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Arctic lagoon and nearshore food webs: Relative contributions of terrestrial organic matter, phytoplankton, and phytobenthos vary with consumer foraging dynamics

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ABSTRACT

Characterizing energy flow and trophic linkages is fundamental to understanding the functioning and resilience of Arctic ecosystems under increasing pressure from climate change and anthropogenic exploitation. We used carbon and nitrogen stable isotopes to examine trophic dynamics and the relative contribution of terrestrial organic matter, water column phytoplankton, and phytobenthos (benthic micro- and macro-autotrophs as well as sea ice algae) to the food webs supporting 45 macroconsumers in three Arctic coastal lagoon ecosystems (Krusenstern, Sisualik, Akulaaq) and the adjacent Kotzebue Sound with varying degrees of connectivity in Cape Krusenstern National Monument, Alaska. A two-source (water column particulate organic matter and benthic sediment organic matter), two-isotope trophic dynamics model informed by a Bayesian isotope mixing model revealed that the Lagoon-Kotzebue Sound coastal ecosystem supported consumers along a trophic position continuum from primary consumers, including amphipods, copepods, and clams to trophic level five predators, such as seastars, piscivorous fishes, seals, and seabirds. The relative contribution of the three primary producer end members, terrestrial organic matter (41 ± 21%), phytoplankton (25 ± 21%), and phytobenthos (34 ± 23%) varied as a function of: 1) consumer foraging ecology and 2) consumer location. Suspension feeders received most of their carbon from food webs based on phytoplankton (49 ± 11%) and terrestrial organic matter (23 ± 5%), whereas herbivores and detritivores received the majority of their carbon from phytobenthos-based food webs, 58 ± 10% and 60 ± 8%, respectively. Omnivores and predators showed more even distributions of resource reliance and greater overall variance among species. Within the invertebrates, the importance of terrestrial organic matter decreased and phytobenthos increased with increasing trophic position. The importance of terrestrial organic matter contribution increased with lagoon proximity to major rivers inputs and isolation from Kotzebue Sound. Several taxa with cultural and subsistence food importance to local communities showed significant reliance (30–90% of baseline carbon) on food chains linked to fresh terrestrial organic matter. Our study indicates that terrestrial-marine linkages are important to the function of Arctic coastal lagoon ecosystems and artisanal fisheries. These linkages are likely to strengthen in the future with regional changes in erosion and runoff associated with climate change and anthropogenic disturbance.

Abbreviations: Particulate Organic Matter (POM), Sediment Organic Matter (SOM).

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1. Introduction

Understanding the energy sources and associated trophic linkages supporting local food webs is critical to understanding the structure, function, and resilience of an ecosystem (Lindeman, 1942; DeAngelis, 1980; Brookes et al., 2005). Quantitative assessments of carbon and nitrogen flux are needed to predict ecosystem responses to increasing perturbations associated with climate change, habitat destruction, and exploitation of natural resources. This is especially important in the Arctic where air temperature is warming more than twice as fast than at lower latitudes, resulting in dramatic shifts in habitat availability and ocean circulation, increases in freshwater discharge and permafrost thawing, and expansion of human activities (Greene et al., 2008; Wassmann et al., 2011; Hobbie et al., 2017; Ng and Song, 2018).

Arctic coastal lagoons, much like estuaries, are dynamic systems where terrestrial, freshwater and marine systems converge to provide habitat for migratory birds and fishes (Dunton et al., 2006; Lawler et al., 2009) and are important locations for subsistence hunting and fishing (Reynolds, 2012). These systems are dependent on multiple sources of carbon, the quantity and quality of which may change in response to environmental change. The bulk of primary productivity in these shallow, coastal estuarine-marine systems is a combination of pelagic phytoplankton, sea ice algae, and benthic microphytobenthos, macroalgae, and seagrass (Dunton and Schell, 1987; Kühl et al., 2001; Glud et al., 2009). Increasing attention, however, is being paid to the importance of allochthonous organic matter from terrestrial sources (Dunton et al. 2006, 2012, 2012; Bell et al., 2016; Harris et al., 2018), which has long been recognized as an important component of the carbon budget of lacustrine systems (e.g., Wetzel, 1995; Tank et al., 2010) and lower latitude coastal marine systems (e.g., Careddu et al., 2015).

The seasonal input of large amounts of terrestrial organic material within barrier island-lagoon systems and near-shore waters is a distinctive feature of the Arctic coast, though the fate of this material in Arctic food webs is only beginning to be fully appreciated. Several studies have started to shed light on how important terrestrial organic carbon can be in coastal Arctic systems (Dunton et al. 2006, 2012, 2012; Bell et al., 2016; Mohen et al., 2016; Harris et al., 2018). A carbon budget constructed for the Simpson Lagoon-Barrier Island ecosystem in the Beaufort Sea revealed that terrestrial inputs accounted for most of the total carbon available to consumers (Schell et al., 1984). Also working in the Beaufort Sea across five lagoons and nearshore, Harris et al. (2018) found that terrestrial carbon made an important contribution to food webs with some members deriving greater than 40% of their carbon from terrestrial sources. Terrestrial carbon was also a significant contributor to the benthic food web in two sub-Arctic Norwegian Fjords (McGovern et al., 2020).

The relative contribution of marine and terrestrial sources of carbon to lagoon food webs is predicted to vary as a function their degree of connection to the marine system and the amount riverine input (e.g., Young et al., 2021). Some lagoons are always open to the coastal waters while others are only periodically or never connected directly to the marine environment. Changes in environmental conditions associated with current and projected warming are also predicted to have differential impacts on the trajectories of these dominant primary producers and the trophic dynamics they support (Tremblay et al., 2012; Connolly et al., 2020). As such, characterizing the roles that these distinct primary production energy channels play as bottom-up drivers of ecosystem structure and function is critical to understanding the resilience and/or adaptive capacity of coastal Arctic ecosystems to change.

Ecological communities are often characterized by the length of their food chains and as such, determining the factors controlling food chain length has long been a focus of ecology (Elton, 1927; Pimm, 2002; Post, 2002b). Factors that influence the quality and quantity of primary production entering a system, when coupled with ecosystem size, can shape food chain length (Post, 2002b). Food chain length, in turn, plays a central role in the function of ecological communities by structuring predator-prey interactions; modulating biogeochemical cycling and primary productivity; and influencing the concentration of contaminants in top predators, including fish and marine mammals that humans eat (Post, 2002b; Sokolowski et al., 2012). Energetic theory predicts that food chain length should increase as resource availability increases (Post, 2002b), for example as detrital carbon sources from terrestrial runoff increase coastal resource availability (Careddu et al., 2015; Bell et al., 2016).

Stable isotope analysis (SIA) has long been used to examine carbon flow pathways and trophic dynamics in marine systems (Boecklen et al., 2011) avoiding many of the challenges associated with conventional gut content analysis and feeding observations (Deb, 1997). Bulk tissue SIA studies rely upon the assumption that the isotope composition of a consumer reflects the weighted average of the isotope composition of its diet with some degree of trophic fractionation (DeNiro and Epstein, 1978, 1981). In polar marine ecosystems that are dominated by several isotopically distinct primary producers (e.g., phytoplankton, ice algae, benthic macro/microalgae, and terrestrial vegetation [Hobson et al., 1995; McMahon et al., 2006; Harris et al., 2018]), $\delta^{13}C$ analysis provides a robust tracer of carbon source utilization at the base of the food web with relatively little trophic fractionation (Post, 2002a). Large terrestrial inputs of particulate organic matter (POM) are reflected in distinctly low $\delta^{13}C$ values of coastal Arctic sediments ($<$-26‰; Naidu et al., 2000), making it possible to track terrestrial carbon through a food web. Nitrogen isotopes are often used in concert with carbon isotopes to provide additional information about trophic dynamics of a system. Nitrogen stable isotope values typically undergo larger trophic fractionations (3‰–4‰; Post, 2002a) between diet and consumer than carbon, providing a temporally integrated index of consumer trophic position once properly scaled to the nitrogen isotope value of baseline primary producers ($\delta^{15}N_{baseline}$). The combined use of stable carbon and nitrogen isotope analysis has proven very useful for identifying important carbon flow pathways and trophic linkages in polar marine ecosystems (Hobson and Welch, 1992; Hobson et al., 1995; Dunton et al., 2006; Tamelander et al., 2006; Harris et al., 2018).

We used carbon and nitrogen SIA to examine trophic dynamics and the relative contribution of terrestrial organic matter, water column phytoplankton, and benthic phytobenthos (micro- and macro-primary producers) to the food webs supporting 45 macroconsumers in three Arctic coastal lagoon ecosystems (Krusenstern, Sisualik, Akulaaq) and in the nearshore of the adjacent Kotzebue Sound in Cape Krusenstern National Monument, Alaska. While most studies of the trophic structure of Arctic lagoons have focused on the lagoons of the Northeast Chukchi and Beaufort Seas, more southern lagoons, like those of Cape Krusenstern National Monument, have received limited attention (but see stomach content assessment Tibbles and Robards, 2018), despite being important for subsistence hunting and fishing (Uhl and Uhl, 1977; Georgette and Shiedt, 2005; Reynolds, 2012). The three lagoons we examined vary in their degree of connectivity to Kotzebue Sound (Table 1), which we hypothesized would impact the relative importance of terrestrial and marine primary production to local food webs. Given its seasonal and indirect connection to Kotzebue Sound, we predicted that Krusenstern Lagoon would receive the least marine influence and have the highest contribution of terrestrial organic matter to its food web. Conversely, we hypothesized that Sisualik Lagoon, which is open to Kotzebue Sound year-round, would have the strongest marine influence on its local food web of the three lagoons. Akulaaq Lagoon is intermittently open to Kotzebue Sound and its macroconsumers were hypothesized to rely on a more even mix of terrestrial and marine organic matter sources than the other lagoons. Two major rivers, the Noatak and the Kobuk, discharge into Kotzebue Sound, and consequently, we hypothesized that terrigenous sources of carbon would be a component of the Sound food web, though not as important as in the lagoons. Similarly, we hypothesized that consumer foraging ecology would play a role in the relative contribution of distinct primary producer carbon sources, such that

Table 1
Size, relative openness to Kotzebue Sound (I–O = intermittently open, O = open, S–C = seasonally closed, NA = not applicable), water depth, and environmental conditions sampled in [a]April or [b]July (mean ± SD): water temperature, salinity, dissolved oxygen, and near-surface chlorophyll-a and phaeophytin concentrations in three Arctic lagoons in Cape Krusenstern National Monument, Alaska and adjacent Kotzebue Sound ([c]Outer boundary - Cape Krusenstern to Cape Blossom, along the ~10 m isobath). Data are summarized from Jewett et al. (2009), Reynolds (2012), and collected for this study (Kotzebue Sound phaeopigments).

Location	Size (km^2)	Relative openness	Water depth (m)	Water temperature (°C)[b]	Salinity[b]	Dissolved oxygen (mg L^{-1})[b]	Chlorophyll-a (μg L^{-1})[a]	Phaeophytin (ug L^{-1})[a]
Krusenstern Lagoon	56	S–C	2.0 ± 0.2	8.9 ± 0.1	3.6 ± 0.1	11.0 ± 0.2	29.6 ± 8.2	32.2 ± 8.9
Akulaaq Lagoon	9	I–O	1.3 ± 0.1	8.9 ± 0.1	8.1 ± 0.1	10.4 ± 0.2	4.3 ± 7.1	3.9 ± 5.6
Sisualik Lagoon	34	O	0.9 ± 0.1	17.2 ± 0.6	7.3 ± 1.6	10.0 ± 0.2	6.0 ± 1.9	6.9 ± 3.6
Kotzebue Sound	6,700[c]	NA	10–18	8.9 ± 4.0	19.2 ± 9.0	9.8 ± 0.7	2.1 ± 1.1	0.8 ± 0.5

suspension and deposit feeders would show opposite patterns of reliance on water column and benthic production while generalist predators would more closely mirror the lagoon-averaged relative contribution patterns.

2. Materials and methods

2.1. Study area

We collected primary producer and consumer samples from lagoons within Cape Krusenstern National Monument and from adjacent Kotzebue Sound in Northwestern Alaska (Fig. 1). Cape Krusenstern National Monument was established in 1978 and designated as part of the Alaska National Interest Lands Conservation Act in 1980 (ANILCA, 16 USC 3101). It is located approximately 72 km above the Arctic Circle (67°26′N, 163°32′W) and encompasses 2670 km^2 of land and water bordered to the west and south by the Chukchi Sea and Kotzebue Sound, respectively. The region is a largely treeless coastal plain underlain by thick permafrost in a semi-maritime climate (Allen and Weedfall, 1966). There are several coastal lagoons within Cape Krusenstern National

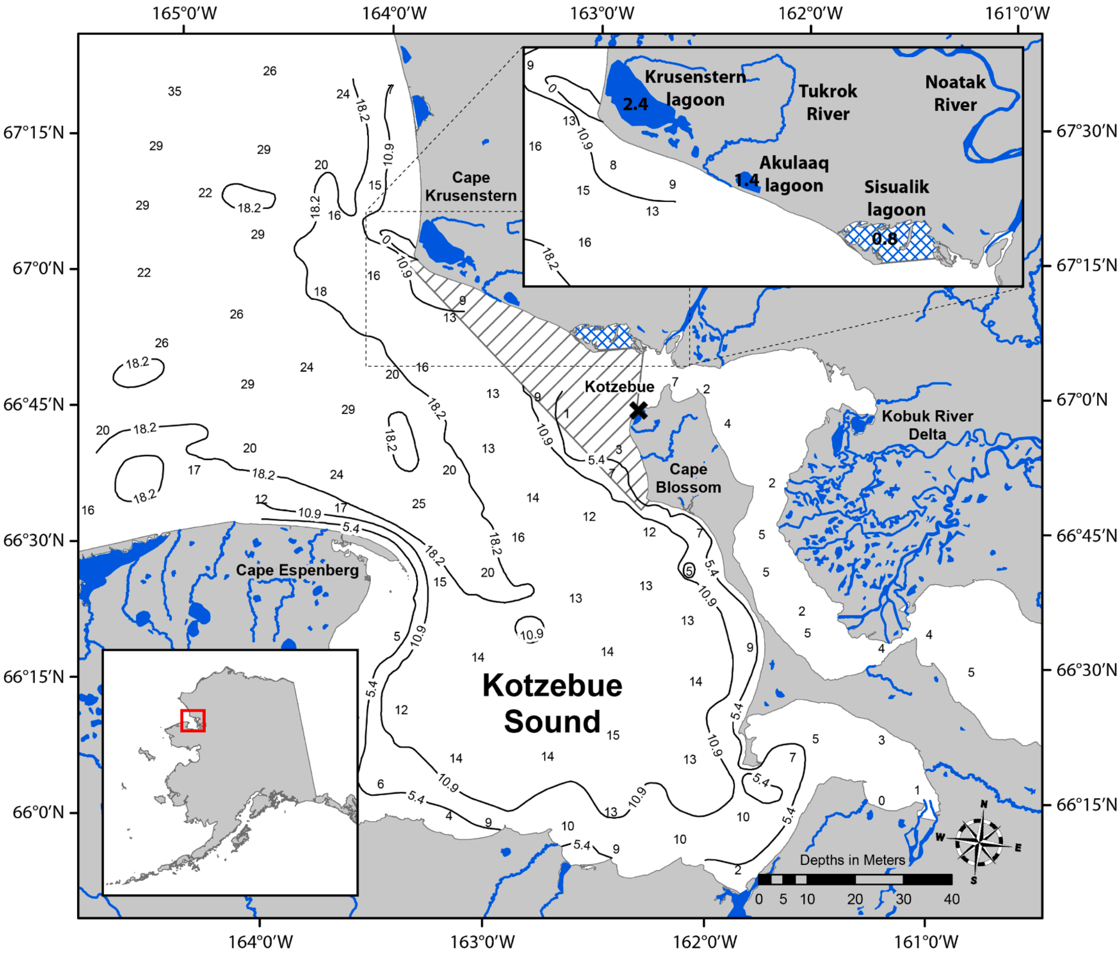

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Fig. 1. Site map: Map of sampled lagoons (inset: Krusenstern, Akulaaq, Sisualik) in Cape Krusenstern National Monument, Alaska and adjacent Kotzebue Sound. Samples in Kotzebue Sound were collected within the 10 m isobath between Cape Blossom and Cape Krusenstern (gridded area). Sisualik Lagoon (blue cross hatch) is always open to the Sound while Krustenstern and Akulaaq Lagoons (solid blue) are intermittently connected to the Sound. Major named rivers noted in blue. Depth soundings (m) and key isobaths indicated in the Sound and lagoons. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Monument fed by streams and rivers that often transport large amounts of terrestrial organic matter during the spring thaw (Guo et al., 2007).

We sampled the shallow waters (<10 m) of Kotzebue Sound from near Cape Krusenstern to Cape Blossom. Kotzebue Sound is a shallow (average water depth 10–18 m) embayment (Fig. 1). The area is characterized by long, cold winters and a short, cool spring, summer and fall from June into October when ice begins to form (Whiting et al., 2011).

Data on the physical and biological conditions and macrobenthic community parameters during the sample periods and methods of collection can be found in Jewett et al. (2009) and are summarized in Table 1. Briefly, poorly to very poorly sorted sediments are primarily sand to sandy mud, with a minor portion of gravel (Jewett et al., 2009). Discharge from the Noatak and Kobuk rivers (10–13 km^3/yr, 1976–2019 average; Global Runoff Data Centre, 2020) into the Sound along with the Sound's shallow depth result in large seasonal changes in both the temperature and salinity of the Sound's near shore waters (seasonal water temperature range of −0.8 to 15 °C and a salinity range of 0.1–35.1 ppt, in 3 m of water off Kotzebue town beach, unpublished data).

The three coastal lagoons we sampled varied in size and degree of openness to Kotzebue Sound (Table 1). Detailed descriptions of the study sites with in-depth characterization of physiochemical parameters and species composition among lagoons can be found in Reynolds (2012). Briefly, Krusenstern Lagoon (67°9′15.9″ N, 163°38′46.9″ W) is the largest and deepest lagoon in Cape Krusenstern National Monument. The lagoon extends longitudinally along the coast and a number of small creeks and rivers flow into the lagoon from the surrounding wide expanse of wetlands with interconnecting sloughs. Krusenstern Lagoon has limited, indirect connection to Kotzebue Sound via a series of sloughs that empty into the Tukrok River, which eventually reaches Kotzebue Sound (15 km downstream), though the opening of the river to the Sound is typically limited to the spring thaw (May to June). Krusenstern Lagoon has the highest chlorophyll-a concentration of the lagoons examined (Table 1). Sisualik Lagoon (67°1′30.5″ N, 162°51′53.9″ W) is intermediate in size and is open to Kotzebue Sound year-round with a mean tidal range of 0.6 m (Table 1). Sisualik Lagoon has the highest species richness of the three lagoons (Reynolds, 2012). Akulaaq Lagoon (67°4′10.0″ N, 163°15′35.0″ W) is one of the smallest lagoons in Cape Krusenstern National Monument and is intermittently open to Kotzebue Sound via periodic barrier beach washouts associated with strong storm events, often flooding the lagoon with water from Kotzebue Sound until the alongshore drift repairs the barrier beach. During the sampling period there were several strong storm events that likely opened Akulaaq Lagoon intermittently, as indicated by the lagoon's high salinity (Table 1).

2.2. Sample collection

A variety of methods were used to collect source end members and macroconsumers, including: hand collections, plankton tows (250 μm mesh), Van Veen grabs (1 mm mesh sieve for invertebrates), minnow traps, beach seines, and gillnets (5-panel with stretch measurements of 2.5 cm, 3.8 cm, 5.1 cm, 7.6 cm, and 10.2 cm). Sampling occurred between April and October 2002–2006 between Cape Blossom and Cape Krusenstern (Fig. 1) shallower than the 10 m isobath. A detailed report of sampling procedures, following that of Blaylock and Houghton (1983a, b), can be found in Reynolds Ch. 3 (2012).

We identified four potentially important source end members for the Lagoon-Sound system: 1) terrestrial organic matter, 2) water column phytoplankton, 3) benthic phytobenthos, and, 4) sea ice algae. Terrestrial organic matter consisted of leaves of the dominant coastal vegetation *Salix herbacea, Betula nana,* and *Sphagnum* sp. The isotopic values for phytoplankton were back calculated from Kotzebue Sound copepods using the $\delta^{X}Y_{corr}$ equation in section 2.4.2 and standard trophic discrimination factors ($\Delta^{13}C = 0.4‰$, $\Delta^{15}N = 3.4‰$ Post, 2002a). While sampling phytoplankton directly was not feasible given sampling logistics with partners in the Native Village of Kotzebue, we have multiple lines of evidence that give us confidence in our approach of using small bodied copepods as a proxy for local phytoplankton. 1) Phytoplankton from the northeast Chukchi Sea near Utqiaġvik (formerly Barrow), Alaska (McTigue and Dunton, 2017) had nearly identical carbon isotope values ($\delta^{13}C = -24.0 \pm 0.4‰$) to the back calculated phytoplankton carbon isotope values in our study (−24.0 ± 0.9‰). These values agree well with regional plankton $\delta^{13}C$ values predicted from a global carbon isoscape (McMahon et al., 2013). 2) Herbivorous copepods (*Calanus hyperboreus*) in northern coastal Alaskan lagoons (Beaufort Sea) had isotope values ($\delta^{15}N = 9.9 \pm 0.4‰$, $\delta^{13}C = -24.3 \pm 0.4$) that align well with the copepods in this study ($\delta^{15}N = 10.0 \pm 0.6$, $\delta^{13}C = -23.4 \pm 0.9$), lending confidence to the herbivorous diet assignment of copepods in this study used to back calculate local phytoplankton isotope values. The phytobenthos end member represented an equally weighted average of isotopic values of microphytobenthos from the literature ($\delta^{13}C = -16.9 \pm 1.2‰$, $\delta^{15}N = 6.4 \pm 1.2‰$; McTigue and Dunton, 2017), location-specific benthic green macroalgae, and location-specific seagrass, *Zostera marina*, and ice algae (Table S1). Equal weighting was chosen as the most parsimonious weighting option given the isotopic similarity among these end members and a lack of empirical data on foraging patterns needed to *a priori* weight contributions in a particular direction. The sea ice algae end member was considered a potential source end member in Kotzebue Sound but not the lagoons. The shallow nature of the lagoons and their rapid freeze and thaw cycle means that no ice algae were observed or collected during the multi-year field campaign in this system. The lack of ice algae in the lagoon systems was corroborated by reports from partners in the Native Village of Kotzebue. The ice algae end member in Kotzebue Sound was an equally weighted average of local field collected ice algae isotope values from a single ice core collected in April 2004 from Kotzebue Sound, *Melosira* sp., $\delta^{13}C = -15.0‰$, $\delta^{15}N = 6.5‰$) and regional literature ice algae isotope values ($\delta^{13}C = -18.7‰$, $\delta^{15}N = 7.8‰$) from a single core collected in May 2002 from the Chukchi Sea station 020510 (Gradinger, 2009). In both cases, ice samples were melted in a dark cold room through a pre-ashed glass-fiber filter. We note that the isotope values of ice algae and phytobenthos strongly overlap in dual isotope space, meaning we were not able to distinguish these end members, as has been seen in other Arctic marine systems (Wang et al., 2014; Oxtoby et al., 2016). As such, in this paper we use phytobenthos to include macro- and microalgae, seagrass, and sea ice algae. We acknowledge that ice algae are not explicitly a benthic production source, however, previous literature indicates rapid sinking and deposition of ice algae in coastal Arctic systems during rapid spring thaws (Sun et al., 2007; Boetius et al., 2013; Koch et al., 2020). Furthermore, the carbon and nitrogen isotope values of water column POM sampled in this system fell along a continuum between terrestrial organic matter and phytoplankton, showing no strong evidence of significant contribution of ice algae or other phytobenthic production sources. Conversely, the carbon and nitrogen isotope values of sediment organic matter did show a strong signal of phytobenthic contribution that likely includes both macro-and micro-algae, seagrass, and rapidly deposited ice algae. Water column particulate organic matter was sampled by filtering 0.5–1 L of water collected with a Niskin bottle through pre-ashed glass-fiber filters. Frozen filters were subdivided for SIA and fluorometric analysis of chlorophyll *a* and phaeophytin concentrations. Sediment organic matter (SOM) was collected from the top 1 cm of the sediment by hand in shallow water or from the top of a sediment grab. POM and SOM represent water column and benthic composites of these source end members as well as consumer waste and biomass fragments.

Small invertebrates (e.g., copepods, amphipods, isopods) were sampled whole, sometimes as multiple organisms pooled, after a 24-hr period of depuration. Muscle tissue was sampled from all organisms (fish, seals, birds, and large invertebrates, such as bivalves, seastars, crabs) large enough to permit sufficient sample sizes for isotopic analysis. Vertebrate samples were collected opportunistically from species already in possession by a Fisheries Subsistence Management Specialist at the Western Arctic National Parklands such that no additional permission was required for lagoon sampling. Sea bird and marine mammal muscle tissues were collected by the Alaska Department of Fish and Game (Permit No. 358-1585-07) in Kotzebue Sound and data were shared with us via formal data request approval. Consumer foraging ecology was characterized as herbivores, deposit feeders, suspension feeders, zooplanktivores, omnivores, and predators according to www.fishbase.de and www.sealifebase.ca. All samples were frozen (−20 °C) until analysis.

2.3. *Stable isotope analysis*

A subset of all animal tissue samples was lipid extracted in chloroform/methanol (2:1 v/v) to remove lipids and filtered onto pre-ashed glass-fiber filters for δ^{13}C analysis. δ^{15}N analysis was conducted on non-lipid extracted samples. Sediment samples for organic δ^{13}C analysis were pretreated with acid to remove inorganic (carbonate) carbon (Harris et al., 2001). Briefly, sediment samples in silver capsules were moistened with 50 μL of deionized water, placed in a vacuum desiccator and exposed to HCl vapor for 24 h, after which samples were dried at 60 °C for 4 h. Sediment samples for δ^{15}N analysis were not acid-treated. All samples frozen at −20 °C then lyophilized (freeze-dried) for 48 h prior to homogenization with a mortar and pestle. Samples were analyzed for stable carbon and nitrogen isotope values using a ThermoFinnigan Delta Plus Advantage isotope ratio mass spectrometer coupled to a Costech elemental analyzer via a Conflo III combustion interface in the Environmental Geochemistry Laboratory, Bates College, Lewiston, ME. Stable isotope values were expressed in standard δ (‰) notation relative to Pee Dee Belemnite for carbon and Air for nitrogen. The accuracy and precision (±0.2‰ for both δ^{13}C and δ^{15}N) of analyses were determined by multiple analyses of a working standard (acetanilide: C_8H_9NO) run every sixth sample.

2.4. *Data analysis*

2.4.1. *Trophic position estimation*

Individual consumer trophic positions (TP_c) were calculated using a two-source, two-isotope Bayesian isotope mixing model within the tRophicPosition package (ver. 0.7.7, Quezada-Romegialli et al., 2018) in R using Δ^{15}N (= 3.4 ± 1.0‰, Post, 2002a) as the nitrogen isotope trophic discrimination factor and setting the trophic positions of the two baselines $\lambda_{b1,b2} = 1$. We paired location-specific POM and SOM with local consumers for each of the four locations (Table S1) to reflect the baseline pelagic and benthic end members, respectively. This model uses a secondary mixing model to determine the relative contribution (α_c) of the pelagic and benthic baselines in the TPc calculation, which accounts for carbon trophic discrimination factor (0.4 ± 1.3‰, Post, 2002a). We used the function “multiSpeciesTP” to define and initialize the Bayesian model and to sample the posterior distribution of $TP_{c.}$ The Bayesian model ran 10,000 iterations used for the parameters “n.adapt,” “n.iter, ”and “burnin” and used five parallel Markov Chain Monte Carlo(MCMC) simulations using the JAGS (ver. 4.3.0) Gibbs sampler (Plummer, 2003).

2.4.2. *End member source model*

We estimated the relative contributions of potential source end members, terrestrial organic matter, marine phytoplankton, and phytobenthos (a composite of benthic macro- and microalgae, seagrass, and ice algae), to water column POM, benthic SOM, and macroconsumers (invertebrates, fishes, birds, and marine mammals) among the four locations within this study using a fully Bayesian approach within the MixSIAR package (ver. 3.1, Stock et al., 2018). We adjusted the stable isotope values of macroconsumers back to their source end member equivalents by correcting their bulk δ^{13}C and δ^{15}N values for trophic fractionation using the equation $\delta^{X}Y_{corr} = \delta^{X}Y_c$ - (TP_c – 1)$\Delta^{X}Y$, where $\delta^{X}Y_{corr}$ represent the trophic transfer-corrected consumer isotope values of δ^{13}C or δ^{15}N, $\delta^{X}Y_c$ represents the original, uncorrected consumer $\delta^{13}C_c$ or $\delta^{15}N_c$ values, TP_c represents the individual calculated consumer trophic position from the tRophicPosition package in section 2.4.1, and $\Delta^{X}Y$ represents the trophic discrimination factors between diet and consumer (Δ^{13}C = 0.4‰, Δ^{15}N = 3.4‰ Post, 2002a). In MixSIAR, species were characterized as random effects and location as a fixed effect. Each model was run with chain length = 1,000,000, burn-in = 500,000, thin = 500, chains = 3 to ensure the model satisfied the Gelman-Rubin and Geweke Diagnostics. An uninformative prior was used. Note, this approach identifies the relative contribution of primary producer end members at the base of the food web supporting these consumers and does not necessarily reflect direct consumption of these end members by macroconsumers.

2.4.3. *Statistical analyses*

Separate one-way Analyses of Variance (ANOVA) were used to compare the system averaged δ^{13}C and δ^{15}N values among the end members: terrestrial organic matter, water column phytoplankton, and phytobenthos to confirm that our end members were isotopically different from each other. Separate one-way ANOVAs were used to test whether δ^{13}C and δ^{15}N values of POM and SOM were different among locations, as hypothesized based on differences in hydrography. Mean trophic positions of invertebrates, fishes, seabirds, and mammals were compared with a one-way ANOVA. Prior to all ANOVAs, data were confirmed to exhibit normal distributions using the F_{max} test. When an ANOVA revealed a significant difference among tested groups, differences between pairs of means were assessed using the Tukey Highly Significant Difference (HSD) *post hoc* test with the Bonferroni correction to the results of the *post hoc* tests to correct for the increased risk of a type I error with multiple testing. An ordinary least squares model II regression was used to examine relationships between consumer trophic position and the relative contribution of terrestrial organic matter, phytoplankton, and phytobenthos as a function of broad consumer taxa: invertebrates, fishes, seabirds, and mammals.

3. Results

3.1. *Source end member and consumer δ^{13}C and δ^{15}N values*

Primary producer end members exhibited a ~11.3‰ range in mean δ^{13}C values and a ~4.3‰ range in mean δ^{15}N values (Fig. 2, Table S1). Terrestrial organic matter (δ^{13}C = −28.8 ± 3.2‰; δ^{15}N = 0.8 ± 1.0‰), water column phytoplankton (δ^{13}C = −24.0 ± 0.9‰; δ^{15}N = 5.1 ± 0.6‰), and phytobenthos (benthic micro- and macro-primary production: δ^{13}C = −18.3 ± 0.6‰; δ^{15}N = 4.7 ± 0.5‰) had significantly different δ^{13}C values (One-way ANOVA, $F_{2,35} = 31.7$, $p = 1.4e^{-8}$) and δ^{15}N values (One-way ANOVA, $F_{2,35} = 97.0$, $p = 5.3e^{-15}$) within this system (Fig. 2, Tables S1, S2A,B). Water column POM varied significantly in δ^{13}C values (One-way ANOVA, $F_{3,52} = 32.9$, $p = 4.5e^{-12}$) and δ^{15}N values (One-way ANOVA, $F_{3,52} = 54.3$, $p = 4.9e^{-16}$) among the four locations, as did benthic SOM δ^{13}C (One-way ANOVA, $F_{3,8} = 16.4$, $p = 8.9e^{-4}$) and δ^{15}N (One-way ANOVA, $F_{3,8} = 14.6$, $p = 1.3e^{-3}$), though not all lagoons were significantly different from each other (Fig. 2, Tables S1, S2C,D,E,F).

Macroconsumers exhibited a range of δ^{13}C values (~10.6‰) among taxa and locations similar to the range in primary producers but macroconsumer δ^{15}N values (15.4‰) exhibited a much wider range than the primary producers (Fig. 2, Table S1). Trophic transfer-corrected consumer $\delta^{13}C_{adj}$ and $\delta^{15}N_{adj}$ values were well constrained within the end member isotope space of this system.

3.2. *Contribution of primary producer end members to consumers*

All three primary producer end members, terrestrial organic matter (41 ± 21%), phytoplankton (25 ± 21%), and phytobenthos (34 ± 23%),

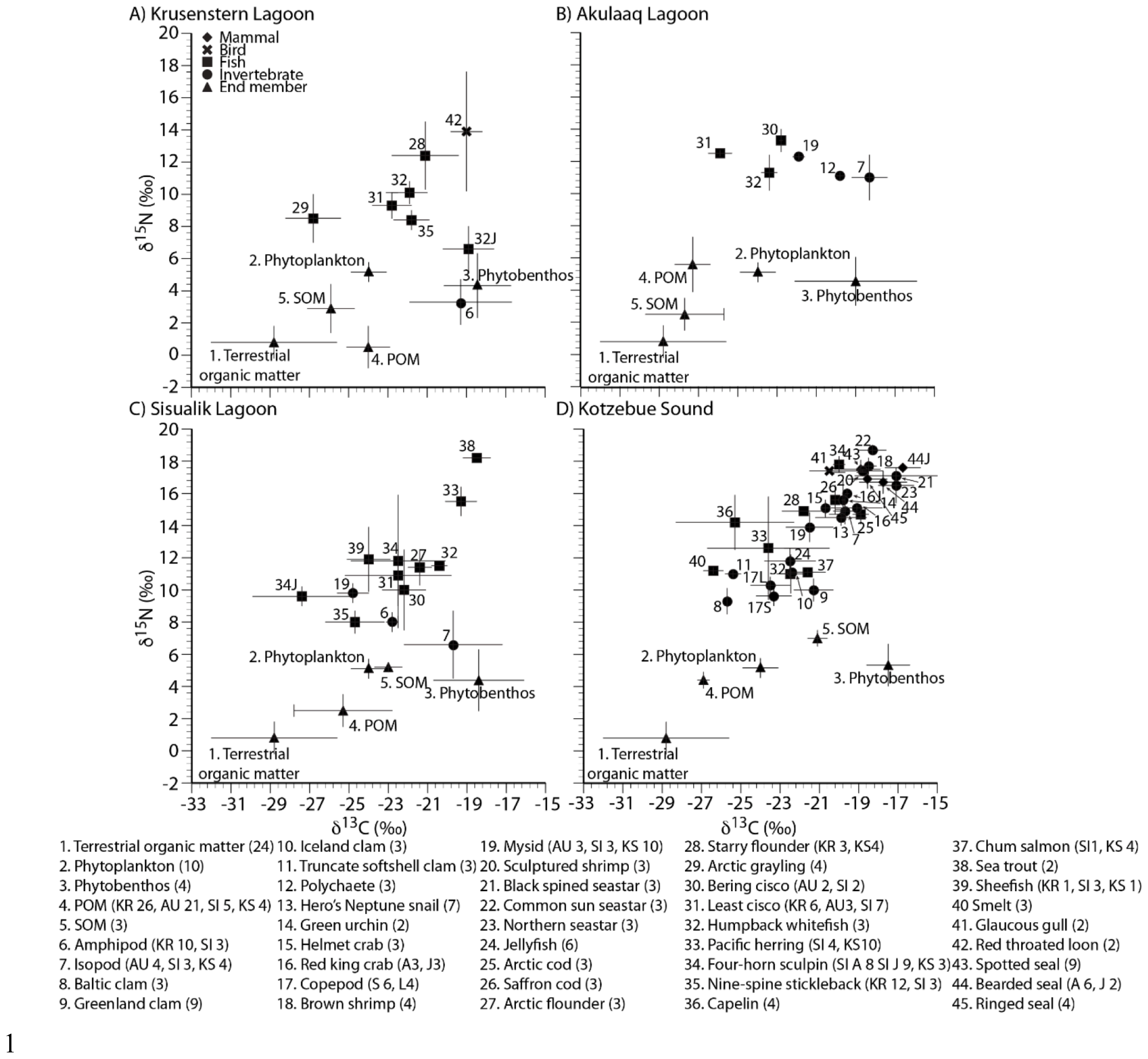

Fig. 2. Dual isotope plot: Mean (±SD) δ^{13}C and δ^{15}N values of end members (triangles: Terrestrial organic matter in green, phytoplankton in blue, phytobenthos in orange), particulate organic matter (triangles in light gray), sediment organic matter (triangles in dark gray), invertebrates (circles), fishes (squares), birds (crosses), and mammals (diamonds) from A) Krusenstern Lagoon, B) Akulaaq Lagoon, C) Sisualik Lagoon, and D) Kotzebue Sound in Cape Krusenstern National Monument, Alaska. All consumers were adults unless indicated as juvenile (#J). Copepod 19 S were <2 mm and 19 L were >2 mm. Sample sizes in parentheses after ID apply to all sampled locations with that organism present unless specified by lagoon or life stage.

contributed to food webs supporting macroconsumers in Cape Krusenstern National Monument; however, the relative contribution of each end member to local food webs varied among locations (Fig. 3, Table S1). Terrestrial organic matter was the dominant carbon contribution to the food web of Krustenstern and Sisualik Lagoons, while the least important source to the food web in Kotzebue Sound. Phytoplankton had much lower contributions to the food web in Krustenstern and Sisualik Lagoons than in Akulaaq Lagoon and Kotzebue Sound. Phytobenthos followed by phytoplankton contributed the most carbon to Kotzebue Sound. Akulaaq Lagoon had relatively even distributions of all three end members.

The relative contribution of each end member to local food webs also varied among consumer taxa (Fig. 4). Across all locations (Fig. 4), phytobenthos was the dominant end member supporting invertebrates (50 ± 20%), sea birds (53 ± 5%), and marine mammals (75 ± 8%), while terrestrial organic matter was the dominant end member supporting fishes (45 ± 22%). Invertebrates showed a significant positive relationship between trophic position and the relative contribution of benthic algae to their food web but a significant negative relationship between trophic position and terrestrial organic matter contribution (Fig. 5). No such relationships existed for fishes, seabirds, or mammals in this study. Consumer foraging ecology also played an important role in determining the relative contribution of carbon from the three primary producers (Fig. 6). Suspension feeders received most of their carbon from food webs based on phytoplankton (49 ± 11%) and terrestrial organic matter (23 ± 5%), whereas herbivores and detritivores received the majority of their carbon from phytobenthos-based food webs, 58 ± 10% and 60 ± 8%, respectively. Omnivores and predators showed more even distributions of resource reliance and greater overall variance. While the comparison of the relative contributions of the end members

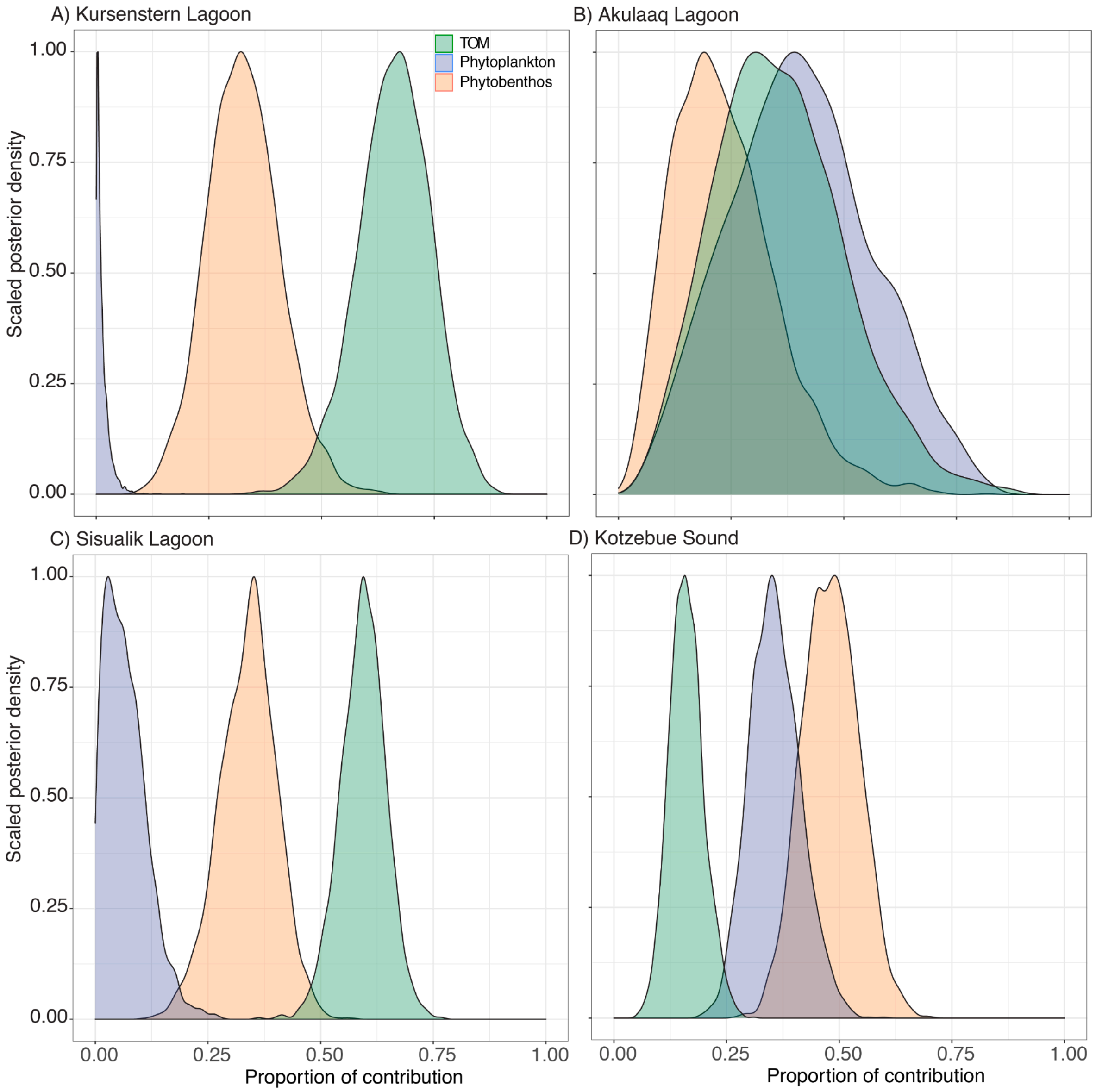

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Fig. 3. End member contributions by location: Scaled posterior density of the proportion of contribution of primary producer end members - terrestrial organic matter (TOM - green), water column phytoplankton (blue), and phytobenthos (orange) - to food webs supporting particulate organic matter, sediment organic matter, invertebrates, fishes, birds, and mammals from A) Krusenstern Lagoon, B) Akulaaq Lagoon, C) Sisualik Lagoon, and D) Kotzebue Sound in Cape Krusenstern National Monument, Alaska. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

to the food webs in the lagoon-sound system may be confounded by species distribution patterns among the different lagoons, comparison of POM/SOM composition and resource utilization patterns among taxa that exist across multiple sites generally follows the patterns previously described (Fig. 7).

3.3. Consumer trophic positions

The Cape Krusenstern National Monument coastal ecosystem of connected lagoons and the Sound supported organisms along a continuum of five trophic levels from primary producers at the base to the sea-run Dolly Varden, *Salvelinus malma*, in Sisualik Lagoon (TP = 5.5 ± 0.1) at the top (Fig. 8). There was a significant difference in mean trophic level among major taxonomic groups (One-way ANOVA, $F_{3,58} = 5.39$, $p = 2.4e^{-3}$; Table S2G); with invertebrates (3.4 ± 0.9) and fishes (3.5 ± 0.7) occupying a similar trophic position that was significantly lower than birds (4.7 ± 0.7) and mammals (4.6 ± 0.2).

4. Discussion

Our stable isotope investigation of the coastal lagoon ecosystems of Cape Krusenstern National Monument and adjacent Kotzebue Sound revealed a long food web with strong pelagic-benthic and terrestrial-marine coupling. Our results indicate that ecosystem location relative to marine and riverine input, along with consumer foraging ecology, play important roles in mediating the relative contribution of different sources of primary production in Arctic coastal food webs. Terrestrial organic matter fueled, directly and indirectly (through local POM), a number of primary and secondary macroconsumer species that support marine mammals, migratory birds, and subsistence fisheries that are culturally and nutritionally important to local communities. Our study lends strong support to the growing appreciation for how important terrestrial organic matter is to the function of coastal Arctic ecosystems (e.g., Dunton et al., 2006, 2012; Bell et al., 2016; Harris et al., 2018). This nuanced understanding of terrestrial-marine and pelagic-benthic

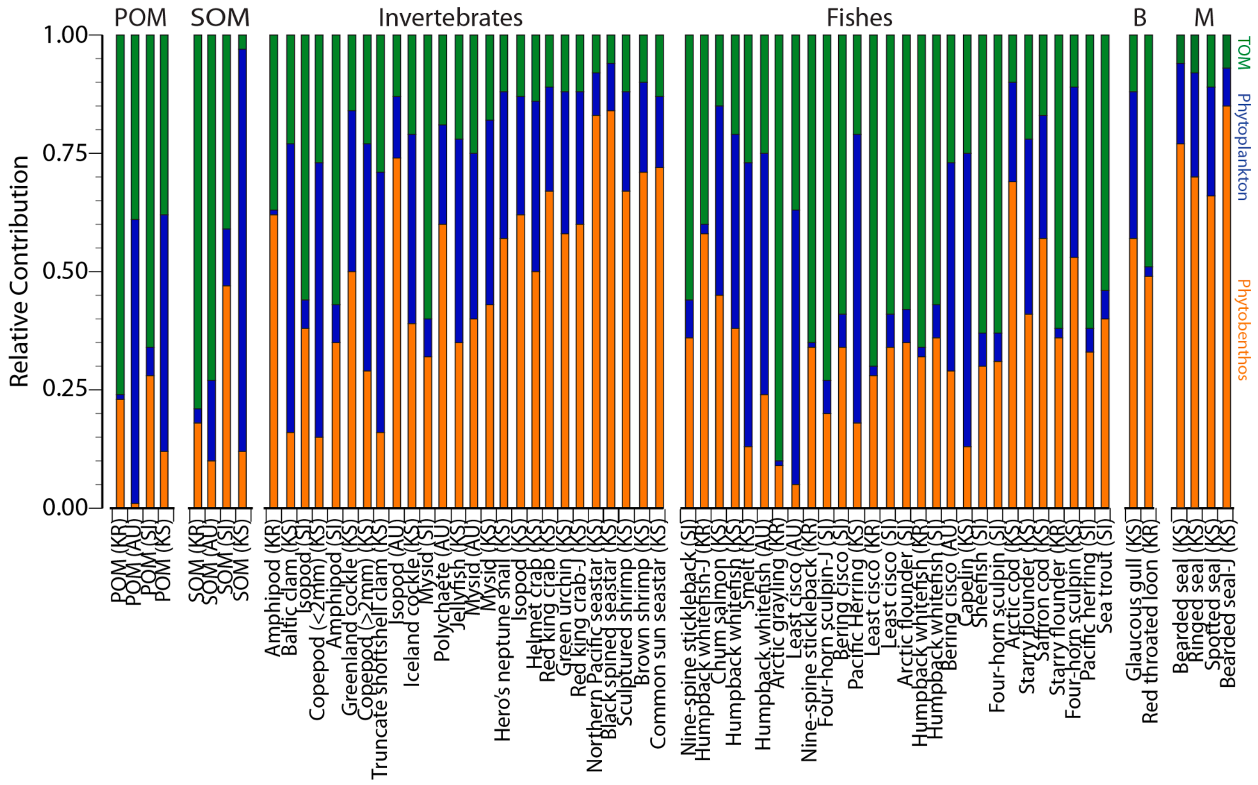

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Fig. 4. End member contributions by species: Mean relative contribution of primary producer end members - terrestrial organic matter (TOM - green), water column phytoplankton (blue), and phytobenthos (orange) - to food webs supporting particulate organic matter (POM), sediment organic matter (SOM), invertebrates, fishes, birds (B), and mammals (M) from Krusenstern Lagoon (KR), Akulaaq Lagoon (AU), Sisualik Lagoon (SI), and Kotzebue Sound (KS) in Cape Krusenstern National Monument, Alaska. Columns are ordered in increasing trophic position (left to right) within each group. All consumers were adults unless indicated as juvenile (juv). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

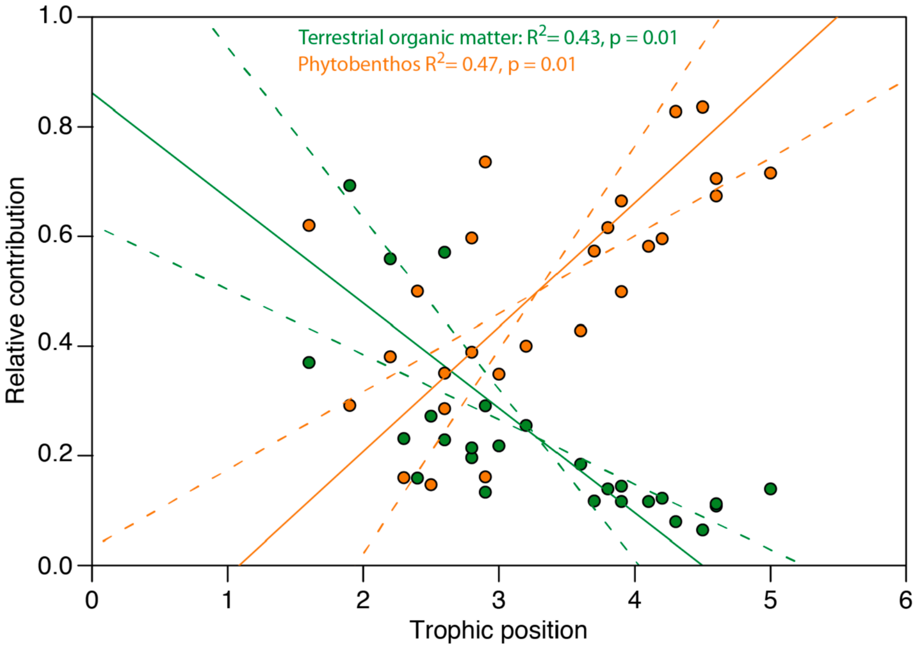

Fig. 5. End member contributions by trophic position: Model II regression of the relative contribution of terrestrial organic matter (green) and phytobenthos (orange) to food webs supporting invertebrates across all locations versus invertebrate trophic position. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

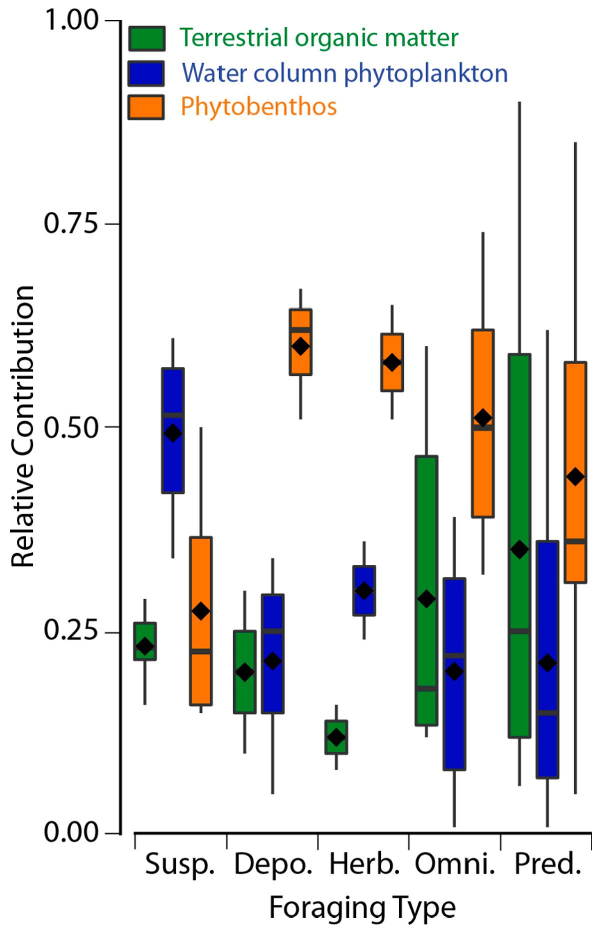

Fig. 6. End member contributions by consumer foraging type. Comparison of relative contribution of terrestrial organic matter (green), water column phytoplankton (blue), and phytobenthos (orange) to suspension feeders (Susp.), deposit feeders (Depo.), herbivores (Herb.), omnivores (Omni.), and predators (Pred) for macroconsumers in Cape Krusenstern National Monument Lagoon-Sound system. Dashes denote the median, diamonds denote the mean, box denotes the 25th and 75th percentile, whiskers denote approximately 95% confidence intervals, and dots denote outliers. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

coupling is important to ecosystem modeling efforts to project how Arctic ecosystems, and the food webs they support, will respond to current and emerging climatic and anthropogenic perturbations.

The food webs of the coastal lagoons in Cape Krusenstern National Monument and Kotzebue Sound were fueled to varying degrees by multiple ecologically and isotopically distinct primary producer end members. System-wide, terrestrial organic matter (41 ± 21%) was the dominant carbon source supporting the regional food web, followed by phytobenthos (consisting of macro- and micro-algae, seagrass, and sea ice algae) (34 ± 23%) and water column phytoplankton (25 ± 21%) (Fig. 3). Terrigenous input of nutrients and organic material, one of the major processes that promotes high productivity in temperate coastal waters (Cloren, 2001; Mann and Lazier, 2005), has been shown to contribute, directly or indirectly, to nutrition of taxa from bacteria (Sipler et al., 2017) to invertebrates (Hoffman et al., 2008; Mohen et al., 2016; Harris et al., 2018) to fish (Darnaude, 2005; Romanuk and Levings, 2005; Harris et al., 2018) to mammals (Derocher et al., 2000; Harris et al., 2018). While the assimilation of terrestrial carbon sources into coastal Arctic food webs was originally discounted based on the general absence of low ^{14}C in most invertebrates and fishes (Schell et al., 1984), work by Benner et al. (2004) and O'Donnell et al. (2020) clearly demonstrates the incorporation of terrestrial DOC into the aquatic Arctic food webs. Similarly, a wide diversity of taxa in lagoons along the Beaufort Sea have also shown a strong signal of terrestrial organic carbon in their tissues (Bell et al., 2016; Harris et al., 2018). Here, we add strong evidence to the growing number of studies that show the important role of terrestrial organic matter to Arctic ecosystems around the world. Our study helps uncover patterns of how terrestrial organic matter use varies spatially and across taxa.

Cape Krusenstern National Monument contains numerous coastal lagoons that are essential fish nurseries and major feeding locations along coastal bird and marine mammal migration routes. Nearly all the species we examined relied at least in part on a food web rooted in terrestrial organic matter. Rural Alaskan villagers rely heavily on coastal artisanal fisheries (Georgette and Loon, 1993), which often provide all their necessary protein and over a third of their total caloric intake (Wolfe, 2000). Several culturally and nutritionally important species (Uhl and Uhl, 1977; Georgette and Loon, 1993), including Arctic Grayling, Least Cisco, Humpback Whitefish (*Coregonus pidschian*), Sheefish (*Stenodus leucichthys*), Chum Salmon (*Oncorhynchus keta*), Smelt (*Osmerus mordax*) and Starry Flounder (*Platichthys stellatus*) receive the majority of their carbon from a terrestrial-based food web in at least one fished lagoon.

Perhaps unsurprisingly, the fate of terrestrial organic matter in the marine environment has evolved into an important issue as the current warming trend in the Arctic accelerates and anthropogenic disturbance from land-use practices continue to grow in the coastal Arctic. The amount of terrestrial organic carbon entering these coastal systems is only projected to increase as a function of changing human land-use practices and climate warming-induced increases in sea level, storm activity and coastal erosion, river discharge, and permafrost thaw (Zhang et al., 2004; Fritz et al., 2017). This may alter trophic and metabolic pathways, impact growth rates, and shift species abundance and distribution patterns, as has been speculated for lacustrine systems (Wauthy et al., 2018; O'Donnell et al., 2020). Our study illustrates the importance of terrestrial organic matter to the function of coastal Arctic ecosystems, which may in turn affect the sustainability of cultural and artisanal fisheries.

The importance of primary producers to Cape Krusenstern National Monument food webs was not uniform across the system, but rather varied as a function of consumer: 1) foraging ecology and 2) foraging location (proximity to Kotzebue Sound and major river inputs). For example, suspension feeders received most of their carbon from food webs based on phytoplankton (49 ± 11%) and terrestrial organic matter (23 ± 5%) (Fig. 6). Harris et al. (2018) recorded large amounts of terrestrial organic carbon in suspension/filter feeders in the Beaufort Sea lagoons and hypothesized that members of this feeding group may be assimilating terrestrial organic carbon indirectly by feeding on phytoplankton that are using terrestrially-derived dissolved organic matter after remineralization by microbes. Herbivores and detritivores, unsurprisingly, received the majority of their carbon from phytobenthos-based food webs, 58 ± 10% and 60 ± 8%, respectively. Omnivores and predators showed more even distributions of resource reliance among the three primary producer food webs but also substantially higher variance in end member reliance among species within these feeding guilds. This pattern has been observed in other Arctic (Pedro et al., 2020), temperate (Udy et al., 2019), and tropical (McMahon et al., 2016) systems.

Interestingly, as invertebrate trophic position increased, so did their reliance on a phytobenthos-based food web, with a concomitant decrease in reliance on terrestrial organic matter (Fig. 5). Fishes received more of their carbon from a terrestrial organic matter-based food web (45 ± 22%) than any other carbon source while birds (53 ± 5%) and marine mammals (75 ± 8%) relied predominantly on phytobenthos as the dominant carbon source. This may suggest that fishes relied on food web pathways routed through different invertebrate communities than birds and mammals. Invertebrate groups that showed

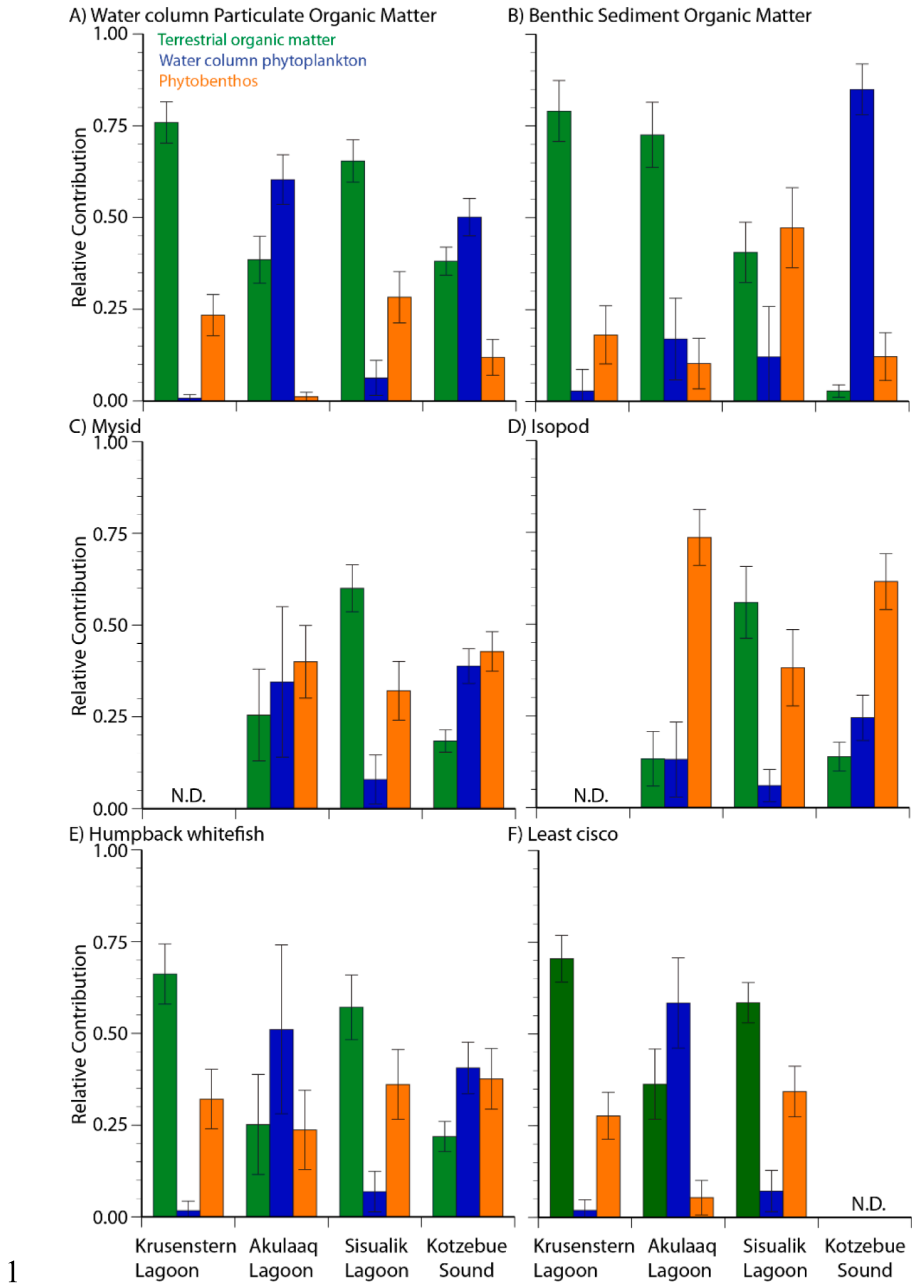

Fig. 7. End member contributions by location and species: Comparisons across sites of mean (±SD) relative contribution of primary producer end members - terrestrial organic matter (TOM - green), water column phytoplankton (blue), and phytobenthos (orange) - to A) water column particulate organic matter, B) benthic sediment organic matter, C) Mysids, D) Isopods, E) Humpback whitefish, and F) Least cisco found in at least three of the locations sampled. All consumers were adults. N.D. indicates no data available. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

strong dependence (>50%) on terrestrial organic matter, such as mysids, chironomids, and select amphipods in the lagoon-Sound system and more northern Arctic lagoon systems (Dunton et al., 2012), are often very abundant in coastal Arctic lagoons and nearshore waters and can be important food sources for upper trophic level macroconsumers, including birds and anadromous fishes (Truett, 1984; O'Donnell et al., 2020). The reliance of fishes in the lagoon-sound system on terrestrial organic matter mirrors a similar dependence in more northern Beaufort Sea coastal systems (Brewster et al., 2018; Harris et al., 2018) as well as more inland rivers of the Cape Krusenstern National Monument (O'Donnell et al., 2020). Conversely, deposit feeding polychaetes, isopods, red king crabs, and select amphipods relied heavily (>50% carbon contribution) on phytobenthos in select lagoons and the Sound and may serve as vectors of organic matter to birds and marine mammals in this system. This signal likely reflects contributions from both benthic macro- and microalgae as well as recently deposited sea ice algae, both of which have similar isotope values. Numerous studies using isotopes and essential fatty acid biomarkers have documented the important role that ice algae play in the nutritional condition of deposit feeding benthic organisms (Schollmeier et al., 2018; Koch et al., 2020).

In addition to foraging ecology, consumer foraging location also played an important role in determining the primary production fueling macroconsumers. For example, while phytoplankton was an important component of POM (50 ± 5%)/SOM (85 ± 7%) in Kotzebue Sound, as hypothesized, surprisingly, phytobenthos (52 ± 22%) was the largest contributor to the food web supporting macroconsumers in the Sound. Benthic sources of primary production are important contributors to coastal food webs in the Arctic (Renaud et al., 2015; Harris et al., 2018) and at lower latitudes (Newell et al., 1995; Rigolet et al., 2014). Despite low water visibility due to runoff and resuspension, Kotzebue Sound is shallow enough to support benthic micro- and macroalgae., Some of the "phytobenthos" isotope signal in Kotzebue Sound consumers, however, may reflect consumption, directly or indirectly, of ice algae, which has a similar carbon and nitrogen isotope value to seagrass, and macro- and

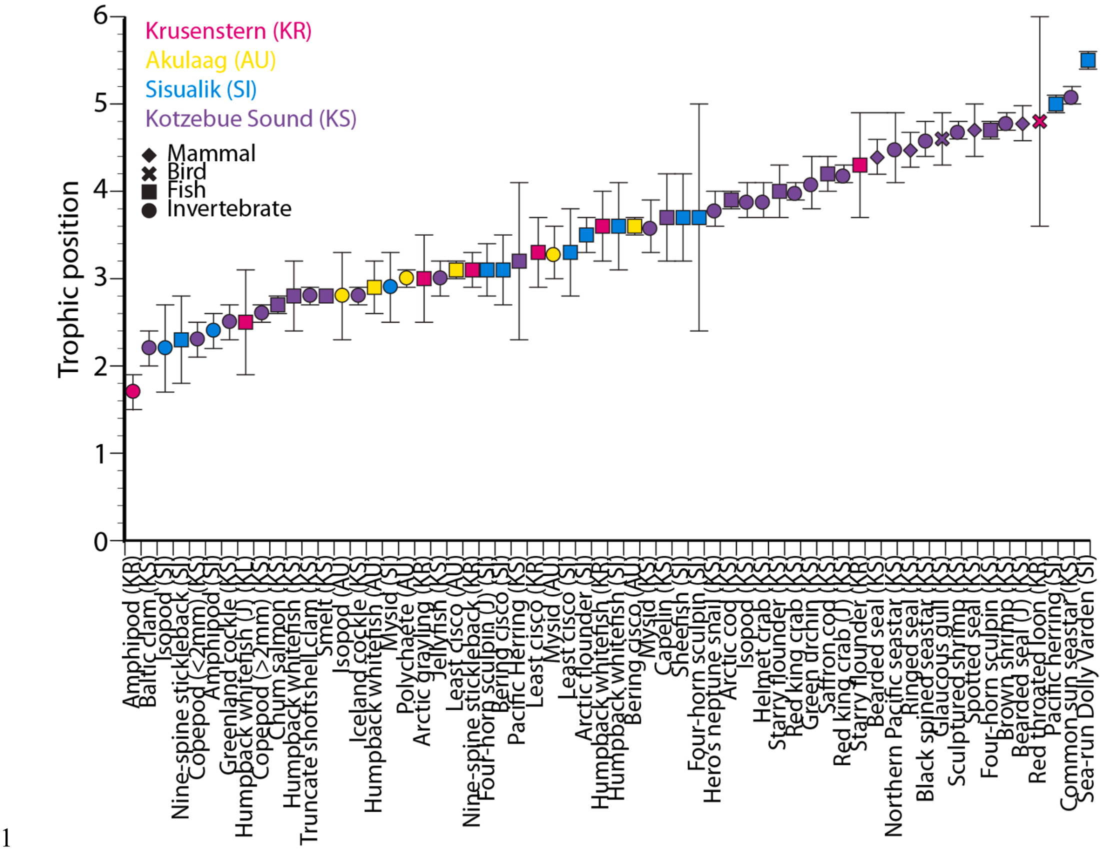

Fig. 8. Macroconsumer trophic positions: Trophic positions (Posterior Mode ± SD) of invertebrates (circles), fishes (squares), birds (crosses), and mammals (diamonds) from Krusenstern Lagoon (magenta), Akulaaq Lagoon (yellow), Sisualik Lagoon (cyan), and Kotzebue Sound (purple) in Cape Krusenstern National Monument, Alaska. All consumers were adults unless indicated as juvenile (J). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

microalgae in this system. This may explain why several suspension feeding bivalves in Kotzebue Sound showed high contributions of phytobenthos, e.g., Greenland cockle (*Serripes groenlandicus*) 50 ± 6% and Iceland cockle (*Clinocardium ciliatum*) 38 ± 8%. Ice algae sinks rapidly during the spring thaw (Sun et al., 2007; Boetius et al., 2013; Koch et al., 2020), providing an important lipid-rich (high quality) early season food source for many benthic suspension feeders (McMahon et al., 2006; Mäkelä et al., 2017; Koch et al., 2020) and the upper trophic level predators they support (e.g., Szpak et al., 2018), such as the bearded seals (*Erignathus barbatus*) in this study that showed phytobenthos contribution = 85 ± 7% for juveniles and 77 ± 7% for adults. In fact, the seasonal influx of ice algae to the sea floor has been shown to initiate substantial benthic biological production owing to the high total concentrations of essential fatty acids (C20:5(n-3), 18:2(n-6) and C22:6 (n3)) in ice algae (Arrigo & Thomas 2004; Morata et al., 2011). The stable isotope signals of this massive foraging effort on ice algae are evident in a wide range of benthic consumers (McMahon et al., 2006; Schollmeier et al., 2018; Koch et al., 2020). Alternatively, the phytobenthos isotope signal in suspension feeding bivalves could reflect feeding on resuspended benthic algal production but the POM isotope values in Kotzebue Sound do not support this alternative hypothesis.

As we hypothesized, terrestrial organic matter was the most important contributor to POM (76 ± 6%)/SOM (79 ± 8%) as well as macroconsumers (60 ± 17%) in Krusenstern, the lagoon that is the most isolated from Kotzebue Sound. These data suggest strong terrestrial-lagoon and pelagic benthic coupling that aligns well with the lagoon location and depth. Yet, terrestrial organic matter was almost equally important to POM (65 ± 6%)/SOM (41 ± 8%) and macroconsumers (60 ± 5%) in Sisualik, the lagoon that is always open to Kotzebue Sound (Fig. 4). Though not what we hypothesized, the large contribution of terrestrial organic matter in Sisualik Lagoon is likely a function of the lagoon's proximity to the mouths of the Noatak and Kobuk rivers (Fig. 1) causing large seasonal inputs of terrestrial organic matter to overwhelm local marine production signals. Similarly, Schell (1983) and Schell et al. (1984) also found that macroconsumers relied heavily on terrestrial organic matter in Northern Alaskan nearshore ecosystems, particularly in spring when erosion and fluvial transport of terrestrial organic matter can equal the magnitude of *in situ* primary production within 10 km of shore.

With its intermittent connectivity to Kotzebue Sound, Akulaaq Lagoon showed more evenly distributed reliance on the three primary producer end members as we hypothesized. Surprisingly, despite its shallow depth, Akulaaq Lagoon showed the strongest divergence in dominant carbon source to POM (phytoplankton 60 ± 7%) and SOM (terrestrial organic matter 73 ± 9%), suggesting lower pelagic-benthic coupling than at the other locations in this system where POM and SOM exhibited similar contribution patterns. Tight pelagic-benthic coupling is typically a hallmark of Arctic marine ecosystems (Grebmeier et al., 1988; Ambrose and Renaud, 1995; McMahon et al., 2006; Stasko et al., 2018). This divergence may reflect a recent breaching of Akulaaq Lagoon by Kotzebue Sound water, corroborated by the lagoon's relatively higher salinity compared to the other lagoons, that likely brought in fresh phytoplankton in the water column (POM record) despite sediment records reflecting terrestrial organic matter input.

Our interpretation of the differences in the relative contributions of the end members to the food webs may be confounded by species distribution patterns among the different locations. Relatively few taxa occurred in all four locations in our study and given low sample sizes of select individuals, we have tried to focus on larger scale patterns of resource utilization. Nevertheless, where inter-location comparisons were possible (Fig. 7), they generally support the overall trends discussed previously. Isopods, which can both be surface detritivores and carnivores, showed dietary plasticity that followed location-based trends. In the intermittently open Akulaaq Lagoon, isopods (TP 2.8 ± 0.5) relied primarily on a phytobenthos food chain (74 ± 8%), whereas isopods from the open Sisualik Lagoon (TP 2.2 ± 0.5) relied on terrestrial organic matter (56 ± 10%), mirroring the dominant carbon source of both POM and SOM. Interestingly, isopods from Kotzebue Sound appear to be quite carnivorous (TP 3.9 ± 0.2) and occupied a phytobenthos-based food web like many other macroconsumers in the Sound. Mysids also relied heavily on terrestrial organic matter (60 ± 6%) in Sisualik, which is similar to their diet in lagoons in the Eastern Alaska Beaufort Sea (Harris et al., 2018), but a mixture of phytobenthos (43 ± 5%) and phytoplankton (39 ± 5%) in Kotzebue Sound as hypothesized. Higher in the food web, humpback whitefish (*Coregonus pidschian*) and least cisco (*C. sardinella*) relied heavily on terrestrial organic matter-based food webs in Krusenstern and Sisualik Lagoons, but more heavily on phytoplankton-based food webs in Akulaaq, reflecting the lagoon's POM composition. Similar spatial variation in carbon source patterns as a function of location within an estuary have been observed in Kushida Estuary, Japan, where Kasai and Nakata (2005) found that the infaunal suspension-feeding bivalve corbicula (*Corbicula japonica*) relied heavily on terrestrial POM (>90%) in the uppermost reach of the estuary and shifted to a predominantly marine phytoplankton-based diet (>70%) closer to the mouth of the estuary.

The diverse primary producer carbon sources in this lagoon-sound system supported characteristically long Arctic food chains (Fig. 8). We calculated individual consumer trophic positions using a two-source, two-isotope Bayesian mixing model with local δ^{13}C and δ^{15}N values of POM and SOM as pelagic and benthic baseline end members, which fell along predictable mixing lines between terrestrial organic matter, phytoplankton, and phytobenthos. Given challenges of properly characterizing the specific isotope baselines for each species (Post, 2002a) and the sometimes-small sample sizes of certain species, however, we chose to focus on the overall patterns of trophic dynamics rather than the exact trophic positions of individual species. In the lagoon-Sound system, macroconsumers fell along a continuum of trophic positions, from amphipods, isopods, and bivalves (TP 2 to 3) to sea-run Dolly Varden, seastars, seabirds, and seals at the top of the food chain (TP 4.5 to 5.5). Trophic positions of top predators >5 make the food chain length in this system longer than the global average of 4.0 (Vander Zanden and Fetzer, 2007). These long food chains, characteristic of coastal Arctic systems (Hobson and Welch, 1992; Hobson et al., 1995; McMeans et al., 2013), play important roles in mediating the flow of organic matter from benthic, pelagic, and terrestrial primary producers through the food web, modulating biogeochemical cycling, and influencing the distribution and abundance of upper trophic level consumers, like fish and marine mammals, that humans eat (Post, 2002b; Renaud et al., 2011; Sokolowski et al., 2012).

There were some surprises amongst the estimated trophic positions in this system. For example, the trophic position of Pacific herring, *Clupeas pallasii* (5.0 ± 0.1 in Sisualik Lagoon) was higher than expected for a species that typically forages on large crustaceans and small fishes, as was the trophic position of the putative herbivore green urchin, *Strongylocentrotus droebachiensis* (4.1 ± 0.3 in Kotzebue Sound), while the trophic position of the invertivore nine-spine stickleback, *Pungitius pungitius*, (2.3 ± 0.5 in Sisualik Lagoon) was anomalously low. These discrepancies may have some ecological underpinnings, but they may also reflect issues with proper characterization of individual isotope baselines. While the broad trophic dynamics patterns are clear, these fine scale comparisons would benefit from future work using δ^{15}N analysis of individual amino acids to provide better resolved trophic position estimates that are internally indexed to $\delta^{15}\mathrm{N}_{\mathrm{baseline}}$ (reviewed in McMahon and McCarthy, 2016).

Our study was not a comprehensive survey of the many hundreds of species in the system and additional collections of potential prey species are needed to better constrain full carbon flow pathways through the food web. Future work to elucidate fine scale differences in carbon flow pathways and trophic dynamics of macroconsumers in coastal Arctic waters would benefit greatly from compound-specific SIA. For instance, refined trophic position estimates from amino acid δ^{15}N analysis could be coupled with amino acid isotope fingerprinting techniques, which use essential amino acid δ^{13}C values that show minimal trophic fractionation (McMahon et al., 2010) to record unique primary producer isotope "fingerprints" in upper trophic level consumers (Larsen et al., 2009). This molecular geochemistry approach may add greater resolution to the sources of primary production supporting food webs in these coastal Arctic systems (e.g., Rowe et al., 2019).

Arctic coastal waters are often characterized by low productivity (e.g., Grebmeier et al., 1988), yet they support relatively high zooplankton and epibenthic crustacean abundances, particularly in early summer (Craig and Haldorson, 1981; Johnson and Richardson, 1981). This paradox led Craig et al. (1984) to argue that advection of allochthonous phytoplankton and invertebrates into the lagoons must occur to account for the primary and secondary macroconsumer production. While we document significant plasticity in source end member use among macroconsumers in our system that varied across taxa, feeding guilds, and lagoon location relative to marine and riverine sources, terrestrial organic matter was often one of the most important carbon sources fueling coastal Arctic Alaskan food webs. It is important to keep in mind that our data were collected in 2002–2006. The past two decades witnessed an increase in Arctic river discharge (Bring et al., 2017), accelerated rate of permafrost warming (Biskaborn et al., 2019) and lake drainage (Nitze et al., 2020), and in some areas increased coastal erosion (Jones et al., 2018), processes that will contribute more terrestrial carbon to coastal systems. Our data set creates a prime opportunity for a future study to test this hypothesis that the importance of terrestrial carbon to Arctic nearshore foods webs is likely even higher now than reflected in the consumers of this study 15 years ago. While the dietary plasticity of many of the members of these food webs and the different pathways for carbon to move through the food webs suggests resilience, the projected changes in production of terrestrial organic matter, phytoplankton, and phytobenthos in light of impending shifts in climate and human activities will likely have an impact on the resource utilization pathways of coastal Arctic food webs.

Author statement

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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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2021.107388.

References

Allen, P.W., Weedfall, R.O., 1966. Weather and climate. In: Wilimovsky, N.J., Wolfe, J.N. (Eds.), Environment of the Cape Thompson Region, Alaska. United States Atomic Energy Commission, Division of Technical Information, PNE-481, p. 1250. Washington, D.C.

Ambrose Jr., W.G., Renaud, P.E., 1995. Benthic response to water column productivity patterns: evidence for benthic-pelagic coupling in the Northeast Water polynya. J. Geophys. Res. 100, 4411–4421.

Bell, L.E., Bluhm, B.A., Iken, K., 2016. Influence of terrestrial organic matter in marine food webs of the Beaufort Sea shelf and slope. Mar. Ecol. Prog. Ser. 550, 1–24.

Benner, R., Benitz-Nelson, B., Kaiser, K., Amon, R.M.W., 2004. Export of young terrigenous dissolved organic carbon from rivers to the Arctic Ocean. Geophys. Res. Lett. 31, L05305. https://doi.org/10.1029/2003GLO19251.

Biskaborn, B., Smith, S., Noetzli, J., 45 other authors. 2019. Permafrost is warming at a global scale. Nat. Commun. 10, 264. doi: 10.1038/s41467-018-08240-4.

Blaylock, W.M., Houghton, J.P., 1983a. Benthic Investigations. Dames and Moore, Los Angeles, CA.

Blaylock, W.M., Houghton, J.P., 1983b. Lagoon Investigations. Dames and Moore, Los Angeles, CA.

Boecklen, W.J., Yarnes, C.T., Cook, B.A., James, A.C., 2011. On the use of stable isotopes in trophic ecology. Ann. Rev. Mar. Sci. 42, 411–440.

Boetius, A., Albrecht, S., Bakker, K., Bienhold, C., Felden, J., Fernández-Méndez, M., Hendricks, S., Katlein, C., Lalande, C., Krumpen, T., Nicolaus, M., 2013. Export of algal biomass from the melting Arctic sea ice. Science 339 (6126), 1430–1432.

Brewster, J.D., Giraldo, C., Choy, E.S., MacPhee, S.A., Hoover, C., Lynn, B., McNicholl, D. G., Majewski, A., Rosenberg, B., Power, M., Reist, J.D., 2018. A comparison of the trophic ecology of Beaufort Sea Gadidae using fatty acids and stable isotopes. Polar Biol. 41, 149–162.

Bring, A., Shiklomanov, A., Lammers, R.B., 2017. Pan-Arctic river discharge: prioritizing monitoring of future climate change hot spots. Earth's Fut. 5, 72–92. https://doi.org/10.1002/2016EF000434.

Brookes, J.D., Aldridge, K., Wallace, T., Linden, L., Ganf, G.C., 2005. Multiple interception pathways for resource utilization and increased ecosystem resilience. Hydrobiologia 552, 135–146.

Careddu, G., Costantini, M.L., Calizza, E., Carlino, P., Bentivoglio, F., Orlandi, L., Rossi, L., 2015. Effects of terrestrial input on microbenthic food webs of coastal sea are detected by stable isotope analysis in Gaeta Gulf. Estuar. Coast Shelf Sci. 154, 158–168.

Cloren, J.E., Canuel, E.A., Harris, D., 2001. Stable carbon and nitrogen isotope composition of aquatic and terrestrial plants of San Francisco Bay estuarine system. Limnol. Oceanogr. 47, 713–729.

Connolly, C.T., Cardenas, M.B., Burkart, G.A., Spencer, R.G., McClelland, J.W., 2020. Groundwater as a major source of dissolved organic matter to Arctic coastal waters. Nat. Commun. 11, 1–8.

Craig, P.C., Griffiths, W.B., Johnson, S.R., Schell, D.M., 1984. Trophic dynamics in an arctic lagoon. In: Barnes, P.W., Schell, D.M., Reimnitz, E. (Eds.), The Alaskan Beaufort Sea: Ecosystems and Environments. Academic Press, New York, NY, pp. 347–380.

Craig, P.C., Haldorson, L., 1981. Beaufort Sea barrier island-lagoon ecological process studies: Fish. In: US Department Commerce NOAA, OCSEAP Final Rep, 7, pp. 384–678.

Darnaude, A.M., 2005. Fish ecology and terrestrial carbon use in coastal areas: implications for marine fish production. J. Anim. Ecol. 74, 864–876.

DeAngelis, D.L., 1980. Energy flow, nutrient cycling, and ecosystem resilience. Ecology 61, 764–771.

Deb, D., 1997. Trophic uncertainty vs. parsimony in food web research. Oikos 78, 191–194.

DeNiro, M.J., Epstein, S., 1978. Influence of diet on distribution of carbon isotopes in animals. Geochem. Cosmochim. Acta 42, 495–506.

DeNiro, M.J., Epstein, S., 1981. Influence of diet on the distribution of nitrogen isotopes in animals. Geochem. Cosmochim. Acta 4, 341–351.

Derocher, A.E., Wiig, Ø., Bangjord, G., 2000. Predation of Svalbard reindeer by polar bears. Polar Biol. 23, 675–678.

Dunton, K.H., Schell, D.M., 1987. Dependence of consumers on macroalgal (*Laminaria solidungula*) carbon in an arctic kelp bed. Mar. Biol. 93, 615–625.

Dunton, K.H., Schonberg, S.V., Cooper, L.W., 2012. Food web structure of the Alaskan nearshore shelf and estuarine lagoons of the Beaufort Sea. Estuar. Coast 35, 416–435.

Dunton, K.H., Weingartner, T., Carmack, E.C., 2006. The nearshore western Beaufort Sea ecosystem: circulation and importance of terrestrial carbon in arctic coastal food webs. Prog. Oceanogr. 71, 362–378.

Elton, C.S., 1927. Animal Ecology. Sidgewick and Jackson, London, U.K., p. 207

Fritz, M., Vonk, J.E., Lantuit, H., 2017. Collapsing arctic coastlines. Nat. Clim. Change 7, 6–7.

Georgette, S., Loon, H., 1993. Subsistence Use of Fish and Wildlife in Kotzebue: A Northwest Alaska Regional Center (Paper 167). Alaska Department of Fish and Game, Juneau.

Georgette, S., Shiedt, A., 2005. Whitefish: Traditional Ecological Knowledge and Subsistence Fishing in the Kotzebue Sound Region. Alaska Department of Fish and Game, Division of Subsistence, Alaska. No. 290.

Global Runoff Data Centre. 56068 koblenz, Germany. https://www.bafg.de/GRDC/EN/02_srvcs/21_tmsrs/210_prtl/prtl_node.html. (Accessed 30 December 2020).

Glud, R.N., Kühl, M., Wenzhöfer, F., Rysgaard, S., 2009. Benthic diatoms of a high Arctic fjord (Young Sound, NE Greenland): importance for ecosystem primary production. Mar. Ecol. Prog. Ser. 238, 15–29.

Gradinger, R., 2009. Sea-ice algae: major contributors to primary production and algal biomass in the Chukchi and Beaufort seas during may/june 2002. In: Deep sea research Part II: Topical Studies in Oceanography, 56, pp. 1201–1212, 17.

Grebmeier, J.M., McRoy, C.P., Feder, H.M., 1988. Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas. I. Food supply source and benthic biomass. Mar. Ecol. Prog. Ser. 48, 57–67.

Greene, C.H., Pershing, A.J., Cronin, T.M., Ceci, N., 2008. Arctic climate change and its impacts on the ecology of the North Atlantic. Ecology 89, S24–S38.

Guo, L., Ping, C.-L., Macdonald, R.W., 2007. Mobilization pathways of organic matter from permafrost to Arctic rivers in a changing climate. Geophys. Res. Lett. 34, L13603. https://doi.org/10.1029/2007GL030689.

Harris, D., Horwath, W.R., van Kessel, C., 2001. Acid fumigation of soils to remove carbonates prior to total organic carbon or carbon-13 isotopic analysis. Soil Sci. Soc. Am. J. 65, 1853–1856.

Harris, C.M., McTigue, N.D., McClelland, J.W., Dunton, K.H., 2018. Do Arctic coastal food webs rely on a terrestrial carbon subsidy? Food Webs 15, e00081. https://doi.org/10.1016/j.fooweb.2018.e00081.

Hobbie, J.E., Shaver, G.R., Rastetter, E.B., Cherry, J.E., Goetz, S.J., Guay, K.C., Gould, W. A., Kling, G.W., 2017. Ecosystem responses to climate change at a low Arctic and a high Arctic long-term research site. Ambio 46, S160–S173.

Hobson, K.A., Ambrose Jr., W.G., Renaud, P.E., 1995. Sources of primary production benthic-pelagic coupling, and trophic relationships within the Northeast Water Polynya: insights from $\delta^{13}C$ and $\delta^{15}N$ analysis. Mar. Ecol. Prog. Ser. 128, 1–10.

Hobson, K.A., Welch, H.E., 1992. Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}C$ and $\delta^{15}N$ analysis. Mar. Ecol. Prog. Ser. 84, 9–18.

Hoffman, J.C., Bronk, D.A., Olney, J.E., 2008. Organic matter sources supporting lower food web production in the tidal freshwater portion of the York River estuary, Virginia. Estuar. Coast 31, 898–911.

Jewett, S.C., Clough, L.M., Blanchard, A.L., Ambrose Jr., W.G., Feder, H.M., Hoberg, M. K., Whiting, A.V., 2009. Nearshore macrobenthos of northern Kotzebue Sound, Alaska, with reference to local sewage disposal. Polar Biol. 32, 1665–1680. https://doi.org/10.1007/s00300-009-0667-5.

Johnson, S.R., Richardson, W.J., 1981. Beaufort Sea barrier island-lagoon ecological process studies: Birds. In: US Department Commerce NOAA, OCSEAP Final Report, 7, pp. 109–383.

Jones, B.M., Farquharson, L.M., Baughman, C.A., 2018. A decade of remotely sensed observations highlight complex processes linked to coastal permafrost bluff erosion in the Arctic. Environ. Res. Lett. 13, 115001. https://doi.org/10.1088/1748-9326/aae471, 23 other authors.

Kasai, A., Nakata, A., 2005. Utilization of terrestrial organic matter by the bivalve *Corbicula japonica* estimated from stable isotope analysis. Fish. Sci. 71, 151–158.

Koch, C.W., Cooper, L.W., Lalande, C., Brown, T.A., Frey, K.E., Grebmeier, J.M., 2020. Seasonal and latitudinal variations in sea ice algae deposition in the Northern Bering and Chukchi Seas determined by algal biomarkers. PloS One 15 (4), e0231178.

Kühl, M., Glud, R., Bourm, J., Roberts, R., Rysgaard, S., 2001. Photosynthetic performance of surface-associated algae below sea ice as measured with a pulse-amplitude-modulated (PAM) fluorometer and O_2 microsensors. Mar. Ecol. Prog. Ser. 223, 1–14.

Larsen, T., Taylor, D.L., Leigh, M.B., O'Brien, D.M., 2009. Stable isotope fingerprinting: a novel method for identifying plant, fungal, or bacterial origins of amino acids. Ecology 90, 3526–3535.

Lawler, J.P., Miller, S.D., Sanzone, D.M., Ver Hoef, J., Young, S.B., 2009. Arctic Network Vital Signs Monitoring Plan. Natural Resource Report NPS/ARCN/NRR-2009/088. National Park Service, Fort Collins, CO.

Lindeman, R.L., 1942. The trophic-dynamic aspect of ecology. Ecology 23, 399–417.

Mäkelä, A., Witte, U., Archambault, P., 2017. Ice algae versus phytoplankton: resource utilization by Arctic deep sea macroinfauna revealed through isotope labelling experiments. Mar. Ecol. Prog. Ser. 572, 1–18.

Mann, K.W., Lazier, J.R.N., 2005. Dynamics of Marine Ecosystems. Wiley-Blackwell Scientific, London, U.K, p. 512.

McGovern, M., Poste, A.E., Oug, E., Renaud, P.E., Hilde, C.T., 2020. Riverine impacts on benthic biodiversity and functional traits: a comparison of two sub-Arctic fjords. Estuar. Coast Shelf Sci. 240, 106774. https://doi.org/10.1016/j.ecss.2020.106774.

McMahon, K.W., Ambrose Jr., W.G., Johnson, B.J., Sun, M.-Y., Lopez, G.R., Clough, L.M., Carroll, M.L., 2006. Benthic community response to ice algae and phytoplankton in Ny Ålesund, Svalbard. Mar. Ecol. Prog. Ser. 310, 1–14.

McMahon, K.W., Hamady, L.L., Thorrold, S.R., 2013. Ocean ecogeochemistry: a review. Oceanogr. Mar. Biol. Annu. Rev. 51, 327–374.

McMahon, K.W., Fogel, M.L., Elsdon, T., Thorrold, S.R., 2010. Carbon isotope fractionation of amino acids in fish muscle reflects biosynthesis and isotopic routing from dietary protein. J. Anim. Ecol. 79, 1132–1141.

McMahon, K.W., McCarthy, M.D., 2016. Embracing variability in amino acid δ^{15}N fractionation: mechanisms, implications, and applications for trophic ecology. Ecosphere 7, e01511. https://doi.org/10.1002/ecs2.1511.

McMahon, K.W., Thorrold, S.R., Houghton, L.A., Berumen, M.L., 2016. Tracing carbon flow through coral reef food webs using a compound-specific stable isotope approach. Oecologia 180 (3), 809–821.

McMeans, B.C., Rooney, N., Arts, M.T., Fisk, A.T., 2013. Food web structure of a coastal Arctic marine ecosystem and implications for stability. Mar. Ecol. Prog. Ser. 482, 17–28.

McTigue, N.D., Dunton, K.H., 2017. Trophodynamics of the Hanna Shoal Ecosystem (Chukchi Sea, Alaska): connecting multiple end-members to a rich food web. Deep Sea Res., Part II 144, 175–189.

Mohen, S.D., Connelly, T.L., Harris, C.M., Dunton, K.H., McClelland, J.W., 2016. Seasonal trophic linkages in Arctic marine invertebrates assessed via fatty acids and compound-specific stable isotopes. Ecosphere 7, e01429. https://doi.org/10.1002/ecs2.1429.

Morata, N., Poulin, M., Renaud, P.E., 2011. A multiple biomarker approach to tracking the fate of an ice algal bloom to the sea floor. Polar Biol. 34, 101–112.

Naidu, A.S., Cooper, L.W., Finney, B.P., Macdonald, R.W., Alexander, C., Semiletov, I.P., 2000. Organic carbon isotope ratios (δ^{13}C) of Arctic Amerasian continental shelf sediments. Int. J. Earth Sci. 89, 522–532.

Newell, R.I.E., Marshall, N., Sasekumar, A., Chong, V.C., 1995. Relative importance of benthic microalgae, phytoplankton, and mangroves as sources of nutrition for penaeid prawns and other coastal invertebrates from Malaysia. Mar. Biol. 123, 595–606.

Ng, A.K.Y., Song, D.-W., 2018. Special issue on 'Arctic shipping, transportation, and regional development'. Marit. Pol. Manag. 45, 419–421.

Nitze, I., Cooley, S.W., Duguay, C.R., Jones, B.J., Grosse, G., 2020. The catastrophic thermokarsk lake drainage events of 2018 in northwestern Alaska: fast-forward into the future. Cryosphere 14, 4279–4297.

O'Donnell, J.A., Carey, M.P., Koch, J., Zimmerman, C.E., 2020. Permafrost carbon in stream food webs of Arctic Alaska. Alaska Park Sci. 19, 76–79.

Oxtoby, L.E., Mathis, J.T., Juranek, L.W., Wooller, M.J., 2016. Estimating stable carbon isotope values of microphytobenthos in the Arctic for application to food web studies. Polar Biol. 39 (3), 473–483.

Pedro, S., Fisk, A.T., Ferguson, S.H., Hussey, N.E., Kessel, S.T., McKinney, M.A., 2020. Broad feeding niches of capelin and sand lance may overlap those of polar cod and other native fish in the eastern Canadian Arctic. Polar Biol. 43 (11), 1707–1724.

Pimm, S.L., 2002. Food Webs. Univ. of Chicago Press, Chicago, IL, p. 258.

Plummer, M., 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In: Proceedings of the 3rd International Workshop on Distributed Statistical Computing, vol. 124, pp. 1–10.

Post, D.M., 2002a. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83, 703–718. https://doi.org/10.1890/0012.

Post, D.M., 2002b. The long and short of food-chain length. Trends Ecol. Evol. 17, 269–277.

Quezada-Romegialli, C., Jackson, A.L., Hayden, B., Kahilainen, K.K., Lopes, C., Harrod, C., 2018. tRophicPosition, an R package for the Bayesian estimation of trophic position from consumer stable isotope ratios. Methods Ecol. Evol. 9, 1592–1599.

Renaud, P.E., Løken, T.S., Jørgensen, L.L., Berge, J., Johnson, B.J., 2015. Macroalgae detritus and food-web subsidies along an Arctic fjord depth-gradient. Front. Mar. Sci. 2, 31. https://doi.org/10.3389/fmars.2015.00031.

Renaud, P.E., Tessmann, M., Evenset, A., Christensen, G.N., 2011. Benthic food-web structure of an arctic fjord (kongsfjorden, svalbard). Mar. Biol. Res. 7 (1), 13–26.

Reynolds, M.J., 2012. Arctic Coastal Lagoons of Cape Krusenstern National Monument: Subsistence, Ecosystem Characterization, and Management. Ph.D. thesis, East Carolina University. Retrieved from the Scholarship. http://hdl.handle.net/10342/3996.

Rigolet, C., Thiébaut, É., Dubois, S.F., 2014. Food web structures of subtidal benthic muddy habitats: evidence of microphytobenthos contribution supported by an engineer species. Mar. Ecol. Prog. Ser. 500, 25–41. https://doi.org/10.3354/meps10685.

Romanuk, T.N., Levings, C.D., 2005. Stable isotope analysis of trophic position and terrestrial vs. marine carbon sources for juvenile Pacific salmonids in nearshore habitats. Fish. Manag. Ecol. 12, 113–121.

Rowe, A.G., Iken, K., Blanchard, A.L., O'Brien, D.M., Døving Osvik, R., Uradnikova, M., Wooller, M.J., 2019. Sources of primary production to Arctic bivalves identified using amino acid stable carbon isotope fingerprinting. Isot. Environ. Health Stud. 55, 366–384.

Schell, D.M., 1983. Carbon-13 and carbon-14 abundances in Alaskan aquatic organisms: delayed production from peat in arctic food webs. Science 219, 1068–1071.

Schell, D.M., Ziemann, P.J., Parrish, D.M., Dunton, K.H., Brown, E.J., 1984. Food web and nutrient dynamics in nearshore Alaska Beaufort Sea waters. In: US Department of Commerce, NOAA, OCSEAP Final Report, 25, pp. 327–499.

Schollmeier, T., Oliveira, A.C.M., Wooller, M.J., Iken, K., 2018. Tracing sea ice algae into various benthic feeding types on the Chukchi Sea shelf. Polar Biol. 41 (2), 207–224.

Sipler, R., Kellogg, C.T.E., Connelly, T.L., Roberts, Q.N., Yager, P.L., Bronk, D.A., 2017. Microbial community response to terrestrial derived dissolved organic matter in the coastal Arctic. Front. Microbiol. 8, 1018. https://doi.org/10.3389/fmicb.2017.01018.

Sokołowski, A., Wołowicz, M., Asmus, H., Asmus, R., Carlier, A., Gasiunaité, Z., Grémare, A., Hummel, H., Lesutiené, J., Razinkovas, A., Renaud, P.E., Richard, P., Kędra, M., 2012. Is benthic food web structure related to diversity of marine macrobenthic communities? Estuar. Coast Shelf Sci. 108, 76–86.

Stasko, A.D., Bluhm, B.A., Michel, C., Archambault, P., Majewski, A., Reist, J.D., Swanson, H., Power, M., 2018. Benthic-Pelagic trophic coupling in an Arctic marine food web along vertical water mass and organic gradients. Mar. Ecol. Prog. Ser. 594, 1–19.

Stock, B.C., Jackson, A.L., Ward, E.J., Parnell, A.C., Phillips, D.L., Semmens, B.X., 2018. Analyzing mixing systems using a new generation of Bayesian tracer mixing models. PeerJ 6, e5096. https://doi.org/10.7717/peerj.5096.

Sun, M.Y., Carroll, M.L., Ambrose, W.G., Clough, L.M., Zou, L., Lopez, G.R., 2007. Rapid consumption of phytoplankton and ice algae by Arctic soft-sediment benthic communities: evidence using natural and 13C-labeled food materials. J. Mar. Res. 65 (4), 561–588.

Szpak, P., Buckley, M., Darwent, C.M., Richards, M.P., 2018. Long-term ecological changes in marine mammals driven by recent warming in northwestern Alaska. Global Change Biol. 24 (1), 490–503.

Tamelander, T., Renaud, P.E., Hop, H., Carroll, M.L., Ambrose Jr., W.G., Hobson, K.A., 2006. Trophic relationships and pelagic–benthic coupling during summer in the Barents Sea Marginal Ice Zone, revealed by stable carbon and nitrogen isotope measurements. Mar. Ecol. Prog. Ser. 310, 33–46.

Tank, S.E., Lesack, L.F.W., Gareis, J.A.L., Osburn, C.L., Hesslein, R.H., 2010. Multiple tracers demonstrate distinct sources of dissolved organic matter to lakes of the Mackenzie Delta, western Canadian Arctic. Limnol. Oceanogr. 56, 1297–1309.

Tibbles, M., Robards, M.D., 2018. Critical trophic links in southern Chukchi Sea lagoons. Food Webs 15, e00099. https://doi.org/10.1016/j.fooweb.2018.e00099.

Tremblay, J.É., Robert, D., Varela, D.E., Lovejoy, C., Darnis, G., Nelson, R.J., Sastri, A.R., 2012. Current state and trends in Canadian Arctic marine ecosystems: I. Primary production. Climatic Change 115, 161–178.

Truett, J.C., 1984. Environmental characterization and biological use of lagoons in the eastern Beaufort Sea. In: US Department of Commerce, NOAA, OCSEAP Final Report, 24, pp. 129–579.

Udy, J.A., Wing, S.R., Connell-Milne, S.O., Durante, L.M., McMullin, R.M., Kolodzey, S., Frew, R.D., 2019. Regional differences in supply of organic matter from kelp forests drive trophodynamics of temperate reef fish. Mar. Ecol. Prog. Ser. 621, 19–32.

Uhl, W.R., Uhl, C.K., 1977. Tagiumsinaaqmiit, Ocean Beach Dwellers of the Cape Krusenstern Area: Subsistence Patterns. Anthropology and Historic Preservation, Cooperative Park Studies Unit. University of Alaska, Fairbanks, Alaska. Occasional Paper No. 14.

Vander Zanden, J., Fetzer, W.W., 2007. Global patterns of aquatic food web length. Oikos 116, 1378–1388.

Wang, S.W., Budge, S.M., Gradinger, R.R., Iken, K., Wooller, M.J., 2014. Fatty acid and stable isotope characteristics of sea ice and pelagic particulate organic matter in the Bering Sea: tools for estimating sea ice algal contribution to Arctic food web production. Oecologia 174, 699–712.

Wassmann, P., Durate, C.M., Agusti, S., Sjer, M.K., 2011. Footprints of climate change in the Arctic marine ecosystem. Global Change Biol. 17, 1235–1249.

Wauthy, M., Rautio, M., Christoffersen, K.S., Forsstöm, L., Laurion, I., Mariash, H.L., Perua, S., Vincent, W.F., 2018. Increasing dominance of terrigenous organic matter in circumpolar freshwaters due to permafrost thaw. Limnol. Oceanogr. Lett. 3, 186–198. https://doi.org/10.1002/lol2.10063.

Wetzel, R.G., 1995. Death, detritus, and energy flow in aquatic ecosystems. Freshw. Biol. 33, 83–89.

Whiting, A., Griffith, D., Jewett, S., Clough, L.M., Ambrose Jr., W.G., Johnson, J., 2011. Combining Inupiaq and Scientific Knowledge: Ecology in Northern Kotzebue Sound, Alaska. Alaska Sea Grant. University of Alaska Fairbanks, Fairbanks, AK, p. 71.

Wolfe, R.J., 2000. Subsistence in Alaska: A Year 2000 Update. Alaska Department of Fish and Game, Juneau.

Young, M., Howe, E., O'Rear, T., Berridge, K., Moyle, P., 2021. Food web fuel differs across habitats and seasons of a tidal freshwater estuary. Estuar. Coast 44, 286–301.

Zhang, K., Douglas, B.C., Leatherman, S.P., 2004. Global warming and coastal erosion. Climatic Change 64, 41–58.