



Barrier islands influence the assimilation of terrestrial energy in nearshore fishes

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ABSTRACT

We examined the relative importance of landscape features on estuarine fish trophic structure and dependence on terrestrial organic matter (OM_{terr}) in four barrier island lagoon systems along the Alaskan Beaufort Sea coast. Our study compared two relatively large lagoon systems characterized by high river discharge and relatively free ocean water exchanges (central region near Prudhoe Bay, Alaska) with two highly protected lagoons characterized by low river discharge and limited exchange with ocean waters (eastern region near Kaktovik, Alaska). We hypothesized that freshwater discharge would be a strong determinant of food web structure for both resident marine and diadromous fishes if more discharge increases availability of OM_{terr} relative to lagoons with limited or no river inputs. To consider differences in trophic characteristics in fishes between study regions, we estimated community-wide measures of trophic structure (hereafter, community metrics) and the relative use of OM_{terr} from mixing models using stable isotope composition ($\delta^{13}C$ and $\delta^{15}N$; muscle tissue) among 12 species and identified the influences of region and body size. Fish captured in lagoons well protected by barrier islands had more distinct and diverse isotopic niches relative to those in more exposed lagoons based on community metrics. The use of OM_{terr} by nearshore fishes in both regions was substantial and was >50% for diadromous species. Between regions, OM_{terr} use differed in 6 of the 8 species considered but was not consistently higher in one region. The relative importance of OM_{terr} varied with fish size in 7 of 10 species considered, with more OM_{terr} used by smaller individuals. This work highlights the importance of OM_{terr} to Arctic fishes and fisheries, some of which are of subsistence importance, even when feeding grounds are primarily marine. We propose that landscape features, particularly barrier islands, play an important role in structuring nearshore food webs. Barrier islands may provide a previously undocumented ecosystem service of increasing food web complexity, which may promote system resilience.

1. Introduction

The intersection of terrestrial and marine ecosystems creates highly productive estuarine and coastal waters where multiple sources of primary production mix (Beger et al., 2010; McClelland et al., 2012; Sheaves, 2009). Globally, coastal habitats including lagoons, river deltas, sea grass beds, salt marshes, kelp forests, and mangroves reflect landscape features that support varied nearshore communities and their food webs. The importance of allochthonous terrestrial and freshwater-derived nutrients and organic matter (together, OM_{terr}) in nearshore marine systems is widespread across tropical (Gorman et al.,

2019), temperate (Deegan and Garritt, 1997; Martineau et al., 2004; Simenstad and Wissmar, 1985; Tallis, 2009), and Arctic locales (Bell et al., 2016; Dunton et al., 2006; von Biela et al., 2013). Yet the way landscape features influence the use of OM_{terr} by coastal food webs is poorly understood, which limits our ability to anticipate climate change related shifts in food web structure across different habitats or over time. Significant and accelerating warming across the Arctic has contributed to landscape change including increased terrestrial inputs through permafrost thaw, increased erosion, and earlier river break-up with higher freshwater discharge (Fritz et al., 2017; Günther et al., 2015; McClelland et al., 2012; Post et al., 2019). Shifts in the allochthonous

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inputs to coastal food webs are likely to accompany these physical changes (McClelland et al., 2014, 2016).

In the coastal Arctic, the pace of landscape change is rapid, and change in the distribution and use of OM_{terr} is likely (Post et al., 2019; Terhaar et al., 2021). Currently, approximately one third of primary production in the Arctic Ocean is derived from OM_{terr} via river input and coastal erosion (Rachold et al., 2004; Terhaar et al., 2021). The primary source of OM_{terr} to the Beaufort Sea shelf and slope is the Mackenzie River, Northwest Territories, Canada, which discharges a tremendous amount of freshwater ($306 \pm 10 \text{ km}^3$ annually, McClelland et al., 2016) and OM_{terr} into the Beaufort Sea with the plume extending westward (Goñi et al., 2000; McClelland et al., 2016; Terhaar et al., 2021). Smaller rivers and groundwater seeps are also likely to input OM_{terr} into the coastal Beaufort Sea and support marine food webs (Connolly et al., 2020; Divine et al., 2015).

The amount of freshwater discharge appears to be an important determinant of OM_{terr} use by marine fauna in the Mackenzie River plume (Bell et al., 2016; Divine et al., 2015). Multiple studies investigating the dynamics of Beaufort Sea lagoons show that benthic and epibenthic fauna in the nearshore incorporate OM_{terr} (Dunton et al., 2006, 2012; Harris et al., 2018). Invertebrates and microbes inhabiting these nearshore marine environments serve a unique role in marine ecosystems by integrating organic matter from benthic marine, pelagic marine, freshwater, and terrestrial sources, and transferring energy and nutrients to higher trophic level organisms, including fish (Craig and Halderson, 1981; Harris et al., 2018), birds (Rizzolo et al., 2015), and marine mammals (Crawford et al., 2015; Quakenbush et al., 2015). The productivity in Beaufort Sea lagoons is attributed, in part, to the flux of OM_{terr} delivered during the spring freshet from local freshwater sources and erosion (Connolly et al., 2020; Dunton et al., 2012; Schreiner et al., 2013; Terhaar et al., 2021).

Here, we investigate the influence of two coastal lagoon landscape features, rivers and barrier islands, on the structure of nearshore food webs and the use of OM_{terr} among Arctic fishes. Our focus is on fish because of their ubiquity across the coastline and importance to higher trophic level animals (e.g., birds, whales, and seals) and people living in the Arctic. This research was conducted in areas that overlap with Inupiat fishing and hunting grounds (Jacobson and Wentworth, 1982). A portion of our study area is within the Arctic National Wildlife Refuge that aims to provide opportunity for subsistence and to maintain healthy fish and wildlife populations per the Alaska National Interest Land Conservation Act of 1980, 16 U.S.C. § 3101–3233. The amount of freshwater discharge draining into the Beaufort Sea is heterogeneous across the coastline (Craig, 1984), but it is not clear if the nearshore assimilation of OM_{terr} is consistent across the Beaufort Sea shelf (Dunton et al., 2006). Protection by barrier islands that form the lagoons could also affect the delivery of marine organic matter (OM_{mar}) sources to lagoon food webs (Craig and Halderson, 1981; Dunton et al., 2006; Underwood et al., 1995) by either limiting advection of OM_{mar} to lagoons or preventing OM_{terr} from flowing out of lagoons into nearshore Beaufort Sea waters. We hypothesized that the amount of freshwater discharge would be a stronger determinant of food web structure compared to protection by barrier islands.

We used the natural variation in carbon and nitrogen stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) to trace OM_{terr} and OM_{mar} in fish food webs in Arctic lagoon systems. We compared trophic structure among multiple fish species and use of OM_{terr} in four lagoons nested within two regions that varied in the relative degree of river discharge and protection by barrier islands. Two lagoons in the eastern region were more protected by barrier islands, but with little or no river discharge. The two lagoons in the central region had less barrier island protection and, thus, more exposure to the marine shelf, but also received waters from three large rivers, including the two largest on the Alaskan Beaufort Sea coast (the Colville and Sagavanirktok rivers). Either high river discharge (in the central region) or isolation from exchanges with Beaufort Sea marine waters by barrier islands (in the eastern region) could result in high

assimilation of OM_{terr} by lagoon fishes. These scenarios do not require fish trophic structure to differ among lagoons, but consistency in trophic patterns should not be assumed. We first assessed fish food web structure by comparing community-wide metrics of trophic diversity (hereafter, community metrics) across the lagoons. Second, we determined the contribution of OM_{terr} to fishes in the lagoon food webs, using recently enhanced species-specific mixing models (Stock et al., 2018) that explicitly consider the importance of region and fish size.

2. Methods

2.1. Study area

Fish were collected at four lagoons in two regions (central and eastern) along the Alaskan Beaufort Sea coast (Fig. 1) in areas of management interest for continued or new oil and gas development. Each site can be categorized in terms of its relative river discharge and protection by barrier islands. The two central sites, Simpson Lagoon and Stefansson Sound, are adjacent to northern Alaska's major river basins (Sagavanirktok River [$14,890 \text{ km}^2$], Kuparuk River [$8,107 \text{ km}^2$], and Colville River [$61,183 \text{ km}^2$]; Milner et al., 2005; U.S. Geological Survey, 2018) and a terrestrial landscape with ample freshwater draining into the Beaufort Sea. Barrier islands in the central region are discontinuous and allow for greater connectivity to the marine environment than the more continuous barrier islands in the eastern region. By contrast, the two eastern sites, Kaktovik Lagoon and Jago Lagoon, are near a smaller river (Jago River [$2,351 \text{ km}^2$]; U.S. Geological Survey, 2018) and tiny unnamed streams that cross a drier landscape (Craig, 1984). Kaktovik Lagoon is surrounded by barrier islands and is only connected to the Beaufort Sea by way of adjacent lagoons, including Jago Lagoon, where semi-continuous barrier islands limit exposure to wind and the marine environment.

2.2. Sample collection and analysis

The central sites were sampled in late July 2018 and 2019, while the eastern lagoons were sampled in early August 2017, 2018, and 2019. Two fyke net stations were installed at each of the four sites for 1–6 days per year, depending on weather. Fyke nets (mesh size of lead and wings was 2.54 cm and 1.7 cm in the trap) were deployed in water ~1 m deep and up to 50 m from shore. Most fish captured in fyke nets were released alive after identification and counting every 24 h, with lethal sampling and collection of epaxial muscle tissue from a subset of individuals from the following species: Arctic cisco (*Coregonus autumnalis*, Qaaktaq in Inupiaq), least cisco (*C. sardinella*, Iqalusaaq), broad whitefish (*C. nasus*, Aanaaktiq), humpback whitefish (*C. pidschian*, Pikuktuuq), Arctic flounder (*Liposetta glacialis*, Nataaḡnaq), fourhorn sculpin (*Myoxocephalus quadricornis*, Kanayuuq), Arctic smelt (*Osmerus mordax*, Ithuaḡniq), ninespine stickleback (*Pungitius pungitus*, Kakalisauraq), and threespine stickleback (*Gasterosteus aculeatus*, Kakiḡaḡnaq). In addition, we analyzed all captured Dolly Varden (*Salvelinus malma*, Iqalukpik), Arctic cod (*Boreogadus saida*, Iqalugaq), and saffron cod (*Eleginus gracilis*, Uugaq). Beam trawls (1 m or 3 m) were opportunistically deployed in 2017 and 2018 near the fyke net stations to ensure that fish using habitat away from the shoreline were represented in this analysis. Only four species (Arctic flounder, fourhorn sculpin, Arctic cod, and saffron cod) were also collected by benthic beam trawl ($n = 47$ across all species). In the laboratory, the length of each fish was measured to the nearest 1 mm. Fork length was measured for species with forked tails and total length was measured for species with truncate or rounded tails (Stanek et al., 2022b). We assigned two or three size categories for each species based on values in the literature, when available (Brown, 2008; Fehsel et al., 1984; Forster, 2019; Knutzen et al., 1990), or natural breaks in our measured lengths (Table 1). Muscle samples were kept frozen at -20°C . Sample collection and animal handling were conducted under Alaska Department of Fish and Game Aquatic Resource Use permits

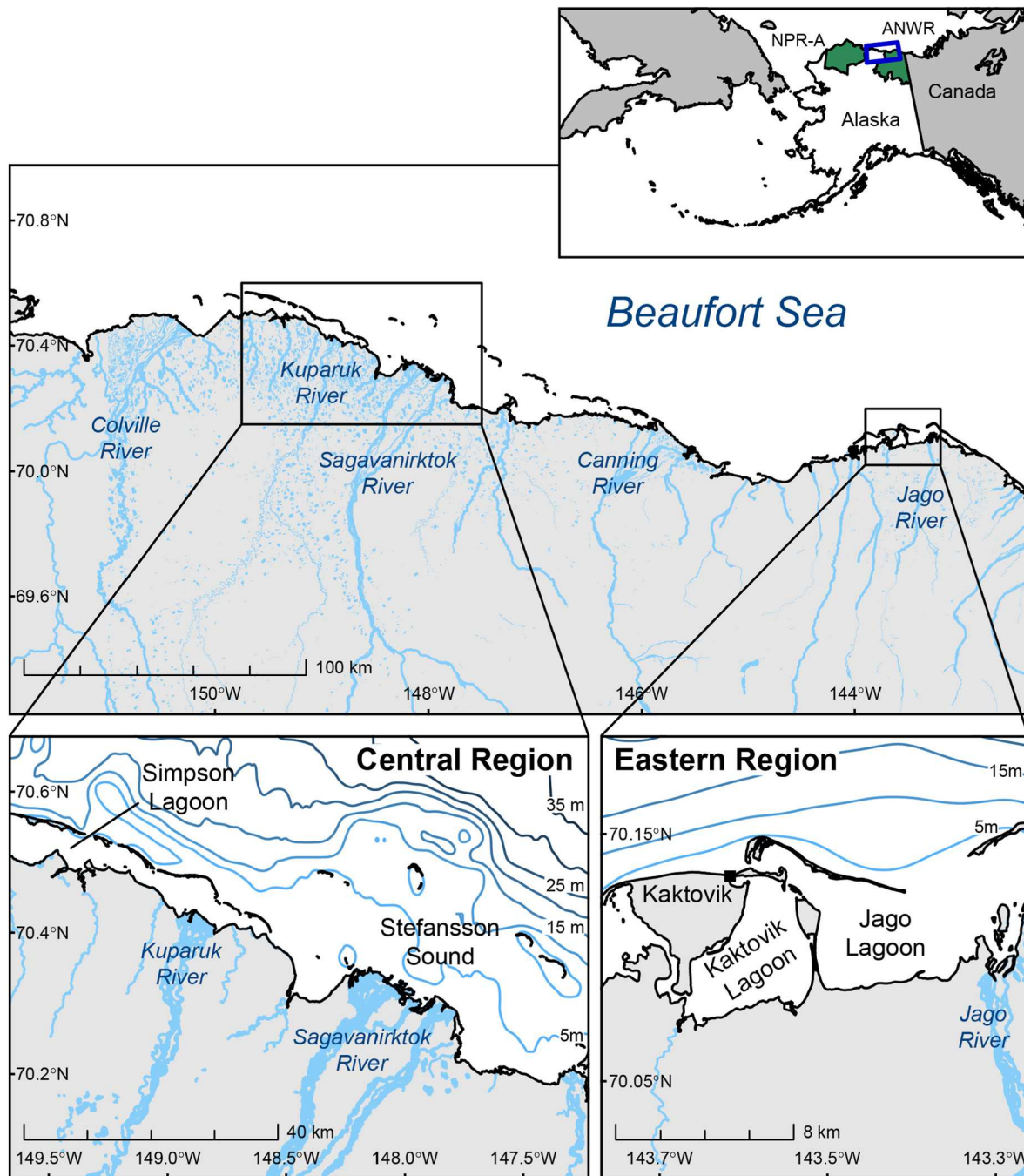


Fig. 1. Study area map showing the two regions and four sites where fish were sampled in the Beaufort Sea, Alaska in summers 2017–2019. Federally managed lands of the National Petroleum Reserve-Alaska (NPR-A) and the Arctic National Wildlife Refuge (ANWR) are identified in green. Contour lines depict 5 m bathymetry (GEBCO Bathymetric Compilation Group 2021). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

CF-2017-100, CF-2018-074, and CF-2019-096, Fish and Wildlife Service Special Use Permit 2017–03 from the Arctic National Wildlife Refuge, and followed protocols approved under Animal Care and Use Committee of the U.S. Geological Survey (USGS) Alaska Science Center (2017–07).

We randomly selected and included up to 15 individuals caught in fyke nets from each lagoon and all individuals captured in benthic beam trawls for stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) analysis. Because the range of isotope values overlapped by gear type for each species, the individuals were combined, and gear type was not considered in any analyses. In total, one muscle sample from each of 792 individual fish from 14 species was analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Table 1). Additionally, we

report isotope values of sporadically captured pink salmon (*Oncorhynchus gorbuscha*, Amaqtuq) and chum salmon (*O. keta*, Qalugruaq). These species are thought to be strays to the Arctic (Nielsen et al., 2013) and we have included their values for reference, but they have not been included in analyses. Fish stable isotope values and associated metadata are available in Stanek et al. (2022b).

Muscle samples were freeze-dried for at least 48 h and homogenized by grinding to a fine powder with a mortar and pestle. Approximately 1 mg of sample was weighed into tin cups. A ThermoFisher Scientific EA-Isolink CNSOH Elemental Analyzer (Waltham, Massachusetts, USA) coupled to a ThermoFisher Scientific Delta V isotope ratio mass

Table 1

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (mean $\pm$ SD) of fish muscle collected from lagoons of the central and eastern regions of the Beaufort Sea, Alaska, in summers 2017–2019. Length (mean $\pm$ SD) measurements are fork length for species with forked tails and total lengths for species with truncate or rounded tails (Stanek et al., 2022b).

Species	Size Category	Central Region				Eastern Region			
		n	Length (mm)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	n	Length (mm)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
Arctic Cod	Small: ≤ 70 mm	6	67 $\pm$ 3	-22.0 $\pm$ 0.7	14.2 $\pm$ 0.3	–	–	–	–
	Medium: 71–130 mm	29	100 $\pm$ 17	-21.5 $\pm$ 0.6	14.8 $\pm$ 0.5	2	86 $\pm$ 19	-22.6 $\pm$ 0.8	14.0 $\pm$ 0.6
	Large: > 130 mm	7	162 $\pm$ 29	-21.9 $\pm$ 0.4	16.3 $\pm$ 0.5	–	–	–	–
Saffron Cod	Small: ≤ 160 mm	5	122 $\pm$ 29	-21.5 $\pm$ 0.5	14.6 $\pm$ 1.0	50	118 $\pm$ 23	-20.2 $\pm$ 0.9	13.3 $\pm$ 0.7
	Medium: 161–300 mm	26	227 $\pm$ 36	-20.8 $\pm$ 1.1	15.2 $\pm$ 1.7	52	212 $\pm$ 37	-19.9 $\pm$ 0.9	14.3 $\pm$ 0.8
	Large: > 300 mm	2	390 $\pm$ 13	-21.4 $\pm$ 0.1	15.1 $\pm$ 0.1	72	398 $\pm$ 33	-19.2 $\pm$ 1.0	15.7 $\pm$ 0.8
Arctic Flounder		34	159 $\pm$ 47	-21.3 $\pm$ 0.6	12.1 $\pm$ 1.0	39	156 $\pm$ 52	-19.5 $\pm$ 0.9	12.6 $\pm$ 1.1
Fourhorn Sculpin	Small: ≤ 177 mm	21	120 $\pm$ 33	-21.5 $\pm$ 0.6	14.2 $\pm$ 0.9	20	126 $\pm$ 37	-19.5 $\pm$ 0.9	14.1 $\pm$ 0.9
	Large: > 177 mm	16	211 $\pm$ 25	-21.1 $\pm$ 0.9	16.0 $\pm$ 1.4	15	217 $\pm$ 23	-19.2 $\pm$ 0.9	15.7 $\pm$ 1.0
Arctic Smelt	Small: ≤ 150 mm	9	105 $\pm$ 27	-23.1 $\pm$ 0.6	13.7 $\pm$ 1.0	6	117 $\pm$ 23	-21.7 $\pm$ 0.6	14.3 $\pm$ 1.0
	Large: > 150 mm	15	228 $\pm$ 37	-21.7 $\pm$ 0.5	15.9 $\pm$ 0.8	20	192 $\pm$ 19	-21.0 $\pm$ 0.8	14.2 $\pm$ 0.4
Chum Salmon		–	–	–	–	3	589 $\pm$ 8	-21.5 $\pm$ 0.6	10.8 $\pm$ 1.3
Pink Salmon		18	429 $\pm$ 42	-21.2 $\pm$ 0.6	10.8 $\pm$ 0.5	13	400 $\pm$ 25	-21.1 $\pm$ 0.6	10.7 $\pm$ 1.0
Threespine Stickleback		12	78 $\pm$ 4	-20.4 $\pm$ 0.4	13.7 $\pm$ 0.6	1	77	-20.3	14.0
Ninespine Stickleback		1	59	-29.8	10.4	6	65 $\pm$ 5	-30.9 $\pm$ 3.1	9.7 $\pm$ 1.2
Arctic Cisco	Small: ≤ 100 mm	2	86 $\pm$ 4	-23.6 $\pm$ 0.1	9.9 $\pm$ 1.0	12	68 $\pm$ 10	-25.5 $\pm$ 1.1	10.0 $\pm$ 0.7
	Medium: 101–250 mm	24	157 $\pm$ 27	-23.4 $\pm$ 0.7	12.0 $\pm$ 0.9	7	170 $\pm$ 27	-24.5 $\pm$ 2.8	10.7 $\pm$ 1.4
	Large: > 250 mm	3	285 $\pm$ 24	-22.3 $\pm$ 0.1	13.7 $\pm$ 0.1	11	353 $\pm$ 26	-23.0 $\pm$ 1.0	13.7 $\pm$ 0.5
Humpback Whitefish		30	314 $\pm$ 84	-22.3 $\pm$ 1.5	11.4 $\pm$ 0.9	–	–	–	–
Broad Whitefish		30	245 $\pm$ 100	-22.9 $\pm$ 1.5	9.6 $\pm$ 1.0	10	335 $\pm$ 17	-22.5 $\pm$ 0.7	9.7 $\pm$ 0.6
Dolly Varden	Small: ≤ 250 mm	17	147 $\pm$ 11	-28.0 $\pm$ 1.9	8.8 $\pm$ 0.9	29	194 $\pm$ 22	-25.7 $\pm$ 2.6	10.7 $\pm$ 1.7
	Medium: 251–400 mm	4	355 $\pm$ 46	-22.0 $\pm$ 1.1	14.5 $\pm$ 1.1	16	338 $\pm$ 39	-23.2 $\pm$ 1.1	14.4 $\pm$ 0.6
	Large: > 400 mm	19	499 $\pm$ 66	-22.4 $\pm$ 1.1	15.4 $\pm$ 1.5	31	489 $\pm$ 56	-23.6 $\pm$ 1.4	15.0 $\pm$ 0.6
Least Cisco	Small: ≤ 200 mm	9	165 $\pm$ 36	-23.4 $\pm$ 0.4	12.3 $\pm$ 1.2	3	135 $\pm$ 40	-28.8 $\pm$ 5.1	11.6 $\pm$ 1.9
	Large: > 200 mm	21	290 $\pm$ 39	-22.7 $\pm$ 0.9	13.8 $\pm$ 0.7	14	305 $\pm$ 28	-23.1 $\pm$ 1.0	14.1 $\pm$ 0.8

spectrometer in continuous-flow (He) mode was used to determine fish muscle carbon and nitrogen isotopic compositions. All values are reported in delta (δ) notation, relative to standards VPDB for $\delta^{13}\text{C}$ and air for $\delta^{15}\text{N}$. Calibration of $\delta^{13}\text{C}$ to VPDB and $\delta^{15}\text{N}$ to air was achieved using standards USGS-40 and USGS-41a. Accuracy was evaluated using a casein protein standard purchased from EA Consumables (Pennsauken, New Jersey, USA). Analysis was performed at the University of Texas at Austin Marine Science Institute core facilities in Port Aransas, Texas, USA.

2.3. Community metrics

We described the food web structure of fish communities using trophic-species (species or size categories within a species, see section 2.4 *mixing models*) in each of the four lagoons (two lagoons $\times$ two regions) with six community metrics using the package Stable Isotope Bayesian Ellipses in R (SIBER v.2.1.6, Jackson et al., 2011). SIBER generated ellipses and Bayesian estimates of the community metrics proposed by Layman et al. (2007). Community metrics estimated the distribution of fish isotopic ellipse centroids between lagoons and included the distance to centroid (CD), $\delta^{13}\text{C}$ range, $\delta^{15}\text{N}$ range, mean nearest neighbor distance (NND), standard deviation of nearest neighbor distance (SDNND), and total area (TA). Ellipses were estimated when $n \geq 4$ for each grouping of species by lagoon and/or size category (Jackson et al., 2011). We followed settings recommended in the SIBER vignettes (Jackson et al., 2011) with the following exceptions: 400,000 iterations, with a burn-in of 20,000, and thinning of 100 to achieve model convergence. Model convergence was determined using the Gelman-Rubin diagnostic ($\hat{r} < 1.05$) (Gelman et al., 2021).

Small Dolly Varden and ninespine stickleback were excluded in the analysis of community metrics because of concerns that collection timing or gear would introduce a bias in comparison among lagoons. Small Dolly Varden were excluded because they have recently out-migrated from rivers. This life history phase includes the transition from freshwater to marine feeding, rapid growth, and likely rapid isotope turnover times such that minor difference (a few weeks) in collection dates can be associated with major isotope differences. Indeed, differences between regions can be explained by this bias

because small Dolly Varden collected in the eastern lagoons in early August are 32% longer and are enriched in $\delta^{13}\text{C}$ by $>2\%$ on average compared to those collected in the central lagoons in mid to late July (Table 1). Ninespine stickleback were excluded because only the largest individuals were captured by the mesh size of our capture gear such that our collections were not representative of the species or even their presence/absence.

2.4. Mixing models

We estimated the relative importance of OM_{terr} and OM_{mar} to fish using Bayesian mixing models in R package MixSIAR (v. 3.1.13, Stock et al., 2018). We provided MixSIAR with four types of input: 1) stable isotope values of consumers (i.e., $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of individual fish muscle samples), 2) stable isotope values of organic matter sources ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of OM_{terr} and OM_{mar}), 3) diet-to-tissue discrimination values, and 4) covariates (i.e., region, and either size category or length associated with each fish). MixSIAR was run with the consumer values from each species separately.

Stable isotope values of organic matter sources were obtained from the literature and public data repositories online: values for OM_{terr} were compiled from river particulate organic matter (POM) reported by Dunton et al. (2012), McClelland et al. (2014) and Harris et al. (2018). Values of OM_{mar} were obtained from the ANIMIDA III cruise data release (Dunton, 2016; Kasper et al., 2017). In summary, POM was collected on the Beaufort Sea shelf from August 1–5, 2014 from seven stations within 60 km from shore and at depths up to 54 m. POM was collected at two locations in the water column: within 3 m of the seabed and at the depth of the chlorophyll maximum as determined by CTD measured fluorescence. We used individual source values as the input for MixSIAR; however, for comparison, the mean $\pm$ SD were as follows: OM_{terr} $\delta^{13}\text{C} = -27.8\text{‰} \pm 1.3\text{‰}$ and $\delta^{15}\text{N} = 2.4\text{‰} \pm 0.8\text{‰}$ ($n = 29$); OM_{mar} $\delta^{13}\text{C} = -22.1\text{‰} \pm 0.8\text{‰}$ and $\delta^{15}\text{N} = 7.2\text{‰} \pm 0.7\text{‰}$ ($n = 24$).

Because we were interested in the use of OM_{terr} and OM_{mar} by fishes two trophic levels above basal resources, we multiplied discrimination values reported by Post (2002) by two (Harding and Reynolds, 2014; Harris et al., 2018). The total diet-to-tissue discrimination input to MixSIAR for each end member was mean $\pm$ SD: $\Delta^{13}\text{C} = 0.78\text{‰} \pm 2.6\text{‰}$,

$\Delta^{15}\text{N} = 6.8\text{‰} \pm 1.96\text{‰}$. Accounting for two trophic steps was supported by estimating fish trophic levels relative to “lagoon POM”, which reflects a mixture of OM_{terr} and OM_{mar} . Lagoon POM $\delta^{15}\text{N} = 5.6\text{‰} \pm 1.4\text{‰}$ was obtained from several existing sources (Beaufort Lagoon Ecosystem LTER Core Program, 2020; Connelly et al., 2015; Dunton et al., 2012; Harris et al., 2018). Relative fish trophic position of approximately 2.2 was then estimated using the equation from Post (2002), such that relative fish trophic position = $(\delta^{15}\text{N}_{\text{fish}} - \delta^{15}\text{N}_{\text{lagoon POM}}) / 3.4\text{‰}$.

MixSIAR allowed for inclusion of covariates and for model comparison to determine which variables likely influence variation in consumer mixture proportions (Stock et al., 2018). The mixing models differentiated by region, but not by lagoon, because community metrics indicated

similarity between lagoons within a region, and MixSIAR models cannot consider both variables given the limitations on number of covariates. We included fixed effects of region (central and eastern), fish size (length as grouped categories or as a continuous variable [Francis et al., 2011]), and their combinations as candidate models. Up to six models were examined for each species separately; candidate models included 1) “Null” (no covariates), 2) “Region” (central, eastern), 3) “sizeCat” (size class: small, medium, large), 4) “Length” (length as a continuous variable in mm), 5) “Region + sizeCat”, and 6) “Region + Length”. The models constructed for a species depended on its presence in both regions and size range. For example, we could not consider models with “Region” for Arctic cod or humpback whitefish as too few samples ($n \leq$

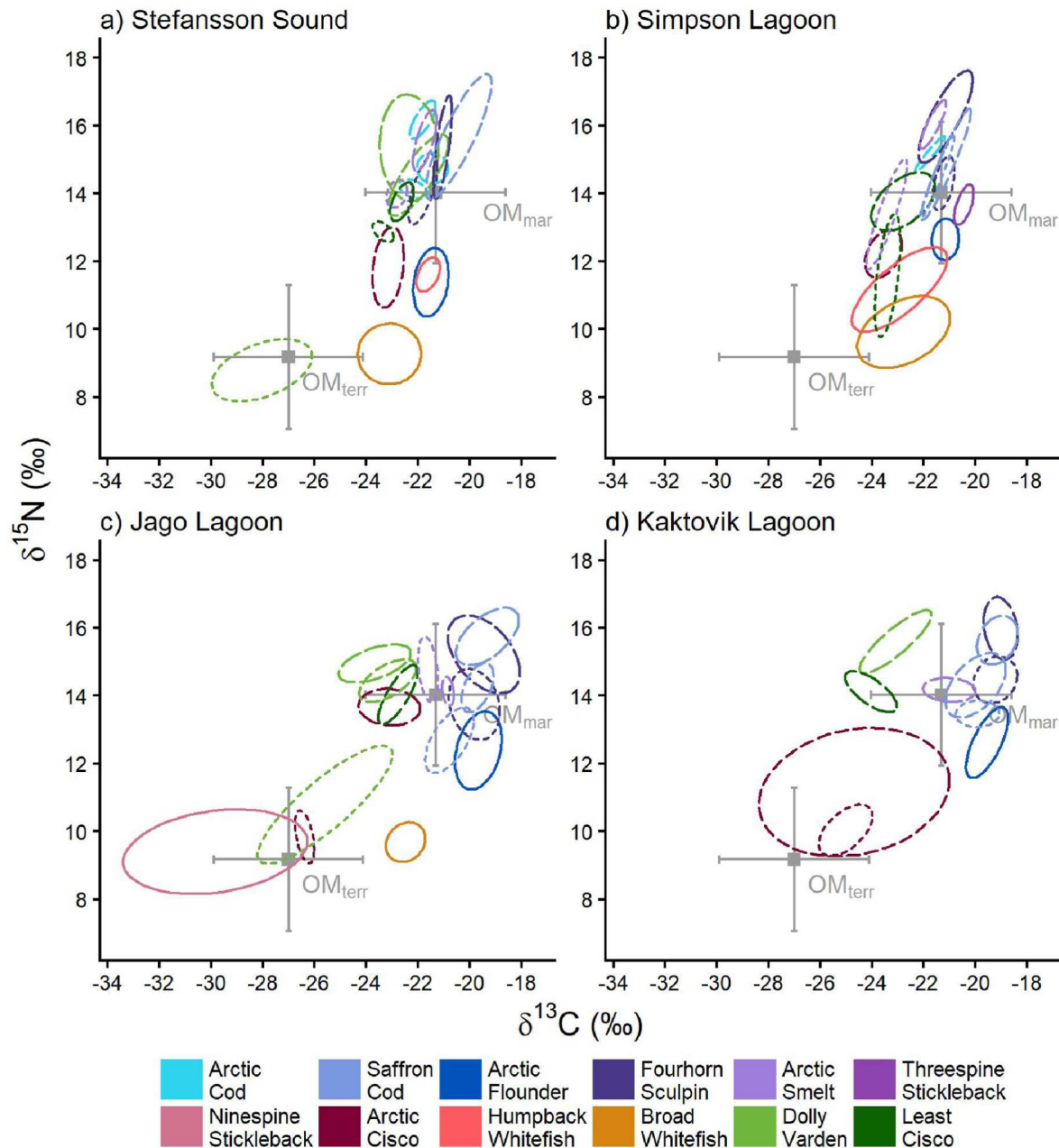


Fig. 2. Standard ellipses of fish muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from four lagoons (a–d) in the Beaufort Sea, Alaska, in summers 2017–2019. Ellipses contain ~40% of the data and are shown when $n \geq 4$ for each combination of species, lagoon, and size category. Mean $\pm$ SD sources of marine and terrestrial organic matter, OM_{mar} (Dunton, 2016) and OM_{terr} (Dunton et al., 2012; Harris et al., 2018; McClelland et al., 2014), are shown as gray squares and have been adjusted for diet-to-tissue discrimination (section 2.4) with error propagated (Stock and Semmens, 2016). Size categories are separated when mixing model results found an effect of size (Table 2, small: dotted, medium: short dashed, large: long dash, or all sizes: solid line). See supplementary file with Figs. S1–S4 for annotated enlargements of each lagoon. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2) were available from the central region. Models with a size variable (“sizeCat” or “Length”) were considered for all but two species (threespine stickleback and ninespine stickleback) with narrow size ranges (<15 mm). Due to the narrow size range of broad whitefish from the eastern region (48 mm) relative to the central region (407 mm) we did not include models with both region and either size category or length as candidates. MixSIAR was run with uninformative priors where the use of each source is equal (to represent a generalist species), and with the multiplicative error term incorporating both residual and process error (Stock et al., 2018). Markov Chain Monte Carlo parameters were initially set to “normal” run length; models that did not converge at “normal” were run until convergence was reached with “long” (Dolly Varden “Length” and rainbow smelt “Region” models), or “very long” (saffron cod “Length” model) settings. We used the Gelman-Rubin diagnostic ($\hat{r} < 1.05$) to ensure convergence (Gelman et al., 2021). For each species, we chose the model with the best out-of-sample predictive ability (best model) as determined by the highest LOOic weight using the compare_models function of MixSIAR (Stock and Semmens, 2016; Vehtari et al., 2017).

3. Results

Fish stable isotope values aligned well between the values for OM_{terr} and OM_{mar} end-members when adjusted for diet-to-tissue discrimination with the error propagated (Stock and Semmens, 2016) (mean $\pm$ SD: OM_{terr} $\delta^{13}\text{C} = -27.0\text{‰} \pm 2.9\text{‰}$ and $\delta^{15}\text{N} = 9.2\text{‰} \pm 2.1\text{‰}$; OM_{mar} $\delta^{13}\text{C} = -21.3\text{‰} \pm 2.7\text{‰}$ and $\delta^{15}\text{N} = 14.0\text{‰} \pm 2.1\text{‰}$, Fig. 2).

3.1. Community metrics

A total of 21 trophic-species across the four lagoons were identified (represented by ellipses in Fig. 2 and Figs. S1–S4). A trophic-species was either all individuals of the same species or a subset grouped by size categories when either size category or length improved the mixing models (Table 2). Species that were separated by size category into two or three trophic-species for community metric analyses included Arctic cod, saffron cod, fourhorn sculpin, Arctic smelt, Arctic cisco, Dolly Varden, and least cisco. The number of trophic-species used to estimate community metrics varied among lagoons. There were more trophic-species at the central sites (16 in Stefansson Sound and 14 in Simpson Lagoon) versus the eastern sites (14 in Jago Lagoon and 11 in Kaktovik Lagoon).

In general, community metrics were more similar between lagoons from the same region, relative to those in the other region. The distance to centroid (CD) is a measure of within-food web trophic diversity, which was higher in both lagoons in the eastern region (posterior mode, >2.3‰, Fig. 3a) and lower in those in the central region (<2‰). Similarly, most other metrics were higher in the eastern region (Jago Lagoon and Kaktovik Lagoon) compared to the central region (Stefansson Sound and Simpson Lagoon). The $\delta^{13}\text{C}$ range, an indicator of the diversity of basal resources used by a community (Fig. 3b) was substantially larger at the eastern sites (~6.7‰) relative to the central sites (~3.3‰). The higher NND (Fig. 3d) in the eastern sites indicated that those species exhibited more divergent trophic niches compared to fishes in the central sites; and the total area (Fig. 3f) was also greater in the eastern sites, indicating larger occupied niche space and more trophic diversity. The SDNND (Fig. 3e), which indicates the distribution of trophic niches, trended similarly, but the variance was high for Kaktovik Lagoon, and values of SDNND did not always appear to differ. Lastly, the $\delta^{15}\text{N}$ range (Fig. 3c), which reflects trophic level diversity within communities, was the metric most similar between regions (~6.7‰ at central sites and ~6.2‰ at eastern sites). Thus, community structure appears to differ between the eastern and central regions according to four of the six metrics we considered.

Table 2

Models compared for each species using MixSIAR (Stock et al., 2018) with the best model in bold. Model options depended on sample size available for each covariate. sizeCat refers to the size categories described in Table 1.

Species	Model	LOOic	Weight
Arctic Cod	Length	-57.1	0.993
	sizeCat	-47.2	0.007
	Null	-39.8	0.000
Saffron Cod	Region + Length	87.9	1.000
	Region + sizeCat	106.1	0.000
	Length	187.7	0.000
	sizeCat	210.4	0.000
	Region	256.8	0.000
Arctic Flounder	Region	22.0	0.675
	Region + sizeCat	24.3	0.214
	Region + Length	25.6	0.112
	sizeCat	85.0	0.000
	Null	86.3	0.000
Fourhorn Sculpin	Region + Length	33.5	0.981
	Region + sizeCat	41.5	0.018
	Region	47.8	0.001
	Length	49.2	0.000
	sizeCat	71.1	0.000
	Null	79.7	0.000
	Region + sizeCat	-2.9	0.986
Arctic Smelt	Region + Length	6.3	0.010
	Length	9.2	0.002
	sizeCat	9.9	0.002
	Null	29.3	0.000
	Region	29.8	0.000
Threespine Stickleback	Null	-	-
Ninespine Stickleback	Null	-	-
Arctic Cisco	Region + Length	83.6	0.998
	Region + sizeCat	96.6	0.002
	Length	102.1	0.000
	sizeCat	110.4	0.000
	Region	165.9	0.000
	Null	170.0	0.000
	Null	72.6	0.582
Humpback Whitefish	Length	74.5	0.225
	sizeCat	74.8	0.194
	Region	102.7	0.402
Broad Whitefish	Null	103.2	0.313
	Length	104.1	0.200
	sizeCat	105.8	0.085
Dolly Varden	sizeCat	263.0	0.998
	Region + sizeCat	275.3	0.002
	Length	279.9	0.000
	Region + Length	285.2	0.000
	Region	412.0	0.000
	Null	412.2	0.000
Least Cisco	Length	87.9	0.808
	Region + Length	90.8	0.190
	Region + sizeCat	99.4	0.003
	sizeCat	117.5	0.000
	Region	127.9	0.000
	Null	129.0	0.000

3.2. Mixing models

Mixing model predictive ability (i.e., the best model determined by LOOic weights) was improved by adding either the size of individuals, region, or both as a covariate in nine of ten species where models were compared (all but Humpback whitefish, Table 2). Best models included size for seven of ten species where it was a possible covariate; for five, it was continuous (length in mm; Arctic cod, saffron cod, fourhorn sculpin, Arctic cisco, least cisco) and for two it was categorical (Arctic smelt and Dolly Varden). Best models included “Region” for six of eight species where it was a possible covariate, including marine residents (saffron cod, Arctic flounder, fourhorn sculpin, and Arctic smelt) and diadromous species (Arctic cisco and broad whitefish). A combination of region and size was selected as the best model for four of seven species

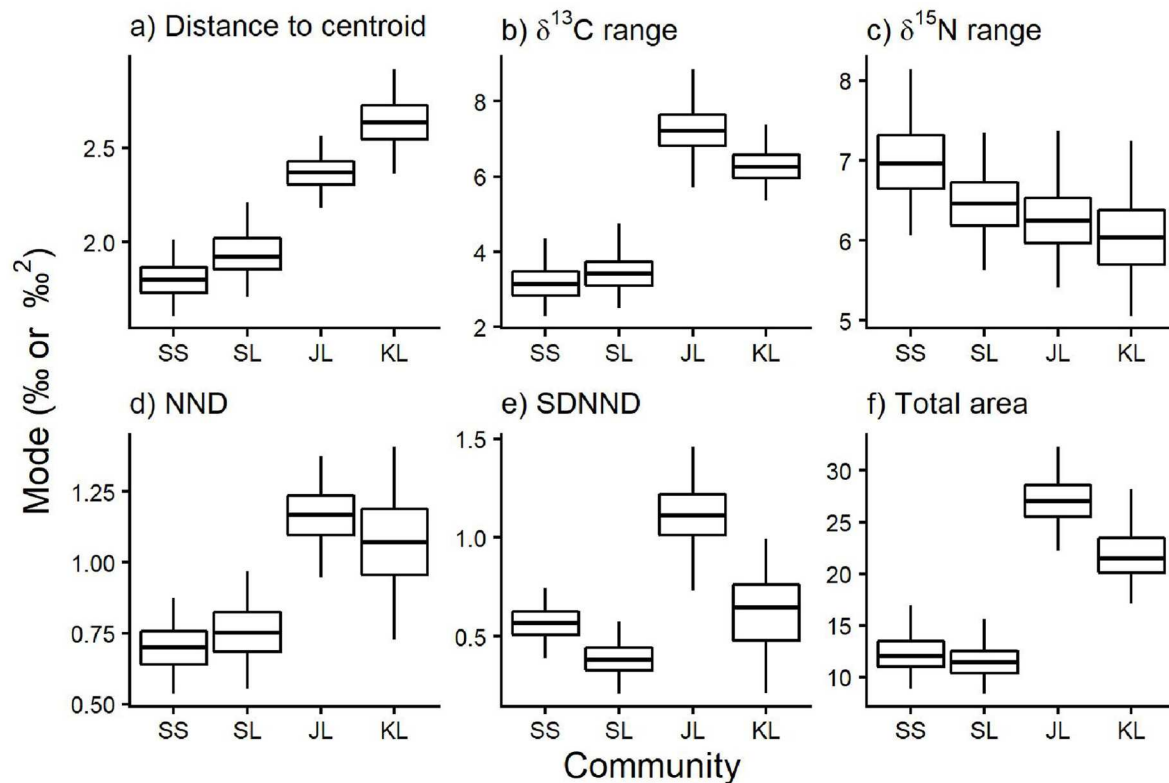


Fig. 3. Most likely value for each of six community metrics (Layman et al., 2007) describing the fish in the Beaufort Sea, Alaska [a) distance to centroid (%), b) $\delta^{13}\text{C}$ range (‰), c) $\delta^{15}\text{N}$ range (‰), d) mean nearest neighbor distance (NND, %), e) standard deviation of nearest neighbor distance (SDNND, %), and f) total area (% 2)]. Boxplots depict the most likely value (posterior mode, horizontal line), with 50% and 95% credible intervals identified by boxes and whiskers, respectively, resulting from estimates generated using SIBER (Jackson et al., 2011). Metrics were estimated for two lagoons in the central region, Stefansson Sound (SS) and Simpson Lagoon (SL), and two lagoons in the eastern region, Jago Lagoon (JL) and Kaktovik Lagoon (KL). Notes: Chum salmon and pink salmon, ninespine stickleback, and small Dolly Varden were excluded from these analyses.

where the combination was possible. “Region + Length” was the preferred model for saffron cod, fourhorn sculpin, and Arctic cisco, while “Region + sizeCat” was the preferred model for Arctic smelt.

The range in relative use of OM_{terr} by fishes caught in the nearshore lagoons spanned nearly the entire range of possibilities (i.e., 0–100%, Fig. 4). Posterior median OM_{terr} use ranged from 0% (large Arctic cod [95% credible interval: 0–2%] and large Arctic smelt in the eastern region [0–2%]) to 87% (ninespine stickleback [64–99%] and small Dolly Varden [77–93%]) among all trophic-species; the range was the same in both regions. The average of posterior median OM_{terr} use was similar between regions and highly variable (mean $\pm$ SD, central: 30% $\pm$ 28%, eastern: 27% $\pm$ 30%).

There were differences in the use of OM_{terr} by region for six species (Table 2, Fig. 4). Four species used more OM_{terr} in the central region relative to their conspecifics in the eastern region (posterior median percent contribution, reported at the median length when there was a continuous effect of length): Arctic flounder (Fig. 4c, central: 25% [19–38%], eastern: 4% [1–19%]), fourhorn sculpin (Fig. 4d, central: 9% [3–18%], eastern: 1% [0–4%]), Arctic smelt (Fig. 4e, small size, central: 26% [18–33%], eastern: 7% [1–15%]), and broad whitefish (central: 73% [63–88%], eastern: 70% [57–87%]). By contrast, two species used more OM_{terr} in the eastern region, saffron cod (Fig. 4b, central: 3% [1–7%], eastern: 16% [11–22%]) and Arctic cisco (Fig. 4h, central: 41% [35–46%], eastern: 65% [56–75%]).

For species with an effect of size, small individuals consistently used more OM_{terr} than larger conspecifics. The greatest difference across a species’ size range was for Arctic cisco (Fig. 4h). The smallest (48 mm) Arctic cisco used 88% (80–94%) OM_{terr} while the largest (405 mm) used only 7% (2–14%). A similar difference was observed in Dolly Varden (Fig. 4k); the contribution was 87% (77–93%) OM_{terr} for small

individuals (≤ 250 mm) and 11% (4–21%) OM_{terr} for large individuals (> 400 mm). Of the marine species, the smallest saffron cod (32 mm) incorporated the most OM_{terr} (Fig. 4b, up to 52% [49–55%]), followed by the smallest fourhorn sculpin (Fig. 4d, central region, 65 mm, 34% [24–44%]). Larger individuals of these marine species shifted to using virtually no OM_{terr} . Lastly, small Arctic smelt (≤ 150 mm) incorporated up to 26% (18–33%) OM_{terr} in the central region while large Arctic smelt (> 150 mm) used less than 2% (0–7%, Fig. 4e). Other fishes incorporated negligible amounts of OM_{terr} , including marine residents Arctic cod (Fig. 4a, $\leq 15\%$) and threespine stickleback (Fig. 4f, 2% [0–8%]).

4. Discussion

Our results suggest that fish trophic structure was influenced by the nature of barrier island systems that enclose lagoons of the Beaufort Sea coast. There was no evidence, however, that the use of OM_{terr} was uniformly higher for fishes of the central Beaufort Sea region that receives substantial river discharge. The ready exchange with the Beaufort Sea waters likely served to dilute OM_{terr} and facilitate advection of OM_{mar} to coastal lagoons. We found the entire structure of the food web differed between lagoons depending on the degree of protection provided by offshore barrier islands. More protection by barrier islands allowed for a wider diversity of trophic niches compared to less protected lagoons. We suspect this pattern arises because OM_{terr} and OM_{mar} are more effectively mixed by wind and currents in the central region where barrier islands offer less protection. The more protective barrier islands in the eastern region likely limit mixing of OM_{terr} and OM_{mar} at the base of the food web, which we saw reflected by less overlap in the trophic niches of fishes. It seems that two major food chains, originating from OM_{terr} and OM_{mar} , respectively, exist in parallel in the more

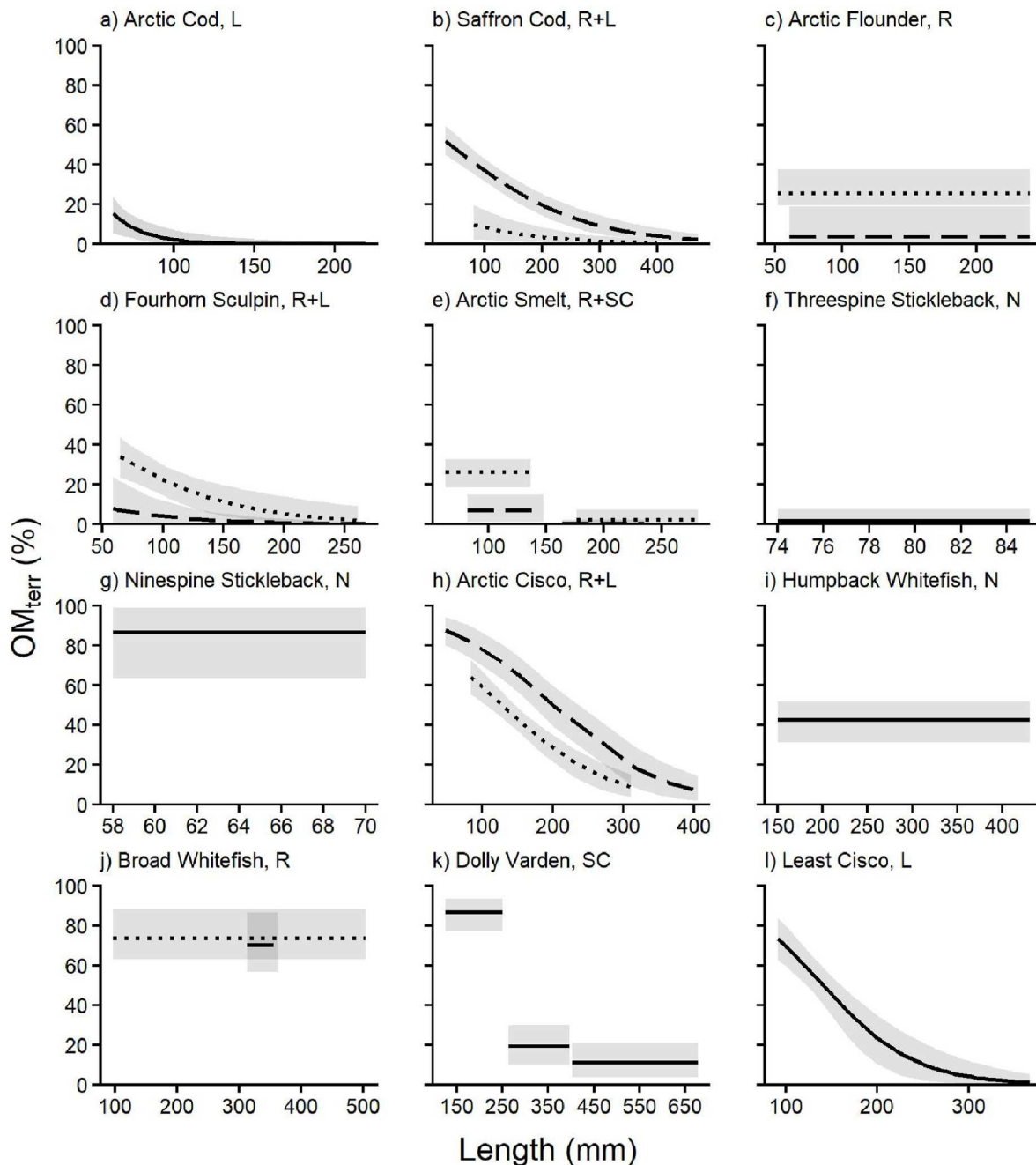


Fig. 4. Contribution (percent) of terrestrial organic matter (OM_{terr}) used by fish in the nearshore Beaufort Sea, Alaska relative to length (mm), in summers 2017–2019. Plots show the estimates of percent OM_{terr} from the best MixSIAR model (Table 2, Stock and Semmens, 2016). The text at the top left corner of each panel identifies the species and abbreviation for the best model, “Region” (R), “Length” (L), “sizeCat” (SC), “Region + Length” (R + L), “Region + sizeCat” (R + SC), or “Null” (N). Lines identify the median contribution $\pm 95\%$ credible interval (shading) across the size range of fish measured. Regional effects are identified by line pattern (central region: dotted line, eastern region: dashed line, no regional difference: solid line). Species are ordered from marine residents toward increasing freshwater affinity and diadromy.

protected lagoons and converge into upper trophic level fish (McMeans et al., 2013). Interestingly, the lack of large rivers in the eastern region was not associated with a dramatic reduction in the use of OM_{terr} and suggests that even small rivers and streams, along with sources from erosion, leaching, and groundwater from the adjacent tundra are effective conduits of OM_{terr} to nearshore marine systems. Indeed, concentrations of dissolved organic carbon and nitrogen were two orders of magnitude higher in groundwater compared to adjacent surface waters in rivers that feed eastern Beaufort Sea lagoons (Connolly et al., 2020).

The distribution of trophic-species’ stable isotope values, as reflected by ellipses (Fig. 2), identified isotopic niches that ranged in the

contribution of organic matters sources from nearly fully terrestrial to fully marine. OM_{terr} has frequently been detected in Beaufort Sea nearshore food webs (Bell et al., 2016; Churchwell et al., 2016; Divine et al., 2015; Harris et al., 2018) and the variation in OM_{terr} use among fish species was also consistent with previous studies in the Beaufort Sea that have primarily focused on benthic invertebrates (Bell et al., 2016; Churchwell et al., 2016; Divine et al., 2015; Harris et al., 2018). The findings presented here demonstrate that use of OM_{terr} and variation in use among species extends up the food chain to fishes of the Beaufort Sea, providing an OM_{terr} -based pathway to piscivorous marine birds (e.g., loons) and mammals (e.g., seals and beluga whales).

4.1. Community comparisons

The striking difference in food web structure across regions was evident in the plot of isotope ellipses (Fig. 2) and community metrics (Fig. 3) even when small Dolly Varden and ninespine stickleback were excluded (see section 2.3 *community metrics*). Substantial overlap in $\delta^{13}\text{C}$ of fish trophic niches in the central region lagoons was notable, as was the position of ellipses in isotope space. For both Stefansson Sound and Simpson Lagoon, most ellipses occupied a relatively narrow $\sim 3\%$ range in $\delta^{13}\text{C}$ (from -23.4% to -20.4%) between the values for OM_{terr} and OM_{mar} (when adjusted for discrimination). In Jago and Kaktovik Lagoons, ellipses spanned a wider $\delta^{13}\text{C}$ range that expanded upon the entire $\delta^{13}\text{C}$ range for the same species in Stefansson Sound and Simpson Lagoon in both directions (i.e., depletion and enrichment). The $\delta^{15}\text{N}$ values of individual species remained similar among the four lagoons and between regions indicating that they fed at the same trophic levels across lagoons. The four remaining community metrics (distance to centroid, total area, NND, and SDNND) indicated similarity among fish species trophic niches in the central region and greater isotopic niche diversity among fish species in the eastern region.

In Jago and Kaktovik Lagoons, there was clear separation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ that distinguished three groups of fish: 1) resident marine fish (all size classes of saffron cod, fourhorn sculpin, Arctic flounder, and Arctic smelt) 2) larger diadromous fishes that have likely been feeding in the marine environments but still have depleted $\delta^{13}\text{C}$ relative to resident marine fish (large Arctic cisco, medium and large Dolly Varden, large least cisco) and 3) smaller diadromous fishes that recently entered lagoons and still had relatively depleted $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values that likely reflect varying degrees of freshwater feeding (ninespine stickleback, small and medium Arctic cisco, broad whitefish, and small Dolly Varden).

We interpreted differences in the spatial arrangement of trophic-species ellipses and the community metrics to be a product of terrestrial and marine organic matter mixing via wind driven currents and exchanges. In the central region, most species rely on a homogenous mixture of organic matter compared to the eastern region where species have more distinct niches. Wind is known to mix organic matter sources along with planktonic primary consumers (Dunton et al., 2006; Goñi et al., 2009). It is unlikely that the differences in food web structure between regions are explained by differences in prey resource diversity. There is no evidence that fish have access to different prey resources between the regions. Diet studies of Arctic nearshore fishes consistently indicate the importance of just a few invertebrate taxa: mysid shrimp, gammarid amphipods, and to a lesser extent, zooplankton (Craig and Haldorson, 1981; Fechtel et al., 1984; Knutzen et al., 1990). Instead, we suspect that invertebrate prey have narrower carbon isotope ranges in the central region that reflect uptake of a homogenous mixture of OM_{terr} and OM_{mar} .

4.2. Organic matter sources between regions

One of our hypotheses was greater use of OM_{terr} by fishes in Simpson Lagoon and Stefansson Sound (central region) because of greater freshwater discharge, in line with previous work on the Beaufort Shelf that has found higher use of OM_{terr} at locations closer to the Mackenzie River (Bell et al., 2016; Divine et al., 2015). We also considered an alternative hypothesis where OM_{terr} use would be higher in Kaktovik and Jago Lagoons (eastern region) if protective barrier islands in this region excluded more OM_{mar} , which would result in relatively higher availability, and consequently, use of OM_{terr} . We did not find a consistent regional difference in the use of OM_{terr} ; however, regional differences were typically detected when the species occurred in both regions with sufficient sample size (6 of 8 species; Table 2). Use of OM_{terr} was slightly more common among species in the central region (4 of 6 species; Arctic flounder, fourhorn sculpin, Arctic smelt, and broad whitefish) than in the eastern region (2 of 6 species; saffron cod and Arctic

cisco). These regional differences in OM_{terr} use within a species were smaller (range 3%–21% absolute difference in OM_{terr} use) than differences among species (up to 87%) or within species due to size (up to 81% for Arctic cisco). Harris et al. (2018) similarly assessed whether consumer $\delta^{13}\text{C}$ varied across sites in the Beaufort Sea and did not find a relationship between consumer stable isotope values and a proxy for freshwater discharge (% meteoric water; study sites included Kaktovik Lagoon and Jago Lagoon).

Regional differences within species appeared more often for species where individuals move less. For example, Arctic flounder and fourhorn sculpin varied in their OM_{terr} use between regions and previous research suggests minimal movement (Fig. 4, Craig and Haldorson, 1981). Highly motile species like Arctic cod and Dolly Varden had similar OM_{terr} use by region, in agreement with long-distance movements for feeding (Courtney et al., 2018; Logerwell et al., 2015). Arctic cisco were notable in that they are highly motile but differed in OM_{terr} use by region. Arctic cisco may be foraging in closer proximity to their overwintering freshwater habitats than Dolly Varden. Additionally, Arctic cisco forage at a different trophic level and likely use different prey species than Dolly Varden (Craig and Haldorson, 1981).

4.3. Organic matter sources among species

Marine and diadromous species in the lagoons used a mix of OM_{terr} and OM_{mar} . High use of OM_{terr} across all sizes was noted for two diadromous species, broad whitefish and ninespine stickleback (Fig. 4). This finding is consistent with their strong association with freshwater habitats and the likelihood that feeding areas include rivers and lakes in addition to the lower salinity lagoon waters (Brown, 2008; Thorsteinson and Love, 2016). Near complete use of OM_{mar} was only apparent for two species, Arctic cod and threespine stickleback. Arctic cod are the primary Arctic forage fish and a key link between lower and upper trophic levels (Divoky et al., 2021; Jarvela and Thorsteinson, 1999; Marsh and Mueter, 2020). The negligible use of OM_{terr} is consistent with primarily feeding on the marine shelf instead of lagoons. Shifts in Arctic cod distribution away from nearshore habitat has become apparent in recent years and is attributed to warming (Divoky et al., 2021; Jarvela and Thorsteinson, 1999; Marsh and Mueter, 2020). As recently as 2004, Arctic cod captured in Beaufort Sea lagoons were shown to have much higher OM_{terr} contributions based on $\delta^{13}\text{C}$ values depleted by 3–4‰ as compared to individuals captured on the seaward side of the barrier islands in the coastal Beaufort Sea, implying that at least some Arctic cod fed primarily in lagoons (Dunton et al., 2006). Little is known about the threespine stickleback in the Arctic, but their life history strategies are diverse and include marine, diadromous, and freshwater populations such that the high use of OM_{mar} could arise from marine or diadromous life histories (Thorsteinson and Love, 2016).

4.4. Organic matter sources and fish size

Individual size strongly influenced use of organic matter sources in several species, and the difference in OM_{terr} use was typically greater across a species' size range than between regions (Fig. 4). More OM_{terr} was used by smaller fish relative to larger conspecifics in both diadromous (Dolly Varden, Arctic cisco, and least cisco) and marine species (Arctic cod, Saffron cod, and fourhorn sculpin). Among the diadromous Dolly Varden and Arctic cisco, the smallest individuals used $>90\%$ OM_{terr} while larger individuals had diets with $<15\%$ OM_{terr} . Freshwater rearing explains high use of OM_{terr} among smaller Dolly Varden. Dolly Varden rear and feed for 2–5 years in freshwater before migrating to sea when a size of ~ 200 – 250 mm is reached (Brown, 2008). Thus, small Dolly Varden (≤ 250 mm) are likely smolts, and their high use of OM_{terr} reflects freshwater feeding in rivers (Brown, 2008). Arctic cisco are also diadromous and spawn in rivers, but their life history does not include any freshwater rearing or feeding (Zimmerman et al., 2013). Arctic cisco migrate to sea at age-0 with spring flooding shortly (days to weeks) after

hatching. The age-0 Arctic cisco in Alaska's Beaufort Sea all undergo a wind-driven recruitment from the Mackenzie River delta in Canada (Zimmerman et al., 2013). Their high use of OM_{terr} likely comes from feeding in the Mackenzie River plume, and a shift in carbon resources has been previously noted within their first summer at sea (von Biela et al., 2013). Larger Dolly Varden and Arctic cisco feed almost exclusively in nearshore and offshore marine waters consistent with less OM_{terr} use (Courtney et al., 2018; Craig and Haldorson, 1981).

Among marine fishes, shifts in organic matter sources with size were less pronounced compared to diadromous fishes. Shifts in saffron cod organic matter use in eastern Beaufort Sea lagoons stood out among the marine fishes with the smallest individuals using ~50% OM_{terr} and the largest using almost none. This pattern suggests that the smallest saffron cod are either feeding closer to shore or selecting different prey than larger saffron cod. The difference in OM_{terr} use with size underscores the possibility that the shallowest nearshore waters are particularly important for saffron cod rearing as in other regions (Johnson et al., 2009) and other gadid species (Laurel et al., 2007). Saffron cod are a species of interest in the Arctic given their eurythermal temperature tolerance in a warming Arctic and their future fishery potential (Laurel et al., 2016). Indeed, saffron cod catch and lengths have increased dramatically since the late 1980s in the eastern Beaufort Sea lagoons (Stanek et al., 2022a).

5. Conclusions

In this study, stable isotopes revealed food web differences between fish communities, which were linked to regional landscape features, species, and size of individuals. At the community level, fishes in less protected lagoons occupied a lower diversity of trophic niches. A lack of trophic diversity has been linked to reduced food web resilience and stability because food limitations may lead to a simultaneous decline in species that share resources (Gabara et al., 2021; McMeans et al., 2013). There is growing concern and evidence that climate change may lead to simpler food webs (Rooney et al., 2006) and, thus, less resilient ecosystems through several mechanism including warming, changes in pH, and disturbance by storms (Bernhardt and Leslie, 2013).

We propose that the differences in the food web structure of estuarine fish communities between protected and exposed lagoons arose from different degrees of mixing between fresh and offshore marine waters. Although there are insufficient data to test these causal hypotheses, ongoing studies are focused on measurements that will enable us to link ecological processes with physical structure, water exchange, winds, and storm events. Climate change is likely to drive increases in mixing as coastlines and barrier islands erode and migrate from the effects of sea-level rise and increases in storm intensity and duration (Bonsell and Dunton, 2018; Erikson et al., 2020; Jones et al., 2020; Schreiner et al., 2013). Our work contributes to the fundamental understanding of the fishery ecology of Arctic nearshore systems that are vital to the Inupiat communities, especially with respect to their cultural traditions and subsistence lifestyle (Harcharek et al., 2018; Jacobson and Wentworth, 1982; Pedersen and Linn, 2005).

CRediT authorship contribution statement

Ashley E. Stanek: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation. **Vanessa R. von Biela:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Sarah M. Laske:** Writing – review & editing, Writing – original draft, Investigation. **Rebecca L. Taylor:** Writing – review & editing, Validation, Methodology, Formal analysis. **Kenneth H. Dunton:** Writing – review & editing, Project administration, Investigation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data used in this study and associated metadata are available in the U.S. Geological Survey data release at <https://doi.org/10.5066/P9DAFMJD>.

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Appendix A. Supplementary figures

Supplementary figures (S1–S4) can be found online at <https://doi.org/10.1016/j.ecss.2022.108094>.

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