (non-metric multidimensional scaling analysis, a ordination technique that serves as a means of visualizing the level of fatty acid similarity in individual fish from the whole dataset) output showing (**a**) both large and small fish from four different survey collections in 2012–2013, $n = 156$ (**b**) just small fish (FL <55 mm, $n = 68$) from three different research surveys and (**b**) large juvenile saffron cod (FL >75 mm, $n = 72$) from three different research surveys. Percentage similarity groupings from cluster analyses are superimposed on nMDS plots

linear relationship; however, the rate of change was steeper in small age-0 saffron cod than in larger fish. The relationships were described by the following equations: Small saffron cod lipids per WW (mg/g) = 4.9 + 30.1 (16:1n-7/16:0), $r^2 = 0.32$, $p < 0.001$ in Fig. 7, and large saffron cod lipids per WW (mg/g) = 8.5 + 12.0 (16:1n-7/16:0), $r^2 = 0.26$, $p < 0.001$ in Fig. 7.

Stable isotopes of field-collected saffron cod

Overall, there was a significant positive linear relationship between $\delta^{13}C$ and length ($p < 0.01$; $r^2 = 0.12$), however

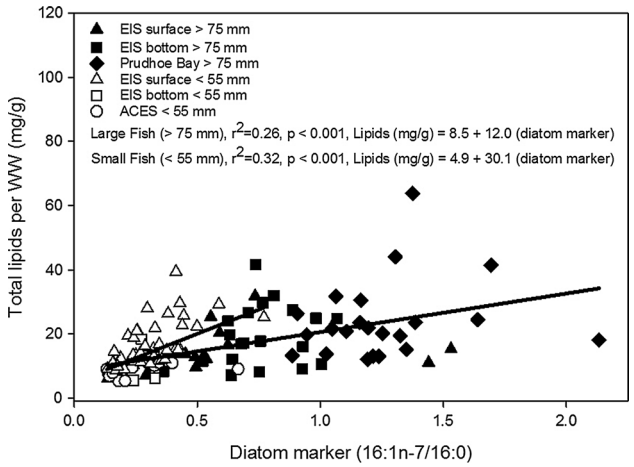

Fig. 7 Relationship between diatom marker (% 16:1n-7/ % 16:0) and total lipids per WW (mg/g) in small (<55 mm, $n = 68$) juvenile saffron cod (*Eleginus gracilis*) and large (>75 mm, $n = 72$) saffron cod from four different research surveys. *Colors* represent fish size (fish <55 mm = *open*; fish >75 mm = *filled*)

not for $\delta^{15}N$ ($p < 0.10$; $r^2 = 0.06$) (Fig. 8a, b). Among regions, the large size class from the EIS bottom survey was significantly more enriched in $\delta^{13}C$ ($p < 0.04$; Fig. 8c) than the other regions including the small size class with a difference of 1.3 ‰. The small size class of juvenile saffron cod from the EIS bottom survey was also significantly enriched in $\delta^{13}C$ relative to the small size classes of fish in both the EIS surface survey and ACES ($p < 0.01$). The small size class juvenile saffron cod from the EIS bottom survey was not significantly different than large juvenile saffron cod from Prudhoe Bay ($p = 0.27$) nor the large fish from the EIS surface survey ($p = 0.23$); in fact the three varied by <0.6 ‰. There was no difference between size classes of juvenile saffron cod collected from the EIS surface in $\delta^{13}C$ ($p = 0.16$) nor relative to saffron cod from the ACES survey ($p = 0.10$).

Significant overall variation in $\delta^{15}N$ was observed among regions and size classes ($F_{5,106} = 29.24$; $p < 0.001$). As with carbon, large saffron cod from the EIS bottom survey were more enriched in $\delta^{15}N$ (16.21 ± 0.56 ‰), but not significantly different than large saffron cod from the EIS surface (15.47 ± 0.21 ‰) nor the small size class from the EIS bottom survey (14.88 ± 0.28 ‰; $p = 0.29$). These three were significantly more enriched than the small saffron cod from the EIS surface survey (13.10 ± 1.26 ‰; $p < 0.001$), which was at 1.78 ‰ more depleted than the small fish from the EIS bottom survey. Based on the pairwise comparisons, small saffron cod from the ACES survey and large cod from Prudhoe Bay were not significantly different ($p = 0.10$), with a mean difference in $\delta^{15}N$ of 0.62 ‰. Additionally, pairwise comparisons of cod from Prudhoe Bay and small saffron cod from the EIS surface survey indicated negligible differences, with a

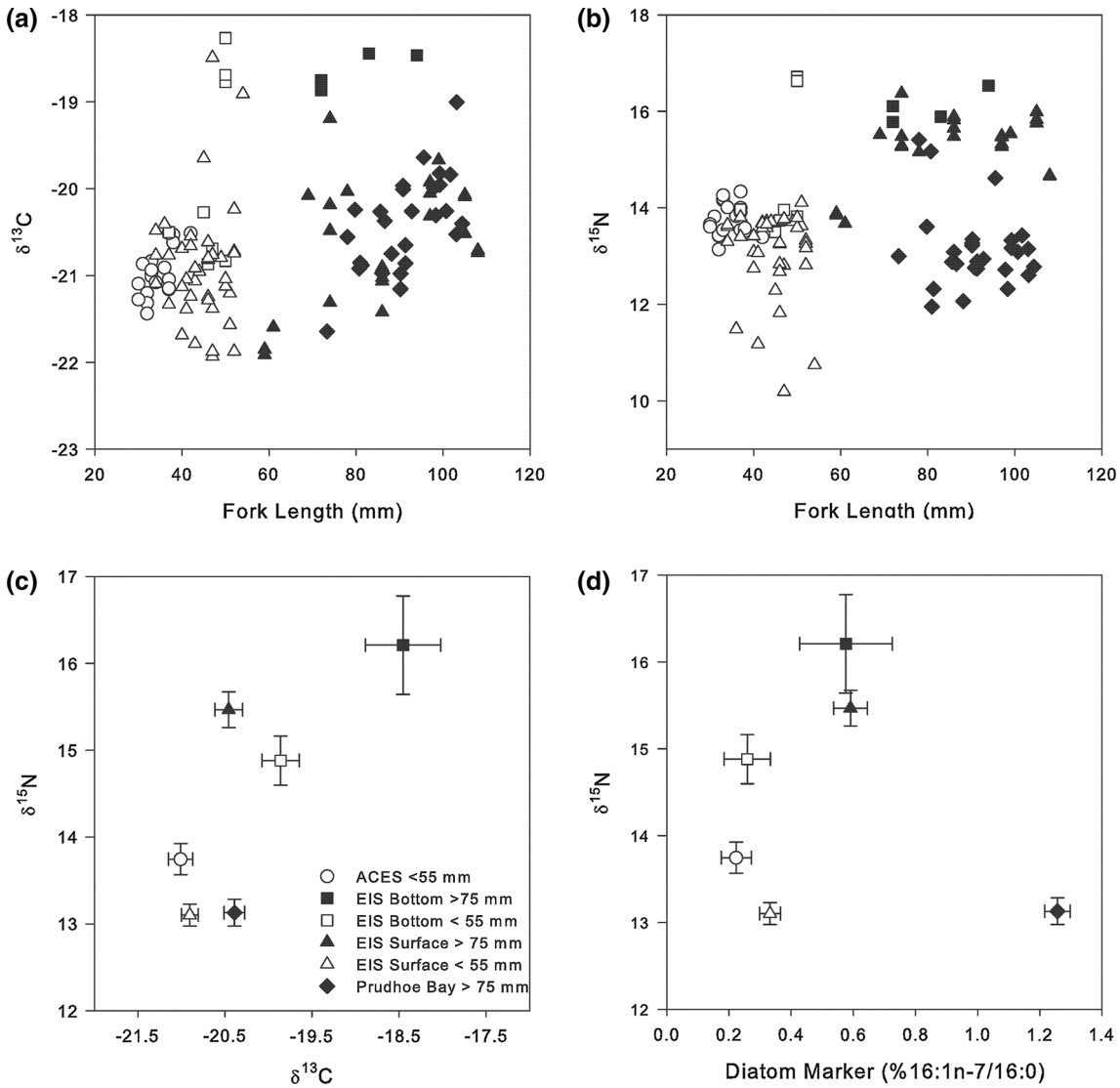

Fig. 8 Relationship between **a** $\delta^{13}C$ and FL (mm), **b** δ^{15} N and FL (mm), **c** $\delta^{13}C$ and δ^{15} N as well as **d** δ^{15} N and the fatty acid diatom marker 16:1n-7/16:0. Data are shown for 105 saffron cod (*Eleginus gracilis*) of known ages on which complimentary fatty acid and isotope data are available. *Error bars* represent standard error derived from pairwise comparisons. *Colors* represent fish size (fish <55 mm = *open*; fish >75 mm = *filled*). *Error bars* represent standard error

mean δ^{15}N difference of 0.02 ‰ ($p = 0.90$, Fig. 8c). Prudhoe Bay fish showed a unique combination of lower mean δ^{15}N values and elevated diatom markers (Fig. 8d).

The trophic breadth (convex hull area, CHA) among regions and size classes suggested that saffron cod varied by region in their dietary breadth. Saffron cod from EIS surface survey exhibited the greatest trophic breadth (CHA = 14.32) with most of the variation driven by separation between the large and small size classes, with each contributing a much smaller areal extent (CHA = 5.66 and 1.36, respectively). Additionally, the large saffron cod from Prudhoe Bay exhibited relatively extensive trophic breadth (CHA = 5.60) when considering the proximity of sampling stations, suggesting a variety in resource availability. Saffron cod from the EIS bottom and ACES survey showed the narrowest breadth (CHA = 2.52 and 0.93, respectively).

Condition of temperature-growth laboratory experiment saffron cod

The effects of temperature on lipid allocation were clearly evident following results of the laboratory experiment. Although not apparent in the hepatosomatic indices (Fig. 9a), lipid class analyses indicated saffron cod stored significantly more total lipid and triacylglycerols (TAGs) in their livers at higher temperatures (up to 20 °C) than at

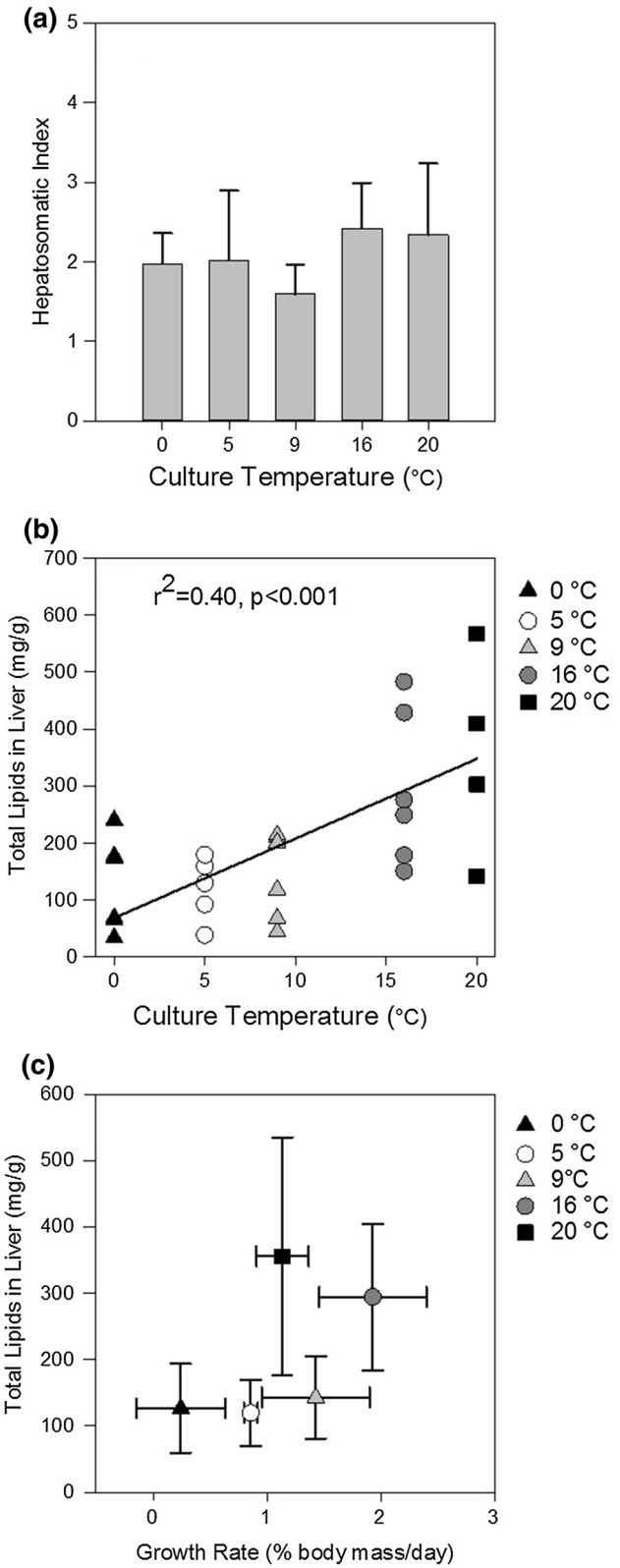

Fig. 9 Comparison of the **a** hepatosomatic index, $n = 6 \pm 2$ SE per temperature **b** total lipids (mg/g, each symbol represents one fish) and **c** total lipids as a function of growth rate from saffron cod (*Eleginus gracilis*) reared at five temperature treatments ranging from 0 to 20 °C. *Each symbol* represents mean ± 2 SE, $n = 6$

lower culture temperatures (0 °C, total lipids only shown in Fig. 9b). Linear regression significantly described the relationship of temperature on lipid storage: Liver TAG (mg/g) = 55.8 + 8.9 (temperature °C) ($r^2 = 0.37$, $p < 0.001$) and liver total lipid (mg/g) = 84.3 (mg/g) + 12.2 (temperature °C) ($r^2 = 0.40$, $p < 0.001$). However, upper thermal stress was apparent at 20 °C by way of variable lipid storage and reduced growth compared to 16 °C (Fig. 9c).

Discussion

This is the first investigation of the ontogeny of lipid storage in a juvenile Arctic gadid. It is clear that saffron cod in the Arctic are a highly variable prey species in terms of lipid content. Based on the combined biomarker approaches, otoliths-based age data and live-animal temperature experiments, our mechanistic understanding of the lipid dynamics in saffron cod is that: (1) lipid storage is dependent on ontogeny, (2) within an ontogenetic stage, regional conditions can alter energy storage, (3) growth and energy storage are both food and temperature dependent, and (4) higher lipid storage in Arctic Beaufort fish was associated with slower growth and feeding at lower trophic levels than fish from farther south in the Bering Sea. The mechanisms and consequences of these patterns are discussed in turn below.

Energetic density and variability

Lipid storage in juvenile saffron cod was variable (5–45 mg/g WW) with averaged survey values ranging from 10 mg/g in age-0 ACES fish to 21 mg/g WW in age-1 Prudhoe Bay fish. Comparative data of juvenile saffron cod in other regions are unavailable, but walleye pollock from the Lynn Canal and Frederick Sound in SE, AK, are reported to have considerably higher lipid density 22.5 mg/g; age-0 and 27.4 mg/g; age-1 (Heintz and Vollenweider 2010). In contrast, Van Pelt et al. (1997) described lower lipid densities of 9.8 mg/g in Pacific cod and 14.4 mg/g in juvenile walleye pollock collected around puffin breeding grounds in the Eastern Aleutian Islands. Similar variation is also reported in the Atlantic cod (*Gadus morhua*) that undergo high seasonal variation in lipids following settlement in coastal eelgrass habitats around Newfoundland, Canada. Lipid values within these fish ranging from a high of 25 mg/g in the late summer to a low of 5 mg/g WW in late fall (Copeman et al. 2008). Overwintering survival in juvenile fish may be determined by the amount of lipid energy individuals can store during the summer and fall period. Siddon et al. (2013a) proposed that recruitment

dynamics in walleye pollock are largely determined by the amount of energy storage age-0 juveniles can acquire prior to the onset of their first winter in the Bering Sea. Juvenile saffron cod demonstrated dramatic increases in lipids per WW throughout all regions within the age-0 period (30–55 mm size range), with individuals collected at Barrow, AK, being very small and having the lowest lipid density compared to similar size offshore fish sampled within the Chukchi and Bering Seas. Similarly, age-0 saffron cod from surface waters had higher lipid densities than age-0 juveniles collected from bottom trawls. These patterns are likely due to an interaction of temperature and food availability (see below), but raise interesting questions about the fate of these individuals and overall contribution to the adult population.

We observed a break-point in the relationship between fish size and lipid storage on a WW basis. Originally, this break-point appeared to represent different storage strategies between age-0 and age-1 fish, with the break-point representing overwintering lengths. Indeed, fish collected in Chukchi and Arctic waters that were <55 mm were age-0, while fish >75 mm were age-1. However, otolith analyses on fish samples from Bering Sea surface surveys indicated that these fish had accelerated growth and/or an extended growing season that allowed them to reach 110 mm during the age-0 period (Helser et al. in revision). Therefore, the break-point we observed for juvenile saffron cod is more likely an ontogenetic pattern, possibly around the time of settlement. This pattern could result from changes in foraging behavior, settling behavior with fish moving from shallow to deeper habitats, or changes in the physiology of lipid storage with increased storage of lipid in liver versus muscle tissues. Such a break-point in lipid storage with size has previously been noted by Copeman et al. (2008) to occur in Atlantic cod at 59 mm in standard length. Copeman et al. (2008) hypothesized that decreased lipid storage with increasing length in age-0 cod was likely due to trade-offs in fast growth and energy storage in response to high predation pressure. By allocating more energy to growth and avoidance behaviors, juvenile fish can reduce size-dependent predation at the expense of energetic storage in the flesh or liver (Post and Parkinson 2001; Hurst 2007).

Alterations in diet commonly occur in gadids between 55 and 80 mm in length. For example, a strong size-dependent foraging strategy was obvious in Arctic cod from Svalbard, with smaller fish (<80 mm) feeding primarily on small copepods and *Calanus* spp., and larger fish on a higher proportions of the Arctic amphipod, *Themisto* spp. (Renaud et al. 2012). Relatively little is known about juvenile saffron cod feeding habits, although Buckley et al. (unpublished data) have been analyzing the size-dependent differences in saffron cod diets (% weight) from Bering and Chukchi Seas. Small fish (<55 mm) from the Bering Sea had up to 89 % of their diets as copepods with 71 % specifically from the family Calanidae. Conversely, larger fish (75–110) collected off-bottom had only 0.4 % calanoid copepods and a much higher diversity of prey items including ~25 % mysids and ~45 % amphipods. Trends in the Chukchi Sea were similar with small fish having ~88 % copepods with 57 % from the family Calanidae. Larger fish (75–110 mm) had <1 % copepods and elevated proportions of shrimp, amphipods, polychaetes and euphausiids. Therefore, it is likely that the ontogenetic energy storage shift we observed in cod is due to changes in prey type and/or quality that occurs at ~60 mm in length.

The condition of juvenile fish varied by way of an interaction between fish size and collection region. Small saffron cod (<55 mm) collected in the nearshore around Barrow, AK, represented the smallest and poorest condition individuals, whereas larger age-1 cod from nearshore Prudhoe Bay, AK, were in the highest condition compared to similarly sized fish from the offshore. Juvenile Pacific and Atlantic gadids settle in nearshore regions where summer temperatures are warm and they can maintain growth, avoid predation and have access to an abundant food supply (Grant and Brown 1999; Laurel et al. 2003, 2007). In Temperate Regions, coastal nursery areas with eelgrass and kelp are essential to many juvenile fish and invertebrates, and also maintain bay-scale population structure in Atlantic cod juveniles (Orth et al. 1984; Bradbury et al. 2008). Despite the importance of this life history stage to gadid recruitment, little is known about cod trophic ecology and bioenergetics during this critical nearshore settlement period. Further, shallow (<15 m) nearshore habitats in Arctic Regions around Barrow and Prudhoe Bay have little to no structured habitat, and temperatures at Prudhoe Bay, AK, can reach over 15 °C during late summer. It is conceivable that throughout early juvenile stages (<55 mm) prey quality may be more important than during the later age-1 juvenile stages (>75 mm). If food quantity and quality in the offshore are elevated, this could provide more of a growth and condition advantage in the early juvenile stages compared to the later juvenile stages, where temperature may be more influential on growth and condition. Further research needs to be done to tease apart the interactive effects of temperature and food quality on different ontogenetic stages of Arctic fish.

Dietary sources and variability

We predicted that trophic biomarker differences between nearshore and offshore surveys would reflect the input of nearshore carbon sources into the diet of juvenile saffron cod. Fatty acids (FAs) and isotopes provide integrated (weeks to months) dietary information compared to gut

content analyses that represents feeding over hours to days (St John and Lund 1996; Budge et al. 2006; Copeman et al. 2013). C_{20} and C_{22} polyunsaturated FAs (PUFA) are particularly important in cold water marine organisms as they allow animals to maintain cell membrane fluidity at very low temperatures (Hall et al. 2002; Laurel et al. 2012). These C_{20+22} FAs are considered essential and must be provided in the diet as marine fish generally cannot synthesize adequate quantities of long-chain PUFAs from shorter-chain precursors to satisfy their metabolic requirements (Sargent et al. 1999). Long-chain PUFAs formed in primary production are transferred and concentrated in consumers throughout the food web (Dalsgaard and St John 2004). Other sources of PUFAs in nearshore marine environments include shorter-chain C_{18} PUFA from terrestrial, macrophyte and fresh water sources; however, these are of lower nutritional value than longer-chain PUFAs (Takeuchi 2014). We have previously observed higher proportions of C_{18} PUFA in fish from nearshore habitats around Newfoundland, Canada (Copeman et al. 2009, 2013; Ramos et al. 2003), and in Kodiak, AK, USA (Copeman, unpublished data) at levels ranging from 3 to 6 % of total FAs. However, we did not see these elevated proportions of C_{18} PUFA in saffron cod from nearshore Arctic Regions. This was surprising given that salinity in Prudhoe Bay was often very low, suggesting a significant input of freshwater from the Sag and Sagavanirktok Rivers. Lack of retention of this C_{18} PUFA in saffron cod tissues could be due to an absence of structural habitat that traps nearshore organic carbon, as seen in many temperate gadid nurseries (Copeman et al. 2008).

FA trophic markers were used to indicate variability in diet due to both ontogeny and sampling location. Although we do not have direct measurements of FAs in prey items, there is existent knowledge on the characteristic FAs present in different primary producers in both marine pelagic and benthic systems (Dalsgaard et al. 2003; Kelly and Scheibling 2012). Specifically, diatom production is associated with higher levels of 20:5n-3, 16:1n-7 and an increased ratio of 16:1n-7/16:0 (Dalsgaard and St John 2004). Earlier research has found a positive significant correlation between diatom markers (16:1n-7/16:0, 20:5n-3/22:6n-3) and the biomass percentage of diatoms during the spring bloom off both Greenland and Newfoundland, Canada (Budge and Parrish 1998; Reuss and Poulsen 2002). Further, Dalsgaard and St John (2004) noted that a diatom ratio (16:1n-7/16:0) value >2 represented diatom dominancy in the food web, while a ratio <0.3 reflected flagellate dominancy. Collections of *Calanus marshallae* and *C. glacialis* in the Chukchi and Bering Seas in 2010 and 2011 showed diatom indicators ranging from 0.6 during maximum ice extent to a high of 2.4 during blooms in ice-free periods (Wang et al. 2015).

Diatom-sourced diets for larval and juvenile fish may contribute to increased condition. St John and Lund (1996) used a combination of laboratory feeding studies and analyses of field-collected larvae to show that diatom biomarkers are associated with improved condition in juvenile North Sea Atlantic cod fed in frontal upwelling zones. More recently, Litz et al. (2010) and Pethybridge et al. (2014) noted improved condition of forage fish when feeding during elevated diatom production in both the California Current and the Mediterranean Ecosystems, respectively. We have shown that both size classes of juvenile saffron cod have a significant positive relationship between the diatom marker ratio (16:1n-7/16:0) in their tissue and their total lipid storage. Further, the slope and strength of the relationship were higher in small age-0 saffron cod than in larger juveniles, indicating that prey quality could be even more crucial during late larval and early juvenile development than in the later age-1 juvenile stage.

Copepods from the family Calanidae store excess lipid as both triacylglycerols (TAGs) and wax esters (WEs). TAGs and WEs are considered to be short- and long-term storage, respectively. Wax esters are simple esters comprised of both a FA chain that is generally dietary in origin and an alcohol chain that is synthesized '*de novo*' within the copepod. The alcohol chains are often characterized by high proportions of 20:1 and 22:1 MUFAs (Lee et al. 2006; Wold et al. 2011). Across all surveys, small juvenile saffron cod had on average 7.1 ± 0.4 % of total FAs as copepod marker ($\sum$20:1 + 22:1), while larger saffron cod had only 4.7 ± 0.5 %. These trends agree with increased proportions (% weight) of calanoid copepods in small cod stomachs as compared to larger cod. The lowest biomarker proportions were found in nearshore Prudhoe Bay cod (2 %), while highest values were found in EIS fish (7.4 %). These levels of copepod biomarkers are in contrast to similarly sized co-occurring Arctic cod collected in 2013 in the Chukchi and Beaufort regions ($\sim$30 % of FAs, Copeman et al. unpublished data). Further, Graham et al. (2014) noted proportions of calanoid copepod markers as high as $\sim$25 % in age-0 and age-1 Arctic cod collected in three locations throughout the Beaufort Sea in 2011. Low proportions of copepod FA biomarkers in saffron cod here is somewhat perplexing given that up to 89 % of the prey mass in small saffron cod stomachs is comprised of calanoid copepods. Although speculative, the following hypotheses to explain this discrepancy include: (1) preferential catabolism of C_{20} and C_{22} MUFA, (2) incomplete digestion of copepod WE, (3) targeted feeding on ontogenetic stages of copepods with lower WE proportions, (4) differential lipid class storage or (5) stomach content analyses only provides a snapshot of prey items with hard parts while fatty acids provide time-integrated (4–8 weeks) dietary markers.

Consideration of lipid classes and total lipids are important for the correct interpretation of biomarker results. In the case of copepod WE assimilation, we must reflect that C_{20} and C_{22} MUFA (copepod FA markers) are not accommodated in fish polar membranes (Bell and Dick 1991; Tocher et al. 2008) and are rather re-esterified after hydrolysis into neutral TAG storage. Small saffron cod have on average only 20 mg/g total lipid per WW at 55 mm FL, while Arctic cod have double that amount at ~40 mg/g WW (Copeman, unpublished data). Further, in saffron cod, neutral lipids comprise only 38 %, while Arctic cod have very high proportions of neutral lipids, ~70 % (Copeman, unpublished data). Therefore, lower levels of copepod markers in saffron cod feeding on calanoid copepods are likely due to their overall lower level of total lipids and specifically, reduced neutral lipid storage.

Larger saffron cod (>75 mm) from Prudhoe Bay were characterized by higher total lipids and in particular high proportions of neutral lipids. FA markers indicate a significant input of diatom production to these saffron cod. Saffron cod at this size class had a predominance of benthic and semi-benthic prey such as mysids, gammarid amphipods, polychaetes and euphausiids in their stomachs (Buckley et al., unpublished data). Marine polychaete worms from cold water systems have been found to preferentially and readily assimilate diatom and ice-algae production (McMahon et al. 2006). As an example, the polychaete *P. gouldii* from cold water Labrador, Canada, had over 13 % of its total FAs represented by the diatom indicator 16:1n-7 (Copeman and Parrish 2003).

Arctic gadid species are known to exploit variable prey resources resulting in spatial and temporal variation in isotopic composition (Craig et al. 1982; Budge et al. 2008; von Biela et al. 2013), and proximity to terrestrial sources or inputs into marine systems can significantly act to structure food web processes (von Biela et al. 2013) that are expressed in isotopic analyses. We observed variation between the saffron cod collected from different regions as well as size classes which may be attributable to diversification in trophic pathways and also available basal resources, but might also reflect the importance of ontogeny. This is most noticeable in the differences between the saffron cod collected in the EIS bottom and surface surveys, where the small cod collected in the surface and mid-water region had a mean $\delta^{15}N$ nearly 2 ‰ less than the corresponding cod captured in the bottom waters. The difference between these groups might be due to the relatively high variance measured in $\delta^{15}N$ for the small EIS surface fish, where these samples represent fish collected across a wide geographic range, spanning approximately 6.5° of latitude. For example, when examining these samples, the cod collected in the north Pt. Lay region were significantly ($p = 0.02$) enriched by a mean of 1.16 ‰ relative to the fish south of Pt. Lay despite having a narrow range in fish size (40–51 mm). While we cannot extend inference based on any specific evidence, these differences might be related to variable oceanographic and fine-scale processes.

Prudhoe Bay fish showed a unique combination of lower mean $\delta^{15}N$ values and elevated diatom markers as well as increased storage lipids per WW. This suggests that feeding at a lower trophic level in age-1 fish resulted in saffron cod with elevated condition in nearshore Arctic waters. The clear association between diatom markers and condition in saffron cod is seen throughout both age-0 and age-1 fish. However, Prudhoe Bay fish were only sampled in 2013 compared to the rest of the saffron cod that were collected during 2012. Further collections and analyses of saffron cod are required to disentangle inter-annual variation from differences due to regional variation in temperature and food quantity or quality (Soreide et al. 2007).

The laboratory experiments indicated a clear, positive effect of temperature on saffron cod growth (Laurel et al. this issue) and lipid density in the liver (this study). Together, these results indicate that saffron cod are able to both grow fast and store energy at high temperatures, with some possible decreased growth potential above 16 °C. Collection sites in coastal Prudhoe Bay, AK, can often reach a surprising 16 °C, which is even higher than nearshore regions in the Gulf of Alaska (Kodiak) where they are also found in high abundance (Laurel et al. 2007). Clearly, warm shallow brackish nearshore nursery areas such as those found around Prudhoe Bay and around Kotzebue, AK, favor growth and elevated condition in age-1 juvenile saffron cod. This is in sharp contrast to Arctic cod where temperatures above 9 °C are considered stressful and 16 °C is lethal (Laurel et al. this issue).

Conclusions

Bluhm and Gradinger (2008) reviewed possible food web change scenarios in the Arctic in relation to food availability for Arctic marine mammals. Within, they describe warming as contributing to increased river runoff and nutrient input into coastal/shelf areas. However, the effect on keystone species such as Arctic cod remained uncertain. This is largely due to uncertainty about which species can take advantage of the increased growth potential (warm temperatures and variable food) and which will be more negatively impacted. Here, we have provided fish condition data and food web relationships for juvenile saffron cod which clearly demonstrate ontogenetic patterns and spatial variability. Further, through laboratory studies we have linked increased energy storage to growth at elevated temperatures. Additional research is required to tease apart

how annual variation, food quality/quantity and temperature interact to effect cod condition in the field. Nevertheless, data shown here will help improve models aimed at understanding climate change scenarios in Arctic fish communities. Saffron cod appear physiologically capable of taking advantage of increased temperatures in a warming nearshore Arctic environment.

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