

Seasonal variation in trophic structure and community niche dynamics of an Arctic coastal community of marine vertebrates

Matthew Fuirst^{a,b}, Kyle H. Elliott^c, Steven H. Ferguson^{b,d}, Aaron T. Fisk^e, Les N. Harris^b, Kevin J. Hedges^b, Kevin B. Jacobs^b, Kelsey F. Johnson^b, Tracey N. Loewen^b, Cory J. D. Matthews^{b,d}, C.J. Mundy^f, Andrea Niemi^b, Wesley R. Ogloff^{b,g}, Cortney A. Watt^{b,d}, and David J. Yurkowski^{b,d}

^aDepartment of Integrative Biology, University of Guelph, Guelph, ON, Canada, N1G 2W1; ^bArctic and Aquatic Research Division, Fisheries and Oceans Canada, Winnipeg, MB R3T 2N6, Canada; ^cDepartment of Natural Resources Sciences, McGill University, Ste. Anne de Bellevue, QC, H9X 3V9, Canada; ^dDepartment of Biological Sciences, University of Manitoba, Winnipeg, MB, R3T 2N2, Canada; ^eGreat Lakes Institute for Environmental Research, University of Windsor, Windsor, ON, N8N 4P3, Canada; ^fCentre for Earth Observation Science, University of Manitoba, Winnipeg, MB, R3T 2N2, Canada; ^gDepartment of Integrative Biology, University of Windsor, Windsor, ON, N8N 4P3, Canada

Corresponding author: **Matthew Fuirst** (email: mfuirst@gmail.com)

Abstract

Temporal variation in food web structure is widespread among highly seasonal environments, such as the Arctic, and is driven by changes in resource availability. Variation in resource availability can lead to species differences in diet composition, isotopic niche width, and trophic position (TP) across seasons. Here, we used tissue samples that represent two distinct turnover rates for diet (liver = shorter term, muscle = longer term) from 18 fish and three marine mammal species to investigate seasonal (i) variation in TPs within the Southampton Island marine ecosystem of Hudson Bay, (ii) variation in consumer isotopic niche width within this part of the food web, and (iii) variation in community niche dynamics among a fish and marine mammal community using stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope analyses. Many zooplanktivores and piscivores increased in TP in summer (i.e., shorter-term turnover period), whereas benthic feeders dependent on ice-obligate prey decreased in TP. Most isotopic niche widths and community metrics ($\delta^{15}\text{N}$ range, total ellipse area, mean centroid distance) were higher in liver than muscle. Our findings demonstrate seasonal changes in TPs, which suggests that Arctic communities may be differentially affected by longer ice-free periods and earlier onset of primary production due to accelerated climate change.

Key words: Southampton Island, marine mammals, marine fishes, food webs, stable isotopes

Introduction

Ecosystems are characterized by environmental seasonality that shapes temporal variation in resource availability and resource abundance for consumers (Finlay and Kendall 2007; McMeans et al. 2015; Barbedo et al. 2020). Therefore, quantifying seasonal changes in species assemblages, trophic diversity, and food web structure is integral for understanding the abiotic and biotic drivers of ecosystem processes (Paine 1966; Thompson et al. 2012). This is particularly important for polar ecosystems, which are experiencing continual warming and poleward alterations in species distributions (Root et al. 2003; Hickling et al. 2006; IPCC 2014). These alterations are subsequently driving long-term changes in food web structure and function (Kortsch et al. 2015), species abundances (Wassmann et al. 2011), and growth and condition of Arctic species (Wassmann et al. 2011). In polar environments, drastic seasonal variation in temperature and light availabil-

ity govern ice cover thickness and extent (Polyak et al. 2010) and consequently the levels of organic carbon inputs derived from ice algae production in spring and phytoplankton in summer (Grebmeier and Barry 1991; Riedel et al. 2008; Søreide et al. 2010; Barbedo et al. 2020; Gradinger and Bluhm 2020). However, due to logistical challenges associated with sampling numerous vertebrate consumer species across seasons in the Arctic, seasonal variation in the trophic structure of coastal Arctic systems has seldom been studied. Studies in spring are particularly limited since most research on Arctic consumers to date occur in the summer and fall, thus highlighting a trophic structure based on solely after the phytoplankton bloom (e.g., during the open water period; Dunton et al. 2006; Renaud et al. 2011; Yurkowski et al. 2018).

A well-established method to study the trophic structure of communities is the application of stable isotope analysis (Hobson and Welch 1992; Middelburg 2014). Stable carbon

($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios in tissues of animals provide information on spatiotemporal variation in their resource use and diet (Boecklen et al. 2011; Layman et al. 2012). Specifically, $\delta^{15}\text{N}$ can be used to estimate the trophic position (hereafter; TP) of consumers (i.e., diet; higher $\delta^{15}\text{N}$ corresponds to higher position in food web), while $\delta^{13}\text{C}$ estimates the carbon energy source of an animal's prey and, in turn, habitat use of the consumer (i.e., benthic, pelagic, or freshwater inputs; France 1995; Szpak and Buckley 2020). In the Arctic, $\delta^{13}\text{C}$ signatures of ice algae and phytoplankton are generally unique enough to discern the reliance of a given organism on each carbon source, with $\delta^{13}\text{C}$ often being higher in sea-ice algae compared to phytoplankton (Hobson et al. 1995; Pineault et al. 2013; Yurkowski et al. 2020). Due to the distinct biomarker signature of sea-ice algae and phytoplankton, bulk isotope biomarkers (e.g., bulk and compound-specific stable isotopes) have been used as a valuable tool to quantify human- and climate-driven variation in trophic structure and community dynamics (Yurkowski et al. 2018; Ogloff et al. 2019). Using tissues from marine predators in Arctic ecosystems, both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ have been used to quantify trophic diversity and redundancy (Yurkowski et al. 2018; Ogloff et al. 2019; Amiriaux et al. 2023). Trophic diversity refers to the diversity of diet, habitat, and resource use among a community of consumers where higher trophic diversity signifies more spread among these species in isotopic niche space. Trophic redundancy is defined by the degree to which multiple species function similarly within a community, resulting in less spread of consumers in isotopic niche space thus leading to competition and overlap in resource use across these consumers (Polis et al. 2000; Yurkowski et al. 2018).

The marine region around the coasts of Southampton Island, northwest Hudson Bay (Nunavut) has been identified as a biological hotspot (Yurkowski et al. 2019) and an Area of Interest for Marine Protected Area (MPA) designation by Fisheries and Oceans Canada (DFO, Loewen et al. 2020). The waterways around Southampton Island are characterized by strong tides and currents, which lead to well-mixed, nutrient-rich waters (Carmack and Wassmann 2006) and the formation of polynyas, both of which promote primary production and rich benthic communities (Hannah et al. 2009). Southampton Island and the surrounding marine region supports some of Canada's largest winter and summer aggregations of Arctic marine mammals including bowhead whales (*Balaena mysticetus*), narwhal (*Monodon monoceros*), beluga (*Delphinapterus leucas*), ringed seals (*Pusa hispida*), bearded seals (*Erignathus barbatus*), and Atlantic walrus (*Odobenus rosmarus rosmarus*). Southampton Island is also a biological hotspot for many benthic and zooplanktivorous fishes such as Arctic cod (*Boreogadus saida*), sand lance (*Ammodytes* sp.), slender eelblenny (*Lumpenus fabricii*), and capelin (*Mallotus villosus*; Loewen et al. 2020). The wealth of biodiversity in and around Southampton Island has also been the backbone for local subsistence by Indigenous peoples for millennia (Clarke 1980; Loewen et al. 2020). Even though Southampton Island has a unique physical and biological marine environment, little is known about how the trophic diversity of the food web and consumer niche dynamics across numerous vertebrate species may vary between the winter-

summer (~February–June) and summer (~June–August) seasons.

Our goal was to better understand the seasonal variation in food web dynamics of the Southampton Island system using liver and muscle tissues of fish and marine mammal assemblages. Variation in resource abundance and migratory routes between winter–summer and summer can lead to changes in the diet of marine vertebrates. These seasonal changes are reflected by the tissue-specific turnover rates of liver (short-term turnover that represents the summer period) and muscle (long-term turnover that represents the winter–summer period), respectively. The objectives of this study were to use liver (short term; summer) and muscle (long term; winter–summer) tissues from 16 marine fish species and three marine mammal species (narwhal, beluga, and Atlantic walrus) to examine the effect of season on (1) TP, (2) isotopic niche width, and (3) trophic diversity and redundancy.

Materials and methods

Sample collection

Demersal and pelagic fish and marine mammal samples were collected in 2016, 2018, and 2019 in the waters surrounding Southampton Island, Nunavut, Canada (Fig. 1). Fish samples were collected each year in early-August to early-September aboard the *MV Nulijjuk* (2016) and the *RV William Kennedy* (2018 and 2019). In 2016, fishes were collected using a Yankee style bottom trawl (~40 m wide mouth opening with 8 mm liner) that was towed at 2–3 knots for 30 min on bottom. In 2018 and 2019, fish samples were collected using a 3 m pelagic trawl (0.5 cm cod-end mesh) that was towed between 2 and 3 knots for 15 min targeting the mid-depth part of the water column. A 3 m benthic trawl (0.5 cm cod-end mesh) was towed at 2–3 knots for 15 min on bottom. Opportunistic fish samples from the breeding ledges of thick-billed murre (*Uria lomvia*) at Coats Island were also collected (Fig. 1).

To examine differences in TP, isotopic niche width, and community niche dynamics across seasons, we collected both liver and muscle samples from fishes and marine mammals sampled between July and September. Liver tissue has a faster turnover rate than muscle, with an isotopic half-life on a weekly scale, whereas muscle tissue is typically representative of diet integrated over several months (~1–4 months; Vander Zanden et al. 2015). For example, based on body mass of ectothermic fishes from existing studies, 95% turnover of liver can occur within several weeks (range of 39–58 days; MacNeil et al. 2006; Barton et al. 2019) and muscle within several months (range 98–122 days; MacNeil et al. 2006; Barton et al. 2019). For marine mammals, turnover of liver (~14–17 days) is also much shorter than muscle (approximately 202 days; Browning et al. 2014; Vander Zanden et al. 2015). To examine population-level differences in trophic structure and isotopic niche width, we used samples from 16 fish species, which included 178 liver samples and 250 muscle samples. Fish species that were collected included Arctic cod, fourline snakeblenny (*Eumesogrammus praecisus*), Arctic staghorn sculpin (*Gymnocanthus tricuspis*), Atlantic poacher

Fig. 1. Data collection study sites were located in the marine area surrounding Southampton Island and Coats Island as well as samples collected from Inuit communities at Coral Harbour and Naujaat in Nunavut, Canada. This map includes an ESRI World Ocean basemap under a Lambert Conformal Conic projection in ArcGIS Pro version 3.1.1.



(*Leptagonus decagonus*), daubed shanny (*Leptoclinius maculatus*), slender eelblenny, Arctic sculpin (*Myoxocephalus scorpioides*), shorthorn sculpin (*Myoxocephalus scorpius*), fish doctor (*Gymnelus viridis*), banded gunnel (*Pholis fasciata*), Arctic shanny (*Stichaeus punctatus*), twohorn sculpin (*Icelus bicornis*), spatulate sculpin (*Icelus spatula*), moustache sculpin (*Triglops murrayi*), snailfish (*Liparis sp.*), and ribbed sculpin (*Triglops pingelii*).

Marine mammal samples consisted of 24 liver and 31 muscle samples from Atlantic walrus (liver = 4, muscle = 4), narwhal (liver = 12, muscle = 15), and beluga (liver = 8, muscle = 12). Muscle and liver samples from marine mammals were collected from July to September in 2016, 2018, and 2019 by Inuit hunters from Naujaat and Coral Harbour, Nunavut as part of their subsistence harvests and ongoing

community-based monitoring programs in collaboration with DFO (Fig. 1). All tissue samples were frozen at -20°C and shipped to the Freshwater Institute in Winnipeg, Manitoba before processing. Samples were collected through approved Nunavut Research Institute Licenses (03 009 19R-M and 03 015 18R-M) and Licenses to Fish for Scientific Purposes (S-18/19-1038-NU and S-19/20-1046-NU).

Stable isotope analysis

All tissue samples from fishes and marine mammals were freeze-dried for 48 h and subsequently homogenized using a mortar and pestle. Due to the abundance of lipids in Arctic vertebrates, lipids in marine mammal (Yurkowski et al. 2015) and fish (Post et al. 2007) liver and muscle were ex-

tracted with 2:1 chloroform:methanol solvent using a modified version of the [Bligh and Dyer \(1959\)](#) method. Stable isotope analysis was performed at the Chemical Tracers Laboratory, Great Lakes Institute for Environmental Research, at the University of Windsor using a Delta V Advantage Mass spectrometer (Thermo Finnigan, San Jose, CA, USA) coupled to a Costech 4010 Elemental Combustion system (Costech, Valencia, CA, USA) and a ConFlo IV gas interface. For $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis, subsamples of 400–600 μg of tissue were weighed into tin capsules. All stable isotope ratios are expressed in per mil (‰) in standard delta (δ) notation relative to the international standards Pee Dee Belemnite for carbon and atmospheric N_2 for nitrogen ([Craig 1957](#); [Mariotti 1983](#)) using the following equation:

$$(1) \quad \delta X = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 10^3$$

In this equation, X is ^{13}C or ^{15}N and R equals $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. During the analysis, instrumentation accuracy was checked and based on NIST standards 8573, 8547, and 8574 for $\delta^{15}\text{N}$ ($n = 50$ for all) and 8542, 8573, 8574 for $\delta^{13}\text{C}$ ($n = 50$ for all). The mean difference from the certified NIST standard values were 0.09‰, 0.14‰, 0.06‰ for $\delta^{15}\text{N}$ and 0.09‰, 0.01‰, and 0.08‰ for $\delta^{13}\text{C}$. Precision for all the standards, which was assessed by the standard deviation of replicate analyses of three standards—NIST1577c (internal lab standard, tilapia muscle), USGS 40, and Urea; $n = 22$ for all—was measured at $\leq 0.2\%$ for $\delta^{15}\text{N}$ and $\leq 0.1\%$ for $\delta^{13}\text{C}$.

Calculating trophic position

Trophic position (TP) was calculated for each species/taxonomic group using a one-source TP model ([Post 2002](#)) to determine whether TP varies seasonally across species.

$$\text{TP}_{\text{consumer}} = \text{TP}_{\text{baseline}} + \frac{\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{baseline}}}{\Delta^{15}\text{N}}$$

In benthic and pelagic ecosystems, the $\delta^{15}\text{N}$ of primary producers can often vary depending on species, diet, and environmental factors ([Post 2002](#)). However, in the marine waters around Southampton Island, the $\delta^{15}\text{N}$ of the pelagic-feeding copepod *Calanus hyperboreus* ($9.5 \pm 0.4\%$) was comparable to that of sea urchins ($\delta^{15}\text{N} = 8.7 \pm 1.6\%$; [Paar et al. 2019](#)) and filter-feeding bivalves ($\delta^{15}\text{N} = 8.5 \pm 0.1\%$), and therefore *C. hyperboreus* was used as the baseline ($\delta^{15}\text{N}_{\text{baseline}}$) when calculating TP for all fish species using a scaled one-source TP model because diet-tissue discrimination factors (DTDFs; $\Delta^{15}\text{N}$) decrease with each trophic step up the food chain ([Hussey et al. 2014](#)). The baseline ($\text{TP}_{\text{baseline}}$) used to estimate the TP of all fishes was 2, which represented the TP of *C. copepods* since it was comparable to the TP of benthic grazers (i.e., sea urchins and bivalves). To estimate the TP of fishes, DTDFs of 3.67‰ and 2.80‰ were used for muscle and liver, respectively, ([McCutchan et al. 2003](#); [Caut et al. 2009](#); [Canseco et al. 2022](#)) with *C. hyperboreus* as the baseline. Since beluga and narwhal are primarily piscivorous and consume small pelagic fish species such as capelin and Arctic

cod ([Marcoux et al. 2012](#); [Matley et al. 2015](#); [Watt and Ferguson 2015](#)), we used the mean TP baseline (3.4) and $\delta^{15}\text{N}_{\text{baseline}}$ (14.25) averaged between Arctic cod ($\delta^{15}\text{N} = 14.9 \pm 1.1\%$) and capelin ($\delta^{15}\text{N} = 13.6 \pm 0.8\%$) to estimate the TP of narwhal and beluga. For Atlantic walrus, the TP baseline ($\text{TP}_{\text{baseline}} = 2$) was used since Bivalvia are their main prey ([Dehn et al. 2006](#)). The muscle and liver diet discrimination factors used for $\Delta^{15}\text{N}$ of marine mammals were 2.4‰ and 3.1‰, respectively ([Hobson et al. 1996](#); [McCutchan et al. 2003](#); [Caut et al. 2009](#)). We subtracted from the $\delta^{15}\text{N}$ for fishes and marine mammals their respective $\Delta^{15}\text{N}$ mentioned above to standardize for tissue-specific DTDFs for each species group. The muscle and liver diet discrimination factors used for $\Delta^{13}\text{C}$ of fishes were 1.7‰ and 0.6‰, respectively ([Canseco et al. 2022](#)). For the $\delta^{13}\text{C}$ diet discrimination factors of marine mammals, we used 1.3‰ for muscle and 0.6‰ for liver ([Hobson et al. 1996](#)). There is little published information on diet discrimination factors for marine mammal liver and muscle tissue and thus, we are not able to measure species-specific variation in DTDFs between Atlantic walrus, beluga, and narwhal. Therefore, we decided that the most appropriate DTDFs to use for the marine mammal species in this study were the discrimination factors of pinnipeds from [Hobson et al. \(1996\)](#), which have been used in multiple published studies on other marine mammal species ([Lesage et al. 2001](#); [Newsome et al. 2009](#); [Marcoux et al. 2012](#); [Yurkowski et al. 2018](#); [Simond et al. 2023](#)). Species within TPs between 1.5 and 2.4 are considered primary consumers, whereas secondary consumers occupy TPs between 2.5 and 3.4 and tertiary or top predator consumers between 3.5 and 5.0 ([Gascuel et al. 2011](#); [Woodland et al. 2016](#); FishBase (<https://fishbase.net.br>)).

Statistical analysis

All statistical analyses were carried out using packages in the program R v. 4.0 ([R Core Team 2018](#)). We used a Shapiro-Wilks normality test to determine if the stable isotopes of consumers were normally distributed. Since stable isotopes of prey and consumers can vary annually and were not normally distributed ([Post 2002](#); [Fry 2006](#)), we used a Wilcoxon's signed-rank test to determine if the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for each species differed significantly across the sampling years (2016, 2018, and 2019).

To quantify the trophic diversity of marine mammal and fish assemblages between winter–summer and summer in the marine region around Southampton Island, we used a Bayesian inference package, SIBER (Stable Isotope Bayesian Ellipses in R; version 3.5.1; [Jackson et al. 2011](#)), in R to calculate six community-wide metrics across the combined fishes and marine mammal assemblages. Since we compared community metrics of fishes and marine mammals between liver (summer) and muscle (winter–summer) tissues, we standardized for differences in the species group and tissue-specific DTDFs.

We used samples from nine species of fish and three species of marine mammals (beluga, narwhal, and Atlantic walrus) for which we had at least four samples of both liver and muscle to compare isotopic niche width of each species

and community metrics between seasons. Additionally, given that multiple species of benthic-associated fish (e.g., Arctic alligatorfish, Arctic sculpin, spatulate sculpin, twohorn sculpin, Atlantic poacher, and daubed shanny) had a limited number of samples for both liver and muscle (<10), we combined these species into one functional group (hereafter called “zoobenthic”). All other fish species with at least 10 samples for both liver and muscle (i.e., Arctic cod, Arctic shanny, Arctic staghorn sculpin, banded gunnel, fourline snakeblenny, moustache sculpin, ribbed sculpin, shorthorn sculpin, and slender eelblenny) were not included in this zoobenthic group. The assignments for zoobenthic-feeding fish species were derived from the designations for foraging ecology in World Register of Marine Species (WoRMS; <https://marinespecies.org>) and FishBase (<https://fishbase.net.br>). Specifically, in both databases, each of the abovementioned species was described as a consumer of benthic invertebrate prey.

We used SIBER to calculate four isotopic community metrics of trophic diversity ($\delta^{13}\text{C}$ range, $\delta^{15}\text{N}$ range, mean distance to centroid, and total community area) and two metrics that estimate the extent of trophic redundancy (mean distance to the nearest neighbour and SDNND; Layman et al. 2007; Jackson et al. 2011) for the combined fish and marine mammal assemblages from liver and muscle. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranges are the distances between the individuals in the community with the highest and lowest $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. These ranges represent the variability in basal carbon sources and relative TP. Total ellipse area (TA) is the total isotope area between the means of each species' niche and is less biased by convex hull extremities. The mean distance to centroid (CD) is the average Euclidean distance of each species to the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ centroid of the entire community and provides a measure of the average degree of trophic diversity within a food web. Mean nearest neighbour distance (MNND) is the mean of the Euclidean distances to each species' nearest neighbour in bi-plot space and represents the density of species packing. The standard deviation of the nearest neighbour distance (SDNND) is a measure of the evenness of species packing in bi-plot space and is less influenced by sample size than the nearest neighbour distance (Layman et al. 2007; Jackson et al. 2011). All six metrics were derived from 2 000 000 iterations, with a burn-in of 100 000, and thinned by 10, leaving 90 000 posterior estimates from the posterior probability distribution.

We also used SIBER to generate standard ellipse area (corrected for small sample sizes; SEA_c), using approximately 40% of the data points within the ellipse to infer the population's core isotopic niche width. In addition, the 40% probability Bayesian standard ellipse area (SEA_b) was calculated. Finally, we used SIBER (Jackson et al. 2011) to assess the posterior probability distribution of Layman metrics and SEA_b to examine differences in community-wide metrics between tissue types (i.e., liver and muscle). Posterior probability distributions of Layman metrics were determined by the percentage of estimates from the posterior probability distribution that were lower in muscle compared to liver, relative to the total number of estimates. All error values reported throughout the study are given as standard error (SE).

Results

Stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$)

Among fish, the lowest average $\delta^{13}\text{C}$ for muscle ranged from $-19.5\text{‰} \pm 0.5\text{‰}$ (mean \pm SE) in moustache sculpin to $-16.3\text{‰} (\pm 0.2\text{‰})$ in Arctic staghorn sculpin. The lowest average $\delta^{13}\text{C}$ for liver ranged from $-20.2\text{‰} (\pm 0.6\text{‰})$ in Arctic cod to $-16.4\text{‰} (\pm 0.3\text{‰})$ in Arctic staghorn sculpin. For liver, banded gunnel had the lowest $\delta^{15}\text{N}$ ($13.0 \pm 0.8\text{‰}$) compared to shorthorn sculpin, which had the highest ($15.0 \pm 0.8\text{‰}$). For muscle, slender eelblenny had the lowest average $\delta^{15}\text{N}$ ($13.8 \pm 0.7\text{‰}$) and Arctic shanny had the highest ($15.7 \pm 0.5\text{‰}$). Within marine mammals, the lowest and highest $\delta^{13}\text{C}$ for muscle were from Atlantic walrus ($-17.2 \pm 0.08\text{‰}$) and beluga ($-18.2 \pm 0.2\text{‰}$), respectively. Atlantic walrus had the highest $\delta^{13}\text{C}$ for liver ($-18.5 \pm 0.06\text{‰}$) and narwhal had the lowest for liver ($-18.3 \pm 0.1\text{‰}$). For marine mammal liver and muscle, Atlantic walrus consistently had the lowest average $\delta^{15}\text{N}$ (liver = $9.8 \pm 0.1\text{‰}$; muscle = $10.4 \pm 0.2\text{‰}$; Table 1), whereas beluga had the highest $\delta^{15}\text{N}$ for both tissues (liver = $17.0 \pm 0.4\text{‰}$; muscle = $16.0 \pm 0.4\text{‰}$; Table 1).

Trophic position

Beluga and narwhal had the highest TP in the food web (TP > 4; Table 1; Fig. 2) among sampled species across both time periods. The TP of shorthorn sculpin and Arctic shanny occupied the tertiary consumer position in both muscle (winter to summer) and liver (summer) samples (TP \sim 4; Table 1; Fig. 2). The zoobenthic group, fourline snakeblenny, ribbed sculpin, Arctic cod, banded gunnel, moustache sculpin, Arctic staghorn sculpin, slender eelblenny, and Atlantic walrus occupied the secondary consumer positions across both seasons (TP \sim 2.5–3.5; Table 1; Fig. 2). Overall, the TPs for most species were similar across seasons based on calculations using muscle (winter to summer) and liver (summer) tissue. However, beluga (*t* test; $p = 0.05$, $t = 2.08$), fourline snakeblenny (*t* test; $p = 0.01$, $t = -2.61$), ribbed sculpin (*t* test; $p = 0.004$, $t = -3.45$), and shorthorn sculpin (*t* test; $p = 0.04$, $t = 2.12$), had a higher TP in the summer (TP range: 3.89–4.29) than winter–summer time period (TP range: 3.09–4.13).

Isotopic niche width and community-wide metrics

The posterior probability distributions of the Bayesian standard ellipse areas (SEA_b) were larger in summer (liver) than the winter to summer (muscle) time period for Arctic cod (probability of difference in posterior distributions between tissue types = 76%; liver = 1.82‰ , muscle = 1.56‰ ; Table 1; Fig. 3), Arctic shanny (97%; liver = 1.26‰ , muscle = 0.66‰ ; Table 1; Fig. 3), beluga (72%; liver = 0.48‰ , muscle = 0.37‰ ; Table 1; Fig. 3), fourline snakeblenny (99%; liver = 4.67‰ , muscle = 1.40‰ ; Table 1; Fig. 3), moustache sculpin (72%; liver = 1.28‰ , muscle = 1.07‰ ; Table 1; Fig. 3), ribbed sculpin (79%; liver = 1.10‰ , muscle = 0.87‰ ; Table 1; Fig. 3), and the

Table 1. Fish and marine mammal species' $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (‰, mean \pm SE), C:N ratio, mean and ranges of trophic position (TP), the mode of the standard Bayesian ellipse area (SEA_b), and the 95% Bayesian credible intervals for muscle and liver tissues collected from the marine region surrounding Southampton Island, Nunavut, Canada from 2016 to 2019.

Species	n	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	C:N	Mean TP (Range)	SEA _b mode	SEA _b credibles
Muscle							
Arctic cod	43	-19.4 \pm 0.5	14.9 \pm 0.9	3.1 \pm 0.002	3.47 (3.06–4.06)	1.56	1.17–2.12
Arctic shanny	20	-19.1 \pm 0.3	15.7 \pm 0.5	3.1 \pm 0.002	3.71 (3.40–3.94)	0.66	0.43–1.08
Arctic staghorn sculpin	17	-16.3 \pm 0.2	14.0 \pm 0.5	3.2 \pm 0.007	3.23 (2.79–3.53)	0.44	0.27–0.74
Banded gunnel	17	-19.5 \pm 0.5	14.5 \pm 0.8	3.1 \pm 0.006	3.38 (2.97–3.81)	1.24	0.74–2.24
Fourline snakeblenny	16	-18.2 \pm 0.7	15.7 \pm 0.6	3.1 \pm 0.005	3.70 (3.41–4.04)	1.40	0.86–2.40
Moustache sculpin	21	-19.4 \pm 0.8	14.2 \pm 0.5	3.1 \pm 0.003	3.29 (3.10–3.56)	1.07	0.70–1.70
Ribbed sculpin	20	-19.4 \pm 0.6	15.1 \pm 0.4	3.2 \pm 0.008	3.54 (3.29–3.80)	0.87	0.56–1.40
Shorthorn sculpin	12	-18.9 \pm 0.8	15.7 \pm 1.2	3.0 \pm 0.004	3.70 (3.01–4.26)	3.30	1.86–6.23
Slender eelblenny	13	-17.6 \pm 0.08	13.8 \pm 0.7	3.2 \pm 0.01	3.18 (2.74–3.41)	1.33	0.78–2.45
Zoobenthic	30	-18.9 \pm 0.7	15.2 \pm 0.9	3.1 \pm 0.003	3.57 (2.89–4.17)	2.39	1.64–3.64
Atlantic walrus	4	-17.2 \pm 0.08	10.4 \pm 0.2	3.1 \pm 0.03	3.40 (2.89–3.90)	0.60	0.21–2.11
Beluga	12	-18.2 \pm 0.2	16.0 \pm 0.4	3.1 \pm 0.003	4.13 (3.79–4.43)	0.37	0.21–0.72
Narwhal	15	-18.1 \pm 0.2	15.3 \pm 1.1	3.1 \pm 0.006	3.87 (3.48–5.55)	0.59	0.37–1.06
Liver							
Arctic cod	39	-20.2 \pm 0.6	13.7 \pm 0.9	3.7 \pm 0.009	3.50 (2.85–4.14)	1.82	1.32–2.56
Arctic shanny	19	-19.4 \pm 0.5	14.4 \pm 0.7	3.7 \pm 0.02	3.75 (2.99–4.20)	1.26	0.84–2.13
Arctic staghorn sculpin	17	-16.4 \pm 0.3	12.7 \pm 0.4	3.6 \pm 0.01	3.17 (2.97–3.61)	0.44	0.27–0.74
Banded gunnel	14	-20.1 \pm 0.5	13.1 \pm 0.8	3.5 \pm 0.01	3.27 (2.90–3.78)	0.99	0.60–1.80
Fourline snakeblenny	14	-18.2 \pm 0.3	13.3 \pm 1.2	3.8 \pm 0.03	3.35 (2.11–3.81)	4.67	2.71–8.63
Moustache sculpin	17	-19.8 \pm 0.6	13.2 \pm 0.8	3.6 \pm 0.01	3.34 (2.82–4.01)	1.28	0.80–2.17
Ribbed sculpin	11	-19.3 \pm 0.5	13.1 \pm 1.0	4.1 \pm 0.04	3.23 (2.68–3.56)	1.10	0.62–2.20
Shorthorn sculpin	12	-18.8 \pm 0.3	15.0 \pm 0.8	4.1 \pm 0.07	3.99 (3.47–4.63)	3.00	1.76–5.80
Slender eelblenny	11	-17.0 \pm 0.8	12.6 \pm 0.6	3.4 \pm 0.01	3.14 (2.51–3.33)	1.07	0.59–2.10
Zoobenthic	22	-19.1 \pm 0.1	13.9 \pm 0.9	3.8 \pm 0.02	3.57 (3.02–4.48)	3.21	2.11–5.10
Atlantic walrus	4	-18.5 \pm 0.06	9.8 \pm 0.1	3.9 \pm 0.09	3.11 (2.86–3.44)	0.45	0.17–1.73
Beluga	8	-18.3 \pm 0.3	17.0 \pm 0.4	3.4 \pm 0.01	4.29 (4.06–4.52)	0.48	0.23–1.09
Narwhal	12	-18.3 \pm 0.1	16.3 \pm 0.3	3.3 \pm 0.01	4.08 (3.88–4.26)	0.12	0.07–0.23

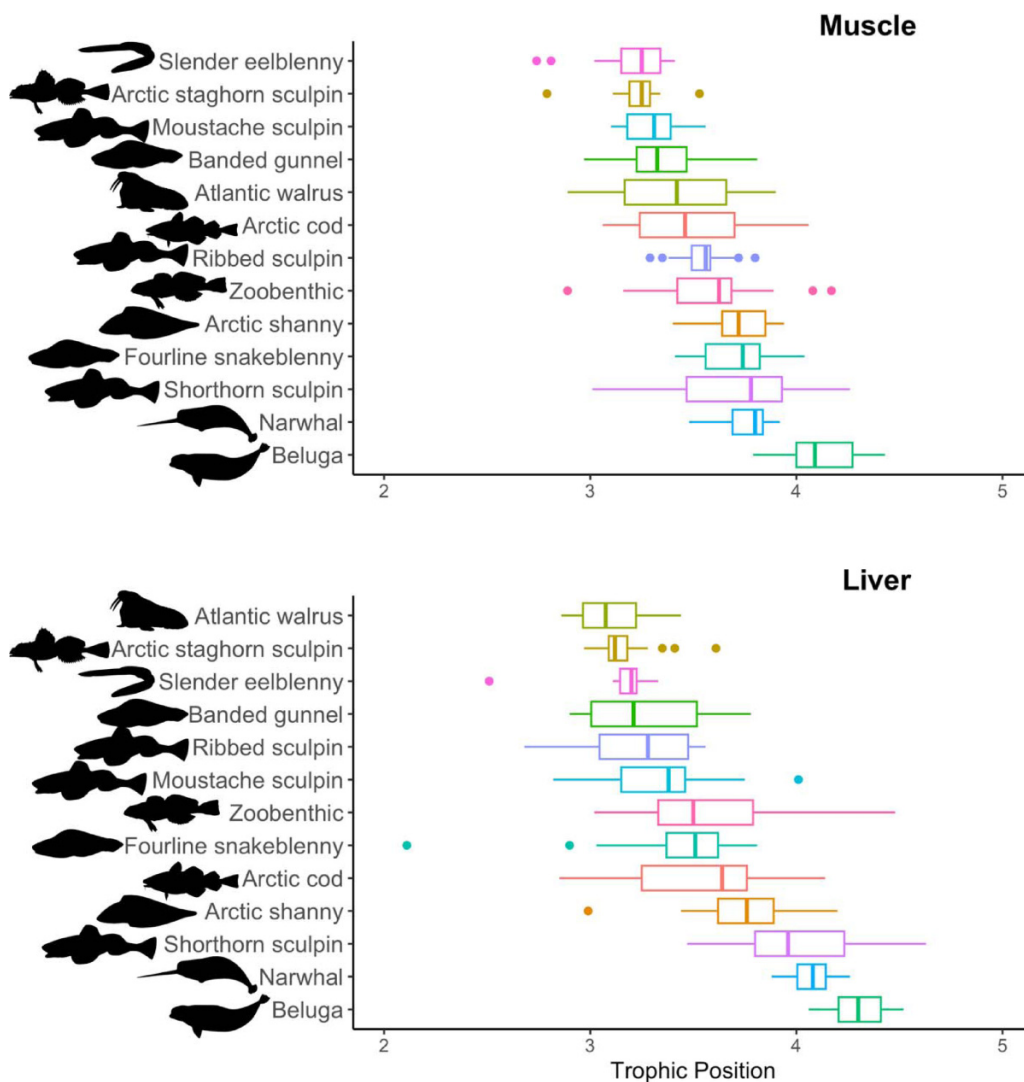
zoobenthic functional group (85%; liver = 3.21‰, muscle = 2.39‰; **Table 1; Fig. 3**). In contrast, posterior probabilities showed that SEA_b was smaller in the summer than the winter to summer time period for banded gunnel (71%; liver = 0.99‰, muscle = 1.24‰; **Table 1; Fig. 3**), shorthorn sculpin (57%; liver = 3.00‰, muscle = 3.30‰; **Table 1; Fig. 3**), slender eelblenny (68%; liver = 1.07‰, muscle = 1.33‰; **Table 1; Fig. 3**), Atlantic walrus (75%; liver = 0.45‰, muscle = 0.60‰; **Table 1; Fig. 3**) and narwhal (99%; liver = 0.12‰, muscle = 0.59‰; **Table 1; Fig. 3**).

Four out of the six community-wide metrics across the combined fish and marine mammal assemblages were higher in the summer (i.e., liver) than the winter to summer (i.e., muscle) periods and included total area (60%), $\delta^{13}\text{C}$ range (variability in basal carbon source; 89%), mean distance to centroid (88%), and MNND (66%; **Table 2; Fig. 4**). In contrast, there was a 79% probability that $\delta^{15}\text{N}$ range (relative TP) was higher in muscle than liver and a 78% probability that the standard deviation of nearest neighbour distance was higher in muscle than liver (**Table 2; Fig. 4**).

Discussion

Given the accelerating decreases in sea-ice cover extent and duration in Arctic ecosystems (**Comiso et al. 2008**), it is important to understand seasonal changes and potential realized niche widths of consumers to recognize how climate change may influence trophic dynamics in the future (**Yurkowski et al. 2018**). In this study, we characterized seasonal variation in the TP, isotopic niche width, and community metrics (total niche area, $\delta^{13}\text{C}$ -range, $\delta^{15}\text{N}$ -range, mean distance to centroid, and nearest neighbour distance) of numerous fish and marine mammal species inhabiting a coastal Arctic ecosystem between the winter to summer and summer time periods. Overall, while primary consumers (i.e., species with TP of 1.5–2.4) had relatively consistent TPs between seasons, some tertiary or top consumers (i.e., species with TP of 3.5–4.4) experienced considerable increases in TP between winter to summer and summer time periods, which may be reflective of their diet breadth or migration (i.e., in beluga; **Loseto et al. 2009**). Many of the zooplankton- and fish-feeding consumers such as Arctic cod, shorthorn sculpin, ribbed sculpin, and moustache sculpin increased in TP during the summer, while

Fig. 2. Boxplot (median and standard deviation) of the trophic positions (TP) of consumer species based on muscle and liver samples collected from the marine region surrounding Southampton Island, Nunavut, Canada from 2016 to 2019.



some species that may be primarily dependent on seasonally available benthic prey, such as slender eelblenny, had a relatively lower TP in the summer than winter to summer, which could be attributed to seasonal changes in depth for vertically migrating fishes (Benoit et al. 2010). For most species, isotopic niche width increased during the summer, which suggests that many consumers are able to adjust their diet in response to an increase in food abundance and diversity related to the phytoplankton bloom and potentially reduced competition for resources (Yurkowski et al. 2018). The fish and marine mammal assemblage also showed a higher $\delta^{13}\text{C}$ ranges, TA, mean distance to centroid, and MNND in summer than winter–summer, which also likely reflects their responses to seasonal variation in resource availability and abundance.

Seasonal variation in trophic position

The TP of tertiary consumers in this study (species that obtain nutrition by consuming secondary consumers), such as beluga, shorthorn sculpin, ribbed sculpin, and fourline snakeblenny, responded variably to seasonal fluctuations in

the marine environment. We found that in the winter to summer period, all fishes had TPs ranging between 3 and 4. In summer, beluga, shorthorn sculpin, ribbed sculpin, slender eelblenny, moustache sculpin, and Arctic cod increased their TP slightly, suggesting that these species may consume marginally higher trophic-level prey during this time period. This slight increase in TP may also be occurring when these consumers are released from competitive pressure in response to increased prey abundance and composition (Dehn et al. 2006). From the winter to summer period in the Arctic, as sunlight increases and snow cover decreases, there is an exponential growth of ice algae, which eventually falls to the seafloor as sea-ice breakup begin in June (Ardyna and Arrigo 2020). This input of ice algae provides the first source of primary production for consumers and subsequent phytoplankton blooms later provide consumers with more food for growth and summer reproduction (Arrigo and Thomas 2004; Ardyna and Arrigo 2020; Barbedo et al. 2020; LeBlanc et al. 2020). The high availability of phytoplankton in late-spring and early-summer leads to an increase in the abundance of

Fig. 3. Stable isotope biplot representing the 40% isotope niche widths (ellipses) of liver and muscle of fishes and marine mammals collected from the marine region surrounding Southampton Island, Nunavut, Canada from 2016 to 2019. The solid lines represent the community metric of standard ellipse area (SEA) and each coloured dot represents a single datum for each species.

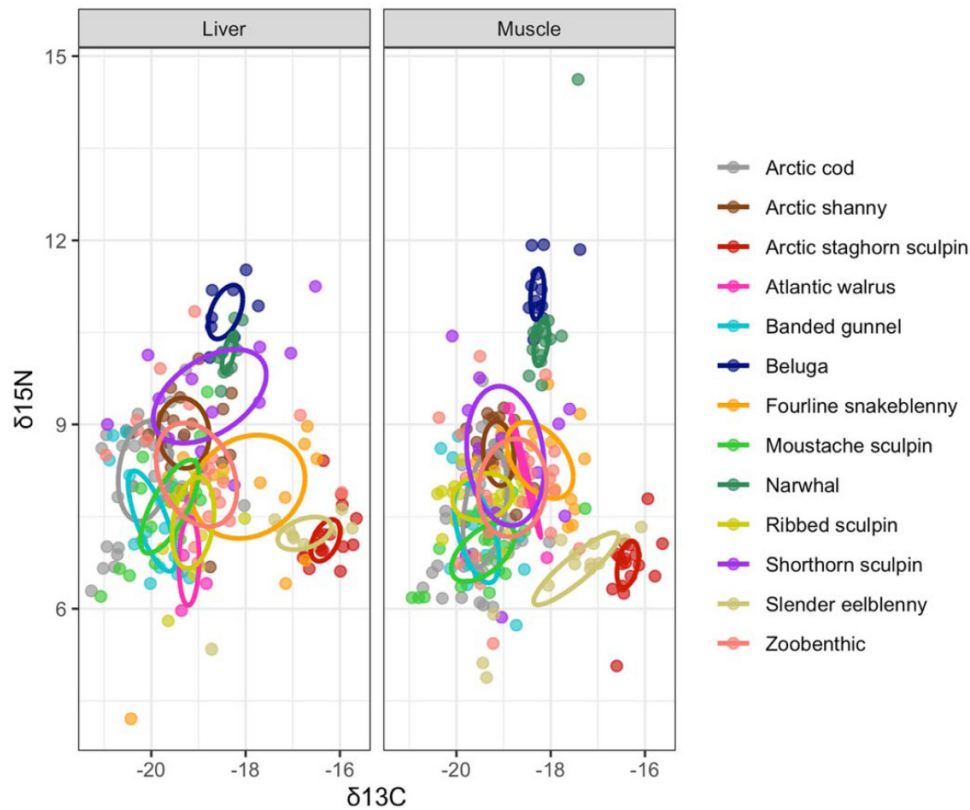


Table 2. Community-wide metrics of trophic diversity and redundancy across liver and muscle tissues collected from the marine region surrounding Southampton Island, Nunavut, Canada from 2016 to 2019 for fishes and marine mammals combined.

Community metric	Liver	Muscle	Probability of difference
Nitrogen range (i.e., food chain length)	4.07	4.69	0.79
Carbon range	3.85	3.22	0.89
Total area	8.47	7.84	0.60
Mean distance to centroid	1.47	1.29	0.88
Mean nearest neighbor distance	0.62	0.51	0.62
Standard deviation nearest neighbor distance	0.16	0.40	0.78

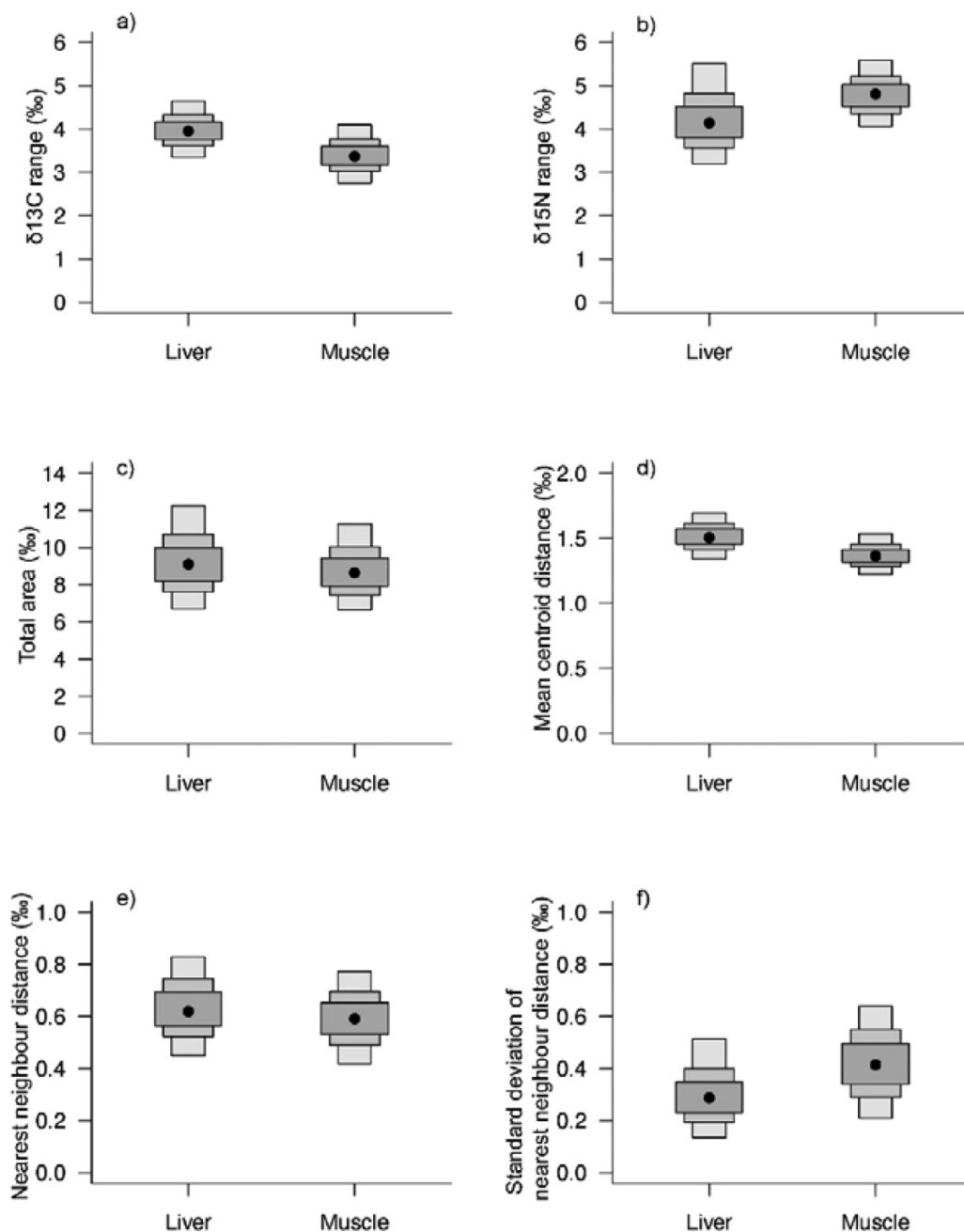
Note: Probability of differences represents the posterior probability that liver and muscle community metrics were significantly different from each other.

pelagic zooplankton grazers, which acts as food for many fish species (Arrigo and Thomas 2004; Mundy et al. 2014; Ardyna and Arrigo 2020; Barbedo et al. 2020). Further, the similarities in TP values across various fish species suggests that many of these planktonic- and benthic-feeding species may be competing within the same foraging niche during a time period of limited food availability before the peak microalgae blooms (Galarowicz et al. 2006; Søreide et al. 2010). Alternatively, since $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are limited in determining specific prey species consumed, it is possible that fishes are feeding on different food items, which have isotopic signatures that are quite variable (McCutchan et al. 2003; Canseco

et al. 2022). Many of these consumer species are generalist foragers (Landry et al. 2018), and the overlap in TPs between these benthic and pelagic-associated fish may instead be due to their wider foraging niche allowing these species to use the same isotopic space.

Further, the seasonal variation in multiple zooplankton-feeding and piscivorous fish species could be attributed to horizontal or vertical migrations of prey species or the consumers themselves (Benoit et al. 2010). That being said, piscivorous top predators (~TP 4–5) in the Southampton Island marine region were beluga (mean TP of 4.1 and 4.3 for muscle and liver, respectively) and narwhal (mean TP of 3.8 and 4.1

Fig. 4. Boxplots representing the Bayesian estimates for each community-wide metric for liver (summer) and muscle (winter to summer) tissues collected from the marine region surrounding Southampton Island, Nunavut, Canada from 2016 to 2019 of fish and marine mammals combined. Community-wide metrics included (a) $\delta^{13}\text{C}$ range ‰, (b) $\delta^{15}\text{N}$ range ‰, (c) total area ‰, (d) mean distance to centroid ‰, (e) mean nearest neighbour distance ‰, and (f) standard deviation of nearest neighbour distance ‰. Boxes indicate Bayesian credible intervals at 50% (dark grey), 75% (medium grey), and 95% (light grey).



for muscle and liver, respectively), both of which remained at the top of the food web across seasons with beluga increasing slightly in TP during summer and narwhal remaining at a similar TP during the summer time period. In summer, beluga and narwhal forage predominantly on Arctic and Greenland cod, squid, and capelin (Finley and Gibb 1982; Loseto et al. 2009; Kelley et al. 2010; Matley et al. 2015; Breton-Honeyman et al. 2016), and while information on the winter to summer diet of these whales is limited, it is suggested that

both species will feed on Greenland halibut (*Reinhardtius hippoglossoides*), *Gonatus* squid sp., and capelin (Finley and Gibb 1982; Laidre and Heide-Jørgensen 2005; Watt and Ferguson 2015). It was, therefore, surprising that we did not see a stronger seasonal changes in diet for narwhals given that it is known they begin to forage primarily on secondary consumers in summer (Matley et al. 2015; Watt and Ferguson 2015). The general seasonal consistency in TP for these two apex predators, despite an increase in TP by belugas, sug-

gests that, even with changes in resource abundance, these whales mainly relied on piscivorous prey that are available year-round (Breton-Honeyman et al. 2016; Yurkowski et al. 2018; Louis et al. 2021). However, these are migratory animals (Lewis et al. 2009; Watt and Ferguson 2015) and it is also possible that diet could change concurrently with geography, which may be masking the seasonal changes in trophic structure that we observed.

Seasonal changes in isotopic niche width

Isotopic niche width was higher in summer (i.e., liver) than winter to summer (i.e., muscle) across most species. Niche width differed between seasons with tertiary consumers (e.g., Arctic cod, Arctic shanny, and fourline snakeblenny, beluga) increasing in isotopic niche width during the summer, whereas other benthic consumers (e.g., shorthorn sculpin, banded gunnel, and Atlantic walrus) experienced a decrease in isotopic niche width. Our results indicate that consumers such as Arctic cod, Arctic shanny, fourline snakeblenny, moustache sculpin, ribbed sculpin, and the zoobenthic group consumed prey items that had more variable isotopic signatures than lower trophic-level consumers such as banded gunnel, slender eelblenny, and Atlantic walrus. Marine mammals, specifically narwhal and beluga, are mostly piscivorous in winter–summer and summer (Finley and Gibb 1982; Loseto et al. 2009; Matley et al. 2015), and are likely consuming similar small pelagic fish species between seasons. Given that belugas and narwhals both forage on fish, which can include Arctic cod, polar cod, and capelin (Matley et al. 2015), the general consistency in TP across seasons for these two toothed whale species could be due to a high abundance of fish prey that enables the two species to avoid competition (Hobbs et al. 2019). This result, however, may be attributed to differences in the sex of individuals sampled, which we did not have information on, since toothed whales can exhibit sex-specific variation in foraging behaviours (Louis et al. 2021).

Given the dynamic annual changes in food web structure in the Arctic due to spring ice algal blooms and spring and late-summer phytoplankton blooms (Ardyna and Arrigo 2020), it is possible that marine fishes occupy a larger niche than marine mammals due to their ability to use more flexible foraging tactics throughout the year. Arctic fishes forage on a wide range of prey such as zooplankton, bivalves, macro algae, kelp, and other fishes, which is likely the underlying mechanism driving large seasonal variation in TP and isotopic niche width (Hobson et al. 1995; Amiraux et al. 2023). Species may change their prey base entirely across seasons (e.g., transition from algae to fish) or they may switch within a prey group (i.e., from amphipods to copepods). The dynamic stability of ecosystems (Leigh et al. 2010) is often associated with the diversity of foraging habitats used by a community of animals and the resilience of these communities to environmental change (Pettit et al. 2017; McMeans et al. 2019). Further, competitive pressures of larger individuals or species, or species with larger gapes, may lead to a competitive advantage for some apex and tertiary consumers (e.g., Arctic charr; Adams and Huntingford 2002). This potential advantage may allow

some species to expand their niche in summer compared to smaller-sized species in the food chain (e.g., banded gunnel) that might narrow their niche in response to a higher abundance of competitors (Schoener 1983; Ogloff et al. 2020). In addition to overall body size of consumers, gape size limitations may force certain fish species to feed on the diverse array of marine invertebrates rather than consuming other fish species (Adams and Huntingford 2002).

Seasonality and community metrics

The overall increase in $\delta^{13}\text{C}$ range and TA of the fish and marine mammal assemblage from winter to summer is likely due to a greater abundance of carbon resources in the waters around Southampton Island from the transition between the spring sea-ice algae bloom followed by the phytoplankton blooms, which lead to higher primary production and grazer abundance in summer (Arrigo et al. 2012; Leu et al. 2015; Loewen et al. 2020). Many of the fish species in this study forage on a wide range of marine benthic and pelagic invertebrate and fish species (Matley et al. 2013; Amiraux et al. 2023). Therefore, some species of fish in this study may occupy a more narrow niche in spring, which they can then expand in summer when primary production allows for increased prey availability. For example, Arctic cod experience seasonal changes in diet where in spring they forage primarily on larger pelagic zooplankton such as *Mysis spp.* and *Themisto spp.*, but then transition to more abundant, smaller food sources such as *Calanoida* copepods in late summer as secondary production increases (Matley et al. 2013; Cusa et al. 2019). Consequently, the increase in $\delta^{13}\text{C}$ range is likely due to an ecosystem-wide increase in productivity of both carbon source end-users during summer, which likely allow generalist species to be more flexible in their alternative foraging strategies (Matley et al. 2013). For example, some species may feed on invertebrate prey when an individual's diet might otherwise be primarily piscivorous. Populations of beluga in the Beaufort Sea, for instance, are known to consume more small, pelagic fish during the summer in comparison to the winter to summer period when they rely more heavily on Greenland halibut or Arctic cod, the latter of which is associated with sea ice (Loseto et al. 2009; Yurkowski et al. 2017).

Trophic redundancy was higher in summer for the fish and marine mammal assemblages, indicating that Arctic marine species play a similar role to each other across the Southampton Island system in summer compared to the winter to summer. During the summer, carbon sources from phytoplankton are more available and thus fish species may be converging on the small pelagic fish species that feed on the phytoplankton resource base during this time (Matley et al. 2013; Cusa et al. 2019; Ardyna and Arrigo 2020). Benthic species such as Arctic shanny, ribbed sculpin, moustache sculpin, and fourline snakeblenny, for example, exhibited substantial increases in isotopic niche width between winter to summer and summer time periods and, therefore, may be playing a large role in the inter-seasonal variation in $\delta^{13}\text{C}$ range and, in turn, trophic redundancy. Lastly, seasonal variation in trophic redundancy could reflect the growing reliance on marine vegetation and benthic habitats in summer by fishes.

Our results suggest that both fishes and marine mammals are able to expand their niche and act more as generalists in summer, thus increasing both trophic diversity and redundancy.

Effects of tissue-specific turnover

A couple knowledge gaps could have affected our ecological interpretation of this study. Both narwhal and beluga whales that summer around Southampton Island spend winter nearby in the eastern Hudson Strait (Lewis et al. 2009; Hobbs et al. 2019), and thus their muscle tissues may be incorporating prey resources from nearby and adjacent Hudson Strait. However, when visually inspecting the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of plankton (i.e., baseline of the food web) from isoscape maps developed by Graham et al. (2010) in the Southampton Island and Hudson Strait area, the baseline $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are relatively similar and within 1‰ between areas. In addition, given the shorter turnover rate of liver tissue compared to muscle, we expect the liver tissues to solely reflect the summer diet of these marine mammal species within the general Southampton Island area. The isotopic turnover rates examined in this study are from interpretations of meta-analyses previously done on fishes (Caut et al. 2009) and mammals (Vander Zanden et al. 2015), and there are no species-specific turnover rates for any of the species examined in this study. In addition, DTDFs were derived from a meta-analysis on teleost fishes (Canseco et al. 2022) and from a case study on pinnipeds (Hobson et al. 1996) that analyzed both liver and muscle tissue. DTDFs may vary slightly between sampled fish and marine mammal species in this study, but, given the lack of DTDFs for all of these species, we used values established from the literature on teleost fish and piscivorous marine mammals. This being said, DTDFs from Hobson et al. (1996) have been applied to analyses in other published studies on marine mammal species (Lesage et al. 2001; Newsome et al. 2009; Marcoux et al. 2012; Yurkowski et al. 2018; Simond et al. 2023). Overall, we recognize that there may be within- and between-species variation in both isotopic turnover rates and DTDFs, which we cannot control for in this study. To address this in the future, there is a need for more feeding experiments that can use captive animals to understand the degree to which stable isotope signatures of prey species are reflected in tissues (Barton et al. 2019). Additionally, larger geographic spread of isotopic studies are required to better understand the seasonal turnover and DTDFs of liver and muscle tissues in various species of Arctic fishes and marine mammals.

Conclusions

In conclusion, the results from this study can be used as a reference point for future work to monitor seasonal variation in the trophic structure and community dynamics of fishes and marine mammals inhabiting the Southampton Island marine area. This work will be particularly important when evaluating the effects of anthropogenic stressors, such as vessel impacts from tourism and shipping and climate change, on Arctic food webs. With continued anthropogenic stressors, ecosystem changes in the Arctic may lead to depletions in prey availability and changes in species distribu-

tion (Fossheim et al. 2015; Florke et al. 2021), thus increasing the potential for seasonal variation in resource use. This could lead to both individual- and population-level consequences related to habitat use, reproduction, and survival. Both fishes and marine mammals are important for subsistence fishing/hunting and for recreational activities in the Arctic. Therefore, exaggerated seasonal variation in habitat use and prey availability are important to monitor since they can directly impact harvest practices of Inuit communities. Finally, future changes in the distribution and structure of Arctic marine consumers should be studied to better inform the planning of MPAs and the management and practice of marine mammal harvests for northern communities.

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Data availability

Data used for the analyses in this paper can be found on FigShare at the following DOI (<https://doi.org/10.6084/m9.figshare.22696102.v1>)

Author information

Author ORCIDs

Matthew Fuirst <https://orcid.org/0000-0001-7488-4150>

Steven H. Ferguson <https://orcid.org/0000-0002-3794-0122>

Kevin J. Hedges <https://orcid.org/0000-0002-2219-2360>

Wesley R. Ogloff <https://orcid.org/0000-0001-7399-4323>

Cortney A. Watt <https://orcid.org/0000-0003-4062-5729>

David J. Yurkowski <https://orcid.org/0000-0003-2264-167X>

Author notes

David Yurkowski serves as Associate Editor at the time of manuscript review and acceptance and did not handle peer review and editorial decisions regarding this manuscript.

Author contributions

Conceptualization: MF, SHF, DJY
 Data curation: KHE, SHF, ATF, LNH, TNL, AN, DJY
 Formal analysis: MF, ATF, CAW, DJY
 Funding acquisition: DJY
 Investigation: MF, SHF, CAW, DJY
 Methodology: AN, DJY
 Project administration: DJY
 Resources: SHF, DJY
 Supervision: DJY
 Validation: DJY
 Visualization: MF, DJY
 Writing – original draft: MF
 Writing – review & editing: MF, KHE, SHF, ATF, LNH, KJH, KBJ, KFJ, TNL, CJDM, CJM, AN, WRO, CAW, DJY

Competing interests

The authors declare there are no competing interests.

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References

- Adams, C.E., and Huntingford, F.A. 2002. The functional significance of inherited differences in feeding morphology in a sympatric polymorphic population of Arctic charr. *Evolutionary Ecology*, **16**: 15–25. doi:10.1023/A:1016014124038.
- Amiriaux, R., Mundy, C.J., Pierrejean, M., Niemi, A., Hedges, K.J., and Brown, T.A., 2023. Tracing carbon flow and trophic structure of a coastal Arctic marine food web using highly branched isoprenoids and carbon, nitrogen and sulfur stable isotopes. *Ecological Indicators*, **147**: 109938. doi:10.1016/j.ecolind.2023.109938.
- Ardyna, M., and Arrigo, K.R. 2020. Phytoplankton dynamics in a changing Arctic Ocean. *Nature Climate Change*, **10**: 892–903. doi:10.1038/s41558-020-0905-y.
- Arrigo, K.R., and Thomas, D.N. 2004. Large scale importance of sea ice biology in the Southern Ocean. *Antarctic science*, **16**(4): 471–486. doi:10.1017/S0954102004002263.
- Arrigo, K.R., Perovich, D.K., Pickart, R.S., Brown, Z.W., Van Dijken, G.L., and Lowry, K.E., 2012. Massive phytoplankton blooms under Arctic sea ice. *Science*, **336**(6087): 1408–1408. doi:10.1126/science.1215065. PMID: 22678359.
- Barbedo, L., Bélanger, S., and Tremblay, J.É. 2020. Climate control of sea-ice edge phytoplankton blooms in the Hudson Bay system. *Elementa: Science of the Anthropocene*, **8**(1): 039.
- Barton, M.B., Litvin, S.Y., Vollenweider, J.J., Heintz, R.A., Norcross, B.L., and Boswell, K.M. 2019. Experimental determination of tissue turnover rates and trophic discrimination factors for stable carbon and nitrogen isotopes of Arctic Sculpin (*Myoxocephalus scorpioides*): a common Arctic nearshore fish. *Journal of Experimental Marine Biology and Ecology*, **511**: 60–67. doi:10.1016/j.jembe.2018.11.005.
- Benoit, D., Simard, Y., Gagné, J., Geoffroy, M., and Fortier, L. 2010. From polar night to midnight sun: photoperiod, seal predation, and diel

- vertical migrations of polar cod (*Boreogadus saida*) under landfast ice in the Arctic Ocean. *Polar Biology*, **33**: 1505–1520. doi:10.1007/s00300-010-0840-x.
- Bligh, E.G., and Dyer, W.J. 1959. A rapid method of total lipid extraction and purification. *Canadian Journal of Biochemistry and Physiology*, **37**(8): 911–917. doi:10.1139/o59-099.
- Boecklen, W.J., Yarnes, C.T., Cook, B.A., and James, A.C. 2011. On the use of stable isotopes in trophic ecology. *Annual Review of Ecology, Evolution, and Systematics*, **42**: 411–440. doi:10.1146/annurev-ecolsys-102209-144726.
- Breton-Honeyman, K., Hammill, M.O., Furgal, C.M., and Hickie, B. 2016. Inuit Knowledge of beluga whale (*Delphinapterus leucas*) foraging ecology in Nunavik (Arctic Quebec), Canada. *Canadian Journal of Zoology*, **94**(10): 713–726. doi:10.1139/cjz-2015-0259.
- Browning, N.E., Dold, C., I-Fan, J., and Worthy, G.A. 2014. Isotope turnover rates and diet–tissue discrimination in skin of ex situ bottlenose dolphins (*Tursiops truncatus*). *Journal of Experimental Biology*, **217**(2): 214–221. PMID: 24072795.
- Cansco, J.A., Niklitschek, E.J., and Harrod, C. 2022. Variability in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ trophic discrimination factors for teleost fishes: a meta-analysis of temperature and dietary effects. *Reviews in Fish Biology and Fisheries*, **32**: 313–329.
- Carmack, E., and Wassmann, P. 2006. Food webs and physical–biological coupling on pan-Arctic shelves: unifying concepts and comprehensive perspectives. *Progress in Oceanography*, **71**(2-4): 446–477. doi:10.1016/j.pocean.2006.10.004.
- Caut, S., Angulo, E., and Courchamp, F. 2009. Variation in discrimination factors ($\Delta^{15}\text{N}$ and $\Delta^{13}\text{C}$): the effect of diet isotopic values and applications for diet reconstruction. *Journal of Applied Ecology*, **46**(2): 443–453. doi:10.1111/j.1365-2664.2009.01620.x.
- Clark, B. 1980. The Lake site (KkHh-2), Southampton Island, NWT and its position in Sadlermiut prehistory. *Canadian Journal of Archaeology/Journal Canadien d'Archéologie*, **4**: 53–81.
- Comiso, J.C., Parkinson, C.L., Gersten, R., and Stock, L. 2008. Accelerated decline in the Arctic sea ice cover. *Geophysical Research Letters*, **35**(1). doi:10.1029/2007GL031972. PMID: 24347740.
- Craig, H. 1957. Isotopic standards for carbon and oxygen and correction factors for mass-spectrometric analysis of carbon dioxide. *Geochimica et cosmochimica acta*, **12**(1-2): 133–149. doi:10.1016/0016-7037(57)90024-8.
- Cusa, M., Berge, J., and Varpe, Ø. 2019. Seasonal shifts in feeding patterns: individual and population realized specialization in a high Arctic fish. *Ecology & Evolution*, **9**(19): 11112–11121. doi:10.1002/ece3.5615.
- Dehn, L.A., Sheffield, G.G., Follmann, E.H., Duffy, L.K., Thomas, D.L., and O'Hara, T.M. 2006. Feeding ecology of phocid seals and some walrus in the Alaskan and Canadian Arctic as determined by stomach contents and stable isotope analysis. *Polar Biology*, **30**: 167–181. doi:10.1007/s00300-006-0171-0.
- Dunton, K.H., Weingartner, T., and Carmack, E.C. 2006. The nearshore western Beaufort Sea ecosystem: circulation and importance of terrestrial carbon in arctic coastal food webs. *Progress in Oceanography*, **71**(2-4): 362–378. doi:10.1016/j.pocean.2006.09.011.
- Finlay, J.C., and Kendall, C. 2007. Stable isotope tracing of temporal and spatial variability in organic matter sources to freshwater ecosystems. *Stable Isotopes in Ecology and Environmental Science*, **2**: 283–333. doi:10.1002/9780470691854.ch10.
- Finley, K.J., and Gibb, E.J. 1982. Summer diet of the narwhal (*Monodon monoceros*) in Pond Inlet, northern Baffin Island. *Canadian Journal of Zoology*, **60**(12): 3353–3363. doi:10.1139/z82-424.
- Florke, K.R., Tai, T.C., Cheung, W.W., Ferguson, S.H., Sumaila, U.R., Yurkowski, D.J., and Auger-Méthé, M. 2021. Predicting how climate change threatens the prey base of Arctic marine predators. *Ecology Letters*, **24**(12): 2563–2575. doi:10.1111/ele.13866.
- Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R.B., Aschan, M.M., and Dolgov, A.V. 2015. Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nature Climate Change*, **5**(7): 673–677. doi:10.1038/nclimate2647.
- France, R.L. 1995. Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. *Marine Ecology Progress Series*, **124**: 307–312. doi:10.3354/meps124307.
- Fry, B. 2006. *Stable isotope ecology*. Vol. 521, p. Springer, New York. p. 318.

- Galarowicz, T.L., Adams, J.A., and Wahl, D.H. 2006. The influence of prey availability on ontogenetic diet shifts of a juvenile piscivore. *Canadian Journal of Fisheries and Aquatic Sciences*, **63**(8): 1722–1733. doi:10.1139/f06-073.
- Gascuel, D., Guénette, S., and Pauly, D. 2011. The trophic-level based ecosystem modelling approach: theoretical overview and practical uses. *ICES Journal of Marine Science*, **68**(7): 1403–1416. doi:10.1093/icesjms/fsr062.
- Gradinger, R., and Bluhm, B.A. 2020. First analysis of an Arctic sea ice meiofauna food web based on abundance, biomass and stable isotope ratios. *Marine Ecology Progress Series*, **634**: 29–43. doi:10.3354/meps13170.
- Graham, B. S., Koch, P. L., Newsome, S. D., McMahon, K. W., and Auriolles, D. 2010. Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. *Isoscapes: understanding movement, pattern, and process on earth through isotope mapping*. 299–318.
- Grebmeier, J.M., and Barry, J.P. 1991. The influence of oceanographic processes on pelagic-benthic coupling in polar regions: a benthic perspective. *Journal of Marine Systems*, **2**(3-4): 495–518. doi:10.1016/0924-7963(91)90049-Z.
- Hannah, C.G., Dupont, F., and Dunphy, M. 2009. Polynyas and tidal currents in the Canadian Arctic Archipelago. *Arctic*, **62**: 83–95.
- Hickling, R., Roy, D.B., Hill, J.K., Fox, R., and Thomas, C.D. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. *Global change biology*, **12**(3): 450–455. doi:10.1111/j.1365-2486.2006.01116.x.
- Hobbs, R.C., Reeves, R.R., Prewitt, J.S., Desportes, G., Breton-Honeyman, K., and Christensen, T., 2019. Global review of the conservation status of monodontid stocks. *Marine Fisheries Review*, **81**(3-4): 1–62.
- Hobson, K.A., and Welch, H.E. 1992. Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. *Marine Ecology Progress Series*, **84**: 9–18. doi:10.3354/meps084009.
- Hobson, K. A., Ambrose, W. G., Jr, and Renaud, P.E. 1995. Sources of primary production, benthic-pelagic coupling, and trophic relationships within the Northeast Water Polynya: insights from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. *Marine Ecology Progress Series*, **128**: 1–10. doi:10.3354/meps128001.
- Hobson, K.A., Schell, D.M., Renouf, D., and Noseworthy, E. 1996. Stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: implications for dietary reconstructions involving marine mammals. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**(3): 528–533. doi:10.1139/f95-209.
- Hussey, N.E., MacNeil, M.A., McMeans, B.C., Olin, J.A., Dudley, S.F., and Cliff, G., 2014. Rescaling the trophic structure of marine food webs. *Ecology Letters*, **17**(2): 239–250. doi:10.1111/ele.12226.
- IPCC. 2014. *Climate change 2014. Impacts, adaptation and vulnerability. Working group II contribution to the IPCC fifth assessment report*. Cambridge University Press, Cambridge, UK.
- Jackson, A.L., Inger, R., Parnell, A.C., and Bearhop, S. 2011. Comparing isotopic niche widths among and within communities: SIBER—Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology*, **80**(3): 595–602. doi:10.1111/j.1365-2656.2011.01806.x.
- Kelley, T.C., Loseto, L.L., Stewart, R.E.A., Yurkowski, M., and Ferguson, S.H. 2010. Importance of eating capelin: unique dietary habits of Hudson Bay beluga. In *A little less Arctic: top predators in the world's largest Northern Inland Sea*. Edited by S.H. Ferguson, L.L. Loseto and M.L. Springer, Dordrecht. p. 53–70.
- Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A.V., and Aschan, M. 2015. Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. *Proceedings of the Royal Society B Biological Sciences*, **282**(1814): 20151546. doi:10.1098/rspb.2015.1546.
- Laidre, K.L., and Heide-Jørgensen, M.P. 2005. Winter feeding intensity of narwhals (*Monodon monoceros*). *Marine Mammal Science*, **21**(1): 45–57. doi:10.1111/j.1748-7692.2005.tb01207.x.
- Landry, J.J., Fisk, A.T., Yurkowski, D.J., Hussey, N.E., Dick, T., Crawford, R.E., and Kessel, S.T. 2018. Feeding ecology of a common benthic fish, shorthorn sculpin (*Myoxocephalus scorpius*) in the high arctic. *Polar Biology*, **41**: 2091–2102. doi:10.1007/s00300-018-2348-8.
- Layman, C.A., Arrington, D.A., Montaña, C.G., and Post, D.M. 2007. Can stable isotope ratios provide for community-wide measures of trophic structure?. *Ecology*, **88**(1): 42–48. doi:10.1890/0012-9658(2007)88%5b42:CSRIPF%5d2.0.CO;2.
- Layman, C.A., Araujo, M.S., Boucek, R., Hammerschlag-Peyer, C.M., Harrison, E., and Jud, Z.R., 2012. Applying stable isotopes to examine food web structure: an overview of analytical tools. *Biological reviews*, **87**(3): 545–562. doi:10.1111/j.1469-185X.2011.00208.x.
- LeBlanc, M., Geoffroy, M., Bouchard, C., Gauthier, S., Majewski, A., Reist, J.D., and Fortier, L. 2020. Pelagic production and the recruitment of juvenile polar cod *Boreogadus saida* in Canadian Arctic seas. *Polar Biology*, **43**: 1043–1054. doi:10.1007/s00300-019-02565-6.
- Leigh, C., Burford, M.A., Sheldon, F., and Bunn, S.E. 2010. Dynamic stability in dry season food webs within tropical floodplain rivers. *Marine and Freshwater Research*, **61**(3): 357–368. doi:10.1071/MF09107.
- Lesage, V., Hammill, M.O., and Kovacs, K.M. 2001. Marine mammals and the community structure of the Estuary and Gulf of St Lawrence, Canada: evidence from stable isotope analysis. *Marine Ecology Progress Series*, **210**: 203–221. doi:10.3354/meps210203.
- Leu, E., Mundy, C.J., Assmy, P., Campbell, K., Gabrielsen, T.M., and Goselin, M., 2015. Arctic spring awakening—Steering principles behind the phenology of vernal ice algal blooms. *Progress in Oceanography*, **139**: 151–170. doi:10.1016/j.pocean.2015.07.012.
- Lewis, A.E., Hammill, M.O., Power, M., Doidge, D.W., and Lesage, V. 2009. Movement and aggregation of eastern Hudson Bay beluga whales (*Delphinapterus leucas*): a comparison of patterns found through satellite telemetry and Nunavik traditional ecological knowledge. *Arctic*, **62**: 13–24.
- Loewen, T.N., Hornby, C., Johnson, M., Chambers, C., Dawson, K., and MacDonell, D., et al. 2020. *Ecological and Biophysical Overview of the Southampton Island Ecologically and Biologically Significant Area in support of the identification of an Area of Interest*. Research document, 1919-5044, 2020/032. Canadian Science Advisory Secretariat (CSAS), Ottawa, ON.
- Loseto, L.L., Stern, G.A., Connelly, T.L., Deibel, D., Gemmill, B., and Prokopowicz, A., 2009. Summer diet of beluga whales inferred by fatty acid analysis of the eastern Beaufort Sea food web. *Journal of Experimental Marine Biology and Ecology*, **374**(1): 12–18. doi:10.1016/j.jembe.2009.03.015.
- Louis, M., Skovrind, M., Garde, E., Heide-Jørgensen, M.P., Szpak, P., and Lorenzen, E.D. 2021. Population-specific sex and size variation in long-term foraging ecology of belugas and narwhals. *Royal Society Open Science*, **8**(2): 202226. doi:10.1098/rsos.202226.
- MacNeil, M.A., Drouillard, K.G., and Fisk, A.T. 2006. Variable uptake and elimination of stable nitrogen isotopes between tissues in fish. *Canadian Journal of Fisheries and Aquatic Sciences*, **63**(2): 345–353. doi:10.1139/f05-219.
- Marcoux, M., McMeans, B.C., Fisk, A.T., and Ferguson, S.H. 2012. Composition and temporal variation in the diet of beluga whales, derived from stable isotopes. *Marine Ecology Progress Series*, **471**: 283–291. doi:10.3354/meps10029.
- Mariotti, A. 1983. Atmospheric nitrogen is a reliable standard for natural ^{15}N abundance measurements. *Nature*, **303**(5919): 685–687. doi:10.1038/303685a0.
- Matley, J.K., Fisk, A.T., and Dick, T.A. 2013. The foraging ecology of Arctic cod (*Boreogadus saida*) during open water (July–August) in Allen Bay, Arctic Canada. *Marine Biology*, **160**: 2993–3004. doi:10.1007/s00227-013-2289-2.
- Matley, J.K., Fisk, A.T., and Dick, T.A. 2015. The foraging ecology of ringed seals (*Pusa hispida*), beluga whales (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) in the Canadian High Arctic determined by stomach content and stable isotope analysis. *Polar Research*, **34**(1): 24295. doi:10.3402/polar.v34.24295.
- McCutchan, J. H., Jr, Lewis, W. M., Jr, Kendall, C., and McGrath, C.C. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos*, **102**(2): 378–390.
- McMeans, B.C., McCann, K.S., Humphries, M., Rooney, N., and Fisk, A.T. 2015. Food web structure in temporally-forced ecosystems. *Trends in Ecology and Evolution*, **30**(11): 662–672.
- McMeans, B.C., Kadoya, T., Pool, T.K., Holtgrieve, G.W., Lek, S., and Kong, H., 2019. Consumer trophic positions respond variably to seasonally fluctuating environments. *Ecology*, **100**(2): e02570. doi:10.1002/ecy.2570.

- Middelburg, J.J. 2014. Stable isotopes dissect aquatic food webs from the top to the bottom. *Biogeosciences*, **11**(8): 2357–2371. doi:10.5194/bg-11-2357-2014.
- Mundy, C.J., Gosselin, M., Gratton, Y., Brown, K., Galindo, V., and Campbell, K., 2014. Role of environmental factors on phytoplankton bloom initiation under landfast sea ice in Resolute Passage, Canada. *Marine Ecology Progress Series*, **497**: 39–49. doi:10.3354/meps10587.
- Newsome, S.D., Tinker, M.T., Monson, D.H., Oftedal, O.T., Ralls, K., and Staedler, M.M., 2009. Using stable isotopes to investigate individual diet specialization in California sea otters (*Enhydra lutris nereis*). *Ecology*, **90**(4): 961–974. doi:10.1890/07-1812.1.
- Ogloff, W.R., Yurkowski, D.J., Davoren, G.K., and Ferguson, S.H. 2019. Diet and isotopic niche overlap elucidate competition potential between seasonally sympatric phocids in the Canadian Arctic. *Marine Biology*, **166**(8): 103. doi:10.1007/s00227-019-3549-6.
- Ogloff, W.R., Ferguson, S.H., Tallman, R.F., and Davoren, G.K. 2020. Diet of capelin (*Mallotus villosus*) in the Eastern Canadian Arctic inferred from stomach contents and stable isotopes. *Polar Biology*, **43**(9): 1273–1285. doi:10.1007/s00300-020-02707-1.
- Paar, M., Lebreton, B., Graeve, M., Greenacre, M., Asmus, R., and Asmus, H. 2019. Food sources of macrozoobenthos in an Arctic kelp belt: trophic relationships revealed by stable isotope and fatty acid analyses. *Marine Ecology Progress Series*, **615**: 31–49. doi:10.3354/meps12923.
- Paine, R.T. 1966. Food web complexity and species diversity. *The American Naturalist*, **100**(910): 65–75. doi:10.1086/282400.
- Pettit, N.E., Naiman, R.J., Warfe, D.M., Jardine, T.D., Douglas, M.M., Bunn, S.E., and Davies, P.M. 2017. Productivity and connectivity in tropical riverscapes of northern Australia: ecological insights for management. *Ecosystems*, **20**: 492–514. doi:10.1007/s10021-016-0037-4.
- Pineault, S., Tremblay, J.É., Gosselin, M., Thomas, H., and 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. *Journal of Geophysical Research: Oceans*, **118**(1): 287–300. doi:10.1029/2012JC008331.
- Polis, G.A., Sears, A.L., Huxel, G.R., Strong, D.R., and Maron, J. 2000. When is a trophic cascade a trophic cascade? *Trends in Ecology and Evolution*, **15**(11): 473–475.
- Polyak, L., Alley, R.B., Andrews, J.T., Brigham-Grette, J., Cronin, T.M., and Darby, D.A., 2010. History of sea ice in the Arctic. *Quaternary Science Reviews*, **29**(15-16): 1757–1778. doi:10.1016/j.quascirev.2010.02.010.
- Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, **83**(3): 703–718. doi:10.1890/0012-9658(2002)083%5b0703:USITET%5d2.0.CO;2.
- Post, D.M., Layman, C.A., Arrington, D.A., Takimoto, G., Quattrochi, J., and Montana, C.G. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia*, **152**: 179–189. doi:10.1007/s00442-006-0630-x.
- R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from <https://cran.r-project.org/> [Accessed January 2023].
- Renaud, P.E., Tessmann, M., Evenset, A., and Christensen, G.N. 2011. Benthic food-web structure of an Arctic fjord (Kongsfjorden, Svalbard). *Marine Biology Research*, **7**(1): 13–26. doi:10.1080/17451001003671597.
- Riedel, A., Michel, C., Gosselin, M., and LeBlanc, B. 2008. Winter–spring dynamics in sea-ice carbon cycling in the coastal Arctic Ocean. *Journal of Marine Systems*, **74**(3-4): 918–932. doi:10.1016/j.jmarsys.2008.01.003.
- Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., and Pounds, J.A. 2003. Fingerprints of global warming on wild animals and plants. *Nature*, **421**(6918): 57–60. doi:10.1038/nature01333.
- Schoener, T.W. 1983. Field experiments on interspecific competition. *The American Naturalist*, **122**(2): 240–285. doi:10.1086/284133.
- Simond, A.E., Ross, P.S., Cabrol, J., Lesage, V., Lair, S., and Woudneh, M.B., 2023. Declining concentrations of chlorinated paraffins in endangered St. Lawrence Estuary belugas (*Delphinapterus leucas*): Response to regulations or a change in diet? *Science of the Total Environment*, 161488. doi:10.1016/j.scitotenv.2023.161488.
- Søreide, J.E., Leu, E.V., Berge, J., Graeve, M., and Falk-Petersen, S.T.I.G. 2010. Timing of blooms, algal food quality and *Calanus glacialis* reproduction and growth in a changing Arctic. *Global change biology*, **16**(11): 3154–3163.
- Szpak, P., and Buckley, M. 2020. Sulfur isotopes ($\delta^{34}\text{S}$) in Arctic marine mammals: indicators of benthic vs. pelagic foraging. *Marine Ecology Progress Series*, **653**: 205–216. doi:10.3354/meps13493.
- Thompson, R.M., Brose, U., Dunne, J.A., Hall, R.O., Hladyz, S., and Kitching, R.L., 2012. Food webs: reconciling the structure and function of biodiversity. *Trends in Ecology and Evolution*, **27**(12): 689–697.
- Vander Zanden, M.J., Clayton, M.K., Moody, E.K., Solomon, C.T., and Weidel, B.C. 2015. Stable isotope turnover and half-life in animal tissues: a literature synthesis. *PLoS ONE*, **10**(1): e0116182. doi:10.1371/journal.pone.0116182.
- Wassmann, P., Duarte, C.M., Agusti, S., and Sejr, M.K. 2011. Footprints of climate change in the Arctic marine ecosystem. *Global Change Biology*, **17**(2): 1235–1249. doi:10.1111/j.1365-2486.2010.02311.x.
- Watt, C.A., and Ferguson, S.H. 2015. Fatty acids and stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) reveal temporal changes in narwhal (*Monodon monoceros*) diet linked to migration patterns. *Marine Mammal Science*, **31**(1): 21–44. doi:10.1111/mms.12131.
- Woodland, R.J., Warry, F.Y., Evrard, V., Clarke, R.H., Reich, P., and Cook, P.L. 2016. Niche-dependent trophic position distributions among primary, secondary and tertiary consumers. *Oikos*, **125**(4): 556–565. doi:10.1111/oik.02486.
- Yurkowski, D.J., Hussey, N.E., Semeniuk, C., Ferguson, S.H., and Fisk, A.T. 2015. Effects of lipid extraction and the utility of lipid normalization models on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in Arctic marine mammal tissues. *Polar Biology*, **38**: 131–143. doi:10.1007/s00300-014-1571-1.
- Yurkowski, D.J., Hussey, N.E., Fisk, A.T., Imrie, K.L., Tallman, R.F., and Ferguson, S.H. 2017. Temporal shifts in intraguild predation pressure between beluga whales and Greenland halibut in a changing Arctic. *Biology Letters*, **13**(11): 20170433. doi:10.1098/rsbl.2017.0433.
- Yurkowski, D.J., Hussey, N.E., Ferguson, S.H., and Fisk, A.T. 2018. A temporal shift in trophic diversity among a predator assemblage in a warming Arctic. *Royal Society Open Science*, **5**(10): 180259. doi:10.1098/rsos.180259.
- Yurkowski, D.J., Auger-Méthé, M., Mallory, M.L., Wong, S.N., Gilchrist, G., and Derocher, A.E., 2019. Abundance and species diversity hotspots of tracked marine predators across the North American Arctic. *Diversity and Distributions*, **25**(3): 328–345. doi:10.1111/ddi.12860.
- Yurkowski, D.J., Richardson, E.S., Lunn, N.J., Muir, D.C., Johnson, A.C., and Derocher, A.E., 2020. Contrasting temporal patterns of mercury, niche dynamics, and body fat indices of polar bears and ringed seals in a melting icescape. *Environmental Science & Technology*, **54**(5): 2780–2789.