Food Webs xxx (2018) e00081

Contents lists available at ScienceDirect

Food Webs

journal homepage: www.journals.elsevier.com/food-webs

Do high Arctic coastal food webs rely on a terrestrial carbon subsidy?

Carolynn M. Harris [a,*,1], Nathan D. McTigue [b], James W. McClelland [a], Kenneth H. Dunton [a]

[a] The University of Texas at Austin - Marine Science Institute, 750 Channel View Drive, Port Aransas, TX 78373, USA
[b] National Oceanographic and Atmospheric Administration, National Centers for Coastal Ocean Science, 101 Pivers Island Rd, Beaufort, NC 28516, USA

ARTICLE INFO

Article history:
Received 19 March 2018
Accepted 19 March 2018
Available online xxxx

Keywords:
Food webs
Terrestrial subsidies
Stable carbon and nitrogen isotopes
Simmr
Beaufort Sea

ABSTRACT

Lagoons are a prominent feature of Arctic coastlines, support diverse benthic food webs, and provide vital feeding grounds for fish, migratory birds, and marine mammals. Across the Arctic, loading of terrestrial/freshwater-derived organic carbon (C_T) from watershed runoff and coastal erosion is predicted to increase with global warming, and may subsidize marine organic carbon as an energy source. To assess the importance of C_T, we analyzed the trophic links and carbon assimilation pathways of twenty genera in five trophic guilds (suspension and filter feeders (Su/FF), surface and subsurface deposit feeders (Ss/De), epibenthic omnivorous invertebrates (Ep/Om), omnivorous fishes (Fish), and mammalian carnivores (Mam/Carn) as well as end-member organic matter (OM) sources. Because end-members had distinct carbon and nitrogen isotopic ratios, we employed a Bayesian stable isotope mixing model (*simmr*) to determine the contributions of C_T, shelf OM, and marine microphytobenthos, to the diets of resident fauna. Ss/De and Ep/Om mainly assimilated marine-derived OM end-members. Su/FF, Fish, and beluga whales derived large portions of their diet from C_T (>40%). We conclude that (1) coastal food webs are characterized by a high degree of omnivory and plasticity, (2) C_T is an important OM subsidy to food webs, and (3) omnivorous fish transfer C_T from lower to upper trophic levels.

© 2018 Elsevier Inc. All rights reserved.

1. Introduction

Arctic estuarine ecosystems are threatened by dramatic climate-driven changes that are occurring on land and at sea (McClelland et al., 2012). These changes include warming temperatures, thawing permafrost, increasing river discharge, and loss of shore-fast ice, which when coupled with enhanced storm activity, has resulted in greatly increased coastal erosion rates over the past 15 years (Peterson et al., 2006; Lantuit et al., 2012; Barnhart et al., 2014). In addition to erosion rates of the bordering coastline, the quantity and concentrations of organic matter (OM) in freshwater discharge from Arctic rivers control the magnitude of terrestrial carbon input to the coastal Beaufort (McClelland et al., 2012; Goñi et al., 2013). In the Alaskan Beaufort Sea, the annual load of organic carbon delivered from both fluvial transport and coastal erosion is roughly equal to the integrated marine primary production within 10 km of the coast (Schell, 1983). Because light limitation results in a short growing period for autochthonous algal sources, such as phytoplankton and benthic microalgae, Arctic nearshore ecosystems may rely on terrestrial and freshwater-derived OM inputs (collectively referred to as C_T herein) to sustain their characteristically productive and diverse food webs (Dunton et al., 2006, 2012; McClelland et al., 2012, 2014).

Coastal lagoons, which are bounded by barrier islands to the north and Alaska's Arctic slope to the south, span over 50% of the Alaskan Beaufort Sea coastline. These lagoons link marine and terrestrial ecosystems and support productive biological communities that provide valuable habitat and feeding grounds for many ecologically and culturally important species. Over 150 species of migratory birds from six continents, including waterfowl (Brown, 2006), and marine and anadromous fish (von Biela et al., 2011), rely on Arctic lagoons and nearby river deltas for summer habitat and feeding grounds (Churchwell et al., 2016). Beluga (*Delphinapterus leucas*) and bowhead whales (*Balaena mysticetus*), which are important to the subsistence and cultural heritage of communities living on the Beaufort Sea coast, forage in the open water outside of lagoons during summer months (Pedersen and Linn, 2005).

Food web studies in the coastal Beaufort Sea have shown that lagoon benthos provide a concentrated area of preferred invertebrate prey items to upper trophic consumers (i.e. Craig et al., 1982b; Dunton et al., 2006, 2012). Lagoon invertebrate communities are dominated by opportunistic omnivores and detritivores (Craig, 1984) and include bivalves, gastropods, polychaetes, ascidians, sponges and crustaceans (Dunton et al., 2012). These invertebrates employ a range of feeding modes, such as deposit-feeding, filter feeding, and omnivory, and inhabit several habitats, including living in and on benthic sediments (Dunton et al., 2006; Macdonald et al., 2010). Epibenthic organisms, in

---

[*] Corresponding author.
E-mail address: carolynn.harris@utexas.edu. (C.M. Harris).

[1] Current address: Department of Land Resources and Environmental Science, Montana State University, Bozeman, MT 59717, USA.

https://doi.org/10.1016/j.fooweb.2018.e00081
2352-2496/© 2018 Elsevier Inc. All rights reserved.

particular polychaetes, mysids, and amphipods, are important prey items for larger consumers such as fish and birds during the brief open water period (Brown et al., 2012).

Some lagoon fauna, such as mysids, amphipods, and fishes, seasonally migrate or are advected to adjacent nearshore areas outside the barrier islands and contribute to the diets of fishes and marine mammals living within the shelf domain (Dunton et al., 2006; Fechhelm et al., 2009). Dominant fish species include Arctic cod (*Boreogadus saida*), Arctic flounder (*Plueronectes glacialis*), Arctic char (*Salvelinus alpinus*), and several sculpin species (*Myoxocephalus* spp.) (Craig et al., 1982a, 1982b). Seals, toothed whales, and polar bears, as well as local subsistence hunters, consume these fishes (Kruse, 1991). Arctic cod, in particular, are one of the most abundant fishes in the Beaufort Sea and may be a key link that transfers energy from primary consumers to upper trophic levels (Bradstreet and Cross, 1982; Craig et al., 1982b; Hop and Gjøsæter, 2013).

It is important to understand what carbon/energy sources are assimilated by lagoon-dwelling biota because of expected climate-driven changes in both terrestrial inputs and marine production in the coastal Beaufort Sea. Knowledge of C_T assimilation by a variety of consumers will improve our ability to predict how nearshore food webs may be affected by climate change. Stable isotope analysis (SIA) is one method of assessing the relative contribution of isotopically distinct OM sources to an organism's diet (Hobson et al., 1995; Phillips et al., 2014). In the eastern Alaskan Beaufort Sea Coast, depleted $\delta^{13}C$ values may imply greater reliance on terrestrially-derived organic matter and/or organic matter produced within fresh waters, reflecting major inputs from the Mackenzie River in Canada as well as inputs from numerous smaller rivers along the coast (Dunton et al., 2006; Iken et al., 2010; Casper et al., 2015; Bell et al., 2016). Two other organic matter sources are present in the coastal Beaufort Sea during the open water period: marine phytoplankton and benthic microalgae, or microphytobenthos (MPB) (Glud et al., 2009). These autochthonous sources are more ^{13}C- and ^{15}N-enriched than C_T (Gradinger, 2009).

Previous work on Beaufort Sea ecosystems concluded that benthic invertebrates assimilate C_T during the open water period, as evidenced by depleted ^{13}C values (Schell, 1983; Dunton et al., 2012). It follows that C_T may be important to apex consumers like adult fishes, seals, toothed whales, and polar bears, though this transfer of C_T to upper trophic levels is inferred and has not been quantitatively explored. Previous work also showed increasingly depleted $\delta^{13}C$ values with decreasing longitude (west to east along the coast) in sediments (−21 to −27‰; Dunton et al., 2012), copepods (−20.9 to −26.7‰; Saupe et al., 1989), benthic invertebrates (−19 to −26‰ for suspension feeders, Dunton et al., 1989), and bowhead whales (−18.8 to −20.7‰ in muscle tissue, Schell et al., 1989). This eastward ^{13}C depletion is likely driven by differences in freshwater inputs and implies the importance of C_T as a basal OM/energy source may vary spatially over the Beaufort Sea.

The purpose of this study is to determine the reliance on OM end-members for twenty genera representing five distinct trophic guilds and multiple trophic levels in a high Arctic coastal ecosystem. To this end, we quantified the importance of C_T as an OM source, relative to phytoplankton and MPB, to genera within each guild using the stable isotope mixing model *simmr*. We hypothesize (1) C_T assimilation will occur within all feeding guilds but deposit feeders and omnivores would assimilate more C_T than filter feeders, and (2) C_T assimilation will vary among lagoons, where fauna inhabiting lagoons with greater freshwater inputs will assimilate more C_T.

2. Methods

2.1. Regional setting and study area

The Beaufort Sea coast experiences weak lunar tides (mean 10 cm) (NOAA, 2010) and is strongly influenced by river runoff. The mouth of the Mackenzie River, the largest river emptying into the Beaufort Sea, is 400 km east of Barter Island and discharges ~380 km^3 of freshwater annually (Macdonald et al., 2004). The Colville River, 200 km west of Barter Island, is the second largest source of freshwater input to the region (~20 $km^3\ y^{-1}$) (McClelland et al., 2014). Numerous smaller rivers and tundra streams that flow directly into the lagoons also greatly influence the physical and chemical environment, especially during the spring freshet period (McClelland et al., 2014; Harris et al., 2017). Exchange between lagoons and the nearshore environment occurs via shallow channels between barrier islands. The shallow lagoons (<4 m) are warm (11 ± 2 °C (mean ± SD)) and estuarine (21 ± 7) during the ice-free months of the summer (July to early-September), and their salinity regimes vary based on rate and magnitude of freshwater inputs (Harris et al., 2017).

Our study area included four shallow sites bounded by barrier islands (lagoon), three sites in adjacent shelf waters (nearshore), and four offshore sites (marine) in the eastern Alaskan Beaufort Sea coast, near Barter Island (Fig. 1, Table 1). Kaktovik Lagoon (KA) is almost fully enclosed and only receives freshwater inputs from small tundra streams and runoff (Dunton et al., 2012; Harris et al., 2017). Jago Lagoon (JA), a more open lagoon east of KA, is separated from KA by a peninsula and receives direct freshwater inputs from the Jago River. Angun (AN) and Nuvagapak (NU) Lagoons, located further east, are semi-enclosed, and receive inputs from smaller rivers. All nearshore sites are located outside of barrier islands within 1 km of the coast.

2.2. End-member collection

We collected suspended particulate organic matter (SPOM) for use as end-members from lagoon, nearshore, marine, and river sites during mid-August 2011–2014. We also collected benthic particulate organic matter (BPOM). Lagoon and nearshore sites were sampled every August from 2011 to 2013. The four marine sites, located 20 km offshore at 35–37 m water depth, were sampled once in 2014. Two North Slope rivers were sampled for SPOM, the Jago River (six times in 2012) and the Hulahula River (three times in 2011). The Jago River empties into JA and the Hulahula River empties into Camden Bay, located 10 km west of Kaktovik lagoon.

Subsurface water samples were collected using 4 L carboys submerged to approximately ~0.5 m depth (lagoon and river stations), 3 m (nearshore), and 10 m (marine). Water samples were sieved (180 μm) to remove zooplankton, detritus, or other large particles. Within hours of collection water samples were filtered in duplicate to collect SPOM onto pre-ashed 25 or 47 mm Whatman GF/F filters and dried at 60 °C in petri dishes. BPOM samples were collected via surface sediment syringe cores (2 cm deep) from Ekman grabs (0.023 m^2), which were repeated twice at every lagoon site. These sediments were stored in plastic vials and dried at 60 °C.

Microphytobenthos (MPB) are a potentially important food web end-member, so they were included in the stable isotope mixing model despite not being sampled directly. MPB production can equal or exceed phytoplankton production in shallow (<30 m) Arctic environments (Glud et al., 2009) and is evidenced by high sediment chlorophyll content at our lagoon and nearshore sites (Dunton and McClelland, unpublished data). MPB can possess variable stable isotope signatures depending on their growth rate and source of dissolved inorganic carbon (Oxtoby et al., 2015; Lebreton et al., 2016). To encapsulate the possible variation in stable isotope values for the Beaufort Sea lagoon MPB, we incorporated average values ($\delta^{13}C$ mean ± SD = −16.9 ± 1.2‰; $\delta^{15}N$ = 6.4 ± 1.2‰) derived from a literature survey that has been successfully applied to mixing models in the Chukchi Sea (McTigue and Dunton, 2017).

Though Oxtoby et al. (2015) estimated $\delta^{13}C$ values for three clades of microalgae that might be components of MPB in the Beaufort Sea shelf sediments using models of ^{13}C-discrimination of bottom water DIC, they did not estimate $\delta^{15}N$ and our mixing model requires both isotope values. Our estimated $\delta^{13}C$ values for lagoonal MPB, however, are

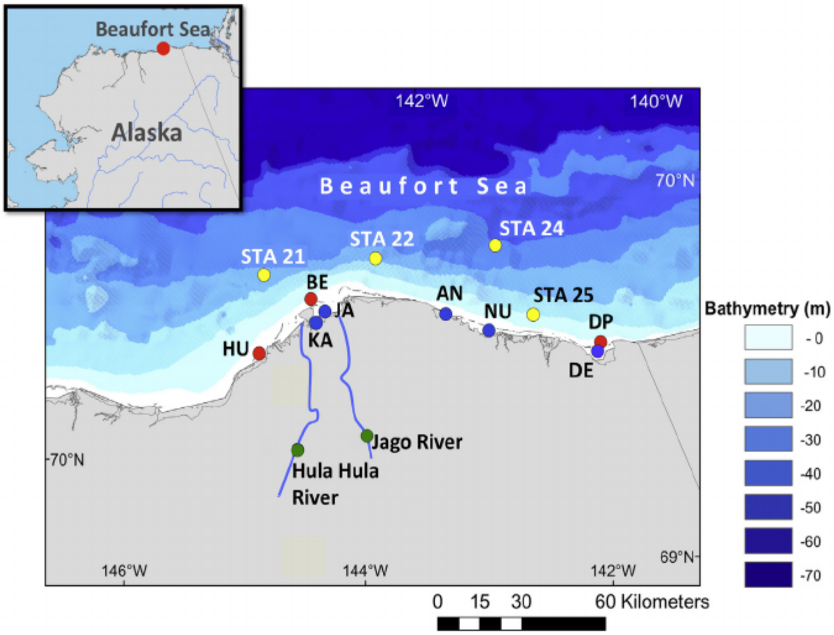


Fig. 1. Lagoon (blue symbols), nearshore (red points), marine (yellow symbols), and river (green symbol) sites along the coast of the eastern Alaskan Beaufort Sea (see Table 1 for site codes). Organic matter samples were collected from all sites and animal samples were collected from nearshore and lagoon sites. All sampling occurred during the open water period between 2011 and 2016.

slightly more ^{13}C-enriched than those estimated for the Beaufort Sea Shelf MPB, which is reasonable assuming that growth rates are higher in the lagoons where photosynthetically active radiation is higher than at shelf sediments. The large standard deviations around the pooled MPB δ^{13}C and δ^{15}N value reflect the uncertainty in this end-member value that was not directly measured.

Ice algae, comprised mainly of pennate diatoms and microflagellates, live on and in the sea ice matrix, and is another potential OM source in the nearshore regions of the Beaufort Sea (Horner and Schrader, 1982; Pineault et al., 2013). It is considered a minor source of autochthonous OM in the lagoons relative to phytoplankton and MPB, however. Though ice algae is present during the winter and spring, blooms of phytoplankton and MPB in lagoons and nearshore waters during and shortly after ice break-up make ice algae contributions proportionally negligible (Horner and Schrader, 1982). This contrasts with deeper offshore waters of the Arctic Ocean, where ice algae production can represent >50% of water column production (Legendre et al., 1992; Gradinger, 2009). It is therefore important to consider ice algae as an OM source to offshore consumers that inhabit the Beaufort Sea slope in summer months. Sea ice algae in the Beaufort is ^{13}C-enriched relative to water column POM, but has similar δ^{15}N values (Gradinger, 2009). Our δ^{13}C and δ^{15}N values for ice algae were observed in the Chukchi Sea in 2012 and have large standard deviations to reflect the uncertainty in this end-member that was not directly sampled in our study region.

2.3. Consumer collection

Benthic invertebrates that live in or on the sediments were collected via Ekman grabs (0.023 m^2) at lagoon and nearshore sites. We obtained two or three grabs per station and sieved (1 mm) the contents to remove sediment and retain invertebrates. Epibenthic invertebrates and small fishes were collected via a 1 m beam trawl (1 mm mesh size) that was towed for ~10 min at each station. Copepods were collected via a vertical plankton net tow (250 μm mesh). Organisms recovered

Table 1
Location and hydrographic and chemical data (mean ± SE (n)) from coastal sites along the Alaskan eastern Beaufort Sea in summer 2011–2014. Hydrographic parameters are means of surface (<1 m) measurements obtained in August at two-three stations in each lagoon and nearshore site. Marine sites are a single measurement obtained in August 2014. Several stations at each river site were visited in August 2011 (Hulahula River) or August 2012 (Jago River), though hydrographic and chemical data was not obtained. "–" indicates data was not collected.

Site type	Site	Site code	Latitude (°N)	Longitude (°W)	Temp (°C)	Salinity	pH	Bottom depth (m)	Years sampled
Marine	STA 21	–	70.28	−143.91	–	36 (1)	–	37	2014
	STA 22	–	70.19	−142.9	–	36 (1)	–	35	2014
	STA 24	–	70.26	−141.76	–	35 (1)	–	52	2014
	STA 25	–	69.85	−141.72	–	34 (1)	–	23	2014
Nearshore	Hulahula Delta	HU	70.07	−144.19	6.2 ± 0.7 (4)	27.7 ± 1.9 (4)	7.9 ± 0.02 (4)	4	2011, 2012
	Bernard Spit	BE	70.16	−143.58	6.4 ± 0.5 (6)	26.6 ± 1.6 (6)	8.0 ± 0.04 (6)	10	2011, 2012, 2013
	Demarcation Point	DP	69.7	−141.31	4.1 ± 1.1 (4)	23.7 ± 4.4 (4)	7.9 ± 0.03 (4)	6	2011, 2012
Lagoon	Kaktovik	KA	70.09	−143.61	11.6 ± 0.4 (9)	23.2 ± 0.8 (9)	7.9 ± 0.1 (9)	4.5	2011, 2012, 2013
	Jago	JA	70.11	−143.5	9.9 ± 0.4 (9)	23.5 ± 1 (9)	8.0 ± 0.03 (9)	4	2011, 2012, 2013
	Angun	AN	69.96	−142.49	10.3 ± 1.1 (6)	22.6 ± 2 (6)	7.9 ± 0.01 (6)	2.5	2011, 2012, 2013
	Nuvagapak	NU	69.86	−142.19	10.1 ± 0.6 (6)	11.0 ± 3.5 (6)	7.9 ± 0.1 (6)	2.5	2011, 2012
	Demarcation Bay	DE	69.66	−141.27	8.6 ± 0.5 (6)	21.0 ± 2.3 (6)	8.0 ± 0.4 (6)	4	2011, 2012, 2013
River	Hulahula River	HU-R1	69.49	−144.36	–	–	–	–	2011
		HU-R2	69.76	−144.16	–	–	–	–	2011
		HU-R3	69.98	−144.02	–	–	–	–	2011
	Jago River	JA-R	69.72	−143.6	–	–	–	–	2012

from grab, trawl, and net samples were rinsed in filtered seawater, sorted into separate vials, and stored in filtered seawater at 5 °C for later identification.

Within one day of collection, all organisms were identified to the lowest taxonomic unit possible, usually species. All organisms were sampled in triplicate when possible, and dried to a constant weight at 60 °C in aluminum dishes. Small organisms were dried whole (e.g., polychaetes, priapulids, and small crustaceans); muscle tissue was isolated from large organisms (bivalves, gastropods, large crustaceans, and fish) prior to drying. When taxa were small, multiple individuals of the same species were pooled to collect sufficient biomass for isotope analysis. All fish were handled in accordance to IACUC permit #AUP-2012-00103.

Most large animal tissue samples (mammals and fish >10 cm) were graciously donated by local Inupiat hunters and fishers or contributed by U.S. Fish and Wildlife Service biologists working within the Arctic National Wildlife Refuge. Samples were provided to us in clean sealed bags, labeled with the organism's common name, date and method of capture, and approximate location. Muscle tissue was isolated from all large animal samples prior to drying to a constant weight at 60 °C in plastic snap-cap vials.

Dried samples were transported to The University of Texas Marine Science Institute (UTMSI) in Port Aransas, TX for stable isotope preparation and analysis. Over 1200 organisms were collected, from which 250 organisms from seven phyla and twenty-four genera were selected for analysis based on their replication and distribution among sampling locations.

2.4. Trophic guild assignment

Invertebrate species were classified a priori into trophic guilds (suspension and filter feeders (Su/FF), surface and subsurface deposit feeders (Ss/De), or epibenthic omnivores (Ep/Om)) based on taxonomic data from Macdonald et al. (2010) and the World Register of Marine Species (Appeltans et al., 2012). Data for the genus was used if species-specific data was unavailable. All fishes are considered to be omnivorous (fish). Carnivorous marine mammals (Mam/Carn) are considered as a separate guild.

2.5. Stable isotope analysis (SIA)

SIA is routinely used to examine trophic structure and carbon assimilation pathways, and has been successfully applied to the Arctic marine environment (e.g. Hobson et al., 1995; Iken et al., 2005; von Biela et al., 2011; Dunton et al., 2012; Connelly et al., 2014; Bell et al., 2016; McTigue and Dunton, 2017). SIA provides a longer-term estimate (weeks to months) of diet than gut content analysis and provides information on what food sources are assimilated after ingestion. Typically, $\delta^{13}C$ values experience little enrichment (~0–1‰) with increasing trophic level and indicate the basal OM source (Fry and Sherr, 1984; McCutchan Jr et al., 2003). $\delta^{15}N$ values also provide information about basal organic matter sources, but with a ~2 to 4‰ enrichment between food source and consumer that is useful for quantifying tropic position (level).

All end-member and consumer samples were analyzed for stable C and N isotope ratios. SPOM filters were analyzed separately for C and N isotope ratios. The C filters were triple acidified with 6% sulfurous acid to remove inorganic carbon prior to analysis; the N filters were not. All BPOM and consumer samples were dried and homogenized with a mortar and pestle. For BPOM, calcifying animals, and animals from which muscle tissue was not isolated, two subsamples were analyzed. One subsample was treated with acid to remove carbonates by soaking in 1 N HCl until bubbling ceased, rinsed twice in de-ionized (DI) water, re-dried at 60 °C, and analyzed for C isotope ratios. N isotope ratios were determined from separate, non-acidified filters. All animal samples that did not require acidification were analyzed once for dual C and N isotope ratios.

Dried samples were weighed into tin capsules and analyzed for C and N content and isotopic composition on a Finnigan MAT Delta Plus continuous flow isotope ratio mass spectrometer (CF-IRMS) coupled to a Carlo Erba 1500 elemental analyzer (EA) at The University of Texas Marine Science Institute. Isotope values are expressed in delta (δ) notation:

$$\delta^{13}\mathrm{C} \quad \text{or } \delta^{15}\mathrm{N} \quad ‰ \qquad R_{\mathrm{sample}} \;\; R_{\mathrm{standard}} \; -1 \quad \mathrm{x}\ 1000$$

where R is $^{13}C/^{12}C$ (or $^{15}N/^{14}N$) and the standard reference is Vienna Pee Dee Belemnite or atmospheric nitrogen (N_2), respectively. Based on internal standards, which were run every 12th sample, instrumental analytical error was ± 0.2‰ for $\delta^{13}C$ and $\delta^{15}N$. Molar C:N ratios for samples analyzed as acidified and non-acidified subsamples were calculated using the carbon and nitrogen content in micromoles from the acidified subsample only.

All samples were collected from late-July to early-September. Therefore, although the process of assimilating carbon into an animal's tissues may take several weeks to several months (half-life for C is ~13–70 days for an Arctic amphipod; Kaufman et al., 2008, four weeks for an Arctic bivalve; McMahon et al., 2006), we assume that the isotopic composition of whole-body and muscle tissue of the animals in this study reflect their diet post-ice break up (which typically occurs in mid-June).

Because lipids are important energy reserves for Arctic animals (Møller and Hellgren, 2006), and the process of lipid extraction may also compromise other tissue constituents, no lipid extractions were performed on our samples to avoid the potential loss of critical information and introduction of error into the food web analysis. This allows us to compare our data to previous work from the Beaufort Sea (Dunton et al., 2006, 2012; Bell et al., 2016) and other areas in the Arctic region (Iken et al., 2010; McTigue and Dunton, 2014, 2017). Though lipids are known to be inherently depleted in ^{13}C relative to other tissues (DeNiro and Epstein, 1977) and may be a confounding variable in food web studies that utilize stable carbon isotopes, previous work shows Arctic benthic consumers have low lipid content (Graeve et al., 1997). A recent study by Mohan et al. (2016) examined the $\delta^{13}C$ of the lipid fraction of the *Calanus* copepods, *Onisimus* amphipods, and mysids (*Mysis*) collected in this study. Mohan et al. found that the $\delta^{13}C$ values of bulk lipids varied by ~6‰ among the crustaceans examined, which questions the utility of a one-size-fits-all mathematical equation to "correct" for lipid content (2016). Consequently, adjustment of the original isotopic value may introduce more bias than it removes.

2.6. Stable isotope models

We quantified the contribution of various OM sources to consumers' diets using a stable isotope mixing model, which determines possible combinations of food web end-members to the consumers' diet based on stable isotope data. We chose to use the R package Stable Isotope Mixing Models in R (*simmr*) for this analysis since it is the upgrade to Stable Isotope Analysis in R (*SIAR*) (Parnell et al., 2013). Like *SIAR*, *simmr* incorporates the variability in both end-member and consumer stable isotope values as well as the uncertainty in trophic enrichment factors (TEF) to provide credible intervals of possible dietary solutions (Parnell et al., 2010, 2013).

TEFs have only been directly measured for a few Arctic organisms (i.e. McMahon et al., 2006), and are known to be variable (Vander Zanden and Rasmussen, 2001; Post, 2002; McCutchan Jr et al., 2003). Therefore, we used literature values that encompass these observations: for all invertebrate guilds (Su/FF, Ss/De, and Ep/Om), we used $\Delta\delta^{13}C = 1.0 \pm 1.0‰$ and $\Delta\delta^{15}N = 3.4 \pm 1.0‰$ to reflect their position as primary consumers. The fish trophic guild used TEFs of 2.0 ± 2.0‰ and 6.8 ±

2.0‰ for $\Delta\delta^{13}C$ and $\Delta\delta^{15}N$, respectively, to reflect their position as secondary consumers compared to basal OM end-members. For the mammalian carnivore group, $\Delta\delta^{13}C$ and $\Delta\delta^{15}N$ were increased to 3.5 ± 3.5‰ and 11.9 ± 3.5‰ to reflect their higher trophic position as well as the increase in uncertainty in TEFs over multiple trophic steps. These TEFs represent expected enrichments in consumers' isotope values relative to basal OM sources. We performed this analysis at the genus level within each trophic guild when replication was sufficient ($n > 4$). *simmr* relies on a Markov Chain Monte Carlo to find possible solutions and disregards those not probabilistically consistent with the data. The iterations run were 10^4, the burn-in was 10^3, the posterior was thinned by 10, and the number of chains fit was 4.

The *simmr* model applies a geometric TEF correction to all end-member isotope values; to graphically represent this extrapolation, minimum and maximum end-member isotope value for each trophic step are represented as:

$$\text{mean}_{\text{end}-\text{member}} \quad \text{SD}_{\text{end}-\text{member}} \qquad \text{mean}_{\text{TEF}} \quad \text{SD}_{\text{TEF}}$$

Gelman-Rubin statistics for analyses were < 1.03, which indicates that the chains were sufficiently long (since values > 1.1 diagnose unsatisfactory runs) (Gelman et al., 2004). The R scripts and raw data used for analysis are available in the Supplemental Methods or available at <https://github.com/nathanmct/Beaufort-Sea-Lagoons>. All analyses were performed in R 3.4.0 (R Core Team, 2017).

Regression analysis relating $\delta^{18}O$-derived meteoric water content of the lagoons (i.e. fresh water from rainfall/runoff) to $\delta^{13}C$ values of POM and consumers was used to further elucidate potential linkages between terrestrial inputs and stable carbon isotope values. The $\delta^{13}C$ values of water column POM and consumers, grouped by genera, were averaged for each lagoon and plotted as a function of meteoric water estimates from Harris et al. (2017). Previous studies have shown an eastward depletion in $\delta^{13}C$ values along the Beaufort coast (Dunton et al., 1989, 2012; Saupe et al., 1989), so we also used regression analysis to relate $\delta^{13}C$ of POM and consumers to longitude. For both analyses, genera were only included where at least 5 samples from at least 3 lagoon sites were available. Because consumer $\delta^{13}C$ data was pooled across several sampling years and several sampling stations within each lagoon, mean meteoric water values were likewise generated by pooling data across sampling stations and over the three sampling years (Table 5).

3. Results

3.1. End-member stable isotope compositions

River OM, lagoon SPOM, and lagoon BPOM were not isotopically distinct end-members; therefore, a conglomerate of river OM, lagoon SPOM, and lagoon BPOM, which we hereafter refer to as terrestrial/freshwater-derived OM, was used as a single end-member for the food web (Table 2). Nearshore SPOM was more ^{13}C depleted in 2012 and 2013 than in 2011, likely reflecting greater C_T inputs in 2012 and 2013. For the nearshore SPOM end-member in the *simmr* model, we chose to use the 2011 mean for $\delta^{13}C$ and $\delta^{15}N$ (−23.0 ± 0.3‰ and 7.5 ± 0.4‰, respectively), as this better represents typical nearshore SPOM composition without the bias of a potentially large C_T input masking it. The marine SPOM end-member possessed slightly more enriched in $\delta^{13}C$ and $\delta^{15}N$ values (−21.9 ± 0.6‰ and 8.9 ± 1.9‰, respectively) than nearshore SPOM. The MPB $\delta^{13}C$ value used was −16.9 ± 1.2‰, which represents a mean of benthic diatom isotope values reported in the literature (see McTigue and Dunton, 2017 for details). The ice algae $\delta^{13}C$ value −17.7 ± 0.2‰ was observed ~40 km offshore in the Chukchi Sea (Dunton, pers. comm.) and was used as an end-member for the non-lagoonal, upper trophic level organisms.

Table 2
End-member organic matter (OM) mean (±SE) $\delta^{13}C$, $\delta^{15}N$, and C:N (molar ratio) for each site type along the Alaskan Beaufort Sea: lagoon, nearshore, marine and river. *n* is the number of samples analyzed for each parameter. Bold values were used as end-members in the *simmr* mixing model. *The terrestrial POM end-member is a grand mean of lagoon SPOM, lagoon BPOM, and river SPOM. **Microphytobenthos (MPB) data is a mean resulting from a literature survey of benthic microalgae and benthic diatoms (McTigue and Dunton, 2017). ***Ice algae data are from the Chukchi Sea collected in 2012 (see Methods Section 2.2).

	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Molar C:N
Marine SPOM				
2014	**4**	**21.9 ± 0.6**	**8.9 ± 1.9**	
Nearshore SPOM				
2011	**3**	**23.0 ± 0.3**	**7.5 ± 0.4**	**6.3 ± 0.2**
2012	3	−28.5 ± 0.3	5.8 ± 1.1	7.1 ± 0.3
2013	1	−27.5	9.4	5.9
Mean	7	−26.0 ± 1.1	7.1 ± 0.7	6.6 ± 0.2
Lagoon SPOM				
2011	4	−24.8 ± 0.7	6.7 ± 0.4	6.6 ± 0.3
2012	4	−28.9 ± 0.6	5.5 ± 0.9	7.2 ± 0.1
2013	3	−28.3 ± 0.3	7.0 ± 0.8	7.7 ± 0.1
Mean	11	−27.2 ± 0.7	6.3 ± 0.4	7.1 ± 0.2
Lagoon BPOM				
2011	4	−27.2 ± 0.3	3.4 ± 0.2	14.1 ± 0.7
2012	4	−27.7 ± 0.8	3.0 ± 0.2	14.9 ± 1.5
2013	3	−27.0 ± 0.4	3.0 ± 0.4	14.0 ± 0.2
Mean	11	−27.3 ± 0.3	3.2 ± 0.2	14.4 ± 0.6
River POM				
2011	3	−29.3 ± 0.4	3.6 ± 0.5	11.4
2012	1	−28.2	2.5	10.9
Mean	4	−29.0 ± 0.5	3.3 ± 0.5	11.1 ± 0.2
*Terrestrial POM	**12**	**27.3 ± 1.5**	**4.2 ± 1.9**	**11.4 ± 3.8**
**MPB		**16.9 ± 1.2**	**6.4 ± 1.2**	
***Ice algae	**3**	**17.7 ± 0.2**	**4.2 ± 1.9**	

3.2. Consumer stable isotope compositions

Mean $\delta^{13}C$ values for consumers ranged from −25.0‰ (*Monoporeia*, amphipod) to −17.1‰ (*Weyprechtia*, amphipod) and mean $\delta^{15}N$ values ranged from 6.6‰ (*Mysis*, peracarid crustacean) to 20.3 (*Ursus maritimus*, polar bear) (Table 3, Fig. 2). The $\delta^{13}C$ and $\delta^{15}N$ values of end-members (Table 2) overlapped with some consumers in the invertebrate guilds. Su/FF was the most depleted guild in ^{13}C and ^{15}N. The other two invertebrate guilds (Ss/De, and Ep/Om) had similar $\delta^{13}C$ and $\delta^{15}N$ ranges, and were more enriched in ^{13}C and ^{15}N relative to the Su/FF group. The Fish guild had the largest range in $\delta^{13}C$ values and intermediate $\delta^{15}N$ values. The Mam/Carn guild had intermediate $\delta^{13}C$ values and was the most enriched in ^{15}N (except for bowhead whale (*Baleana*)). Although every one of the five trophic guilds overlapped with at least one other guild, the most overlap occurred between the Ep/Om and Ss/De groups, both of which had intermediate $\delta^{13}C$ values and lower $\delta^{15}N$ values (Fig. 3).

3.3. End-member OM assimilation (simmr)

The *simmr* mixing model was used to estimate the possible contribution of each end-member OM source to the diet of consumers. As an indicator of the model's ability to discriminate between end-members, the model reports correlations of end-member probabilities for each consumer (Table 4). Large negative correlations may indicate the model cannot discriminate dependably between OM sources. Overall, the model could distinguish very reliably between terrestrial/freshwater POM and MPB (mean correlation = 0.12), and fairly reliably between terrestrial/freshwater POM and shelf POM (−0.72) and between shelf POM and MPB (−0.72).

The proportion of end-member assimilation is represented as the range of the 95% credible interval (analogous to the confidence interval in frequentist statistics) of mixing model solutions. Genera within all trophic guilds assimilated multiple end-member OM sources and

Table 3
Consumer δ^{13}C, δ^{15}N, and C/N (mean ± SD) for taxa collected in 2011–2016 from the eastern Alaskan Beaufort Sea. Organisms with $n > 4$ were included in the *simmr* mixing model.

Trophic guild	Genus	Type	Total length	*n*	δ^{15}N (‰)	δ^{13}C (‰)	C/N (molar)
Su/FF	Alcyonidium	Bryozoan		12	10.34 ± 0.75	−22.89 ± 1.98	6.08 ± 3.19
	Calanus	Copepod		5	10.69 ± 1.68	−23.74 ± 1.35	5.79 ± 2.16
	Eucratea	Bryozoan		5	9.20 ± 2.58	−23.67 ± 2.84	
	Liocyma	Bivalve		16	8.87 ± 0.95	−22.58 ± 1.11	5.52 ± 0.54
	Molgula	Ascidian		1	8.11	−23.51	5.96
Ss/De	Ampharete	Polychaete		2	8.15 ± 0.95	−21.42 ± 1.57	5.58 ± 0.19
	Cistenides	Polychaete		1	8.94	−20.18	6.71
	Cylichna	Gastropod		14	10.59 ± 1.15	−17.5 ± 1.47	5.89 ± 0.72
	Halicryptus	Peanut worm		8	12.00 ± 1.47	−19.77 ± 1.56	
	Monoporeia	Amphipod		1	9.58	−25.02	9.50
	Pontoporeia	Amphipod		10	9.40 ± 0.57	−18.02 ± 1.66	
	Portlandia	Bivalve		6	9.24 ± 0.16	−18.44 ± 1.68	
	Priapulus	Peanut worm		17	12.47 ± 1.36	−18.28 ± 1.25	4.65 ± 0.32
	Prionospio	Polychaete		4	10.19 ± 0.52	−20.59 ± 1.24	
Ep/Om	Atylus	Amphipod		2	9.35 ± 0.29	−21.46 ± 0.12	
	Diastylis	Cumacean		2	12.42 ± 0.46	−21.6 ± 0.15	5.56 ± 0.14
	Gammaracanthus	Amphipod		1	11.29	−20.40	5.75
	Gammarus	Amphipod		9	9.24 ± 1.00	−20.23 ± 2.24	
	Macoma	Bivalve		3	9.00 ± 0.34	−18.28 ± 3.59	
	Mysis	Mysid		13	10.49 ± 1.44	−20.34 ± 1.74	
	Mysis-NU	Mysid		5	6.68 ± 0.60	−17.52 ± 0.19	5.62 ± 0.82
	Nereimyra	Polychaete		5	10.29 ± 1.06	−20.73 ± 1.48	
	Onisimus	Amphipod		8	10.30 ± 1.86	−19.91 ± 2.34	7.12 ± 2.00
	Saduria	Isopod		5	11.97 ± 1.27	−18.99 ± 1.08	6.67 ± 0.85
	Terebellides	Polychaete		7	10.14 ± 0.64	−20.44 ± 1.00	
	Weyprechtia	Amphipod		1	12.41	−17.11	6.43
Fish	Boreogadus (Lagoon)	Arctic cod	<5 cm	6	12.00 ± 0.95	−23.63 ± 1.03	4.70 ± 0.60
	Boreogadus (Shelf)	Arctic cod	3–8 cm	3	12.42 ± 0.77	−24.14 ± 0.96	4.74 ± 0.42
	Coregonus	Arctic cisco	15–34 cm	4	13.21 ± 0.59	−21.91 ± 0.69	4.26 ± 0.39
	Eleginus	Saffron cod	35–40 cm	3	15.23 ± 0.76	−18.87 ± 0.21	3.74 ± 0.07
	Lumpenus	Slender Eelblenny	3–11 cm	12	12.06 ± 0.92	−23.71 ± 2.19	4.78 ± 0.25
	Myoxocephalus (Lagoon)	Sculpin	7–23 cm	12	13.75 ± 1.96	−20.55 ± 1.60	4.05 ± 0.21
	Myoxocephalus (Shelf)	Sculpin	<5 cm	6	12.37 ± 1.07	−24.12 ± 0.91	4.89 ± 0.24
	Pleuronectes	Arctic Flounder	8–12 cm	11	12.67 ± 2.00	−19.47 ± 1.58	4.22 ± 0.71
	Salvelinus	Arctic char	25–55 cm	14	13.39 ± 1.88	−23.55 ± 2.58	4.93 ± 1.97
Mam/Carn	Balaena	Bowhead		3	13.07 ± 0.31	−21.03 ± 0.75	4.51 ± 0.26
	Delphinapterus	Beluga		7	17.85 ± 1.82	−20.35 ± 1.80	
	Erignathus	Bearded Seal		1	17.29	−19.13	4.23
	Ursus	Polar Bear (male)		1	20.25	−20.41	4.15

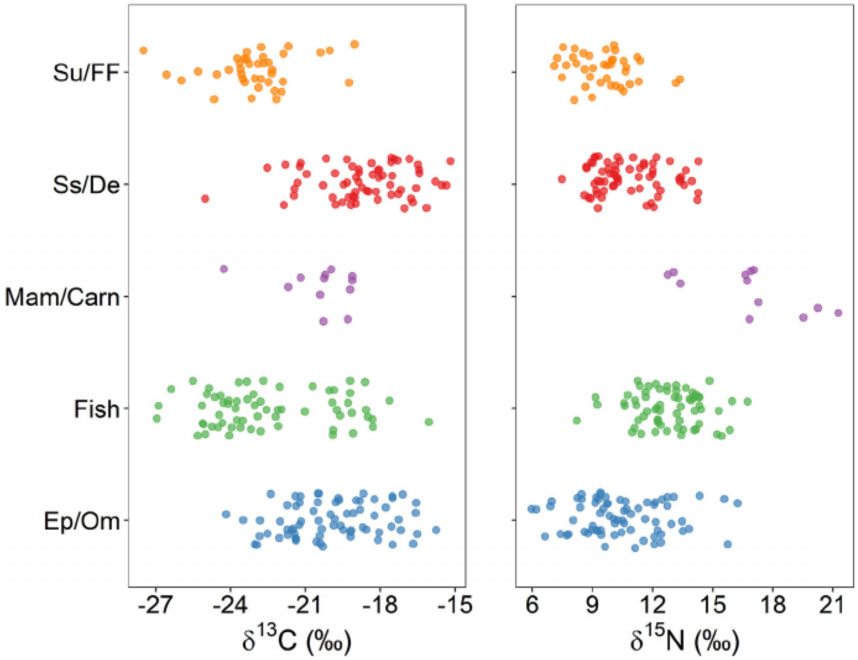


Fig. 2. Jitterplot of (a) δ^{13}C and (b) δ^{15}N isotope range for each trophic guild (indicated by color). Sus/FF = suspension and filter feeders; Ss/De = surface and subsurface deposit feeders; Ep/Om = epibenthic omnivorous invertebrates; Fish = omnivorous fishes, Mam/Carn = mammalian carnivores.

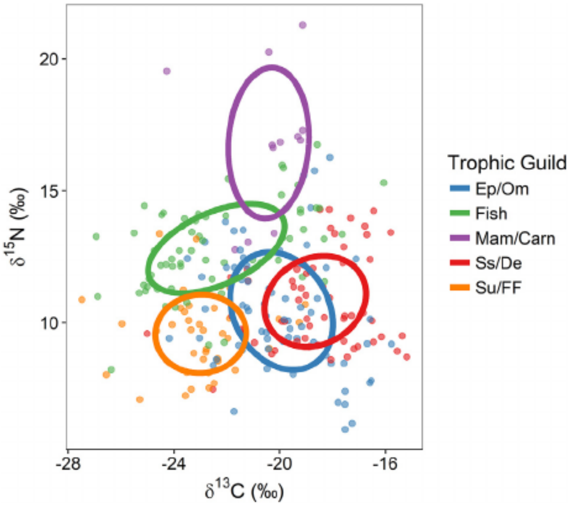


Fig. 3. All consumer samples plotted in $\delta^{13}C$ and $\delta^{15}N$ bivariate space. Points are individual values and ellipses are standard ellipse areas (SEA) including 40% of the observed values.

variation within most trophic guilds and individual genera was high, though this was not correlated with lagoon site or sampling year (except in the case of *Mysis* and *Myoxocephalus*; see explanations below) (Figs. 4a–b, 5). Overall, genera in the Su/FF guild derived most of their diet from shelf POM (28–69%) and terrestrial/freshwater POM (20–49%) and relatively small amounts from MPB. Genera in the Ss/De, and Ep/Om guilds derived most of their diet from MPB (30–76%) and small amounts of terrestrial/freshwater POM (<20%). Fish genera derived most of their diet from terrestrial/freshwater POM and shelf POM (Fig. 5).

Table 4
Summary of *simmr* model capability to discriminate between end-members (when calculating contributions to consumer diets). Values are correlations of end-member probabilities for incorporation into consumer diets for individual genera and overall (mean ± SE). Large negative correlations indicate the model could not distinguish between sources.

Guild	Genus	MPB ~ shelf POM	MPB ~ terrestrial POM	Shelf POM ~ terrestrial POM
Sus/FF	Alcyonidium	−0.65	0.07	−0.80
	Calanus	−0.53	0.12	−0.91
	Eucratea	−0.38	−0.28	−0.78
	Liocyma	−0.87	0.53	−0.88
Dep/SS	Cylichna	−0.90	0.14	−0.55
	Halicryptus	−0.91	0.45	−0.78
	Pontoporeia	−0.76	−0.21	−0.47
	Portlandia	−0.76	−0.42	−0.27
	Priapulus	−0.89	0.46	−0.81
Ep/OM	Gammarus	−0.74	−0.16	−0.53
	Mysis	−0.90	0.45	−0.8
	Mysis-NU	−0.69	−0.50	−0.28
	Nereimyra	−0.84	0.28	−0.75
	Onisimus	−0.86	0.13	−0.61
	Saduria	−0.88	0.19	−0.64
	Terebellides	−0.88	0.47	−0.84
Fish	Boreogadus (Lagoon)	−0.50	−0.04	−0.84
	Lumpenus	−0.51	−0.03	−0.85
	Myoxocephalus (Lagoon)	−0.87	0.60	−0.91
	Myoxocephalus (Shelf)	−0.34	−0.2	−0.84
	Pleuronectes	−0.84	0.45	−0.86
	Salvelinus	−0.43	0.08	−0.93
	Grand Mean	*0.72 ± 0.19*	*0.12 ± 0.32*	*0.72 ± 0.19*
		Ice Agae ~ marine POM	Ice Agae ~ terrestrial POM	Marine POM ~ terrestrial POM
Mam/Carn	Delphinapterus	−0.62	−0.09	−0.72

Table 5
H_2O-$\delta^{18}O$ (mean ± SE) values from water samples collected from 1 to 3 m at each site in August 2011–2013. Meteoric water is the modeled percent of each lagoon determined to be from river inputs or precipitation based on a $\delta^{18}O$ and salinity mixing model. Data from Harris et al. (2017).

Lagoon site	Site Code	n	$\delta^{18}O$ (‰)	Meteoric water (%)
Kaktovik	KA	19	−6.8 ± 0.2	28.8 ± 1.1
Jago	JA	13	−6.0 ± 0.3	24.7 ± 1.7
Angun	AN	10	−6.5 ± 0.7	27.4 ± 3.5
Nuvagapak	NU	11	−11.4 ± 1.7	50.8 ± 8.0
Demarcation Bay	DE	8	−6.7 ± 1.0	27.5 ± 4.9

Within the Su/FF trophic guild, *Eucratea*, *Calanus* and *Liocyma* consumed the most terrestrial/freshwater POM and the least MPB (Figs. 4a, 5). There was little variation among genera in the Ss/De guild: all genera derived the majority (>60%) of their diet from MPB and appeared to assimilate little to no terrestrial/freshwater POM, except for *Halicryptus*, which consumed large amounts of shelf POM (Figs. 4a, 5). Genera within the Ep/Om group showed the most variation (Figs. 4a, 5). Most Ep/Om genera derived the majority (>50%) of their diet from shelf POM. Mysids from NU were isotopically distinct (more depleted in ^{13}C) than mysids from other sites and were treated as a separate group in the *simmr* model. The NU-mysids were unique in their apparent assimilation of large (~70%) amounts of MPB.

Though the fish and Mam/Carn guilds do not consume the end-member OM sources directly, their assimilation of basal OM sources was modeled by using larger TEFs to reflect the multiple trophic steps between them and the end-members in the food web. Within the fish guild, sculpin spp. (*Myoxocephalus*) from lagoon sites were isotopically distinct (more enriched in ^{13}C and ^{15}N) from those at nearshore sites, and were treated as separate groups in the *simmr* model. Most fishes derived the majority of their diet (>50%) from terrestrial/freshwater POM and shelf POM (20–30%), with MPB being a minor component of the diet (<15%) (Figs. 4a, 5). Lagoon *Myoxocephalus* and *Pleuronectes* showed a different pattern, deriving the majority of their diet from shelf POM (>40%) and small amounts of terrestrial/freshwater POM. In the Mam/Carn group, only beluga (*Delphinapterus*) was sampled in sufficient replication to be included in the *simmr* model. Though beluga migrate eastward on the Beaufort coast and feed in the nearshore environment, they do not typically enter the shallow lagoons. To reflect their more offshore habitat, their end-members for *simmr* included terrestrial/freshwater POM, marine SPOM (from marine sites), and ice algae. *Delphinapterus* assimilated large proportions (50%) of terrestrial/freshwater POM, and 20–30% of the other OM sources (Figs. 4b, 6).

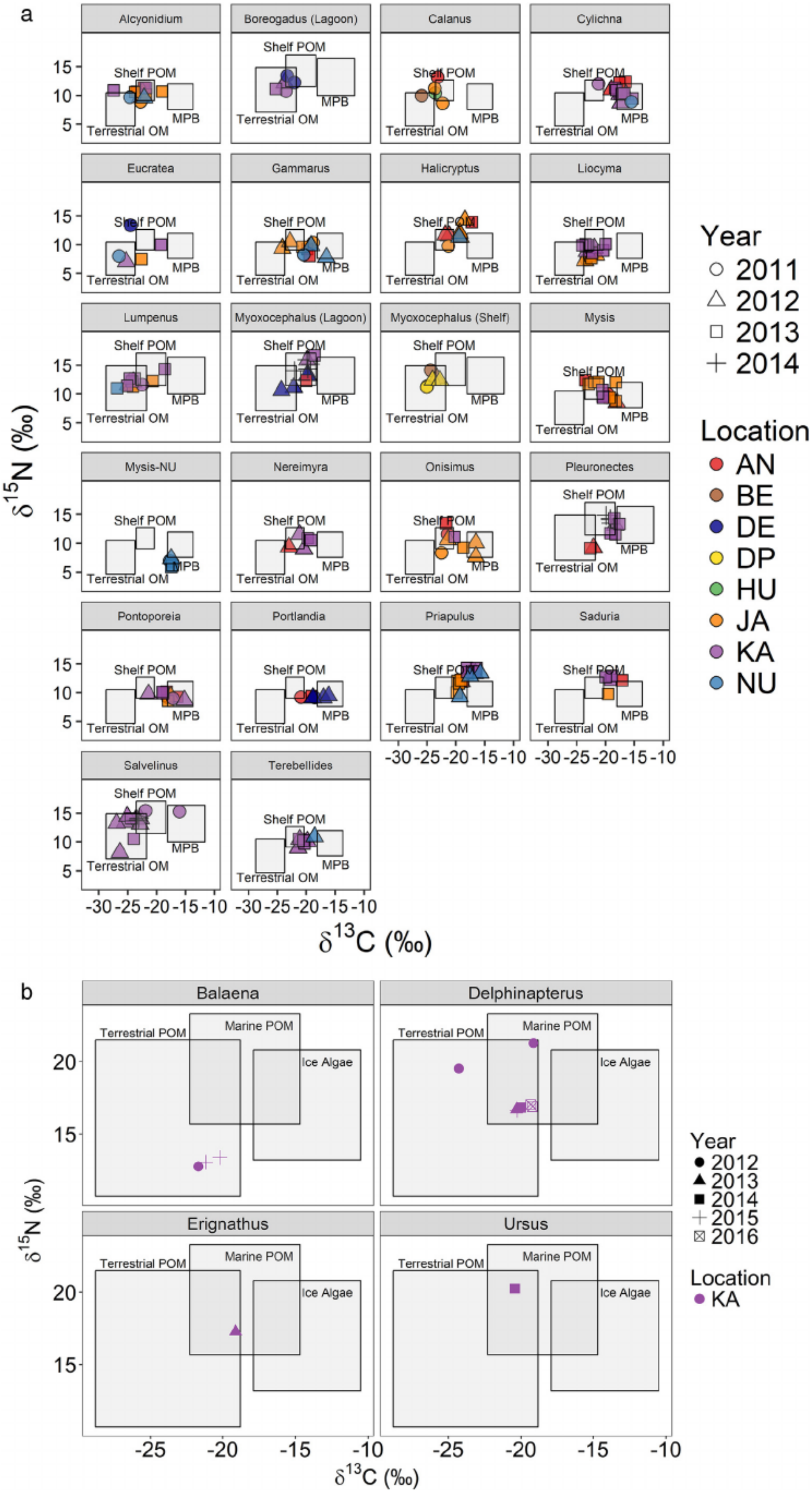
3.4. Spatial differences

Linear regression analysis revealed that % meteoric water was a significant predictor of POM-$\delta^{13}C$ values ($r^2 = 0.85$, $p < 0.0001$) (Fig. 7), but not for any consumer genera $\delta^{13}C$ values (Fig. S1). Longitude was not a significant predictor of $\delta^{13}C$ values for POM or any consumer genera (Figs. S2, S3).

4. Discussion

4.1. Sources of organic matter

Analysis of eastern Beaufort lagoon and nearshore suspended (water column) OM suggest there are at least two distinct sources of OM present in the coastal environment that are distinguishable using C and N stable isotopes: marine primary production (more enriched in ^{13}C and ^{15}N) and terrestrial/freshwater-derived OM inputs. Our terrestrial/freshwater POM end-member encompasses the most depleted lagoon OM value observed in the present study (−28.9‰ in 2012), tundra peat values reported by Schell (1983), and falls within the extremes (−23 to −31‰) observed for North Slope river SPOM by McClelland


a
Alcyonidium
Boreogadus (Lagoon)
Calanus
Cylichna
Eucratea
Gammarus
Halicryptus
Liocyma
Lumpenus
Myoxocephalus (Lagoon)
Myoxocephalus (Shelf)
Mysis
Mysis-NU
Nereimyra
Onisimus
Pleuronectes
Pontoporeia
Portlandia
Priapulus
Saduria
Salvelinus
Terebellides
Shelf POM
MPB
Terrestrial OM
δ15N (‰)
δ13C (‰)
5
10
15
-30
-25
-20
-15
-10
Year
○ 2011
△ 2012
□ 2013
+ 2014
Location
AN
BE
DE
DP
HU
JA
KA
NU
b
Balaena
Delphinapterus
Erignathus
Ursus
Terrestrial POM
Marine POM
Ice Algae
δ15N (‰)
δ13C (‰)
15
20
-25
-20
-15
-10
Year
● 2012
▲ 2013
■ 2014
+ 2015
⊠ 2016
Location
● KA

et al. (2014). We chose to analyze lagoon OM and terrestrial/freshwater POM as a single food web end-member because lagoons contain large amounts of terrestrial/freshwater-derived material in August (Connelly et al., 2015) and they were not isotopically distinct for treatment in the mixing model.

C_T reaches the coastal environment from watershed runoff and coastal erosion as the land margin of the lagoons actively recedes (Jorgenson and Brown, 2005). Erosional inputs and runoff of terrestrial/freshwater sources mix with marine-derived primary production in the coastal environment to produce the intermediate OM δ^{13}C and δ^{15}N values observed at some locations (Table 2, Connelly et al., 2015). Although rivers on the North Slope deliver more dissolved OM than particulate OM (unless inputs from the Colville River are considered), POM inputs from smaller rivers may be an important OM source for lagoon consumers (Macdonald et al., 1998; McClelland et al., 2014). In addition to C_3 plant-derived organic matter from the tundra environment, the C_T pool includes freshwater algae carried in river water (Churchwell et al., 2016) and phytoplankton produced within the lagoons under low salinity conditions. Freshwater algae are typically more ^{13}C-depleted than marine phytoplankton because a larger proportion of the inorganic carbon that they use for photosynthesis comes from CO_2 as opposed to bicarbonate (Marty and Planas, 2008).

Marine primary production includes phytoplankton and microphytobenthos, which can be further distinguished based on ^{13}C content [literature values of MPB are more ^{13}C enriched (e.g. Newell et al., 1995, McTigue and Dunton, 2017) than marine SPOM values reported here]. Though lagoon and nearshore SPOM both contained C_T, lagoon SPOM is characterized by a higher proportion of dinoflagellates relative to diatoms and has a higher polyunsaturated fatty acid content than SPOM from nearshore sites (Connelly et al., 2015). This finding suggests lagoon SPOM is likely an important food source for consumers because of its high nutritional value (Connelly et al., 2015).

While primarily comprised of marine phytoplankton, our marine SPOM samples (<180 μm size fraction) represent a mixture of material that could include resuspended benthic organic matter, small zooplankton, heterotrophic protists, and fecal pellets and other detritus. The inclusion of MPB and/or resuspended benthic organic matter that has been microbially reworked may contribute to our enriched ^{13}C values (McTigue et al., 2015). Mid- to late-summer phytoplankton production is low in lagoons, because of the low inorganic nitrogen concentrations (Dunton et al., 2012), which implies that MPB may be an important source of nutrition for biota. Moreover, MPB is a ^{13}C-enriched end-member that explains the enriched δ^{13}C values of some consumers like *Cylichna*, *Pontoporeia*, *Portlandia*, and *Priapulus*. The δ^{13}C value (-23.0 ± 0.3‰) of the nearshore SPOM end-member agrees well with the mid-water column POM value from the nearshore Beaufort Sea shelf (-24.8‰) reported in Dunton et al. (2012). This value represents a mixture of the more ^{13}C-enriched marine SPOM and more ^{13}C-depleted lagoon/freshwater POM. Nearshore SPOM sampled in the years 2012 and 2013 contained a higher proportion of lagoon/freshwater POM, as reflected in their ^{13}C-depleted values, relative to the samples from 2011 (Table 2).

Ice algae, which are present in the Beaufort Sea during non-summer months, are a distinct fourth carbon source available in the nearshore environment that can have similar isotope values to that of MPB (Gradinger, 2009; Pineault et al., 2013). Our estimated value is similar to the wide range of values observed in the Beaufort Sea (-25 to -14‰, (Gradinger, 2009, Pineault et al., 2013, Bell et al., 2016). Ice algae are not typically found in coastal environments past June, however, and our sampling occurred during the open water period in August. In addition, no ice algae were observed in any of these lagoons during spring 2012 and 2013 (Dunton and McClelland, pers. obs). Consequently, its role as a carbon source in the nearshore environment in August is likely minimal, though it is more important in deeper, offshore waters (Legendre et al., 1992; Connelly et al., 2015).

Although there was high interannual variability in δ^{13}C and δ^{15}N values for lagoon and nearshore OM reported here (as in Connelly et al., 2015), the means for all years are similar to those reported for other studies located in the coastal eastern Alaskan Beaufort Sea (Dunton et al., 2006, 2012; Bell et al., 2016). Therefore, we are confident that the lagoon and nearshore POM isotopic means reported here are robust and representative of typical open water values. Interestingly, the agreement of our values with those of Dunton et al. (2012) also suggests that despite the changing coastal environment over the last decade, the bulk composition of OM during summer, as reflected in stable isotope values along the coast, has not changed substantially.

4.2. Food web structure of the eastern Alaskan Beaufort Sea

Omnivory is a common feeding strategy in the Arctic (Dunton and Schell, 1987) and, as in other marine environments, true herbivores are rare. All three invertebrate feeding groups had similar δ^{15}N ranges, indicating the organisms they contain occupied similar trophic levels near the base of the food web but assimilated different proportions of OM sources. In particular, most overlap occurred between the Ep/Om and Ss/De trophic guilds, which reflects the plasticity of feeding behavior in these organisms and illustrates the substantial degree of trophic redundancy within these estuarine systems. The stable isotope values for the invertebrate feeding guilds Su/FF, Ss/De, and Ep/Om were encapsulated by those of the terrestrial/freshwater-derived OM and MPB end-members, which not only indicates that consumer isotope values can be explained by the representative end-members but also meets the conditions to run a stable isotope mixing model (Phillips et al., 2014).

Other Arctic studies, including those in the Beaufort Sea, have also found benthic invertebrates to be more ^{13}C enriched than marine POM (Dunton et al., 1989; Hobson et al., 1995; McTigue and Dunton, 2014; Connelly et al., 2014). In our model, the ^{13}C enrichment of consumers relative to shelf POM indicates the assimilation of MPB. This enrichment, however, may also reflect assimilation of microbially-reworked organic matter, because microbial processes often result in isotopically-enriched OM substrate (Macko et al., 1987) or ^{13}C-enriched bacteria themselves (Oakes et al., 2016). This explanation has been proposed to explain ^{13}C enrichment of fauna relative to phytoplankton in the Bering and Chukchi Sea (McConnaughey and McRoy, 1979; Hobson et al., 1995; Lovvorn et al., 2005; McTigue and Dunton, 2014; North et al., 2014; McTigue et al., 2015) and for ^{13}C enrichment of benthic POM relative to suspended POM in near-bottom waters near Spitsbergen and on the Beaufort Sea shelf (Tamelander et al., 2006; Connelly et al., 2012).

Overall, genera in the Su/FF guild were the most depleted in ^{13}C and ^{15}N, reflecting the assimilation of large amounts of C_T. The individuals analyzed of the bivalve *Liocyma* ($n = 16$), a surface suspension-feeder (Dunton et al., 2012), exhibit little variation in their stable isotope values across three sampling seasons and two sampling locations, which is reflected in their small range of *simmr* range of diet proportions. The dietary contribution of terrestrial/freshwater POM for *Liocyma* is likely preferential consumption of freshwater phytoplankton since these bivalves are suspension feeders of microalgae; it is possible

Fig. 4. Faceted δ^{13}C and δ^{15}N bivariate plots showing all consumer samples by feeding guild (a: Sus/FF, Dep/Ss, Ep/Om, Fish, b: Mam/Carn). Points are individual values; symbol color indicates sampling location, and symbol shape indicated sampling year (note: colors repeat in each guild). Only genera with $n > 4$ that were included in the simmr model are shown (except for Mar/Carn group, all data shown). Boxes represent the position of end-member carbon sources (a: terrestrial POM, shelf POM, and MPB; b: terrestrial POM, marine POM, and ice algae) in isospace after projecting for different trophic levels (see Table 2 for more details). (a) *Mysis* from Nuvagapuk Lagoon (NU) were distinct from *Mysis* from all other sites, so individuals from this site were analyzed separately. Because *Myoxocephalus* from lagoon and nearshore sites differed in δ^{13}C and δ^{15}N, this genus is plotted separately for each site type.

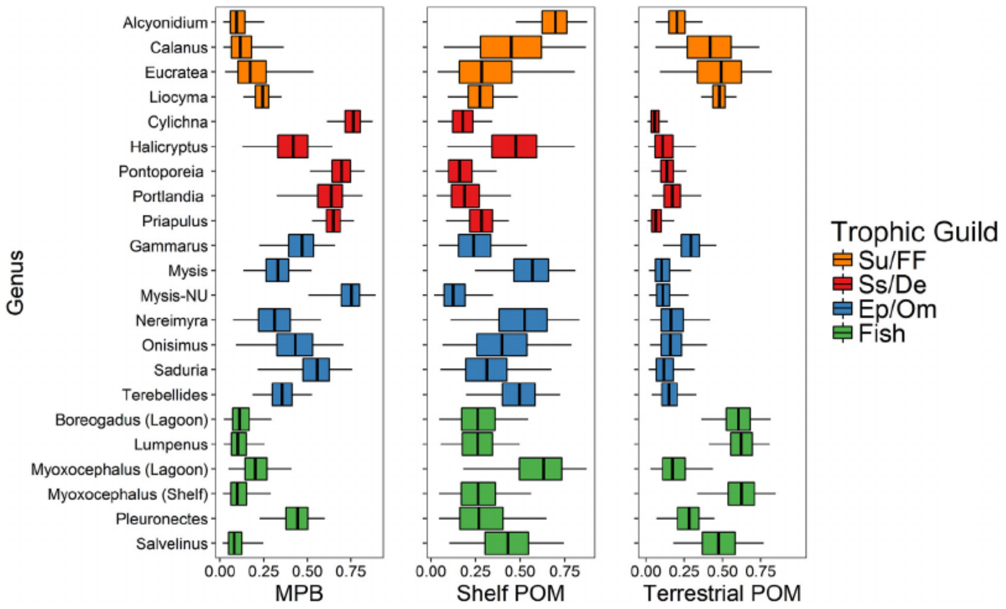


Fig. 5. Boxplots showing modeled proportions of end-member OM sources in consumer diets for each genera within each lower-trophic feeding guild. The centerline is the median of all model solutions, the box encloses 25th and 75th percentiles, and the whiskers extend to the 2.5th and 97.5th percentiles. Outliers were omitted for clarity.

they are indiscriminately consuming and assimilating suspended terrestrial detritus, but seems unlikely. Similarly, our results indicate that *Calanus* copepods, which are herbivorous and consume microalgae and phytoplankton (Macdonald et al., 2010), assimilate both terrestrial/freshwater POM and shelf POM. This suggests *Calanus* consume both freshwater and marine-derived phytoplankton. It is also possible that Su/FF genera are assimilating carbon from semi-labile river-supplied DOM that has been remineralized microbially into dissolved inorganic carbon (DIC) and taken up by phytoplankton that retain the lighter δ^{13}C signal (Sipler and Bronk, 2015). Though previous research showed the bryozoan *Alcyonidium* consumes POM and phytoplankton and the bryozoan *Eucratea* graze mainly on microalgae (Macdonald et al., 2010), the range of δ^{13}C values for these genera indicate assimilation of MPB and terrestrial/freshwater POM, suggesting they are highly plastic in the types of microalgae they assimilate (i.e. assimilate multiple isotopically-distinct OM sources) and are opportunistic feeders.

The Ss/De and Ep/Om groups had similar δ^{13}C and δ^{15}N ranges (Fig. 3) despite feeding primarily on different sediment horizons (subsurface vs. surface) (Macdonald et al., 2010; Appeltans et al., 2012). Studies in the adjacent Bering and Chukchi Seas have found that surface and sub-surface feeders have similar C and N isotopic composition, indicating OM deposited on the sediment surface is mixed to sub-surface via bioturbation (McTigue and Dunton, 2014, 2017; North et al., 2014). Ss/De genera showed little reliance on terrestrial POM and were more ^{13}C-enriched than other consumers, which is surprising given the depleted δ^{13}C values of sediment observed in this study. This finding suggests that these deposit-feeders may be preferentially consuming and/or assimilating carbon from benthic microalgae (as opposed to whole

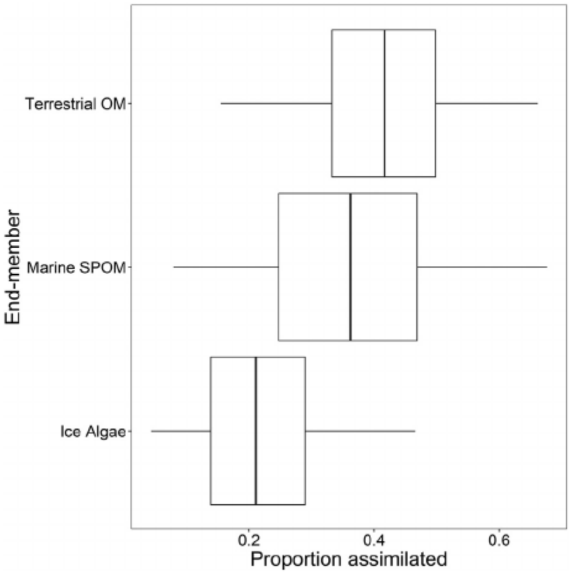


Fig. 6. Boxplots showing modeled proportions of end-member carbon sources in beluga whale (*Delphinapterus*) diet. The centerline is the median, the shaded box encloses 25th and 75th percentiles, and the whiskers extend to the 2.5th and 97.5th percentiles. Only beluga was included in this analysis because of low sample size for other mammals. Because beluga whales are a top predator, the TEFs for this analysis were modified (δ^{13}C = 3.5 ± 3.5, δ^{15}N = 111.9 ± 3.5).

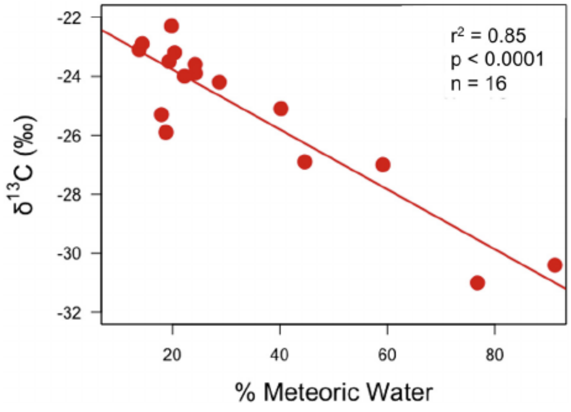


Fig. 7. Relationship between mid-water column POM δ^{13}C value and % meteoric water for 16 samples collected from five lagoon sites in the Eastern Alaskan Beaufort Sea. POM δ^{13}C value decreased significantly with increase % meteoric water (as estimated from a δ^{18}O and salinity mixing model in Harris et al., 2017).

sediments) or the labile OM that is stored in nearshore sediments in the Arctic Ocean (Mincks et al., 2005; McTigue et al., 2015). Labile OM is typically more ^{13}C-enriched than other components of the sediment (McMahon et al., 2006). Dunton et al. (2012) performed a similar study on lagoon and nearshore consumers in the eastern Alaskan Beaufort Sea and also found that deposit-feeders and detritivores were more ^{13}C-enriched relative to suspension-feeding or omnivorous invertebrate consumers. Similarly, McTigue and Dunton (2014, 2017) examined consumers in the Chukchi Sea and found that surface and sub-surface deposit feeders were consistently enriched in ^{13}C and concluded they assimilated more ice algae or MPB relative to particulate OM.

The intermediate δ^{13}C values of the Ep/Om guild agree well with other benthic studies in the Beaufort (Dunton et al., 2006, 2012) and Chukchi Seas (Iken et al., 2010; McTigue and Dunton, 2017). Ep/Om genera may consume POM directly (e.g. *Onisimus* amphipod; Carey and Boudrias, 1987), preferentially consume surface detritus (ex. *Terebellides* worm; (Macdonald et al., 2010)), or switch between predatory and scavenging feeding modes (e.g. *Saduria* isopod; Kvach, 2009, Dunton et al., 2012). These differences in feeding mode (and trophic level) likely cause the range in δ^{15}N values observed (Bunn et al., 2013; McTigue and Dunton, 2014).

Curiously, *Mysis* from Nuvagapuk exhibited δ^{13}C values 2‰ more ^{13}C-enriched than mysids from any other lagoon site and were more ^{15}N depleted than the MPB pool (after adjustment for TEF) despite having similar δ^{13}C values (Fig. 4a). Their position might reflect assimilation of microbially reworked terrestrial POM, which may retain a light δ^{15}N value but become enriched in ^{13}C (Macko et al., 1987). Connelly et al. (2015) reports that invertebrates contained large contributions from bacterial fatty acids, suggesting that a depleted δ^{13}C signal in lower trophic invertebrates (i.e. $TL < 3$) may reflect either the direct consumption of terrestrially-derived OM or indirect terrestrial OM consumption via bacterial food webs. The depleted isotope values may also indicate the mysids were assimilating cyanobacteria, which is present in lagoon margins and has a δ^{15}N value of ~0‰ (Dunton, pers.comm.).

The fish guild similarly displayed a wide range of δ^{13}C values, suggesting Beaufort coast fish are opportunistic generalists who derive their diet from many basal OM sources. This group is comprised of omnivorous fishes of many sizes (from 5 cm (total length) sculpin (*Myoxocephalus*) and eel blennies (*Lumpenus*) to >120 cm Arctic char (*Salvelinus*)). Many of these fishes are gape-limited (i.e. prey size is limited by how wide they can open their mouths) and the large δ^{15}N range of this guild reflects the different trophic positions of individual fish (i.e. smaller fish consume copepods, polychaetes, and amphipods, and larger fish consume larger crustaceans and small fish) (Harris, 1993; Macdonald et al., 2010; Walkusz et al., 2011). For example, mature Arctic cod (*Boreogadus*) feed mainly on amphipods and mysids, though zooplankton are a substantial food source for juveniles (Craig et al., 1982a, 1982b; Walkusz et al., 2011; Dunton et al., 2012). Arctic char (*Salvelinus*) derived ~40% of their diet from shelf POM and ~40% from terrestrial/freshwater POM. These findings imply that *Salvelinus* are plastic in their assimilation of basal OM sources, which might reflect a generalist, omnivorous style of feeding. The size range of this genera was relatively large (25–55 cm), however, so this range in OM source assimilation and large isotopic niche may reflect the inclusion of individual fishes feeding at different trophic levels due to ontogenetic diet shifts.

Because many of these fishes derived large portions of their diet from terrestrial OM, they likely consumed prey items that primarily assimilated terrestrial OM. Su/FF invertebrates, such as bryozoans and copepods, may be important components of fish diets and create one pathway for terrestrial OM to propagate to intermediate trophic levels. *Calanus* copepods, who appear to assimilate large portions of terrestrial OM (likely because they consume freshwater phytoplankton), are residents of the nearshore ecosystems and can be advected into lagoons where they are consumed by larger invertebrates and small fishes (Dunton et al., 2012). Though Ep/Om invertebrates, such as worms, amphipods, and mysids, are some of the most abundant prey items in the coastal Beaufort Sea (Dunton et al., 2006; Bell et al., 2016), these genera consumed small amounts of terrestrial/freshwater OM and therefore are likely not the primary prey items of coastal fishes.

The Mam/Carn guild has a wide δ^{15}N range, reflecting the inclusion of consumers that span several trophic levels. Bowhead whales (*Baleana*) feed on lower trophic level crustaceans (Lowry et al., 2004) whereas large belugas (*Delphinapterus*) and seals (*Erignathus*) feed on large fishes (Frost et al., 1993; Quakenbush et al., 2015). Polar bears, apex predators, feed on large fishes and seals (Frost and Lowry, 1984; Cherry et al., 2011). Gut content analysis of migratory belugas that inhabit the coastal eastern Alaskan Beaufort Sea in summer shows these whales are piscivorous and that saffron cod and Arctic cod are major diet components (Quakenbush et al., 2015). Consumption of omnivorous fishes, in particular Arctic cod, may explain why terrestrial/freshwater OM was found to be a major basal OM source to beluga diet in this study.

4.3. Spatial differences

The δ^{13}C of water column POM showed significant spatial variance related to differences in the magnitude of freshwater inputs (% meteoric water) among lagoons (Fig. 7). In contrast, none of the consumer genera that met our analysis criteria showed significant spatial variance related to % meteoric water or longitude (Figs. S1, S3). Consumers' δ^{13}C values integrate food sources over several months whereas the POM samples represent a shorter temporal window. This spatial homogeneity in consumer δ^{13}C values across several lagoons further justifies our decision to pool consumers from all lagoon sites for our *simmr* mixing model, though it is important to note the low sample size for each consumer genera and the lack of coverage across the full range of % meteoric water spectrum reduced the power of these analyses. It is also possible that the near-bottom salinities and the source of terrestrial/freshwater-derived organic matter are uncoupled because C_T can rain down from fresher waters near the surface of the lagoon. So animals could be feeding in a layer of salty bottom water from marine intrusion and receive C_T from fresher waters above.

Sculpin genera (*Myoxocephalus*), however, showed spatial differences in δ^{13}C and C_T assimilation between lagoon and nearshore sites. Lagoon sculpin were isotopically distinct from those collected from nearshore sites (Figs. 5, 8). Lagoon sculpin assimilated more marine OM sources (MPB and shelf POM) and less terrestrial/freshwater OM. This finding is consistent with previous isotope studies that concluded sculpin rely on a marine phytoplankton carbon source across the Beaufort Sea (sculpin values range from −20.5–23.0‰; Schell, 1983; Loseto et al., 2008; Dunton et al., 2012). Nearshore sculpin, however, derived >50% of their diet from terrestrial/freshwater carbon.

This difference in stable isotope values for the two groups can be explained in two ways: 1) OM source assimilation is related to the size and life history stage of individuals sampled (e.g., ontogenetic shifts in trophic habits), or 2) the location of their capture drives this trend with different OM sources available at different sites. Nearshore sculpin were uniformly smaller (total length: <5 cm) than those collected from lagoons (total length: 7–23 cm). Linear regression analysis revealed a significant positive linear relationship between both C and N isotopes and total length in sculpin (Fig. 8), which is indicative of ontogenetic diet shifts and suggests that smaller sculpin assimilate more terrestrial/freshwater OM. It is also possible that higher lipid-content may cause smaller fish to be more ^{13}C depleted. Younger fishes tend to contain more fats in their muscles than adult organisms (Jobling et al., 1998; Kiessling et al., 2001), which agrees with C:N values reported here (4.9 for small nearshore fish, and 4.1 for larger, lagoon fish). Juvenile sculpin may also feed more on lipid-rich copepod nauplii (Scott et al., 2000), whereas adult sculpin feed mostly on peracarid crustaceans, such as mysids and amphipods, which store less lipids than copepods such as *Calanus hyperboreus* (Connelly et al., 2012).

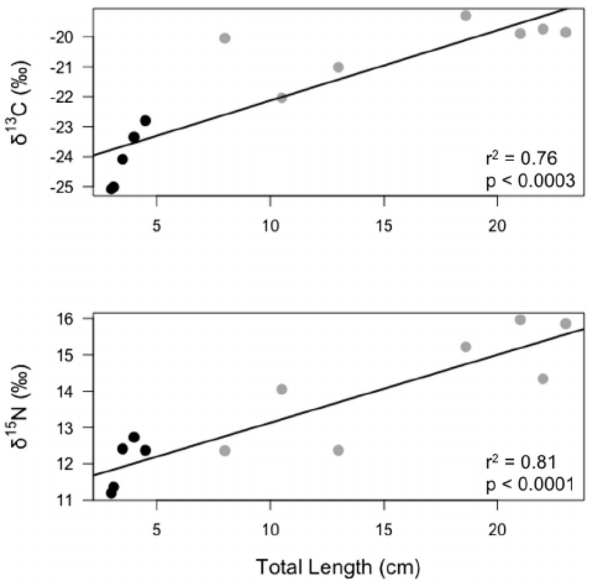


Fig. 8. Linear relationship between total length and (a) δ^{13}C and (b) δ^{15}N for *Myoxocephalus* individuals collected from lagoon (black symbol) and nearshore grey symbol) sites in the eastern Alaskan Beaufort Sea in August 2011–2014.

Motile organisms can travel between lagoon and open water areas, mysids and amphipods are known to migrate between lagoons and nearshore waters (Craig, 1984). Phytoplankton may also be advected into lagoons through channels. These processes help explain the high invertebrate biomass observed in lagoons (Craig, 1984). These movements would further blur any differences in terrestrial/freshwater- vs. marine-derived OM assimilation, should they exist, among lagoons and between lagoon and nearshore sites.

4.4. Conclusions and implications for a changing Arctic

While terrestrial/freshwater contributions to food webs have been well defined in temperate estuaries, their role in Arctic food webs has been given far less attention. This study builds on work from the past decades to assess the role of terrestrial/freshwater carbon in Arctic coastal food webs. Genera within every trophic guild derived >10% of their diet from terrestrial and/or freshwater OM, though this subsidy was assimilated in greater proportions by suspension feeding invertebrates and omnivorous fishes. This finding corroborates previous studies that found benthic food webs are supported by terrestrial carbon subsidies (Dunton et al., 2006, 2012; Bell et al., 2016). These findings confirm that terrestrial/freshwater OM is currently an important subsidy to multiple trophic levels in coastal Arctic waters.

We provide compelling evidence for the transfer of terrestrial and/or freshwater OM from benthic food webs to upper level consumer species, such as beluga whales. Omnivorous fishes, in particular Arctic cod, which is one of the most abundant Arctic fishes and is known to be a key link between benthic and pelagic organisms (Craig et al., 1985; Hop and Gjøsæter, 2013), may be vital in the transfer of terrestrial/freshwater OM subsidies to upper trophic levels. More research is needed that examines multiple terrestrial biomarkers to determine this link conclusively.

Climate change is predicted to alter carbon sources in the Alaskan Beaufort in several ways, which may in turn affect the relative amounts of energy sources available to coastal food webs. Net marine primary productivity, which is tightly coupled to sea ice cover, will likely increase (Arrigo et al., 2008), but the balance between benthic (MPB) and pelagic (phytoplankton) production may change (Glud et al., 2009). Terrestrial/freshwater inputs will be affected by changing river inputs (Peterson et al., 2006), decreased glacial runoff (Nolan et al., 2011), and increased coastal erosion due a longer open water period, larger areas of open water, increased storminess, and decreased permafrost (Overeem et al., 2011; Barnhart et al., 2014). It is not yet clear if these combined phenomena will ultimately result in increased or decreased delivery of C_T to the coastal Beaufort Sea or how this may affect in situ lagoon and nearshore production. Increased terrestrial/freshwater inputs may lower production because erosional processes are often associated with higher water turbidity (Glud et al., 2009), or this terrestrial/freshwater OM may be readily assimilated by lagoon invertebrates. We show that some terrestrial/freshwater OM, which is incorporated into benthic invertebrates, is also transferred to upper trophic levels such as omnivorous fishes and beluga. As such, these larger animals will likely be affected by aspects of climate change that affect land-sea coupling as well those that cause sea-ice loss.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fooweb.2018.e00081.

Acknowledgements

The authors gratefully thank the anonymous reviewer whose constructive criticisms greatly improved the quality of this manuscript. We thank the Captains and crews of the R/V *Proteus* and the R/V *Norseman II* for their invaluable navigation skills and support of our research. We are very grateful to field assistants R. Thompson, S. Linn, S. Mohan, and J. Smith for their long hours and enthusiastic support of this work. T. Connelly contributed greatly to the fieldwork (sample collection and processing) and provided substantive comments that significantly improved the quality of early versions of this manuscript. This field intensive campaign would not have been possible without the support of D. Payer and others at the Arctic National Wildlife Refuge and at U.S. Fish and Wildlife Service headquarters in Fairbanks. We would also like to thank K. Jackson (Texas based logistic support), S. Schonberg (assistance with ArcGIS and invertebrate identification), P. Garlough (isotope sample processing), M. Khosh (river sampling), M. Nolan (river sampling) and R. Churchwell (river sampling). Funding for this work was provided by the National Science Foundation under grant ARC-1023582 and LTER grant OPP-1656026. This research was performed while N. McTigue held an NRC Research Associateship award at the NOAA National Centers For Coastal Ocean Science.

References

Appeltans, W., Bouchet, P., Boxshall, G., DeBroyer, C., DeVoogd, N., Gordon, D., Hoeksema, B., Horton, T., Kennedy, M., Mees, J., Poore, G., Read, G., Stöhr, S., Walter, T., Costello, M., 2012. World Register of Marine Species. http://www.marinespecies.org.

Arrigo, K.R., van Dijken, G., Pabi, S., 2008. Impact of a shrinking Arctic ice cover on marine primary production. Geophys. Res. Lett. 35, 1–6.

Barnhart, K.R., Overeem, I., Anderson, R.S., 2014. The effect of changing sea ice on the vulnerability of Arctic coasts. Cryosphere 8, 2277.

Bell, L., Bluhm, B., 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.

von Biela, V.R., Zimmerman, C.E., Moulton, L.L., 2011. Long-term increases in young-of-the-year growth of Arctic cisco Coregonus autumnalis and environmental influences. J. Fish Biol. 78, 39–56.

Bradstreet, M.S.W., Cross, W.E., 1982. Trophic relationships at high Arctic ice edges. Arctic 1–12.

Brown, S.C., 2006. Arctic Wings: Birds of the Arctic National Wildlife Refuge. Braided River.

Brown, S., Kendall, S., Churchwell, R., Taylor, A., Anna-Marie, B., 2012. Relative shorebird densities at coastal sites in the Arctic National Widlife Refuge. Waterbirds 35, 546–554.

Bunn, S.E., Leigh, C., Jardine, T.D., 2013. Diet-tissue fractionation of δ15N by consumers from streams and rivers. Limnol. Oceanogr. 58, 765–773.

Carey, A.G., Boudrias, M.A., 1987. Feeding ecology of Pseudalibrotus (=Onisimus) litoralis kr??yer (Crustacea: Amphipoda) on the Beaufort Sea inner continental shelf. Polar Biol. 8, 29–33.

Casper, A.F., Rautio, M., Martineau, C., Vincent, W.F., 2015. Variation and assimilation of Arctic riverine sestonin the pelagic food web of the Mackenzie River Delta and Beaufort Sea Transition Zone. Estuar. Coasts 38, 1656–1663.

Cherry, S.G., Derocher, A.E., Hobson, K.a., Stirling, I., Thiemann, G.W., 2011. Quantifying dietary pathways of proteins and lipids to tissues of a marine predator. J. Appl. Ecol. 48, 373–381.

Churchwell, R.T., Kendall, S.J., Blanchard, A.L., Dunton, K.H., Powell, A.N., 2016. Natural disturbance shapes benthic intertidal macroinvertebrate communities of high latitude river deltas. Estuar. Coasts 39:798–814. https://doi.org/10.1007/s12237-015-0028-2.

Connelly, T.L., Deibel, D., Parrish, C.C., 2012. Biogeochemistry of near-bottom suspended particulate matter of the Beaufort Sea shelf (Arctic Ocean): C, N, P, δ13C and fatty acids. Cont. Shelf Res. 43, 120–132.

Connelly, T.L., Deibel, D., Parrish, C.C., 2014. Trophic interactions in the benthic boundary layer of the Beaufort Sea Shelf, Arctic Ocean: combining bulk stable isotope and fatty acid signatures. Prog. Oceanogr. 120, 79–92.

Connelly, T.L., McClelland, J.W.J.W., Crump, B.C., Kellogg, C.T.E., Dunton, K.H., Colleen, K.T., Dunton, K.H., 2015. Seasonalal changes in quantity and composition of suspended particulate organic matter in lagoons of the Alaskan Beaufort Sea. Mar. Ecol. Prog. Ser. 527, 31–45.

Craig, P.C., 1984. Fish use of coastal waters of the Alaskan Beaufort Sea: a review. Trans. Am. Fish. Soc. 113, 265–282.

Craig, P.C., Griffiths, W.B., Haldorson, L., McElderry, H., 1982a. Ecological studies of Arctic cod (*Boreogadus saida*) in Beaufort Sea coastal waters, Alaska. Can. J. Fish. Aquat. Sci. 39, 395–406.

Craig, P.C., Griffiths, W.B., Johnson, S.R., 1982b. Trophic Dynamics in an Arctic Lagoon. Final Reports Outer Continental Shelf Environmental Association Program.

Craig, P.C., Griffiths, W.B., Haldorson, L., Mceiderry, H., McElderry, H., 1985. Distributional patterns of fishes in an Alaskan Arctic Lagoon. Polar Biol. 4, 9–18.

DeNiro, M.J., Epstein, S., 1977. Mechanism of carbon isotope fractionation associated with lipid synthesis. Science 197, 261–263.

Dunton, K.H., Schell, D.M., 1987. Dependence of consumers on macroalgal (Laminaria solidungula) carbon in an arctic kelp community: δ13C evidence. Mar. Biol. 93, 615–625.

Dunton, K.H., Saupe, S.M., Golikov, an N., Schell, D.M., Schonberg, S.V., 1989. Trophic relationships and isotopic gradients among arctic and subarctic marine fauna. Mar. Ecol. Prog. Ser. 56, 89–97.

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.

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. Coasts 35, 416–435.

Fechhelm, R.G., Baker, A.M., Haley, B.E., Link, M.R., 2009. Year 27 of the long-term monitoring of nearshore Beaufort Sea fishes in the Prudhoe Bay region: 2009 annual report. Report for BP Exploration (Alaska) Inc. by LGL Alaska Research Associates. Inc., Anchorage, Alaska. 79.

Frost, K.J., Lowry, L.F., 1984. Trophic relationships of vertebrate consumers in the Alaskan Beaufort Sea. Pages 381–401The Alaskan Beaufort Sea – Ecosystems and Environments. Academic Press, Inc.

Frost, K.J., Lowry, L.F., Carroll, G., 1993. Beluga whale and spotted seal use of a coastal lagoon system in the Northeastern Chukchi Sea. Arctic 46, 8–16.

Fry, B., Sherr, E.B., 1984. d13C measurements as indicators of carbon flow in marine and freshwater ecosystems. Contrib. Mar. Sci. 27, 13–47.

Gelman, A., Carlin, J.B., Stern, H.S., Rubin, D.B., 2004. Bayesian data analysis. Chapman & Hall/CRC, Boca Raton, FL.

Glud, R.N., Woelfel, J., Karsten, U., Kühl, M., Rysgaard, S., 2009. Benthic microalgal production in the Arctic: applied methods and status of the current database. Bot. Mar. 52, 559–571.

Goñi, M.A., O'Connor, A.E., Kuzyk, Z.Z., Yunker, M.B., Gobeil, C., Macdonald, R.W., 2013. Distribution and sources of organic matter in surface marine sediments across the north American Arctic margin. J. Geophys. Res. Oceans 118, 4017–4035.

Gradinger, R., 2009. Sea-ice algae: major contributors to primary production and algal biomass in the Chukchi and Beaufort Seas during May/June 2002. Deep-Sea Res. II Top. Stud. Oceanogr. 56, 1201–1212.

Graeve, M., Kattner, G., Piepenburg, D., 1997. Lipids in arctic benthos: does the fatty acid and alcohol composition reflect feeding and trophic interactions? Polar Biol. 18, 53–61.

Harris, R.K., 1993. Beaufort Sea Coastal Fish Studies Overview and Bibliography.

Harris, C.M., Mcclelland, J.W., Connelly, T.L., Crump, B.C., Dunton, K.H., 2017. Salinity and temperature regimes in Eastern Alaskan Beaufort Sea lagoons in relation to source water contributions. Estuar. Coasts 40, 50–62.

Hobson, K.a., Ambrose, W.G., Renaud, P.E., 1995. Sources of primary production, benthic-pelagic coupling, and trophic relationships within the Northeast Water Polynya: insights from d13C and d15N analysis. Mar. Ecol. Prog. Ser. 128, 1–10.

Hop, H., Gjøsæter, H., 2013. Polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) as key species in marine food webs of the Arctic and the Barents Sea. Mar. Biol. Res. 9, 878–894.

Horner, R., Schrader, G.C., 1982. Relative contributions of ice algae, phytoplankton, and benthic microalgae to primary production in nearshore regions of the Beaufort Sea. Arctic 35, 485–503.

Iken, K., Bluhm, B.a., Gradinger, R., 2005. Food web structure in the high Arctic Canada Basin: evidence from d13C and d15N analysis. Polar Biol. 28, 238–249.

Iken, K., Bluhm, B., Dunton, K., 2010. Benthic food-web structure under differing water mass properties in the southern Chukchi Sea. Deep-Sea Res. II Top. Stud. Oceanogr. 57, 71–85.

Jobling, M., Johansen, S.J.S., Foshaug, H., Burkow, I.C., Jørgensen, E.H., 1998. Lipid dynamics in anadromous Arctic charr, *Salvelinus alpinus* (L.): seasonal variations in lipid storage depots and lipid class composition. Fish Physiol. Biochem. 18, 225–240.

Jorgenson, M.T., Brown, J., 2005. Classification of the Alaskan Beaufort Sea Coast and estimation of carbon and sediment inputs from coastal erosion. Geo-Mar. Lett. 25, 69–80.

Kaufman, M.R., Gradinger, R.R., Bluhm, B.A., O'Brien, D.M., 2008. Using stable isotopes to assess carbon and nitrogen turnover in the Arctic sympagic amphipod Onisimus litoralis. Oecologia 158, 11–22.

Kiessling, A., Pickova, J., Johansson, L., Åsgård, T., Storebakken, T., Kiessling, K.H., 2001. Changes in fatty acid composition in muscle and adipose tissue of farmed rainbow trout (*Oncorhynchus mykiss*) in relation to ration and age. Food Chem. 73, 271–284.

Kruse, J., 1991. Alaska Inupiat subsistence and wage employment patterns: understanding individual choice. Hum. Organ. 50, 317–326.

Kvach, Y., 2009. First report of saduria (Mesidotea) entomon (Linnaeus, 1758) (Isopoda: Chaetiliidae) in the Black Sea. Aquat. Invasions 4, 393–395.

Lantuit, H., Overduin, P.P., Couture, N., Wetterich, S., Aré, F., Atkinson, D., Brown, J., Cherkashov, G., Drozdov, D., Forbes, D.L., et al., 2012. The Arctic coastal dynamics database: a new classification scheme and statistics on Arctic permafrost coastlines. Estuar. Coasts 35, 383–400.

Lebreton, B., Beseres Pollack, J., Blomberg, B., Palmer, T.A., Adams, L., Guillou, G., Montagna, P.A., 2016. Origin, composition and quality of suspended particulate organic matter in relation to freshwater inflow in a South Texas estuary. Estuar. Coast. Shelf Sci. 170, 70–82.

Legendre, L., Ackley, S., Dieckmann, G., Gulliksen, B., Horner, R., Hoshiai, T., Melnikov, I., Reeburgh, W., Spindler, M., Sullivan, C., 1992. Ecology of sea ice biota. Polar Biol. 12, 429–444.

Loseto, L.L., Stern, G.a., Deibel, D., Connelly, T.L., Prokopowicz, a., Lean, D.R.S., Fortier, L., Ferguson, S.H., 2008. Linking mercury exposure to habitat and feeding behaviour in Beaufort Sea beluga whales. J. Mar. Syst. 74, 1012–1024.

Lovvorn, J.R., Cooper, L.W., Brooks, M.L., De Ruyck, C.C., Bump, J.K., Grebmeier, J.M., 2005. Organic matter pathways to zooplankton and benthosunder pack ice in late winter and open water in late summer in the north-central Bering Sea. Mar. Ecol. Prog. Ser. 291, 135–150.

Lowry, L.F., Sheffield, G., George, J.C., 2004. Bowhead whales feeding in the Alaskan Beaufort Sea, based on stomach contents analysis. J. Cetacean Res. Manag. 6, 215–223.

Macdonald, R.W., Solomon, S.M., Cranston, R.E., Welch, H.E., Yunker, M.B., Gobeil, C., 1998. A sediment and organic carbon budget for the Canadian Beaufort shelf. Mar. Geol. 144, 255–273.

Macdonald, R.W., Sakshaug, E., Stein, R., 2004. The Arctic Ocean: Modern status and recent climate change. Pages 6–21. In: Stein, R., Macdonald, R.W. (Eds.), The Organic Carbon Cycle in the Arctic Ocean. Springer-Verlag, Berlin.

Macdonald, T.A., Burd, B.J., Macdonald, V.I., Van Roodselaar, A., 2010. Taxonomic and feeding guild classification for the marine benthic macroinvertebrates of the strait of Georgia, British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 69.

Macko, S.A., Fogel, L., Hare, P.E., Hoering, T.C., 1987. Isotopic fractionation of nitrogen and carbon in the synthesis of amino acids by microorganisms. Chem. Geol. Isot. Geosci. 65, 79–92.

Marty, J., Planas, D., 2008. Comparison of methods to determine algal δ13C in freshwater. Limnol. Oceanogr. Methods 6, 51–63.

McClelland, J.W., Holmes, R.M., Dunton, K.H., Macdonald, R.W., 2012. The Arctic Ocean estuary. Estuar. Coasts 35, 353–368.

McClelland, J.W., Townsend-Small, A., Holmes, R.M., Pan, F., Stieglitz, M., Khosh, M., Peterson, B.J., 2014. River export of nutrients and organic matter from the North Slope of Alaska to the Beaufort Sea. Water Resour. Res. 1823–1839.

McConnaughey, T., McRoy, C.P., 1979. Food-web structure and fractionation of carbon isstopes in the Bering Sea. Mar. Biol. 53, 257–262.

McCutchan Jr., J.H., Lewis Jr., W.M., Kendall, C., McGrath, C.C., 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102, 378–390.

McMahon, K.W., Ambrose, 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.

McTigue, N.D., Dunton, K.H., 2014. Trophodynamics and organic matter assimilation pathways in the northeast Chukchi Sea, Alaska. Deep-Sea Res. II Top. Stud. Oceanogr. 102, 84–96.

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. II 144, 175–189.

McTigue, N.D., Bucolo, P., Liu, Z., Dunton, K.H., 2015. Pelagic-benthic coupling, food webs, and organic matter degradation in the Chukchi Sea: insights from sedimentary pigments and stable carbon isotopes. Limnol. Oceanogr. 60, 429–445.

Mincks, S.L., Smith, C.R., DeMaster, D.J., 2005. Persistence of labile organic matter and microbial biomass in Antarctic shelf sediments: evidence of a sediment "food bank.". Mar. Ecol. Prog. Ser. 300, 3–19.

Møller, P., Hellgren, L., 2006. Lipids and Stable Isotopes in Marine Food Webs in West Greenland: Trophic Relations and Health Implications. Technical University of DenmarkDanmarks Tekniske Universitet, Department of Biochemistry and NutritionInstitut for Biokemi og Ern{æ}ring.

Mohan, 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.

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.

NOAA, 2010. NOAA Tide Predictions: Flaxman Island 2010.

Nolan, M., Churchwell, R., Adams, J., McClelland, J., Tape, K., Kendall, S., Powell, A., Dunton, K., Payer, D., Martin, P., 2011. Predicting the impact of glacier loss on fish, birds, floodplains, and estuaries in the Arctic National Wildlife Refuge. Pages 2011–2016Proceedings of the Fourth Interagency Conference on Research in the Watersheds: Observing, Studying and Managing for Change.

North, C.A., Lovvorn, J.R., Kolts, J.M., Brooks, M.L., Cooper, L.W., Grebmeier, J.M., 2014. Deposit-feeder diets in the Bering Sea: potential effects of climatic loss of sea ice-related microalgal blooms. Ecol. Appl. 24, 1525–1542.

Oakes, J.M., Rysgaard, S., Glud, R.N., Eyre, B.D., 2016. The transformation and fate of sub-Arctic microphytobenthos carbon revealed through 13C-labeling. Limnol. Oceanogr. 61, 2296–2308.

Overeem, I., Anderson, R.S., Wobus, C.W., Clow, G.D., Urban, F.E., Matell, N., 2011. Sea ice loss enhances wave action at the Arctic coast. Geophys. Res. Lett. 38.

Oxtoby, L.E., Mathis, J.T., Juranek, L.W., Wooller, M.J., 2015. Estimating stable carbon isotope values of microphytobenthos in the Arctic for application to food web studies. Pol 1–11.

Parnell, A.C., Inger, R., Bearhop, S., Jackson, A.L., 2010. Source partitioning using stable isotopes: coping with too much variation. PLoS One 5, 1–5.

Parnell, A.C., Phillips, D.L., Bearhop, S., Semmens, B.X., Ward, E.J., Moore, J.W., Jackson, A.L., Grey, J., Kelly, D.J., Inger, R., 2013. Bayesian stable isotope mixing models. Environmetrics 24, 387–399.

Pedersen, S., Linn, A., 2005. Kaktovik 2000–2002 subsistence fishery harvest assessment. U.S. Fish and Wildlife Service, Office of Subsistence Management, Fishery Information Services Division, Federal Subsistence Fishery Monitoring Program, Final Project.

Peterson, B.J., McClelland, J., Curry, R., Holmes, R.M., Walsh, J.E., Aagaard, K., 2006. Trajectory shifts in the Arctic and subarctic freshwater cycle. Science (New York, N.Y.) 313, 1061–1066.

Phillips, D.L., Inger, R., Bearhop, S., Jackson, A.L., Moore, J.W., Parnell, A.C., Semmens, B.X., Ward, E.J., 2014. Best practices for use of stable isotope mixing models in. Can. J. Zool. 835, 823–835.

Pineault, S., Tremblay, J.É., Gosselin, M., Thomas, H., Shadwick, E., 2013. The isotopic signature of particulate organic C and N in bottom ice: key influencing factors and applications for tracing the fate of ice-algae in the Arctic Ocean. J. Geophys. Res. Oceans 118, 287–300.

Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83, 703–718.

Quakenbush, L.T., Suydam, R.S., Bryan, A.L., Lowry, L.F., Frost, K.J., Mahoney, B.A., 2015. Diet of Beluga whales, *Delphinapterus leucas*, in Alaska from stomach contents, March–November. Mar. Fish. Rev. 70–84.

R Core Team, 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing Vienna, Austria. URL. http://www.R-project.org/.

Saupe, S.M., Schell, D.M., Griffiths, W.B., 1989. Carbon-isotope ratio gradients in western arctic zooplankton. Mar. Biol. 103, 427–432.

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., Saupe, S.M., Haubenstock, N., 1989. Bowhead whale (Balaena mysticetus) growth and feeding as estimated by δ13C techniques. Mar. Biol. 103, 433–443.

Scott, C.L., Kwasniewski, S., Falk-Petersen, S., Sargent, J.R., 2000. Lipids and life strategies of Calanus finmarchicus, Calanus glacialis and Calanus hyperboreus in late autumn, Kongsfjorden, Svalbard. Polar Biol. 23, 510–516.

Sipler, R., Bronk, D., 2015. Dynamics of dissolved organic nitrogen. Pages 127–232. In: DAHA, C. (Ed.), Biogeochemistry of Marine Dissolved Organic Matter. Academic Press Bulletin, Boston, MA.

Tamelander, T., Søreide, J.E., Hop, H., Carroll, M.L., 2006. Fractionation of stable isotopes in the Arctic marine copepod Calanus glacialis: effects on the isotopic composition of marine particulate organic matter. J. Exp. Mar. Biol. Ecol. 333, 231–240.

Vander Zanden, M.J., Rasmussen, J.B., 2001. Variation in delta N-15 and delta C-13 trophic fractionation: implications for aquatic food web studies. Limnol. Oceanogr. 46, 2061–2066.

Walkusz, W., Paulic, J.E., Williams, W.J., Kwasniewski, S., Papst, M.H., 2011. Distribution and diet of larval and juvenile Arctic cod (Boreogadus saida) in the shallow Canadian Beaufort Sea. J. Mar. Syst. 84, 78–84.

View publication stats