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NOTE

Energy Condition of Subsistence-Harvested Fishes in Arctic Coastal Lagoons

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Abstract
In Arctic Alaska, Indigenous and rural residents depend on wild-harvested foods for sustenance and the subsistence lifestyle is integral to their culture. Marine and diadromous fishes, which often occupy coastal lagoon habitats, are relied upon for subsistence harvest, particularly Pacific salmon, whitefishes (Coregoninae), cods (Gadidae), and flounder species (Pleuronectidae). However, little research has been conducted that assesses the energetic condition of these fishes, which are harvested by the tens of thousands annually. The effects of accelerating climate change and human development on the metabolic rates, diet, body condition, and energy density of fish is of great concern because these effects will, in turn, affect the people who depend on these species for food security. Consequently, we characterized energy density and percentage of lipid, water, and protein content of 10 fish species in four coastal lagoons within Cape Krusenstern National Monument, Alaska. We found that whitefishes, particularly Bering Cisco *Coregonus laurettae* and Least Cisco *C. sardinella* exhibited the highest energy density, percentage of lipid, and percentage of protein content, significantly greater than that of marine cod and flounder species, Fourhourn Sculpin *Myoxocephalus quadricornis*, freshwater Pond Smelt *Hypomesus olidus*, and values from other regional species that have been in published literature. Additionally, when the relative mean abundance and body weight of each species was taken into account, total energy value by availability in the lagoons was highest for whitefishes when compared with marine taxa and the freshwater Pond Smelt. Given the impending effects of climate change and coastal construction in the region, it will be important to monitor the energy condition of lagoon fishes to ensure their quality and availability for subsistence harvesters.

For residents of remote communities in Arctic Alaska, marine and diadromous fishes can constitute a significant amount of subsistence harvest, supplementing marine and terrestrial mammal and plant food sources (Fechhelm and Streever 2007; Magdanz et al. 2010). Given the

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dependence of residents on wild foods (White et al. 2007), it is important to monitor fish and wildlife population trends and identify long-term changes in population abundance or condition (ICC-A 2015). In the Arctic, accelerating climate change and human activities may have adverse effects on the ecology and population health of these wild food resources (Wassman et al. 2011; Jing et al. 2012; Smith and Stephenson 2013). Quantifying these effects requires baseline surveys and the monitoring of subsistence food resources (Moerlein and Carothers 2012).

Energy density and percentage of lipid content are useful measures of the nutritional quality of wild food resources (Appavoo and Kubow 1991). These measures can allow for the identification food sources of the highest energy per unit biomass harvested, and they can provide baseline values for future comparison. In addition to a direct linkage between fish nutritional quality and subsistence harvest, energy condition can be related to individual survival and population productivity and the energy condition of prey taxa may affect the productivity of predatory subsistence-harvested species (Österblom et al. 2008; Whitfield 2008). For Arctic fishes, increasing water temperatures, changing seasonal timing, range expansion of boreal taxa, and other effects of climate change and human activity may result in changes in their distribution, abundance, diet, metabolic rate, body condition, and tissue proximate composition (Ottersen et al. 2010; Wassman et al. 2011; McMillan et al. 2012; Hollowed and Planque 2013). For example, the worldwide availability of omega-3 fatty acids found primarily in fish is expected to decline with the advance of climate change effects (Colombo et al. 2020). However, the energy density and percentage of lipid composition of subsistence fishes that occur along the Arctic coast of Alaska are poorly documented, hindering our ability to assess such changes. Many studies (e.g., Trudel et al. 2005; Courtney et al. 2020) have focused on Pacific salmon *Oncorhynchus* spp., a universally used food fish throughout the north, but other fishes (e.g., Dolly Varden *Salvelinus malma* and whitefishes [Coregoninae]) can be harvested in greater amounts in the Arctic because the abundance of spawning salmon populations diminishes in the northerly direction (Nielsen and Ruggerone 2013). Furthermore, salmon are largely harvested during seasonal pulses, whereas other species are more consistently available.

Thus, our specific objectives for this investigation were to (1) characterize mean energy density, percentage of lipid, and percentage of water for 10 species of diadromous and marine fishes in coastal habitats within Cape Krusenstern National Monument in Arctic Alaska, with an emphasis on taxa that are of subsistence importance, and (2) compare energy density among species. This study will provide baseline data for the southern Chukchi Sea region and the first quantification of energy density for some species.

METHODS

Study area.— The fish for this study were collected from four Arctic coastal lagoons (Kotlik, Tasaychek, Krusenstern, and Aukulak), a lagoon channel (the Anigaaq channel), and a nearshore oceanic habitat (Anigaaq Ocean) in Cape Krusenstern National Monument, Alaska (Figure 1). The lagoons and lagoon channel are seasonally and intermittently connected to the Chukchi Sea (Tibbles 2018). The fish species that are present in these habitats include those of subsistence importance such as whitefishes, Dolly Varden, Pacific salmon, cods (Gadidae), and flounder species (Pleuronectidae). Additionally, taxa such as sculpins (Cottidae), stickleback (Gasterosteidae), and Pond Smelt *Hypomesus olidus*, among others, occur in these habitats and are ecologically important as prey for predatory fishes, birds, and marine mammals that are of subsistence importance (Quakenbush et al. 2015; Whitehouse and Buckley 2017; Naves 2018).

Fish capture and laboratory processing.— The fish were captured at each location in 2016 and 2017 using beach seining, gill netting, and fyke netting, as part of the National Park Service vital sign component of the Inventory and Monitoring Program for Cape Krusenstern National Monument (Robards 2014). This program was intended to establish biotic and abiotic reference conditions for assessing long-term changes in coastal lagoon habitats. The gill nets had five panels, each 7.62 m in length, with mesh stretch measurements of 2.54, 3.84, 5.08, 7.62, and 10.16 cm. The gill nets were deployed for several hours (dependent on capture success) and checked each hour, the fyke nets were set for 3 h, and two beach-seine sets were conducted at each site. The captured fish were identified and measured, and a subset that was representative of species and sizes that were present at each location were euthanized for a proximate composition analysis with an overdose of anesthetic (AQUI-S 20E; AQUI-S, Lower Hutt, New Zealand, Ltd.) and frozen. Sex was identified for some individuals, although fewer than 20 per species.

In the National Oceanic and Atmospheric Administration's Alaska Fisheries Science Center Auke Bay Laboratory, sex was determined when possible by a visual inspection of the gonads. The fish were dried using one of two methods: in a conventional drying oven or in a Thermogravimetric Analyzer (TGA) 701 (LECO, St. Joseph, Michigan). For conventional drying, whole fish were heated in a convection oven at 55°C (range: 50–60°C), weighed daily, and dried until a constant mass was achieved. For the TGA, the individual whole fish were first homogenized using a Bullet blender and an aliquot of homogenate (<7 g) was then dried at 135°C to constant mass. A quality control sample that was included with each batch consisted of Meat 1546 from the National Institute of Standards and Technology and percentage of

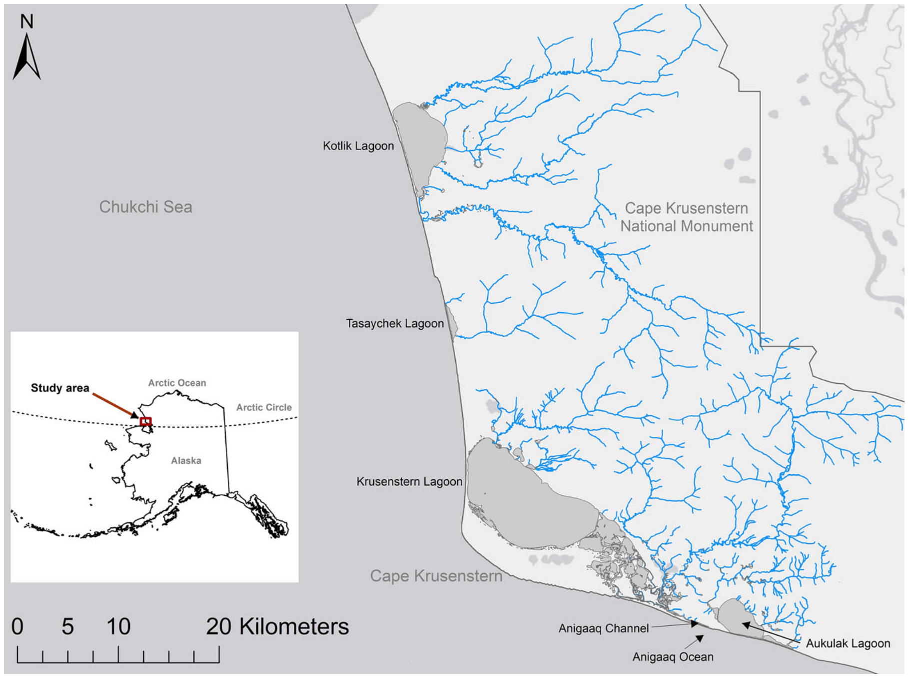

FIGURE 1. Coastal lagoon fish collection locations in Cape Krusenstern National Monument, Alaska.

moisture was verified to vary less than 1%. Additionally, a replicate aliquot of one of the samples was analyzed in each TGA batch to ensure that the coefficient of variation was ≤1. Moisture content (%) was calculated as the mass of water lost relative to the mass of the dried sample. The dried fish and aliquots were pulverized to a fine powder with homogenous consistency by using a bead mill (Next Advance, Troy, New York). All of the proximate composition and energy density values are reported for fish wet weight to allow for comparisons between related studies and because fish wet weights are the most relevant for subsistence harvesters.

For the total lipid analysis, content was determined using a modified version of the microscale lipid protocol described by Van Handel (1985). The values were calculated by comparison of the absorbance values to a calibration curve that was generated by using certified Pacific Menhaden *Ethmidium maculatum* oil from the National Institute of Standards and Technology. The quality control samples that were included with each batch were a sample replicate and an in-house reference of Walleye Pollock *Gadus chalcogrammus*, with a coefficient of variation ≤1 between replicates and from the target value for Walleye Pollock.

The values for energy density were determined by bomb calorimetry. A subsample of 2–15 mg dried fish powder was compressed into a pellet for combustion in a Parr 1425 micro-bomb calorimeter (Parr, Moline, Illinois) to obtain energy content (kJ/g wet weight) following the standard protocols that are outlined in the instrument manual. The quality control measures were (1) the benzoic acid standard included in each analytical run to ensure accuracy, (2) sample replicates to ensure the consistency of sample homogenization, and (3) an in-house reference to ensure consistency with a biological standard.

The values for the protein content of the dried homogenates were calculated from measured nitrogen values using a LECO TruSpec CHN analyzer following the methods that are outlined in the instruction manual (LECO 2007). Briefly, samples of ~0.1 g of dried homogenate were wrapped in foil and combusted at 950°C. Expelled nitrogen was quantified and protein content was estimated by multiplying the total nitrogen content by the Kjeldahl conversion factor of 6.25 to account for the nitrogen content of protein (AOAC 2005). Before the sample analysis, the CHN analyzer was calibrated with ethylene diaminetetraacetic acid and atmospheric blanks. With each batch, the quality control samples included a standard reference material of Meat 1546 from the National Institute of Standards and Technology, with <2% error from the target value, a sucrose blank with <0.2% protein, and a sample replicate varying <1 standard deviation.

Data analysis.— The proximate composition and energy density data were pooled across years and locations by species because too few replicates per species by location and year were available for a more detailed comparison. An ANOVA was conducted in R version 3.1.3 (R Development Core Team 2020) to determine whether energy density and proximate composition differed between the sampled species, formula in R script is aov[(response) ~ species], and a Tukey's honestly significantly different post hoc test was run to determine significant differences ($\alpha < 0.05$) between the pairwise comparisons.

Because simple energy content per unit weight of fish does not fully describe the potential nutritional value of fish species that vary greatly in body size and abundance in Arctic lagoon habitats, an index subsequently referred to as "relative total energy content" was calculated for each species by multiplying the mean energy density by the average fish body weight and average sampling abundance per lagoon per year (units of MJ sampled/lagoon). The results for sampling abundance of the fish species were determined by averaging the values from data that were collected during the 2015–2018 lagoon fisheries monitoring efforts and qualitatively compared among the captured species.

RESULTS

A total of 380 fish were collected and processed for percentage of water content, 356 of these were assessed for percentage of lipid, 313 for energy density, and 352 for percentage of protein in this investigation (Table 1). These included diadromous species, Humpback Whitefish *Coregonus pidschian*, Least Cisco *Coregonus sardinella*, Bering Cisco *Coregonus laurettae*, Inconnu *Stenodus leucichthys*; marine species, Fourhorn Sculpin *Myoxocephalus quadricornis*, Arctic Flounder *Liopsetta glacialis*, Pacific Herring *Clupea pallasii*, Starry Flounder *Platichthys stellatus*, and Saffron Cod *Eleginus gracilis*; and one freshwater species, Pond Smelt. Not all of the taxa were observed at each location or during each year, with the number of species ranging from two to eight among locations and years.

The ANOVA results indicated that the energy content of the sampled fish differed significantly among species with respect to energy density ($F = 47.05$, $P < 0.01$), percentage of lipid content ($F = 42.35$, $P < 0.01$), percentage of protein ($F = 16.02$, $P < 0.01$), and percentage of water ($F = 63.15$, $P < 0.01$). Tukey's honestly significantly different tests results indicated that energy density differed between 21 of 45 species pairs, percentage of lipid between 21 species pairs, percentage of protein between 19 species pairs, and percentage of water between 27 species pairs (Table S1 available in the Supplement separately online; Figure 2). The values for mean energy density ranged from 4 to 12 kJ/g wet weight across species, lipid content was between 2% and 26%, protein content between 13% and 20%, and water content between 60% and 81%. Bering Cisco and Least Cisco exhibited the highest mean energy density, followed by Inconnu, Humpback Whitefish, Arctic Flounder, Pacific Herring, Starry Flounder, Pond Smelt, Saffron Cod, and Fourhorn Sculpin (Table 1). The ranking of percentage of lipid content by species followed a similar order, with all of the Coregoninae species having higher values than marine species and Pond Smelt. The opposite of this was seen for percentage of water content.

TABLE 1. Mean energy density (in decreasing order), percentage of lipid content, and percentage of water content of fishes sampled in coastal habitats of Cape Krusenstern National Monument, Alaska. The values are averaged across locations and years, and standard deviation (SD) values are included. The sample size (*N*) is listed for the energy density values, but the sample sizes for percentage of lipid, water, and protein content are equal to these values or greater (see the full data table in the Supplementary Material [available separately online] for the specific sample sizes). Letters following each species are defined as follows: d = diadromous species, f = freshwater taxa species, m = marine species, and s = fish used by subsistence harvesters.

Species	*N*	Weight range (g)	Size range (mm)	Energy density (kJ/g)	Energy density SD	Lipid content (%)	Lipid content SD	Protein content (%)	Protein content SD	Water content (%)	Water content SD
Bering Cisco (d, s)	18	248–1,039	304–421	11.8	2.1	25.7	7.7	17.1	1.1	60.4	4.8
Least Cisco (d, s)	29	29–827	158–410	8.4	3.0	14.2	11.0	18.8	2.0	67.3	6.2
Inconnu (d, s)	2	1,060–1,730	520–535	7.2	<0.1	8.8	<0.1	18.1	0.2	71.1	0.3
Humpback Whitefish (d, s)	55	51–1,275	178–460	6.9	0.9	9.4	3.9	19.0	1.2	70.3	2.6
Arctic Flounder (m, s)	5	37–143	147–219	6.4	0.3	8.5	0.9	18.5	1.1	71.4	1.5
Pacific Herring (m)	93	0.2–250	38–310	5.6	1.7	6.3	5.9	17.0	2.8	75.6	4.6
Starry Flounder (m, s)	47	1–1,050	40–424	5.0	0.9	4.6	2.9	16.3	1.2	76.0	2.7
Pond Smelt (f)	15	2–7	66–107	4.8	0.5	3.0	2.0	17.6	0.7	76.8	1.2
Saffron Cod (m, s)	41	0.5–574	54–415	4.5	0.7	2.4	1.5	16.2	1.7	78.0	2.3
Fourhorn Sculpin (m)	8	62–256	204–290	4.1	0.6	3.0	1.7	13.5	1.2	80.1	1.6

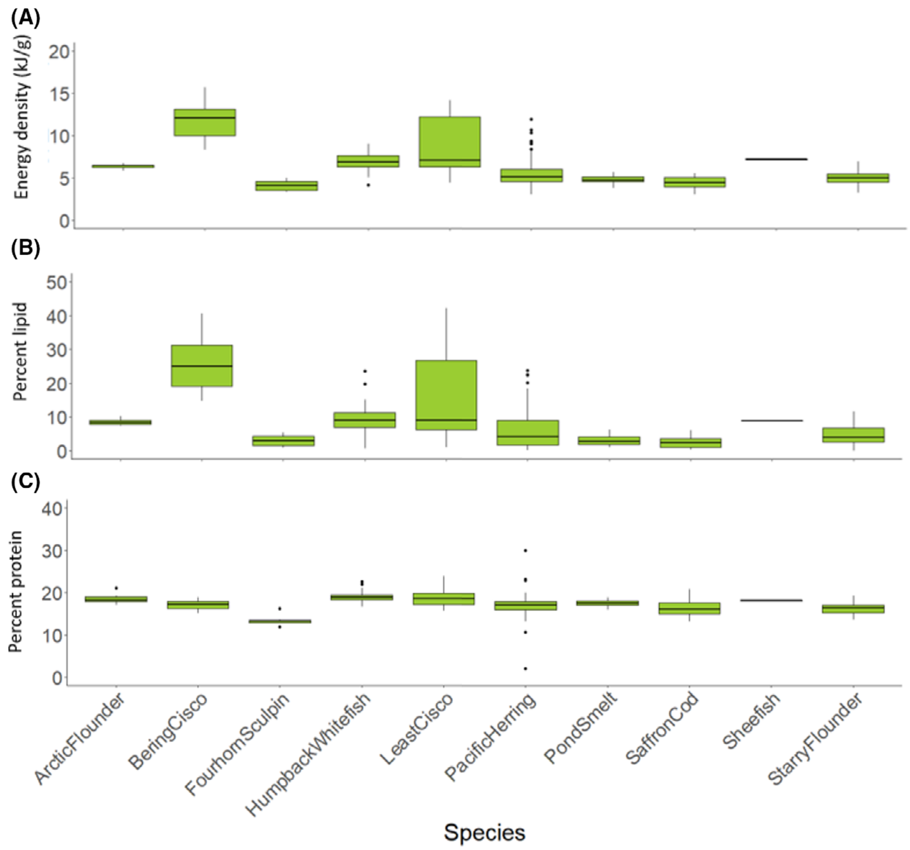

FIGURE 2. The figure shows **(A)** energy density (kJ/g), **(B)** percentage of lipid content, and **(C)** percentage of protein content for fishes that were sampled from coastal habitats in Cape Krusenstern National Monument, Alaska. The specific values for the Tukey's honestly significantly different pairwise tests denoting significant differences between species can be found in Table S1.

For percentage of protein, the Coregoninae species generally had higher mean values than marine taxa and Pond Smelt, with the exceptions of Arctic Flounder and Pond Smelt, which exhibited slightly higher values than Bering Cisco. Finally, relative total energy content by species ranged from 4 to 184 MJ sampled/lagoon and the species rankings mirrored what was seen in the energy density and proximate composition results, with Coregoninae species representing a greater amount of energy content based on their mean size and sampled abundance in Cape Krusenstern lagoons compared with size and abundance for marine taxa and freshwater Pond Smelt (Table 2).

DISCUSSION

The potential nutritional value of the species that we assessed was highest for diadromous Coregoninae in the coastal aquatic habitats of Cape Krusenstern National Monument and lowest for marine species such as Saffron Cod, flounders, and Fourhorn Sculpin. The information we present here is the first we are aware of for species of subsistence importance, including Bering Cisco and Humpback Whitefish, and the first for coastal Inconnu (Appavoo et al. 1991 examined inland Inconnu). Additionally, values have not been previously reported for Fourhorn Sculpin in the literature. For future studies, we recommend that seasonal differences in fish energy density be examined because season is known to be important in driving the body condition and energetic status of fish (Robards et al. 1999; Vollenweider et al. 2011; Falke et al. 2019). Additionally, future assessments of the energetic content of ecologically important forage fishes such as stickleback would be advantageous to give indications about the status of prey quality for piscivorous fishes, marine mammals, and birds, which are often harvested by subsistence users.

In comparison with the results from other studies, the Inconnu from our coastal sites had slightly higher mean percentage of lipid content (8.8%) than those that were assessed in inland waters (6.9%, Appavoo et al. 1991). This is likely the result of greater abundance and diversity of both freshwater and marine-origin prey in the coastal lagoons that we predominantly sampled (Tibbles and Robards 2018) compared with the inland lake and river system as examined by Appavoo et al. (1991). Additionally, the Least Cisco from Cape Krusenstern National

TABLE 2. Mean weight (g), mean sampling abundance per lagoon, and relative total energy content (energy density × mean fish size × mean sampling abundance per lagoon from 2015 to 2018; MJ sampled/lagoon) in decreasing order among fish species that were sampled in the coastal habitats of Cape Krusenstern National Monument, Alaska. Letters following each species are defined as follows: d = diadromous species, f = freshwater taxa species, m = marine species, and s = fish used by subsistence harvesters.

Species	Mean weight (g)	Mean abundance per lagoon	Mean energy density (kJ/g)	Relative total energy content (MJ sampled/lagoon)
Humpback Whitefish (d, s)	489	54.3	6.9	183.3
Inconnu (d, s)	1,808	6.0	7.2	78.1
Least Cisco (d, s)	444	20.7	8.4	77.1
Bering Cisco (d, s)	717	8.3	11.8	70.5
Starry Flounder (m, s)	106	60.5	5	32.1
Pacific Herring (m)	67	82.3	5.6	30.9
Saffron Cod (m, s)	238	20.0	4.5	21.4
Arctic Flounder (m, s)	80	26.7	6.4	13.7
Fourhorn Sculpin (m)	52	19.7	4.1	4.2
Pond Smelt (f)	4	75.7	4.8	1.5

Monument had a mean energy density of 8.4 kJ/g, whereas the Least Cisco that were captured in a Yukon–Kuskokwim Delta estuary were ~5 kJ/g (Ball and Esler 2007). The reasons for this difference are unknown, but it could be attributed to differences between Cape Krusenstern coastal lagoons and the Yukon–Kuskokwim estuary with respect to the seasons during which the fish were sampled, different mean body size, density-dependent population effects, or a contrast in the quality of prey that were available for Least Cisco. Ball et al. (2007) recorded energy density values that are similar to those that we found for Saffron Cod, Starry Flounder, Pacific Herring, and Pond Smelt (<6 kJ/g), although energy density for Arctic Flounder in Cape Krusenstern National Monument habitats (6.4 kJ/g) was slightly higher than that for this species in the Yukon–Kuskokwim Delta estuary (<3 kJ/g). For Pacific Herring, we found mean energy density to be 5.6 kJ/g, while others reported means between 5 and 8 kJ/g for Pacific Herring from various marine sampling locations in Alaska (Anthony and Roby 2000; Logerwell and Schaufler 2005; Vollenweider et al. 2011). However, we collected Pacific Herring of multiple age-classes, and thus body-size-related energetic condition factors may be present.

For subsistence harvesters, Coregoninae present the highest energy content per unit weight of fish caught as well as the highest value when mean body size and relative abundance of these taxa in Cape Krusenstern lagoons are taken into account (i.e., our "relative total energy content" index). Local harvesters indicate that cisco species are particularly prized delicacies in the spring and fall seasons when they are fattest (Georgette and Shiedt 2005; Cyrus Harris and Johnson Stalker, subsistence fishers, personal communication). We found that Coregoninae were of similar or greater energy density than noted elsewhere for salmon. For example, the percentage of fat content ranged from 11% to 20% in Chinook Salmon *O. tshawytscha* and Chum Salmon *O. keta* in the Yukon River (Margraf et al. 2005) and salmon that were species sampled in saltwater in Alaska had mean energy densities between 4 and 5 kJ/g wet weight (Anthony et al. 2000; Logerwell and Schaufler 2005), whereas Bering Cisco from Cape Krusenstern National Monument showed 16–36% lipid content and 11.8 kJ/g mean energy density. In comparison with other studies, cisco species in Cape Krusenstern exhibit the highest wet weight energy density of all of the species that we examined, above the energy-rich lampfish (Myctophidae; 8.49 kJ/g), Eulachon *Thaleichthys pacificus*, and Least Cisco from the Bering Sea (Anthony et al. 2000; Logerwell and Schaufler 2005; Ball et al. 2007; Vollenweider et al. 2011). The energy content of the marine species that were assessed in this study was low in comparison with that of the Coregoninae.

It should be noted that in addition to species, the energy condition of fish is also likely influenced by location, season, and average fish size and age. We were not able to incorporate these additional modulators into our models for evaluating energy condition due to the low numbers of fish for which sex was identified (<20 per species) and low numbers of individuals per species by location/year (<25 per site per year). However, species-specific differences in energy content were clear in many cases, seemingly superseding the influence of other factors.

Supporting this suggestion, energy condition metrics for fish assemblages in each lagoon were qualitatively similar across years and locations (Figure S1 available in the Supplement separately online). In future studies, it would be useful to build on our findings by evaluating the influence of season, location, and fish size and age on energy content, particularly in relation to the timing of subsistence fish harvest.

Given the threats of accelerating climate change and human activity in the Arctic (e.g., warming water temperatures and impending coastal construction projects), it will be important to monitor the energy content of fishes that are of subsistence importance to identify changes in their nutritional value as well as their population productivity and ecosystem function (Paterson et al. 2014). The intrusion of alien species, warming water temperatures, construction projects, and trophic shifts could alter fish habitats, prey, and populations along the southern Chukchi Sea coast of Alaska (Post et al. 2009; Wassman et al. 2011; Jing et al. 2012; Westley 2020; Rubano 2021). These factors could result in changes in fish diet, feeding behavior, prey availability, energetic condition, and, ultimately, their availability and utility for subsistence harvesters (Wassman et al. 2011; Green et al. 2019). Besides the importance of the nutritional quality of fish for subsistence harvest, the energy condition of prey taxa should also be considered, as declining prey quality would affect the productivity of predatory subsistence-harvested species (Österblom et al. 2008; Whitfield 2008) such as Inconnu. A poignant example of a potential climate change effect on fish energy condition and nutritional quality is discussed in a recent study predicting a worldwide decline in the availability of omega-3 fatty acids (found primarily in fish) as a result of climate change effects (Colombo et al. 2020). Thus, it will be important to track the energy condition of fish in Arctic regions to identify, respond to, and mitigate any threats to the food security of rural and Indigenous residents.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.