

Tracing carbon flow and trophic structure of a coastal Arctic marine food web using highly branched isoprenoids and carbon, nitrogen and sulfur stable isotopes

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ABSTRACT

Climate-driven alterations of the marine environment are most rapid in Arctic and subarctic regions, including Hudson Bay in northern Canada, where declining sea ice, warming surface waters and ocean acidification are occurring at alarming rates. These changes are altering primary production patterns that will ultimately cascade up through the food web. Here, we investigated (i) the vertical trophic structure of the Southampton Island marine ecosystem in northern Hudson Bay, (ii) the contribution of benthic and pelagic-derived prey to the higher trophic level species, and (iii) the relative contribution of ice algae and phytoplankton derived carbon in sustaining this ecosystem. For this purpose, we measured bulk stable carbon, nitrogen and sulfur isotope ratios as well as highly branched isoprenoids in samples belonging to 149 taxa, including invertebrates, fishes, seabirds and marine mammals. We found that the benthic invertebrates occupied 4 trophic levels and that the overall trophic system went up to an average trophic position of 4.8. The average $\delta^{34}\text{S}$ signature of pelagic organisms indicated that they exploit both benthic and pelagic food sources, suggesting there are many interconnections between these compartments in this coastal area. The relatively high sympagic carbon dependence of Arctic marine mammals ($53.3 \pm 22.2\%$) through their consumption of benthic invertebrate prey, confirms the important role of the benthic subweb for sustaining higher trophic level consumers in the coastal pelagic environment. Therefore, a potential decrease in the productivity of ice algae could lead to a profound alteration of the benthic food web and a cascading effect on this Arctic ecosystem.

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1. Introduction

Climate warming is forcing rapid changes to Canada's Arctic marine icescape and its associated ecosystems (Amiraux et al., 2022; Gupta et al., 2022; Lukovich et al., 2021; Regehr et al., 2007). Sea ice plays a central role in polar marine ecosystems as it drives the phenology of primary producers that constitute the base of marine food webs. The energy from primary producers then transfers up through successive trophic levels in the pelagic and benthic environments from zooplankton or benthos, to fish, and to top predators including seabirds and marine mammals (Darnis and Fortier, 2012; Welch et al., 1992). In the pelagic environment of the Arctic, microalgal primary production includes two consecutive pulses of marine autotrophs: sea-ice algae and phytoplankton (Loose et al., 2011; Wassmann et al., 2011). An additional autotrophic source is that of benthic micro- and macroalgal production, yet it is restricted to shallow zones where enough light reaches the ocean floor (Filbee-Dexter et al., 2019; Glud et al., 2009). In early spring, increasing irradiance and rising temperatures enable ice algae to grow. Later in the season when snow and sea ice melt, a phytoplankton bloom develops and follows the ice retreat (Amiraux et al., 2022; Barbedo et al., 2020). Measurements of phytoplankton productivity far outnumber those for ice algae; however, it has been estimated that ice algae contribute 3–25 % of the total primary production across Arctic shelves (Legendre et al., 1992), while in the central Arctic Ocean, this contribution can reach 57–83 % (Boetius et al., 2013; Gosselein et al., 1997). Furthermore, because of their relatively high sinking rates and nutritional quality, ice algae play an important role in pelagic-benthic coupling (Amiraux et al., 2021; Yunda-Guarin et al., 2020) and, by extension, the benthic food web and pelagic coastal food webs that make seasonal or occasional use of benthic elements. However, with a decrease in sea ice extent and duration, anthropogenic climate change threatens ice algal productivity with a coinciding increase of net phytoplankton and macroalgal productivity (Kortsch et al., 2012; Lewis et al., 2020; Li et al., 2009; Weslawski et al., 2010). To understand the implications of these predicted productivity shifts, it is crucial to assess the dependency of Arctic species on sea ice and its resources, particularly in terms of food web dynamics such as carbon energy flow and vertical trophic structuring.

Biomarker approaches applied to food web samples allow inferences to be made about the dependency of Arctic consumers on sympagic (*i.e.*, sea ice-associated) and pelagic resources. In particular, conservative bioindicators produced by the two microalgal primary producers and transferred through the food chain, such as stable carbon, nitrogen, and sulfur isotopes and highly branched isoprenoids (HBIs), enable the tracking of the trophic fingerprint of both primary producers. Stable isotopes of nitrogen ($\delta^{15}\text{N}$) provide information on the relative trophic level of consumers (*i.e.*, diet), while carbon ($\delta^{13}\text{C}$) and sulfur ($\delta^{34}\text{S}$) provide information on the energy source (*i.e.*, benthic, sympagic, and pelagic-derived energy; France, 1995; Minagawa and Wada, 1984; Szpak and Buckley, 2020). Indeed, in Arctic regions, the $\delta^{13}\text{C}$ signatures of ice algae and phytoplankton have been commonly employed for the determination of the reliance of an organism on each carbon sources (Hobson et al., 1995; Pineault et al., 2013; Søreide et al., 2006; Yurkowski et al., 2020). However the close $\delta^{13}\text{C}$ signatures between macroalgae and ice algae as well as between phytoplankton and terrestrial organic matter may be in some case, unequivocal and not quantitative (McMeans et al., 2013). To provide an equivocal and quantitative relative contribution of ice algae and phytoplankton that feed consumers and the entire food web, HBI-based methods have recently been widely employed (Brown et al., 2014a; Brown et al., 2014c; Brown and Belt, 2017; Brown, 2018; Brown et al., 2018). HBIs are lipid biomarkers synthesized by diatom species almost exclusively belonging to the genera *Haslea*, *Navicula*, *Rhizosolenia* and *Pleurosigma* (Belt, 2018). Among these HBIs, IP₂₅ (Ice Proxy with 25 carbon atoms; Belt et al., 2007) is a mono-unsaturated C₂₅ HBI produced exclusively by certain Arctic sea ice diatoms (Brown et al., 2014b; Limoges et al., 2018) while a

tri-unsaturated HBI has been proposed as a proxy of pelagic production for the spring marginal ice zone (Amiraux et al., 2019; Belt et al., 2019; Köseoglu et al., 2018; Smik et al., 2016a; Smik et al., 2016b). Numerous HBI-based proxies have been developed in recent years to estimate the relative contributions of sympagic and pelagic algae to consumers and throughout the food web (Brown et al., 2018; Cusset et al., 2019; Yunda-Guarin et al., 2020). For complex coastal habitats, particularly in the Arctic, which include many species with different life histories and varied diets that may also shift seasonally, biomarker approaches provide novel insights into food web structures that would otherwise be impossible to obtain.

The marine region around Southampton Island, northwest Hudson Bay (Nunavut, Fig. 1) is an interesting marine environment because it can be viewed as a shallow inflow shelf, where well-mixed nutrient rich waters flow into Hudson Bay from the more productive Hudson Strait region and fuel a significant benthic community, or as an interior shelf, dominated by freshwater inputs, predominantly pelagic, and having low general biological activity because of lack of external nutrient supply (Carmack and Wassmann, 2006). Although Hudson Bay is generally viewed as oligotrophic overall, the biological evidence supports the notion of high biological productivity and specifically benthic productivity in the Southampton Island region (Castro de la Guardia et al., *in press*; Filbee-Dexter et al., 2022). It, encompasses one of Canada's largest summer and winter aggregations of Arctic marine mammals as well as supporting two migratory bird sanctuaries, including the largest colony of Common Eider (*Somateria mollissima*) in Nunavut (Loewen et al., 2020). Because of the multiple ecosystem services provided by this biological hotspot (Loewen et al., 2020), this region has supported local human habitation for millennia, with confirmed Dorset, Thule, and Sadlermiut occupation sites (Clark, 1980; Collins, 1956; McGhee, 1970). Its marine resources remain critical to the subsistence economy of local communities today. For these reasons, this region has been identified as an Area of Interest for Marine Protected Area (MPA) designation by Fisheries and Oceans Canada (DFO, Loewen et al., 2020). However, surprisingly little scientific data exist about the structure and functioning of the food web surrounding Southampton Island, in terms of its carbon flow and vertical trophic structure. This lack of data, in turn, severely limits our ability to understand and predict temporal changes in this unique and productive marine ecosystem in response to climate change.

In this study, we examined the structure and function of the Southampton Island marine food web across 149 species of benthic and pelagic invertebrates, fishes, marine mammals and seabirds collected from 2016 to 2019, to provide a baseline for future studies that aim to quantify temporal changes in food web structuring. More specifically, we used a multi-biomarker approach combining stable isotopes and HBIs to: (i) determine the vertical trophic structure of the marine food web, (ii) investigate the contribution of benthic and pelagic-derived prey to the higher trophic level species of the Arctic food web, and (iii) determine the role of ice algae and phytoplankton carbon source use across different trophic levels and compartments (pelagic and benthic). By shedding new light on the functioning of the Southampton Island food web and specifically how the contribution of ice algae and benthic habitat shapes its structure, these results will be relevant to adaptive management and conservation initiatives implemented in response to anthropogenic stressors and climate change.

2. Materials and methods

2.1. Sample collection

Benthic and pelagic invertebrate and fish, seabird and marine mammal samples were collected in summer 2016, 2018, and 2019 in the marine waters around Southampton Island, Nunavut, Canada (Fig. 1). In the present paper, benthic food web refers to the benthic invertebrates while the pelagic food web encompasses pelagic invertebrates, benthic

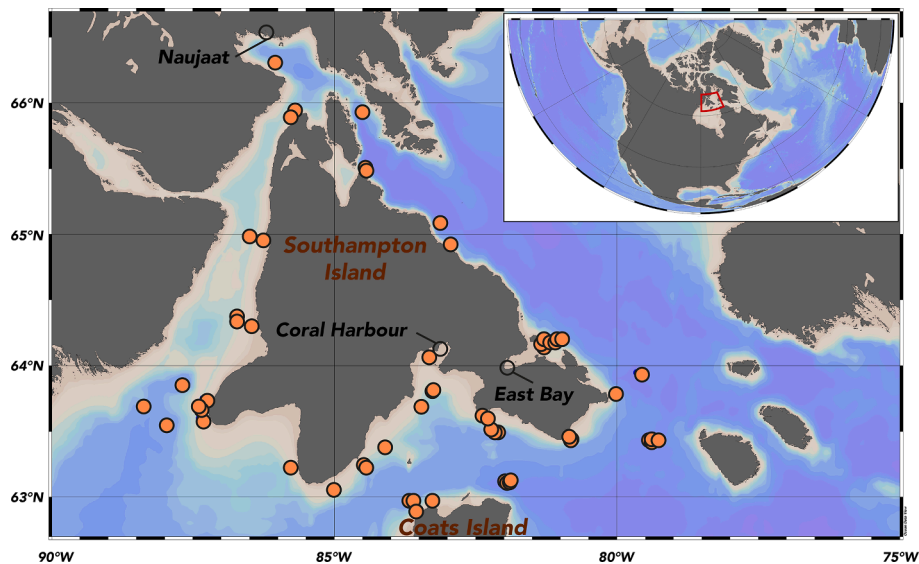


Fig. 1. Map of the study area with location of the stations investigated around Southampton Island in the Hudson Bay.

and pelagic fishes, seabirds and marine mammals. Assignments for habitat (pelagic or benthic) were derived from the designations in World Register of Marine Species (WoRMS; <https://marinespecies.org>) and FishBase (<https://fishbase.net.br>). Benthic and pelagic invertebrates and fishes were collected using a Campelen 1200 research trawl on the *MV Nuliajuk* in 2016 and using benthic and pelagic nets and trawls as well as a Ponar grab and 30-cm box corer on the *RV William Kennedy* in 2018 and 2019 as part of the Southampton Island Marine Ecosystem Project (SIMEP). For larger zooplankton and pelagic fish, a 3-m mid-water trawl (0.5-cm cod-end mesh) was towed at between 2 and 3 knots for 15 min targeting the subsurface chlorophyll maximum depth (SCM) previously identified by fluorescence from an ECO Triplet fluorometer (Sea-bird Scientific) mounted on the rosette. A 3-m benthic beam trawl (0.5-cm cod-end mesh) was towed at 2–3 knots for 15 min on the bottom. Samples were sorted into main groups of zooplankton and identified to the lowest possible taxon level for benthic invertebrates and fishes in the field and were then frozen at -20°C for later food web analysis.

Benthic invertebrates consisted of 881 whole organism, muscle, piece or soft part samples belonging to 97 species and 19 taxonomic groups as follows: amphipod, anthozoan, ascidian, barnacle, bivalve, brachiopod, brittle star, bryozoan, chiton, crinoid, decapod, gastropod, isopod, sea cucumber, sea spider, sea star, sea urchin, sponge, and annelid. For all larger-size benthic invertebrates (e.g. decapods), soft tissue or muscle was dissected and processed for stable isotope and HBI analysis and this included echinoderms, brittle stars and crinoids. Though inorganic carbon that is present as carbonate in echinoderms and crinoid species, these samples were not acidified due to the potential influence on $\delta^{13}\text{C}$ and were instead corrected mathematically using a carbonate proxy following Jacob et al. (2005) and Kazanidis et al. (2019); see Appendix for more details). Corrected values for $\delta^{13}\text{C}$ and C:N are provided in Table S1. For smaller-sized species like amphipods (e.g. *Anonyx* sp), individuals were processed whole. Pelagic invertebrates consisted of 303 whole organism samples belonging to 20 species and 8 taxonomic groups as follows: amphipod, chaetognath, copepod, ctenophore, hydrozoan, krill and mysid, pteropod, and squid. These individuals were all processed whole.

From collected benthic and pelagic fish, both muscle and liver samples were analyzed. In total, 171 muscle samples from 20 demersal fish species and 83 muscle samples from 5 pelagic species were collected. A total of 20 liver samples belonging to 5 demersal fish species and 74 livers from 3 pelagic fish species were also collected. Fish species included Arctic cod (*Boreogadus saida*), Polar cod (*Arctogadus glacialis*),

Fourline snakeblenny (*Eumesogrammus praecisus*), Arctic staghorn sculpin (*Gymnocanthus tricuspsis*), Arctic alligatorfish (*Aspidophoroides olrikii*), Daubed shanny (*Leptoclinus maculatus*), Fish doctor (*Gymnelus viridis*), Twohorn sculpin (*Icelus bicornis*), Spatulate sculpin (*Icelus spatula*), Atlantic poacher (*Leptagonus decagonus*), Snailfish (*Liparis* sp), Slender eelblenny (*Lumpenus fabricii*), Capelin (*Mallotus villosus*), Arctic sculpin (*Myoxocephalus scorpioides*), Shorthorn sculpin (*Myoxocephalus scorpius*), Greenland cod (*Gadus ogac*), Banded gunnel (*Pholis fasciata*), Arctic shanny (*Stichaeus punctatus*), Eelpouts (*Zoarcidae* sp), Moustache sculpin (*Triglops murrayi*), and Ribbed sculpin (*Triglops pingelii*). Arctic char (*Salvelinus alpinus*) muscle samples were collected opportunistically during their upstream run in August as part of Inuit subsistence harvests and in association with ongoing community-based monitoring programs with DFO based in Naujaat, Nunavut.

Marine mammal collections consisted of 72 muscle and 45 liver samples belonging to Atlantic walrus (*Odobenus rosmarus rosmarus*), ringed seal (*Phoca hispida*), narwhal (*Monodon monoceros*), and beluga (*Delphinapterus leucas*), all of which were collected in June to August by Inuit hunters from Naujaat and Coral Harbour (Fig. 1) as part of their subsistence harvests and ongoing community-based monitoring programs in collaboration with DFO.

Samples from three bird species were collected ($n = 62$ samples) by way of long-term monitoring programs coordinated by Environment and Climate Change Canada in East Bay and at the Coats Island murre west colony studied by McGill University, respectively. These samples consisted of blood from Glaucous gulls (*Larus hyperboreus*) and Thick-billed murre (*Uria lomvia*) and plasma from Common eiders (*Somateria mollissima*). For avian blood components, plasma has a faster turnover rate (e.g., days), while red blood cells have a longer turnover rate (e.g., weeks; Barquete et al., 2013; Hahn et al., 2012; Hobson and Clark, 1992). Plasma was analyzed for the Common Eiders as they were pre-incubating at the time of their capture, which took place shortly after arrival in East Bay Island (see Smith et al. (2021) for more details), allowing us to quantify short-term diet after their arrival. In contrast, murre and gulls were sampled during chick-rearing, over a month after arrival at the site, and, thus, red blood cells should reflect local sources. All tissue samples were frozen at -20°C and shipped to the Freshwater Institute in Winnipeg, Manitoba before processing.

2.2. Stable isotope analysis

Frozen samples of whole organisms, soft parts or muscles from invertebrates, muscles for fish and marine mammals and blood or plasma

for seabirds were lyophilized for 48 h at -50°C and then crushed into a fine powder using a mortar and pestle. Due to the ubiquitous presence of lipids in Arctic consumers including invertebrates (Imbs et al., 2021), fish liver and muscle (Post et al., 2007), and marine mammal muscle (Yurkowski et al., 2015), lipids were extracted 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. For $\delta^{34}\text{S}$, 3000–6000 μg of the sample plus 300–500 μg of Vanadim Pentoxide were encapsulated. All stable isotope ratios are expressed in per mil (‰) in standard delta (δ) notation relative to the international standards Pee Dee Belemnite for carbon, atmospheric N_2 for nitrogen, and Vienna Cañon Diablo Triolite for sulfur (Craig, 1957; Mariotti, 1983) using the following equation:

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

where X is ^{13}C , ^{15}N or ^{34}S and R equals $^{13}\text{C}/^{12}\text{C}$, $^{15}\text{N}/^{14}\text{N}$ or $^{34}\text{S}/^{32}\text{S}$. Instrumentation accuracy checked during analysis, was based on NIST standards 8573, 8547 and 8574 for $\delta^{15}\text{N}$ ($n = 50$ for all), 8542, 8573, 8574 for $\delta^{13}\text{C}$ ($n = 50$ for all), and 8555 and 8529 for $\delta^{34}\text{S}$ ($n = 30$ for all). The mean difference from the certified NIST standard values were 0.09, 0.14, 0.06 ‰ for $\delta^{15}\text{N}$, 0.09, 0.01 and 0.08 ‰ for $\delta^{13}\text{C}$, and 0.25 and 0.30 ‰ for $\delta^{34}\text{S}$, respectively. Precision, assessed by the standard deviation of replicate analyses of four standards (NIST1577c, internal lab standard, tilapia muscle), USGS 40 and Urea ($n = 22$ for all), was ≤ 0.25 ‰ for $\delta^{15}\text{N}$ and ≤ 0.13 ‰ for $\delta^{13}\text{C}$ for all the standards. For $\delta^{34}\text{S}$, the precision from standards USGS 42, NIST 8555 and NIST 8529 ($n = 39$ for all) was ≤ 0.43 ‰.

Trophic position (TP) was calculated for each species/taxonomic group using a one-source TP model (Eq. (2); Post, 2002) to determine the food web structure.

$$TP_{\text{consumer}} = TP_{\text{baseline}} + \frac{\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{baseline}}}{\Delta^{15}\text{N}} \quad (2)$$

The $\delta^{15}\text{N}$ of primary producers can sometimes vary between benthic and pelagic systems (Post, 2002); however, in this study system, the pelagic-feeding copepod $\delta^{15}\text{N}$ value (*Calanus hyperboreus*; 9.5 ± 0.4 ‰) was comparable to a more-benthic associated grazer (i.e., the sea urchin *Strongylocentrotus droebachiensis*, Paar et al. (2019); $\delta^{15}\text{N}$ of 8.7 ± 1.6 ‰) and filter-feeding species (i.e., the bivalve taxonomic group, $\delta^{15}\text{N}$ of 8.5 ± 1.7 ‰). Therefore, the following one-source trophic position model with copepod as the baseline (TP = 2) was applied to determine the TP of all taxa. A diet–tissue discrimination factor ($\Delta^{15}\text{N}$) of 3.4 ‰ (Post, 2002) was used for all species. Exceptions were narwhal, beluga and ringed seals, which are primarily piscivorous and 2.4 ‰ was applied as a $\Delta^{15}\text{N}$ (Hobson et al., 1996), with Arctic cod and capelin mean TP of 3.4 employed as a baseline (Table 1) following a scaled trophic position framework (Hussey et al., 2014).

2.3. Highly branched isoprenoid analysis (HBI)

Tissue samples (0.4–2.4 g) of whole organisms, soft parts or muscles for invertebrate, liver for fish and marine mammals were saponified (~ 5 mL H_2O : MeOH, 1:9; 20 % KOH; 60 mins; 70°C) in a flask, extracted with hexane (3×4 mL) to recover HBI fractions and dried (N_2 stream). Dried lipid extracts were fractionated (5 mL hexane) using column chromatography (SiO_2 ; 0.5 g). All extracts were analysed by gas chromatography–mass spectrometry (GC–MS) using a Shimadzu QP2020 system. Extracts were analysed for total ion current (TIC) and selective

ion monitoring (SIM) using a 30-m Rxi-5Sil column (0.25 mm i.d., 0.25- μm film). HBI lipids were identified using TIC mass spectra and retention indices. Relative HBI abundances were obtained from GC–MS SIM output using the mass spectral intensities of the molecular ion for each HBI (i.e., m/z 350.3 for Ice Proxy with 25 carbons (IP₂₅) m/z 348.3 for HBI II, and m/z 346.3 for HBI III), with all HBIs having signal to noise (S/N) ratio > 10 . HBI abundances were normalised according to totals derived from all HBIs. The resulting distribution provides the basis for the HBI fingerprint, referred to hereafter as the H-Print, an analytical method to distinguish between organic matter derived from sea ice and seawater within an Arctic ecosystem (Brown et al., 2014c; Brown and Belt, 2017). H-Print is defined here as the ratio of the HBI contribution from planktonic diatoms (HBI III) vs those from sea ice diatoms (Σ IP₂₅ and HBI II) (Brown et al., 2014c), according to Eq. (3):

$$H - \text{print}(\%) = \frac{III}{(IP_{25} + II + III)} \times 100 \quad (3)$$

Sympagic carbon, as a proportion of marine-origin carbon within organisms, was estimated using Eq. (4) from a previous H-Print calibration ($R^2 = 0.97$, $P = < 0.01$, $df = 23$; Brown and Belt, 2017):

$$\text{Sympagic carbon}(\%) = 101.08 - 1.02 \times H - \text{print} \quad (4)$$

2.4. Statistical analysis

The variable investigated being non-parametric, significant differences of $\delta^{13}\text{C}$, TP, $\delta^{34}\text{S}$ and sympagic carbon percentage (SC%) among the taxonomic groups was determined using non-parametric Kruskal-Wallis tests. Those tests indicated significant differences for each parameter investigated (Kruskal-Wallis chi-squared of 471.92, 654.75, 115.46, 121.61 respectively; $df = 10, 10, 10, 7$ respectively; p -value < 0.001). Following Kruskal-Wallis tests, we applied Dunn's tests with adjusted Bonferroni p -value to identify which taxonomic groups are significantly different. Statistical tests were carried out using R v.4.2 software (R Core Team, 2018).

3. Results

Across the entire Southampton Island marine food web, $\delta^{13}\text{C}$ ranged from -23.9 ± 0.2 ‰ in the sea spider *Boreonymphon abyssorum* to -14.9 in the Bryozoan *Eucratea* sp. For $\delta^{15}\text{N}$, values ranged from 6.5 ± 0.2 ‰ in the benthic bivalve *Crenella* sp to 19.2 ‰ in an asteroidea (seastar), respectively (Table 1, S1). On average, pelagic and benthic invertebrates were lower in $\delta^{15}\text{N}$ (Table 1; Fig. 2A) compared to fishes, seabirds and marine mammals (Fig. 2A). However, likely due to the wide variety of taxonomic groups and species within the invertebrates, it is not surprising this group is both displaying the highest variability in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and some benthic invertebrate species have higher $\delta^{15}\text{N}$ than some marine mammals (Fig. 2B). Although pelagic invertebrates are found in the same ^{13}C isospace as benthic invertebrates, the latter are on average significantly more enriched in $\delta^{13}\text{C}$ (Fig. 2, Table S2). On average, $\delta^{13}\text{C}$ values in pelagic fish ranged from -22.4 ± 1.1 ‰ in sandlance to -17.7 ± 1.1 ‰ in slender eelblenny, and $\delta^{15}\text{N}$ values ranged from 12.8 ± 0.3 ‰ in sandlance to 15.8 ± 1.3 ‰ in shorthorn sculpin (Table 1). Overall, demersal fishes and Arctic char had enriched $\delta^{13}\text{C}$ values compared to all other fish sampled (Fig. 2A). Marine mammals had the lowest $\delta^{13}\text{C}$ variability (SD of 0.4 ‰) observed among taxonomic groups but had the highest $\delta^{15}\text{N}$ variability (SD of 1.7 ‰). Atlantic walrus had the lowest $\delta^{15}\text{N}$ values among marine mammals (12.9 ± 1.0 ‰), while ringed seals had the highest $\delta^{15}\text{N}$ values (17.6 ± 1.3 ‰). Within seabirds, glaucous gulls and thick-billed murres had similar isotopic values with -19.9 ± 0.7 ‰ and -22.2 ± 0.4 ‰ respectively for $\delta^{13}\text{C}$ and 16.0 ± 0.5 and 14.8 ± 0.5 ‰ respectively for $\delta^{15}\text{N}$ values. In contrast, common eiders had higher $\delta^{13}\text{C}$ and lower $\delta^{15}\text{N}$ values with -17.0 ± 1.0 ‰ and 13.3 ± 1.6 ‰, respectively (Table 1; Fig. 2A).

Table 1Carbon, nitrogen and sulfur stable isotope ratio ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$; ‰), C:N ratio, trophic position (TP), and sympagic carbon (%) of organisms in the Southampton Island marine food web at the phylum level.

Taxonomic phyla	Specie	Tissue	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	C:N	TP	n	$\delta^{34}\text{S}$ (‰)	Tissue	n	Sympagic C (%)
Benthic invertebrate		Whole organism, soft part, piece or muscle	881	-17.9 ± 2.3	11.9 ± 2.5	3.8 ± 0.9	2.7 ± 0.7	409	18.5 ± 2.3	Whole organism, soft part or muscle	357	28.0 \pm 20.1
Pelagic invertebrate		Whole organism or piece	303	-20.3 ± 1.3	10.8 ± 1.5	3.4 ± 0.4	2.4 ± 0.4	167	18.4 ± 1.3	Whole organism	66	21.8 \pm 17.3
Benthic fish		Muscle	171	-18.9 ± 1.3	14.9 ± 1.1	3.2 ± 0.1	3.6 ± 0.3	130	17.1 ± 1.7	Liver	20	14.6 \pm 9.6
	Arctic alligatorfish		6	-18.2 \pm 0.4	15.4 \pm 0.4	± 0.2	± 0.1	—*	—		—	—
	Arctic sculpin		7	-18.9 \pm 1.0	15.7 \pm 1.0	3.1 \pm 0.1	3.8 \pm 0.3	7	18.1 \pm 1.8		2	20.8 \pm 0.0
	Arctic shanny		20	-19.2 \pm 0.4	15.8 \pm 0.6	3.1 \pm 0.0	3.8 \pm 0.2	20	17.5 \pm 0.7		—	—
	Arctic staghorn sculpin		17	-16.4 \pm 0.3	14.0 \pm 0.5	3.2 \pm 0.1	3.3 \pm 0.2	17	13.9 \pm 0.4		—	—
	Atlantic poacher		2	-18.8 \pm 1.0	16.3 \pm 1.2	3.1 \pm 0.0	4.0 \pm 0.3	2	18.0 \pm 0.5		—	—
	Banded gunnel		14	-19.6 \pm 0.6	14.6 \pm 0.9	3.1 \pm 0.1	3.5 \pm 0.3	14	18.7 \pm 0.3		—	—
	Daubed shanny		5	-19.5 \pm 0.3	13.9 \pm 0.7	3.1 \pm 0.1	3.3 \pm 0.2	4	16.4 \pm 0.9		—	—
	Eelpouts		1	-19.2	14.6	3.5	3.5	1	17.4		—	—
	Fish doctor		2	-19.5 \pm 0.2	14.9 \pm 0.2	3.3 \pm 0.1	3.6 \pm 0.1	2	18.0 \pm 0.1		—	—
	Fourline snakeblenny		16	-18.2 \pm 0.7	15.8 \pm 0.7	3.2 \pm 0.1	3.8 \pm 0.2	9	16.4 \pm 1.1		2	13.1 \pm 0.0
	Moustache sculpin		21	-19.5 \pm 0.8	14.3 \pm 0.5	3.1 \pm 0.1	3.4 \pm 0.2	20	18.2 \pm 0.9		2	15.2 \pm 0.0
	<i>Myoxocephalus</i> sp		2	-18.2 \pm 0.18	14.1 \pm 1.4	3.2 \pm 0.1	3.3 \pm 0.4	2	17.4 \pm 1.9		—	—
	Ribbed sculpin		20	-19.5 \pm 0.6	15.2 \pm 0.5	3.2 \pm 0.1	3.7 \pm 0.1	5	17.9 \pm 0.2		8	5.9 \pm 3.5
	Sandlance		5	-22.4 \pm 1.1	12.8 \pm 0.3	3.1 \pm 0.1	3.0 \pm 0.1	—	—		—	—
	Shorthorn sculpin		12	-19.0 \pm 0.9	15.8 \pm 1.3	3.1 \pm 0.1	3.8 \pm 0.4	9	18.3 \pm 1.0		6	24.3 \pm 9.2
	Slender eelblenny		13	-17.7 \pm 1.1	13.9 \pm 0.8	3.3 \pm 0.2	3.3 \pm 0.2	13	15.4 \pm 0.9		—	—
	Snailfish		1	-19.2	12.9	3.2	3	1	19		—	—
	Spatulate sculpin		2	-18.5 \pm 0.1	15.3 \pm 0.3	3.3 \pm 0.1	3.7 \pm 0.1	1	17.1		—	—
	<i>Triglops</i> sp		3	-20.2 \pm 0.2	15.3 \pm 0.3	3.1 \pm 0.0	3.7 \pm 0.1	3	18.2 \pm 0.1		—	—
	Twohorn sculpin		2	-18.6 \pm 0.0	15.6 \pm 0.0	3.2 \pm 0.1	3.8 \pm 0.0	—	—		—	—
Pelagic fish		Muscle	83	-19.6 ± 0.7	14.5 ± 1.1	3.1 ± 0.1	3.5 ± 0.3	28	16.9 ± 1.4	Liver	74	6.6 \pm 3.5
	Polar cod		7	-19.5 \pm 0.3	15.3 \pm 0.9	3.1 \pm 0.1	3.7 \pm 0.3	—	—		12	7.8 \pm 2.5
	Arctic cod		38	-19.4 \pm 0.6	14.9 \pm 1.1	3.1 \pm 0.1	3.6 \pm 0.3	14	17.7 \pm 0.7		30	7.6 \pm 3.3
	Greenland cod		5	-20.7 \pm 0.1	15.4 \pm 0.4	3.2 \pm 0.0	3.7 \pm 0.1	—	—		—	—
	Capelin		25	-20.1 \pm 0.8	13.6 \pm 0.8	3.1 \pm 0.1	3.2 \pm 0.2	6	17.2 \pm 0.2		32	5.1 \pm 3.6
	Arctic char		5	-18.8 \pm 0.5	14.5 \pm 0.8	3.2 \pm 0.1	3.5 \pm 0.2	8	15.4 \pm 1.5		—	—
Marine Mammal		Muscle	72	-18.2 ± 0.4	16.6 ± 1.7	3.2 ± 0.1	4.7 ± 0.7	63	17.5 ± 0.6	Liver	45	53.3 \pm 22.2
	Beluga		12	-18.3 \pm 0.3	16.4 \pm 0.7	3.1 \pm 0.0	4.1 \pm 0.2	8	17.5 \pm 0.6		3	22.8 \pm 11.7
	Narwhal		15	-18.1 \pm 0.3	15.4 \pm 1.2	3.1 \pm 0.1	3.9 \pm 0.5	10	17.5 \pm 0.8		3	51.6 \pm 13.0
	Ringed Seal		41	-18.3 \pm 0.4	17.6 \pm 1.3	3.2 \pm 0.1	4.8 \pm 0.5	41	17.4 \pm 0.5		35	57.0 \pm 22.6
	Walrus		4	-18.5 \pm 0.3	12.9 \pm 1.0	3.2 \pm 0.1	3.0 \pm 0.3	4	18.1 \pm 0.4		4	44.5 \pm 7.8
Sea bird			62	-20.1 ± 0.5	15.3 ± 0.8	3.3 ± 0.1	3.9 ± 0.2	62	16.6 ± 2.1		—	—
	Common Eider	Plasma	15	-17.0 \pm 1.0	13.3 \pm 1.6	3.4 \pm 0.1	3.1 \pm 0.5	15	14.7 \pm 3.6		—	—
	Glaucous Gull	Blood	16	-19.9 \pm 0.7	16.0 \pm 0.5	3.2 \pm 0.0	3.9 \pm 0.1	16	17.0 \pm 0.6		—	—
	Thick-Billed Murre	Blood	31	-20.2 \pm 0.4	14.8 \pm 0.5	3.2 \pm 0.1	3.6 \pm 0.1	31	17.3 \pm 0.3		—	—

*Not analyzed

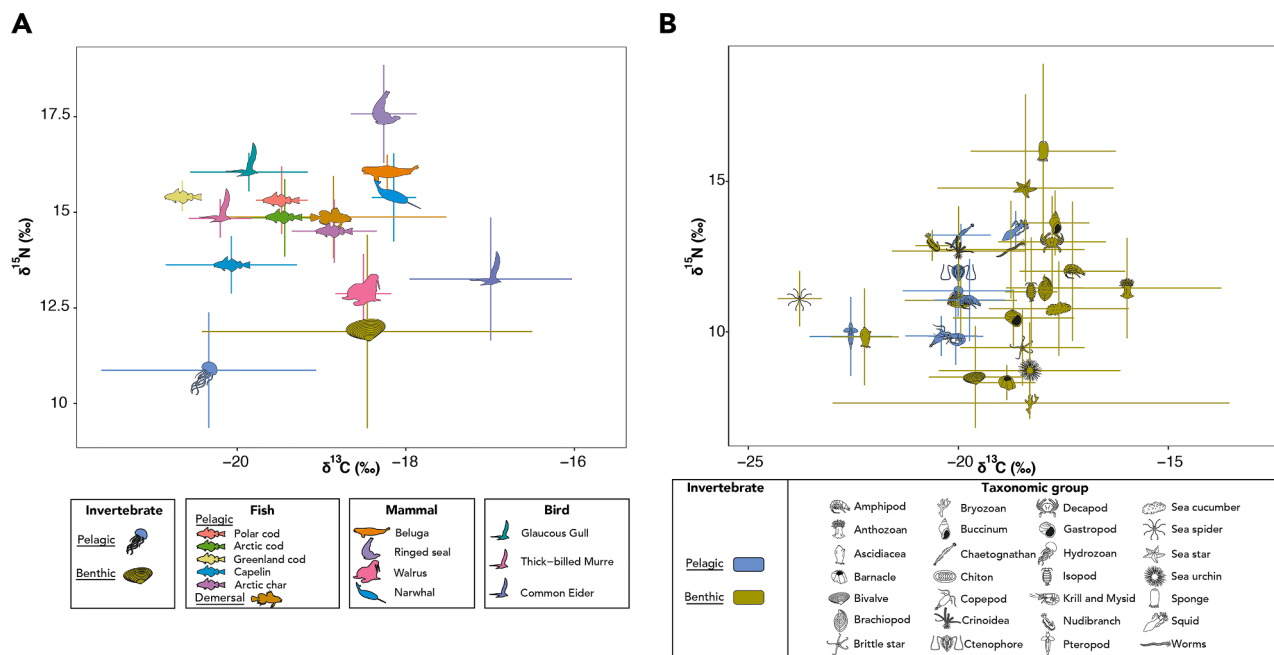


Fig. 2. Relationship of carbon and nitrogen stable isotope ratio ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$; ‰) of organisms in the Southampton Island marine food web at the A) phylum and B) invertebrate taxonomic group level. Pelagic and benthic invertebrates and demersal fish are arithmetic means.

Across the Southampton Island marine food web, average TP ranged from 1.1 ± 0.1 in the bivalve *Crenella* sp. to 4.8 in an asteroidea (sea star) and 4.8 ± 0.5 in ringed seals, with some individual seals occupying TP 5.8 (Fig. S1). In ascending order, pelagic invertebrates occupied a TP of 2.4 ± 0.4 , benthic invertebrates of 2.7 ± 0.7 [1.1–4.8], Atlantic walrus of 3.0 ± 0.3 , common eider of 3.1 ± 0.5 , capelin of 3.2 ± 0.2 , Arctic char of 3.5 ± 0.2 , Arctic cod of 3.6 ± 0.3 , thick-billed murre of 3.6 ± 0.1 , demersal fish of 3.6 ± 0.3 , Greenland cod of 3.7 ± 0.1 , polar cod

of 3.7 ± 0.3 , glaucous gull of 3.9 ± 0.1 , narwhal of 3.9 ± 0.5 , beluga of 4.1 ± 0.2 , and ringed seal of 4.8 ± 0.5 (Table 1; Fig. 3). Benthic and pelagic invertebrate as well as ringed seal had a significant difference in trophic position from almost all other groups (Table S3).

In all taxa investigated, except for Polar cod and Greenland cod, $\delta^{34}\text{S}$ ranged from 12.4 ± 1.6 ‰ in the decapod *Argis dentata* to 22.8 ± 0.5 ‰ in bryozoans. Benthic invertebrates had a mean $\delta^{34}\text{S}$ value of 18.5 ± 2.3 ‰ with high variability observed across benthic taxonomic groups

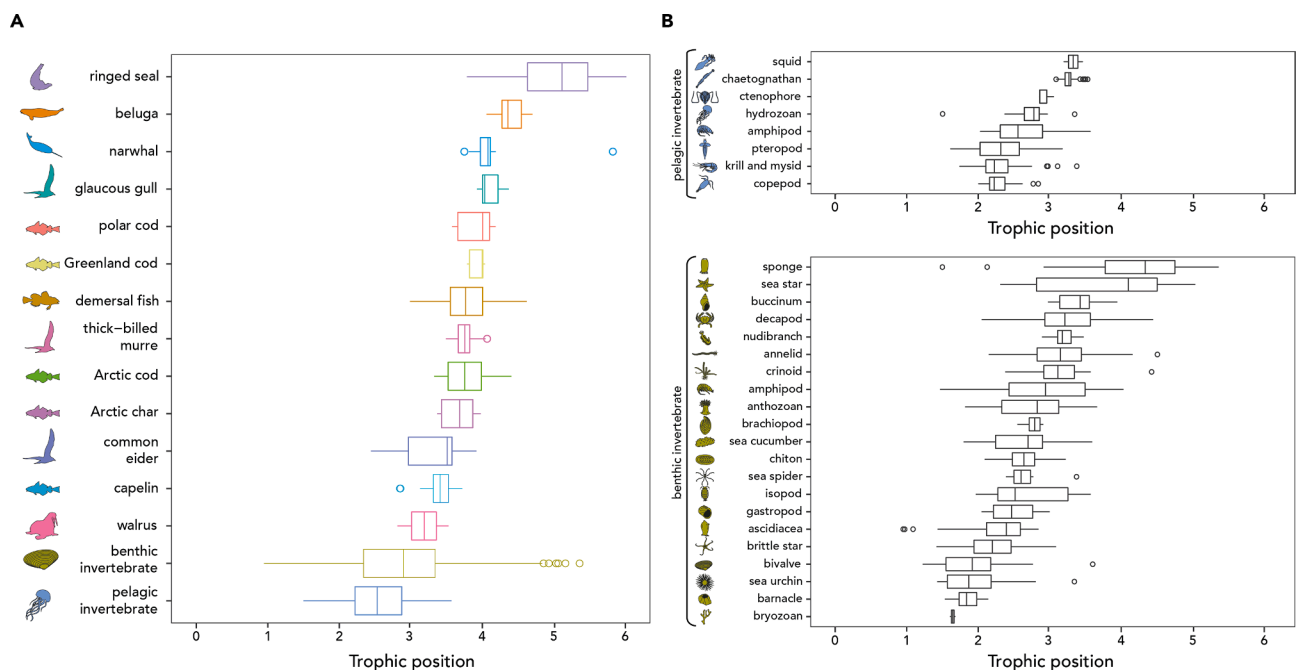


Fig. 3. Trophic position (TP) of organisms in the Southampton Island marine food web at the A) phylum and B) invertebrate taxonomic group level. Pelagic and benthic invertebrates and demersal fish are arithmetic medians.

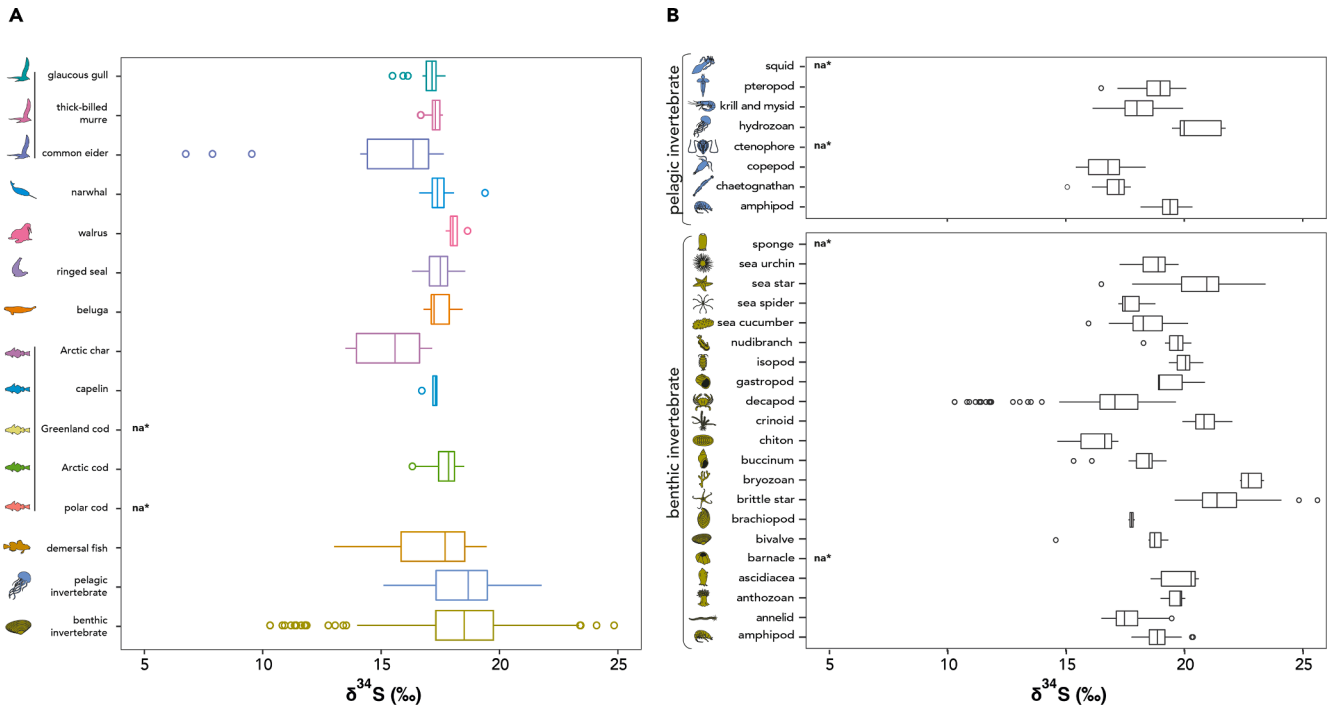


Fig. 4. Sulfur stable isotope ratio ($\delta^{34}\text{S}$; ‰) of organisms in the Southampton Island marine food web at the A) phylum and B) invertebrate taxonomic group level. Pelagic and benthic invertebrates and demersal fish are arithmetic medians.

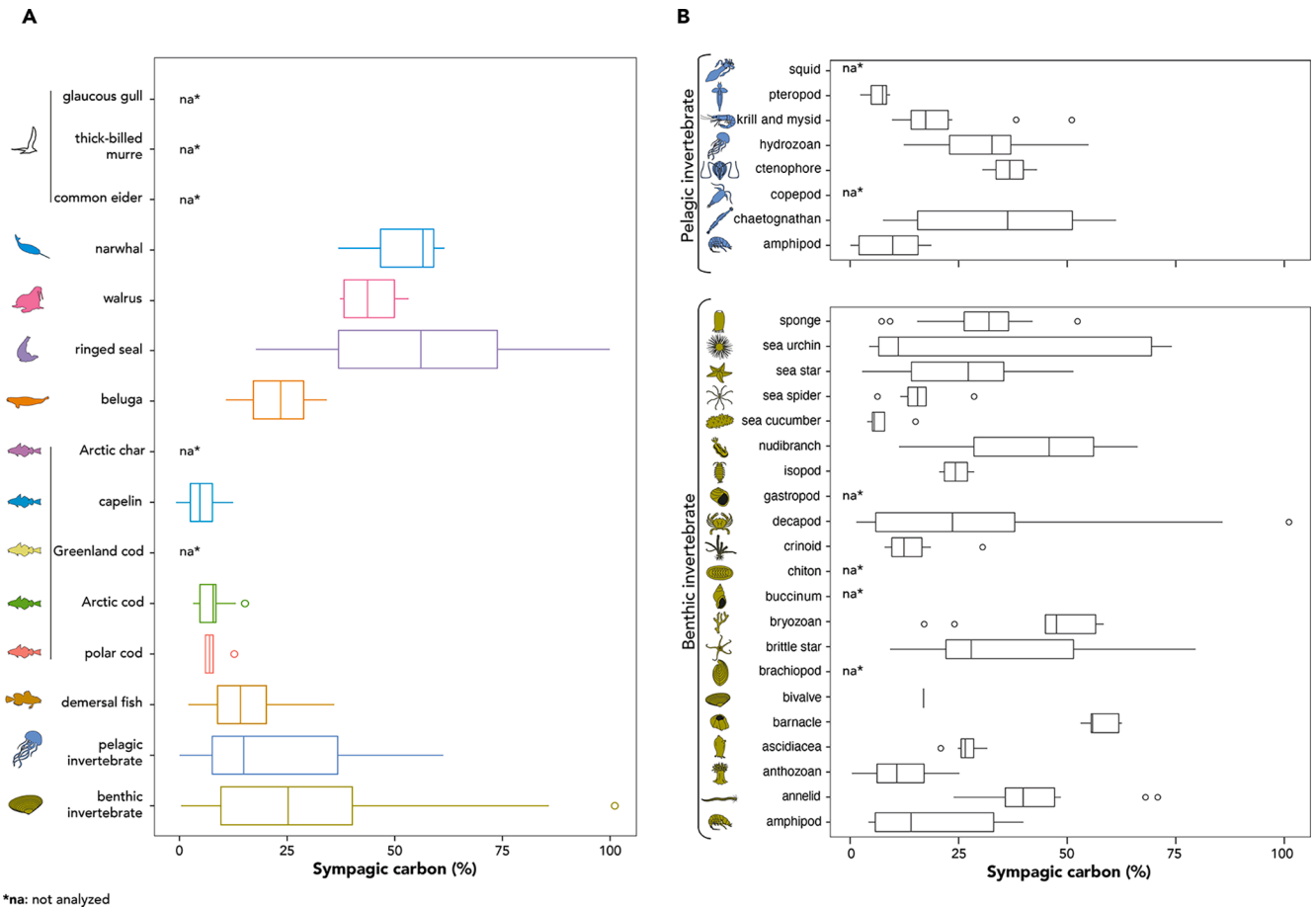


Fig. 5. Sympagic carbon (%) of organisms in the Southampton Island marine food web at the A) phylum and B) invertebrate taxonomic group level. Pelagic and benthic invertebrates and demersal fish are arithmetic medians.

(Fig. 4B). Decapods had the lowest $\delta^{34}\text{S}$ values (16.6 ± 2.1 ‰) while bryozoans had the highest $\delta^{34}\text{S}$ values (22.8 ± 0.5 ‰) (Fig. 4B). Although pelagic invertebrates appeared slightly decreasing and less variable $\delta^{34}\text{S}$ values than benthic invertebrates with 18.4 ± 1.3 ‰, both groups were on average not significantly different (Fig. 4A; Table S4). In pelagic invertebrates, the highest $\delta^{34}\text{S}$ values were observed in hydrozoans (20.6 ± 0.9 ‰) while the lowest $\delta^{34}\text{S}$ values were found in copepods (16.8 ± 0.9 ‰) (Fig. 4B). With the exception of invertebrates, demersal fishes, Arctic char, and common eiders, $\delta^{34}\text{S}$ values in all the other groups had low variation and were not significantly different (Table S4) with $\delta^{34}\text{S}$ values of ca. 17.4 ‰. The mean \pm SD $\delta^{34}\text{S}$ of demersal fish, Arctic char and common eider were 17.1 ± 1.7 ‰, 15.4 ± 1.5 ‰ and 14.7 ± 3.6 ‰, respectively (Fig. 4A, Table 1).

Sympagic carbon percentage (SC%) were not analyzed in seabirds nor in Arctic char and Greenland cod. In all other species investigated, SC% ranged from 1.4 % in the benthic invertebrate *Actiniaria* sp to 57.0 \pm 22.6 % in ringed seals. The taxonomic groups with the highest significant differences in SC% were pelagic fishes, ringed seals, demersal fishes, and benthic invertebrates (Table S5). In benthic invertebrates, average SC% was 28.0 ± 20.1 % and had the highest variability among individuals with values ranging from 0.4 to 101.0 % (Fig. 5A). The highest percentages of sympagic carbon among benthic invertebrates were found in predator functional group such as gastropods, sea stars, decapods, and brittle stars. By contrast, lower percentages of sympagic carbon occurred in filter-feeding or detritivore benthic invertebrates such as crinoids, sea cucumbers and bivalves (Fig. 5B). Pelagic invertebrates had lower SC% than benthic invertebrates with 21.8 ± 17.3 %, but also had high variability among individuals with values ranging from 0.1 to 61.3 % (Fig. 5A). Demersal fish SC% was higher than in pelagic fish with 14.6 ± 9.6 and 6.6 ± 3.5 %, respectively. Among the different groups investigated, marine mammals had the highest average SC% with a mean of 53.3 ± 22.2 % (Table 1; Fig. 5A). Beluga had the lowest SC% among marine mammal species (22.8 ± 11.7 %) while ringed seals had the highest SC% (57.0 ± 22.6 %).

4. Discussion

In the present study, we provide the first characterization of carbon flow (ice algae and phytoplankton-derived carbon use) and vertical trophic structure across the Southampton Island marine food web, from lower to upper trophic levels within invertebrates, fish, marine mammals, and seabirds. The vertical trophic structure of this system included an average trophic position maximum of 4.8 with some ringed seal individuals reaching TP 5.8 which has been observed elsewhere where at least 6 trophic levels occurred in Cumberland Sound, Nunavut (Hussey et al., 2014). Moreover, our results confirm the importance of carbon produced by ice algae for the functioning of this ecosystem, with an averaged ~ 26.0 % carbon of sympagic origin fuelling the local food web. We also highlighted the importance of sympagic carbon to the benthic component and inferred from the low amount of variation in $\delta^{34}\text{S}$ across the majority of benthic and pelagic-associated species, the essential role of the benthic component in transferring this carbon to upper pelagic trophic levels, including marine mammals and birds.

4.1. Trophic structure of the Southampton Island marine food web

4.1.1. Invertebrates

On average, our study suggests a relatively low trophic level for invertebrates. However, benthic invertebrates displayed high variability between species (Fig. 3A), likely explained by their high taxonomic and functional diversity. Previous studies have determined the trophic position of many invertebrates and highlighted the presence of at least 3 and 4 TP in pelagic and benthic invertebrates, respectively (Hobson and Welch, 1992; Iken et al., 2005; Iken et al., 2010; Renaud et al., 2011). Our analyses including a considerable number of invertebrate taxa confirmed these results with 3 and 4 TP observed in pelagic and benthic

invertebrates, respectively (Table S1). The vertical structure of the benthic compartment is composed of filter-feeding taxonomic groups such as bivalves, barnacles or bryozoans occupying the lowest TP, and carnivorous and scavenger groups such as sea stars or decapods occupying the highest TP (Fig. 3B; Fig. S1). Recognized as key predatory species, sea stars exert top-down control over the abundance and distribution of benthic organisms in many ocean regions (Garrido et al., 2021; Menge and Sanford, 2013). Although these species had high TPs, sea stars also had high TP variability with values ranging from 2.1 to 4.8, as previously observed in the Alaska Beaufort Sea shelf (Divine et al., 2015). We suggest that this variability derives from the different feeding habits of the species composing this taxa, with some species feeding on infaunal and epifaunal organisms (e.g., bivalves, crustaceans) while others feed on megafaunal organisms (e.g., sponges and anthozoans such as sea anemones and soft corals) (Gale et al., 2013; Wagstaff et al., 2014). For instance, in our study, the sea star *Leptasterias polaris* had a TP of 2.1, which is explained by its feeding on low TP species such as bivalves and molluscs (Gaymer et al., 2001; Gaymer et al., 2004). Alternatively, the dominant predators, *Pteraster militaris* and *Diploptaster multipes* had a TP of 4.0 and 4.5, respectively, likely due to foraging on various prey, including megafaunal organisms of high TP (Carey, 1972; Sargent et al., 1983). Because of the complexity of the benthic compartment, its many trophic levels, and the presence of the megafaunal predatory sea stars as apex predators, Amiraux et al. (2023) highlighted that the benthic compartment is not a low trophic level reservoir for the marine food web but rather a subweb of the marine food web equal to its pelagic counterpart.

Surprisingly, sponges, a taxonomic group of assumed filter-feeding species, had both one of the highest TPs among benthic invertebrates with 3.9 and variability with TPs ranging from 1.3 to 5.2 in some individuals. We suggest that the high and variable TP of this taxonomic group reveals the presence of both filter-feeding and carnivorous individuals in our sampling. Carnivorous sponges related to the Cladorhizidae family are ubiquitous in the Arctic, including the Hudson Bay Complex (Hestetun et al., 2017) and are known to rely on small crustaceans such as amphipods (Dinn and Leys, 2018; Hestetun et al., 2017), which were one trophic level below that of carnivorous sponges.

4.1.2. Fishes

Benthic and pelagic fishes had similar trophic levels of 3.6 and 3.5, respectively, comparable to those reported in the west Greenland marine food web (see Linnebjerg et al. (2016)). The relatively high variability of demersal fish TP in this study is due to the many different species we included ($n = 20$), that differ markedly in their foraging ecology. For instance, the specialist zooplankton-feeder sandlance (Danielsen et al., 2016) had a lower TP than the more generalist feeder shorthorn sculpin (Landry et al., 2018) with 3.0 ± 0.1 and 3.8 ± 0.4 , respectively, as also previously observed by Pedro et al. (2020). Pelagic invertebrates, and most notably copepods from the *Calanus* genus, are the preferential prey of capelin, which in turn is the key prey species of Greenland cod (Nielsen and Andersen, 2001; O'Driscoll et al., 2001). The similar $\delta^{13}\text{C}$ among these three species associated with their different trophic levels corroborates these trophic links (Figs. 2, 3). Arctic and Polar cod have a similar TP to Greenland cod, likely because all three species feed on copepods and mid-trophic level pelagic invertebrates such as the pelagic amphipods and mysids (Aune et al., 2021; Lønne and Gulliksen, 1989; Majewski et al., 2016; Süfke et al., 1998). Demersal fishes and Arctic char were enriched in ^{13}C compared to all other fishes (Fig. 2; Table S2) suggesting the consumption of ^{13}C enriched benthic prey, though Arctic char generally consume pelagic invertebrates (e.g., *Themisto libellula* and *Onisimus* sp) and fishes (e.g., Arctic cod and capelin; Grainger, 1953; Young et al., 2021).

4.1.3. Seabirds

The diet of glaucous gulls and thick-billed murre consists mainly of pelagic fish, including Arctic cod, capelin, sandlance (Bustnes et al.,

2000; Smith and Gaston, 2012). As such, these sea birds displayed higher TP than their prey associated with no significant $\delta^{13}\text{C}$ enrichment, supporting close diet links (Figs. 2, 3). Although gulls partially subsist on murre, fish likely make up most of their diet given their similar $\delta^{15}\text{N}$ to murre indicating similar trophic position. In contrast, common eiders displayed a much different and lower TP than glaucous gulls and thick-billed murre due to their diet consisting primarily of benthic invertebrates of relatively low TP, such as bivalves (primarily *Mytilus edulis*), gastropods, and benthic amphipods (Waltho and Coulson, 2015). This trophic link is corroborated by the similarity of the $\delta^{13}\text{C}$ signatures between common eider and benthic invertebrates associated with different TP (Figs. 2, 3).

4.1.4. Marine mammals

Marine mammals represented the group with the highest TP, with the exception of Atlantic walrus (Fig. 3A), which feeds to a large part on filter-feeding bivalves (Born et al., 2003; Fisher and Stewart, 1997). Both narwhal and beluga primarily consume pelagic fish, such as Arctic cod, Polar cod and capelin (Louis et al., 2021). However, the TP of beluga was slightly higher than that of the narwhal (Fig. 3, Table 1), which may be due to higher squid consumption by narwhal (Watt et al., 2013). The diet of ringed seals – the apex predator in our study – is varied and consists of fishes, such as capelin, sand lance, sculpin, Arctic char and Arctic cod, pelagic invertebrates such as amphipods (i.e., *Themisto libellula*) and mysids, as well as benthic invertebrates including decapods (e.g., *Hyas coarctatus*, *Eualus fabricii*, *Lebbeus groenlandicus* and *Lebbeus polaris*) (Chambellant et al., 2013; Dehn et al., 2007; Yurkowski et al., 2016). The TP of ringed seals was also highly variable between individuals, further highlighting their dietary plasticity (Yurkowski et al., 2016). However, it is important to note that the ringed seals were sampled during their fasting period of the spring moult. This can lead to increased $\delta^{15}\text{N}$ values, since the seals mainly get their energy from metabolizing their blubber stores, rather than prey, during this period (Hobson et al., 1993; Young and Ferguson, 2013).

4.2. Benthos, an important component for the transfer of carbon to the pelagic food web

The ratio of ^{34}S to ^{32}S , represented in relative terms by $\delta^{34}\text{S}$, is well-known to distinguish benthic from pelagic feeding in a food web, as $\delta^{34}\text{S}$ typically varies little from source to consumer and is, therefore, unaffected by trophic level (Krajcarz et al., 2019; Nehlich, 2015; Szpak and Buckley, 2020; Thomas and Cahoon, 1993). Sulfur dissolved in the water column is primarily present as sulfates while sulfur within sediments is primarily present as sulfides due to anaerobic reduction by bacteria (Hebert et al., 2006; Hobson, 1999). Sulfates are more enriched in ^{34}S compared with sulfides, thus, consumers feeding in the benthic habitats tend to have lower $\delta^{34}\text{S}$ values than pelagic marine consumers (Hobson, 1999; Thomas and Cahoon, 1993).

To our knowledge, this study is the most comprehensive work using sulfur isotope analysis across an Arctic coastal food web. Benthic invertebrates had the highest $\delta^{34}\text{S}$ variability in this system, with values ranging from 12.4 in the decapod *Argis dentata* and 22.8 ‰ in Bryozoan (Table S1). Surprisingly, although $\delta^{34}\text{S}$ values in pelagic invertebrates were less variable than in benthic invertebrates, they were also not significantly different (Table S4). This suggests that $\delta^{34}\text{S}$ would not differentiate between a consumer's diet from benthic or pelagic organisms. However, Southampton Island is subject to strong tidal- and wind-mixing currents (Kitching, 2022) that likely resuspend organic matter from the sediment into the water column. Therefore, we suggest that the relatively depleted $\delta^{34}\text{S}$ of the pelagic invertebrate in this area is rather indicative of their partial reliance on resuspended organic matter than a $\delta^{34}\text{S}$ method limitation, or that many species are not that reliant on the benthic microbial food web. Consequently, the $\delta^{34}\text{S}$ average value of 17.6 ‰ in all the pelagic taxa (invertebrates, fishes, seabirds, marine mammals), suggests that these taxonomic groups are dependent on both

pelagic and benthic-derived resources as part of their diet (Fig. 4). This confirms the findings of Murphy et al. (2016) who showed that benthic–pelagic interactions are numerous in the Arctic food web.

In the present study, $\delta^{34}\text{S}$ is not constantly lower in the benthic compartment compared to the pelagic compartment. Indeed, some benthic taxonomic groups had enriched ^{34}S values that were similar or higher to known pelagic-associated feeders such as capelin, narwhal and beluga. The most ^{34}S -enriched taxonomic groups are either those relying on pelagic food or those inhabiting the epibenthic habitat such as bryozoans and bivalves (filter feeders), brittle stars (surface deposit feeders), sea stars (predators) and crinoids (suspension feeders). The taxonomic groups with the lowest $\delta^{34}\text{S}$ values were those that feed within the sediment layer, such as annelids. Therefore, we suggest that a depleted ^{34}S signature indicates an infaunal feeding habit, which applies only to a portion of the benthic species. This assumption is supported by several examples in our dataset. For example, although Atlantic walrus is a known benthic foraging species (Fisher and Stewart, 1997), it had relatively enriched ^{34}S value that derived from its filter-feeding clams inhabiting the sediment. While situated within the sediment, they consume particulate organic matter from the water column, resulting in lower $\delta^{34}\text{S}$ values. In contrast, the common eider had a relatively depleted ^{34}S value that is explained by its known benthic foraging behavior on various benthic species, such as bivalves, gastropods, annelids, crustaceans and fishes (Merkel et al., 2007), and likely species of infaunal feeding habit.

4.3. Carbon flows supporting the Southampton Island marine ecosystem

Numerous studies have shown that ice algae are a better food source for benthic consumers than phytoplankton due to their higher nutritional quality, a key parameter for growth and reproduction (Amiraux et al., 2021; McMahon et al., 2006; North et al., 2014). The present study confirms the important role of ice algae in the functioning of the benthic component with an average of 28.0 ± 20.1 % of the carbon fueling this component of sympagic origin. However, some benthic taxonomic groups seem more dependent on sympagic carbon than others. For example, gastropods, sea stars, decapods, and brittle stars were highly dependent on this sympagic resource, whereas it appears to be less important for filter-feeding or detritivore taxonomic group such as bivalves, sea cucumbers or crinoids that mostly relied on phytoplankton carbon at the time of sampling (Fig. 4B; Table S1).

The high dependence of marine mammal phyla on ice algae (53.3 ± 22.2 %) is surprising considering that, apart from Atlantic walrus, fish is their preferred prey, and fish, on average, had a relatively low ice algae carbon dependence (Fig. 5). This apparent difference in sympagic carbon dependence between marine mammals and fish could be explained by a different turnover rate of molecules in the livers used to assess the percentage of sympagic carbon in these phyla or spatial differences in collection sites. Previous studies suggested a relatively high turnover of HBIs in invertebrates (days; Amiraux et al., 2021; Brown and Belt, 2017) compared to ringed seals (weeks to months; Brown et al., 2014a). The metabolism of the organisms seems to influence the turnover of HBIs and it is possible that turnover is faster in fishes than in marine mammals. Thus, the sympagic carbon index in the liver of marine mammals collected in summer may be representative of the entire spring bloom production (ice algae and then phytoplankton). Alternatively, for fish collected in summer, this index could be representative only of the phytoplanktonic bloom because of their likely faster turnover of the HBI and, thus, the sympagic carbon proxy. Another explanation may be that in these regions, marine mammals consume a mix of both invertebrates and fish. This assumption is supported by (i) their $\delta^{34}\text{S}$ indicating a mix of pelagic and benthic foraging behavior, (ii) the numerous observations of the dependence of marine mammals on benthic organisms in shallow areas (Maxwell et al., 2012; Szpak and Buckley, 2020), and (iii) by the relatively high SC% content of some of their known invertebrate preys (e.g., decapod, such as *Hyas coarctatus*; krill, and mysids such as

Thysanoessa raschii; Table S1). In any case, although HBI turnover rate in the different phyla constituting the Arctic ecosystem should be better assessed, our study revealed, at least in this coastal environment, the critical role of the benthic component for sustaining the higher trophic level pelagic food web, as well as the importance of sea ice-derived carbon for the diet of Arctic marine mammals (Brown et al., 2014a; Brown et al., 2018).

5. Conclusion

Based on a multi-proxy approach, we examined the structure and function of the Southampton Island marine food web across numerous benthic and pelagic invertebrate species, fishes, marine mammals and seabirds. Interconnections of this benthic component with the pelagic component are numerous in this coastal area as suggested by the low amount of variability in $\delta^{34}\text{S}$ across most organisms, indicating a mix of benthic and pelagic feeding. The relatively high sympagic carbon dependence of marine mammals and their benthic invertebrate prey, also confirm the important role of the benthic component for sustaining the higher trophic levels of the pelagic food web.

By reducing sea ice extent and duration, climate change impacts the patterns of primary productivity with an expected increase in phytoplankton production to the detriment of ice algal production. As such, pelagic-benthic coupling would be altered with a reduced supply of ice algal material to the benthic component. Because of the loss of this material of high nutritional quality that is essential to the reproduction of many benthic organisms, we expect a change in the abundance, diversity and structure of the benthic food web. Through a cascading effect, higher trophic level pelagic organisms that depend on the benthic component will also be impacted, which in the coastal zone represents many fishes, sea birds and the majority of marine mammals. Finally, our study provides a comprehensive baseline of trophic structures and functioning of the Southampton Island marine food web that will be important for monitoring future changes that may occur under accelerated climate change and increased anthropogenic pressures.

Declaration of Competing Interest

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

Data availability

Summary data of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^{34}\text{S}$, HBI and trophic position by species is provided in Table S1.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2023.109938>.

References

- Amiraux, R., Archambault, P., Moriceau, B., Lemire, M., Babin, M., Memery, L., Massé, G., Tremblay, J.-É., 2021. Efficiency of sympagic-benthic coupling revealed by analyses of n-3 fatty acids, IP25 and other highly branched isoprenoids in two filter-feeding Arctic benthic molluscs: *Mya truncata* and *Serripes groenlandicus*. *Org. Geochem.* 151, 104160.
- Amiraux, R., Smik, L., Köseoglu, D., Rontani, J.-F., Galindo, V., Grondin, P.-L., Babin, M., Belt, S.T. 2019. Temporal evolution of IP25 and other highly branched isoprenoid lipids in sea ice and the underlying water column during an Arctic melting season. *Elementa Sci. Anthropocene.* 7. <https://doi.org/10.1525/elementa.377>.
- Amiraux, R., Lavaud, J., Cameron-Bergeron, K., Matthes, L.C., Peeken, I., Mundy, C.J., Babb, D., Tremblay, J.-É. 2022. Content in fatty acids and carotenoids in phytoplankton blooms during the seasonal sea ice retreat in Hudson Bay Complex, Canada. *Elementa Sci. Anthropocene.* 10(1). <https://doi.org/10.1525/elementa.2021.00106>.
- Amiraux, R., Yurkowski, D.J., Archambault, P., Pierrejean, M., Mundy, C.J., 2023. Top predator sea stars are the benthic equivalent to polar bears of the pelagic realm. *PNAS* 120 (1).
- Aune, M., Raskhozheva, E., Andrade, H., Augustine, S., Bambulyak, A., Camus, L., Carroll, J., Dolgov, A.V., Hop, H., Moiseev, D., Renaud, P.E., Varpe, Ø., 2021. Distribution and ecology of polar cod (*Boreogadus saida*) in the eastern Barents Sea: A review of historical literature. *Mar. Environ. Res.* 166, 105262 <https://doi.org/10.1016/j.marenvres.2021.105262>.
- Barbedo, L., Bélanger, S., Tremblay, J.-É., 2020. Climate control of sea-ice edge phytoplankton blooms in the Hudson Bay system. *Elem. Sci. Anth.* 8 <https://doi.org/10.1525/elementa.039>.
- Barquette, V., Strauss, V., Ryan, P.G., 2013. Stable isotope turnover in blood and claws: A case study in captive African Penguins. *J. Exp. Mar. Biol. Ecol.* 448, 121–127. <https://doi.org/10.1016/j.jembe.2013.06.021>.
- Belt, S.T., 2018. Source-specific biomarkers as proxies for Arctic and Antarctic sea ice. *Org. Geochem.* 125, 277–298. <https://doi.org/10.1016/j.orggeochem.2018.10.002>.
- Belt, S.T., Massé, G., Rowland, S.J., Poulin, M., Michel, C., LeBlanc, B., 2007. A novel chemical fossil of palaeo sea ice: IP₂₅. *Org. Geochem.* 38, 16–27. <https://doi.org/10.1016/j.orggeochem.2006.09.013>.
- Belt, S.T., Smik, L., Köseoglu, D., Knies, J., Husum, K., 2019. A novel biomarker-based proxy for the spring phytoplankton bloom in Arctic and sub-arctic settings—HBI T25. *Earth Planet. Sci. Lett.* 523, 115703 <https://doi.org/10.1016/j.epsl.2019.06.038>.
- Bligh, E.G., Dyer, W.J., 1959. A rapid method of total lipid extraction and purification. *Can. J. Biochem. Physiol.* 37, 911–917. <https://doi.org/10.1139/o59-099>.
- Boetius, A., Albrecht, S., Bakker, K., Bienhold, C., Felden, J., Fernández-Méndez, M., Hendricks, S., Katlein, C., Lalande, C., Krumpfen, T., Nicolaus, M., Peeken, I., Rabe, B., Rogacheva, A., Rybakova, E., Somavilla, R., Wenzhöfer, F., Party, R.P.A.-S.S., 2013. Export of Algal Biomass from the Melting Arctic Sea Ice. *Science* 339, 1430–1432. <https://doi.org/10.1126/science.1231346>.
- Born, E., Rysgaard, S., Ehlme, G., Sejr, M., Acquarone, M., Levermann, N., 2003. Underwater observations of foraging free-living Atlantic walrus (*Odobenus rosmarus rosmarus*) and estimates of their food consumption. *Polar Biol.* 26, 348–357. <https://doi.org/10.1007/s00300-003-0486-z>.
- Brown, T.A., 2018. Stability of the lipid biomarker H-Print within preserved animals. *Polar Biol.* 41 (9), 1901–1905.
- Brown, T., Alexander, C., Yurkowski, D., Ferguson, S., Belt, S., 2014a. Identifying variable sea ice carbon contributions to the Arctic ecosystem: A case study using highly branched isoprenoid lipid biomarkers in Cumberland Sound ringed seals. *Limnol. Oceanogr.* 59, 1581–1589. <https://doi.org/10.4319/lo.2014.59.5.1581>.
- Brown, T.A., Belt, S.T., 2017. Biomarker-based H-Print quantifies the composition of mixed sympagic and pelagic algae consumed by *Artemia* sp. *J. Exp. Mar. Biol. Ecol.* 488, 32–37. <https://doi.org/10.1016/j.jembe.2016.12.007>.

- Brown, T.A., Belt, S.T., Tatarek, A., Mundy, C.J., 2014b. Source identification of the Arctic sea ice proxy IP25. *Nature Commun.* 5 <https://doi.org/10.1038/ncomms5197>.
- Brown, T.A., Galicia, M.P., Thiemann, G.W., Belt, S.T., Yurkowski, D.J., Dyck, M.G. 2018. High contributions of sea ice derived carbon in polar bear (*Ursus maritimus*) tissue. *PLoS one.* 13: e0191631. <https://doi.org/10.1371/journal.pone.0191631>.
- Brown, T.A., Yurkowski, D.J., Ferguson, S.H., Alexander, C., Belt, S.T., 2014c. H-Print: a new chemical fingerprinting approach for distinguishing primary production sources in Arctic ecosystems. *Environ. Chem. Lett.* 12, 387–392. <https://doi.org/10.1007/s10311-014-0459-1>.
- Bustnes, J.O., Erikstad, K.E., Bakken, V., Mehlum, F., Skaare, J.U., 2000. Feeding Ecology and the Concentration of Organochlorines in Glaucous Gulls. *Ecotoxicology* 9, 179–186. <https://doi.org/10.1023/A:1008938603257>.
- Carey, A.G., 1972. Food sources of sublittoral, bathyal and abyssal asteroids in the northeast Pacific Ocean. *Ophelia* 10 (1), 35–47.
- Carmack, E., Wassmann, P., 2006. Food webs and physical–biological coupling on pan-Arctic shelves: unifying concepts and comprehensive perspectives. *Prog. Oceanogr.* 71, 446–477. <https://doi.org/10.1016/j.pocean.2006.10.004>.
- Castro de la Guardia, L., Filbee-Dexter, K., Reimer, J., MacGregor, K., Garrido, I., Singh, R.K., Bélanger, S., Konar, B., Iken, K., Johnson, L.E., Archambault, P., Sejr, M.K., Søreide, J.E., Mundy, C.J. in press. Increasing depth distribution of Arctic kelp with increasing light during longer open water days. *Elementa Sci. Anthropocene*.
- Chambellant, M., Stirling, I., Ferguson, S.H., 2013. Temporal variation in western Hudson Bay ringed seal *Phoca hispida* diet in relation to environment. *Mar. Ecol. Prog. Ser.* 481, 269–287. <https://doi.org/10.3354/meps10134>.
- Clark, B., 1980. The Lake site (KkHh-2), Southampton Island, NWT and its position in Sadlermiut prehistory. *Canadian J. Archaeol./J. Canadien d'Archéologie* 53–81.
- Collins, B., 1956. Archaeological investigations on Southampton and Coats Islands, NWT. *National Museums of Canada Bulletin* 142, 82–85.
- Craig, H., 1957. Isotopic standards for carbon and oxygen and correction factors for mass-spectrometric analysis of carbon dioxide. *Geochim. Cosmochim. Acta* 12, 133–149. [https://doi.org/10.1016/0016-7037\(57\)90024-8](https://doi.org/10.1016/0016-7037(57)90024-8).
- Cusset, F., Fort, J., Mallory, M., Braune, B., Massicotte, P., Massé, G., 2019. Arctic seabirds and shrinking sea ice: egg analyses reveal the importance of ice-derived resources. *Sci. Rep.* 9, 15405. <https://doi.org/10.1038/s41598-019-51788-4>.
- Danielsen, N.S., Hedeholm, R.B., Grønkjær, P., 2016. Seasonal changes in diet and lipid content of northern sand lance *Ammodytes dubius* on Fyllas Bank, West Greenland. *Marine Ecology Progress Series* 558, 97–113. <https://doi.org/10.3354/meps11859>.
- Darnis, G., Fortier, L., 2012. Zooplankton respiration and the export of carbon at depth in the Amundsen Gulf (Arctic Ocean). *J. Geophys. Res. Oceans* 117 (C4), n/a–n/a.
- Dehn, L.-A., Sheffield, G.G., Föllmann, E.H., Duffy, L.K., Thomas, D.L., O'Hara, T.M., 2007. Feeding ecology of phocid seals and some walrus in the Alaskan and Canadian Arctic as determined by stomach contents and stable isotope analysis. *Polar Biol.* 30, 167–181. <https://doi.org/10.1007/s00300-006-0171-0>.
- Dinn, C., Leys, S.P., 2018. Field guide to sponges of the Eastern Canadian Arctic. <https://doi.org/10.7939/R3DF6KJ4G>.
- Divine, L.M., Iken, K., Bluhm, B.A., 2015. Regional benthic food web structure on the Alaska Beaufort Sea shelf. *Mar. Ecol. Prog. Ser.* 531, 15–32. <https://doi.org/10.3354/meps11340>.
- Filbee-Dexter, K., Wernberg, T., Fredriksen, S., Norderhaug, K.M., Pedersen, M.F., 2019. Arctic kelp forests: Diversity, resilience and future. *Global Planet. Change* 172, 1–14. <https://doi.org/10.1016/j.gloplacha.2018.09.005>.
- Filbee-Dexter, K., MacGregor, K.A., Lavoie, C., Garrido, I., Goldsmit, J., Castro de la Guardia, L., Howland, K.L., Johnson, L.E., Konar, B., McKindsey, C.W., Mundy, C.J., Schlegel, R.W., Archambault, P., 2022. Sea Ice and Substratum Shape Extensive Kelp Forests in the Canadian Arctic. *Front. Mar. Sci.* 9 <https://doi.org/10.3389/fmars.2022.754074>.
- Fisher, K., Stewart, R., 1997. Summer foods of Atlantic walrus, *Odobenus rosmarus rosmarus*, in northern Foxe Basin, Northwest Territories. *Can. J. Zool.* 75, 1166–1175. <https://doi.org/10.1139/z97-139>.
- France, R., 1995. Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. *Mar. Ecol. Prog. Ser.* 124, 307–312. <https://doi.org/10.3354/meps124307>.
- Gale, K.S.P., Hamel, J.-F., Mercier, A., 2013. Trophic ecology of deep-sea Asteroidea (Echinodermata) from eastern Canada. *Deep Sea Res. Part I* 80, 25–36. <https://doi.org/10.1016/j.dsr.2013.05.016>.
- Garrido, I., Pardo, L.M., Johnson, L.E., Schories, D., 2021. Selective Feeding by a Predatory Sea Star Across a Depth Gradient in Northern Patagonia, Chile. *Front. Mar. Sci.* 355 <https://doi.org/10.3389/fmars.2021.636208>.
- Gaymer, C.F., Himmelman, J.H., Johnson, L.E., 2001. Distribution and feeding ecology of the seastars *Leptasterias polaris* and *Asterias vulgaris* in the northern Gulf of St Lawrence, Canada. *J. Mar. Biol. Assoc. U.K.* 81, 827–843. <https://doi.org/10.1017/S0025315401004660>.
- Gaymer, C.F., Dutil, C., Himmelman, J.H., 2004. Prey selection and predatory impact of four major sea stars on a soft bottom subtidal community. *J. Exp. Mar. Biol. Ecol.* 313, 353–374. <https://doi.org/10.1016/j.jembe.2004.08.022>.
- 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. 52: 559–571. <https://doi.org/10.1515/BOT.2009.074>.
- Gosselin, M., Lavoie, M., Wheeler, P.A., Horner, R.A., Booth, B.C., 1997. New measurements of phytoplankton and ice algal production in the Arctic Ocean. *Deep Sea Res., Part II* 44, 1623–1644. [https://doi.org/10.1016/S0967-0645\(97\)00054-4](https://doi.org/10.1016/S0967-0645(97)00054-4).
- Grainger, E., 1953. On the age, growth, migration, reproductive potential and feeding habits of the Arctic char (*Salvelinus alpinus*) of Frobisher Bay, Baffin Island. *J. Fisher. Board Canada* 10, 326–370. <https://doi.org/10.1139/f53-023>.
- Gupta, K., Mukhopadhyay, A., Babb, D.G., Barber, D.G., Ehn, J.K. 2022. Landfast sea ice in Hudson Bay and James Bay: Annual cycle, variability and trends, 2000–2019. *Elementa Sci. Anthropocene.* 10: 00073. <https://doi.org/10.1525/elementa.2021.00073>.
- Hahn, S., Hoye, B.J., Korthals, H., Klaassen, M. 2012. From food to offspring down: tissue-specific discrimination and turn-over of stable isotopes in herbivorous waterbirds and other avian foraging guilds. *PLoS one.* 7: e30242. <https://doi.org/10.1371/journal.pone.0030242>.
- Hebert, C.E., Arts, M.T., Weseloh, D.V.C., 2006. Ecological Tracers Can Quantify Food Web Structure and Change. *Environ. Sci. Tech.* 40, 5618–5623. <https://doi.org/10.1021/es0520619>.
- Hestetun, J.T., Tompkins-Macdonald, G., Rapp, H.T., 2017. A review of carnivorous sponges (Porifera: Cladorhizidae) from the Boreal North Atlantic and Arctic. *Zool. J. Linn. Soc.* 181, 1–69. <https://doi.org/10.1093/zoolinnean/zw022>.
- Hobson, K.A., 1999. Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* 120, 314–326. <https://doi.org/10.1007/s004420050865>.
- Hobson, K.A., Clark, R.G., 1992. Assessing avian diets using stable isotopes I: turnover of ^{13}C in tissues. *Condor* 94, 181–188. <https://doi.org/10.2307/1368807>.
- Hobson, K.A., 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. *Mar. Ecol. Prog. Ser.* 84, 9–18.
- Hobson, K.A., Alisauskas, R.T., Clark, R.G., 1993. Stable-nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: implications for isotopic analyses of diet. *Condor* 95, 388–394. <https://doi.org/10.2307/1369361>.
- Hobson, K.A., Ambrose Jr, W.G., Renaud, P.E., 1995. Sources of primary production, benthic-pelagic coupling, and trophic relationships within the Northeast Water Polynya: insights from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. *Mar. Ecol. Prog. Ser.* 128, 1–10. <https://doi.org/10.3354/meps128001>.
- Hobson, K.A., Schell, D.M., Renouf, D., Noseworthy, E., 1996. Stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: implications for dietary reconstructions involving marine mammals. *Can. J. Fish. Aquat. Sci.* 53, 528–533. <https://doi.org/10.1139/f95-209>.
- Hussey, N.E., MacNeil, M.A., McMeans, B.C., Olin, J.A., Dudley, S.F.J., Cliff, G., Wintner, S.P., Fennessy, S.T., Fisk, A.T., Hessen, D., 2014. Rescaling the trophic structure of marine food webs. *Ecol. Lett.* 17 (2), 239–250.
- Iken, K., Bluhm, B., Gradinger, R., 2005. Food web structure in the high Arctic Canada Basin: evidence from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. *Polar Biol.* 28, 238–249. <https://doi.org/10.1007/s00300-004-0669-2>.
- Iken, K., Bluhm, B., Dunton, K., 2010. Benthic food-web structure under differing water mass properties in the southern Chukchi Sea. *Deep Sea Res. Part II* 57, 71–85. <https://doi.org/10.1016/j.dsr2.2009.08.007>.
- Imbs, A.B., Ermolenko, E.V., Grigorovich, V.P., Sikorskaya, T.V., Velansky, P.V., 2021. Current Progress in Lipidomics of Marine Invertebrates. *Mar. Drugs* 19, 660.
- Jacob, U., Mintenbeck, K., Brey, T., Knust, R., Beyer, K., 2005. Stable isotope food web studies: a case for standardized sample treatment. *Mar. Ecol. Prog. Ser.* 287, 251–253. <https://doi.org/10.3354/meps287251>.
- Kazanidis, G., Bourgeois, S., Witte, U.F., 2019. On the effects of acid pre-treatment on the elemental and isotopic composition of lightly- and heavily-calcified marine invertebrates. *Ocean Science Journal.* 54, 257–270. <https://doi.org/10.1007/s12601-019-0014-x>.
- Kitching, E. 2022. Physical processes driving phytoplankton production around Southampton Island, Nunavut in late summer 2018 and 2019.
- Kortsch, S., Primicerio, R., Beuchel, F., Renaud, P.E., Rodrigues, J., Lønne, O.J., Gulliksen, B., 2012. Climate-driven regime shifts in Arctic marine benthos. *PNAS* 109 (35), 14052–14057.
- Köseoğlu, D., Belt, S.T., Smik, L., Yao, H., Panieri, G., Knies, J., 2018. Complementary biomarker-based methods for characterising Arctic sea ice conditions: A case study comparison between multivariate analysis and the PIP25 index. *Geochim. Cosmochim. Acta* 222, 406–420. <https://doi.org/10.1016/j.gca.2017.11.001>.
- Krajcarz, M.T., Krajcarz, M., Drucker, D.G., Bocherens, H., 2019. Prey-to-fox isotopic enrichment of 34S in bone collagen: Implications for paleoecological studies. *Rapid Commun. Mass Spectrom.* 33, 1311–1317. <https://doi.org/10.1002/rcm.8471>.
- Landry, J.J., Fisk, A.T., Yurkowski, D.J., Hussey, N.E., Dick, T., Crawford, R.E., Kessel, S. T., 2018. Feeding ecology of a common benthic fish, shorthorn sculpin (*Myoxocephalus scorpius*) in the high arctic. *Polar Biol.* 41, 2091–2102. <https://doi.org/10.1007/s00300-018-2348-8>.
- Legendre, L., Ackley, S.F., Dieckmann, G.S., Gulliksen, B., Horner, R., Hoshiai, T., Melnikov, I.A., Reeburgh, W.S., Spindler, M., Sullivan, C.W., 1992. Ecology of sea ice biota. *Polar Biol.* 12, 429–444. <https://doi.org/10.1007/BF00243114>.
- Lewis, K., Van Dijken, G., Arrigo, K., 2020. Changes in phytoplankton concentration now drive increased Arctic Ocean primary production. *Science* 369, 198–202. <https://doi.org/10.1126/science.aay8380>.
- Li, W.K., McLaughlin, F.A., Lovejoy, C., Carmack, E.C. 2009. Smallest algae thrive as the Arctic Ocean freshens. *Science.* 326: 539–539. <https://doi.org/10.1126/science.1179798>.
- Limoges, A., Massé, G., Weckström, K., Poulin, M., Ellegaard, M., Heikkilä, M., Geilfus, N.-X., Sejr, M.K., Rysgaard, S., Ribeiro, S., 2018. Spring Succession and Vertical Export of Diatoms and IP25 in a Seasonally Ice-Covered High Arctic Fjord. *Front. Earth Sci.* 6 <https://doi.org/10.3389/feart.2018.00226>.
- Linnebjerg, J.F., Hobson, K.A., Fort, J., Nielsen, T.G., Møller, P., Wieland, K., Born, E.W., Rigét, F.F., Mosbech, A., 2016. Deciphering the structure of the West Greenland marine food web using stable isotopes ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$). *Mar. Biol.* 163, 1–15. <https://doi.org/10.1007/s00227-016-3001-0>.
- Loewen, T., Hornby, C., Johnson, M., Chambers, C., Dawson, K., MacDonell, D., Bernhardt, W., Gnanapragasam, R., Pierrejean, M., Choy, E. 2020. Ecological and Biophysical Overview of the Southampton Island Ecologically and Biologically Significant Area in support of the identification of an Area of Interest.

- Lønne, O.J., Gulliksen, B., 1989. Size, age and diet of polar cod, *Boreogadus saida* (Lepechin 1773), in ice covered waters. *Polar Biol.* 9, 187–191. <https://doi.org/10.1007/BF00297174>.
- Loose, B., Miller, L.A., Elliott, S., Papakyriakou, T., 2011. Sea ice biogeochemistry and material transport across the frozen interface. *Oceanography* 24, 202–218. <https://www.jstor.org/stable/24861315>.
- Louis, M., Skovrind, M., Garde, E., Heide-Jørgensen, M.P., Szpak, P., Lorenzen, E.D., 2021. Population-specific sex and size variation in long-term foraging ecology of belugas and narwhals. *R. Soc. Open Sci.* 8, 202226 <https://doi.org/10.1098/rsos.202226>.
- Lukovich, J.V., Tefs, A., Jafarikhazragh, S., Pennelly, C., Myers, P.G., Stadyk, T.A., Sydor, K., Wong, K., Vieira, M., Landry, D. 2021. A baseline evaluation of atmospheric and river discharge conditions in the Hudson Bay Complex during 2016–2018. *Elementa Sci. Anthropocene*. 9: 00126. <https://doi.org/10.1525/elementa.2020.00126>.
- Majewski, A.R., Walkusz, W., Lynn, B.R., Atchison, S., Eert, J., Reist, J.D., 2016. Distribution and diet of demersal Arctic Cod, *Boreogadus saida*, in relation to habitat characteristics in the Canadian Beaufort Sea. *Polar Biol.* 39, 1087–1098. <https://doi.org/10.1007/s00300-015-1857-y>.
- Mariotti, A., 1983. Atmospheric nitrogen is a reliable standard for natural ^{15}N abundance measurements. *Nature* 303, 685–687. <https://doi.org/10.1038/303685a0>.
- Maxwell, S.M., Frank, J.J., Breed, G.A., Robinson, P.W., Simmons, S.E., Crocker, D.E., Gallo-Reynoso, J.P., Costa, D.P. 2012. Benthic foraging on seamounts: A specialized foraging behavior in a deep-diving pinniped. *Marine Mammal Science*. 28: E333. <https://doi.org/10.1111/j.1748-7692.2011.00527.x>.
- McGhee, R., 1970. A quantitative comparison of Dorset Culture microblade samples. *Arct. Anthropol.* 7, 89–96.
- McMahon, K.W., Ambrose Jr, W.G., Johnson, B.J., Yi Sun, M., Lopez, G.R., Clough, L.M., Carroll, M.L., 2006. Benthic community response to ice algae and phytoplankton in Ny Ålesund, Svalbard. *Mar. Ecol. Progr. Ser.* 310, 1–14. <https://doi.org/10.3354/meps310001>.
- McMeans, B.C., Rooney, N., Arts, M.T., Fisk, A.T., 2013. Food web structure of a coastal Arctic marine ecosystem and implications for stability. *Mar. Ecol. Progr. Ser.* 482, 17–28. <https://doi.org/10.3354/meps10278>.
- Menge, B.A., Sanford, E., 2013. *Ecological Role of Sea Stars from Populations. Starfish: biology and ecology of the Asteroidea* 67.
- Merkel, F.R., Jamieson, S.E., Falk, K., Mosbech, A., 2007. The diet of common eiders wintering in Nuuk, Southwest Greenland. *Polar Biology* 30, 227–234. <https://doi.org/10.1007/s00300-006-0176-8>.
- Minagawa, M., Wada, E., 1984. Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochim. Cosmochim. Acta* 48, 1135–1140. [https://doi.org/10.1016/0016-7037\(84\)90204-7](https://doi.org/10.1016/0016-7037(84)90204-7).
- Murphy, E.J., Cavanagh, R.D., Drinkwater, K.F., Grant, S.M., Heymans, J., Hofmann, E. E., Hunt Jr, G., Johnston, N.M., 2016. Understanding the structure and functioning of polar pelagic ecosystems to predict the impacts of change. *Proceedings of the Royal Society B: Biological Sciences* 283 (1844), 20161646. <https://doi.org/10.1098/rspb.2016.1646>.
- Nehlich, O., 2015. The application of sulphur isotope analyses in archaeological research: a review. *Earth Sci. Rev.* 142, 1–17. <https://doi.org/10.1016/j.earscirev.2014.12.002>.
- Nielsen, J.R., Andersen, M., 2001. Feeding Habits and Density Patterns of Greenland Cod, *Gadus ogac* (Richardson 1836), at West Greenland Compared to Those of the Coexisting Cod, *Gadus morhua* L. *J. Northwest Atl. Fish. Sci.* 30, 1–22.
- 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. <https://doi.org/10.1890/13-0486.1>.
- O'Driscoll, R.L., Parsons, M.J., Rose, G.A., 2001. Feeding of capelin (*Mallotus villosus*) in Newfoundland waters. *Sarsia* 86, 165–176. <https://doi.org/10.1080/00364827.2001.10420472>.
- Paar, M., Lebreton, B., Graeve, M., Greenacre, M., Asmus, R., Asmus, H., 2019. Food sources of macrozoobenthos in an Arctic kelp belt: trophic relationships revealed by stable isotope and fatty acid analyses. *Mar. Ecol. Progr. Ser.* 615, 31–49. <https://doi.org/10.3354/meps12923>.
- Pedro, S., Fisk, A.T., Ferguson, S.H., Hussey, N.E., Kessel, S.T., McKinney, M.A., 2020. Broad feeding niches of capelin and sand lance may overlap those of polar cod and other native fish in the eastern Canadian Arctic. *Polar Biol.* 43, 1707–1724. <https://doi.org/10.1007/s00300-020-02738-8>.
- 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. <https://doi.org/10.1029/2012JC008331>.
- Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83, 703–718. [https://doi.org/10.1890/0012-9658\(2002\)083\[0703:USITET\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2).
- Post, D.M., Layman, C.A., Arrington, D.A., Takimoto, G., Quattrochi, J., Montaña, 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. <https://doi.org/10.1007/s00442-006-0630-x>.
- Regehr, E.V., Lunn, N.J., Amstrup, S.C., Stirling, I., 2007. Effects of earlier sea ice breakup on survival and population size of polar bears in western Hudson Bay. *J. Wildl. Manage.* 71, 2673–2683. <https://doi.org/10.2193/2006-180>.
- Renaud, P.E., Tessmann, M., Evenset, A., Christensen, G.N., 2011. Benthic food-web structure of an Arctic fjord (Kongsfjorden, Svalbard). *Mar. Biol. Res.* 7, 13–26. <https://doi.org/10.1080/17451001003671597>.
- Sargent, J.R., Falk-Petersen, I.B., Calder, A.G., 1983. Fatty acid compositions of neutral glycerides from the ovaries of the asteroids *Ctenodiscus crispatus*, *Asterias lincki* and *Pteraster militaris* from Balsfjorden, northern Norway. *Mar. Biol.* 72, 257–264. <https://doi.org/10.1007/BF00396831>.
- Smik, L., Belt, S.T., Lieser, J.L., Armand, L.K., Leventer, A., 2016a. Distributions of highly branched isoprenoid alkenes and other algal lipids in surface waters from East Antarctica: Further insights for biomarker-based paleo sea-ice reconstruction. *Org. Geochem.* 95, 71–80. <https://doi.org/10.1016/j.orggeochem.2016.02.011>.
- Smik, L., Cabedo-Sanz, P., Belt, S.T., 2016b. Semi-quantitative estimates of paleo Arctic sea ice concentration based on source-specific highly branched isoprenoid alkenes: A further development of the PIP25 index. *Org. Geochem.* 92, 63–69. <https://doi.org/10.1016/j.orggeochem.2015.12.007>.
- Smith, R.A., Yurkowski, D.J., Parkinson, K.J., Fort, J., Hennin, H.L., Gilchrist, H.G., Hobson, K.A., Mallory, M.L., Danielsen, J., Garbus, S.E. 2021. Environmental and life-history factors influence inter-colony multidimensional niche metrics of a breeding Arctic marine bird. *Sci. Total Environ.* 796: 148935. <https://doi.org/10.1016/j.scitotenv.2021.148935>.
- Smith, P.A., Gaston, A.J., 2012. Environmental variation and the demography and diet of thick-billed murre. *Mar. Ecol. Progr. Ser.* 454, 237–249. <https://doi.org/10.3354/meps09589>.
- Søreide, J.E., Hop, H., Carroll, M.L., Falk-Petersen, S., Hegseth, E.N., 2006. Seasonal food web structures and sympagic-pelagic coupling in the European Arctic revealed by stable isotopes and a two-source food web model. *Prog. Oceanogr.* 71, 59–87. <https://doi.org/10.1016/j.pocean.2006.06.001>.
- Süfke, L., Piepenburg, D., von Dorrien, C.F., 1998. Body size, sex ratio and diet composition of *Arctogadus glacialis* (Peters, 1874) (Pisces: Gadidae) in the Northeast Water Polynya (Greenland). *Polar Biol.* 20, 357–363. <https://doi.org/10.1007/s003000050314>.
- Szpak, P., Buckley, M., 2020. Sulfur isotopes ($\delta^{34}\text{S}$) in Arctic marine mammals: indicators of benthic vs. pelagic foraging. *Mar. Ecol. Progr. Ser.* 653, 205–216. <https://doi.org/10.3354/meps13493>.
- Team, R.C. 2018. R: A language and environment for statistical computing.
- Thomas, C.J., Cahoon, L.B. 1993. Stable isotope analyses differentiate between different trophic pathways supporting rocky-reef fishes. *Marine Ecology-Progress Series*. 95: 19-19. <https://doi.org/10.3354/meps095019>.
- Wagstaff, M.C., Howell, K.L., Bett, B.J., Billett, D.S., Brault, S., Stuart, C.T., Rex, M.A., 2014. β -diversity of deep-sea holothurians and asteroids along a bathymetric gradient (NE Atlantic). *Mar. Ecol. Progr. Ser.* 508, 177–185. <https://doi.org/10.3354/meps10877>.
- Waltho, C., Coulson, J. 2015l. *The common eider*. Vol: Bloomsbury Publishing.
- Wassmann, P., Duarte, C.M., Agustí, S., Sejr, M.K., 2011. Footprints of climate change in the Arctic marine ecosystem. *Glob. Chang. Biol.* 17, 1235–1249. <https://doi.org/10.1111/j.1365-2486.2010.02311.x>.
- Welch, H.E., Bergmann, M.A., Siferd, T.D., Martin, K.A., Curtis, M.F., Crawford, R.E., Conover, R.J., Hop, H., 1992. *Energy Flow through the Marine Ecosystem of the Lancaster Sound Region, Arctic Canada*. *Arctic* 45, 343–357.
- Weslawski, J.M., Wiktor, J., Kotwicki, L., 2010. Increase in biodiversity in the arctic rocky littoral, Sorkapland, Svalbard, after 20 years of climate warming. *Mar. Biodivers.* 40, 123–130. <https://doi.org/10.1007/s12526-010-0038-z>.
- Young, B.G., Ferguson, S.H., 2013. Seasons of the ringed seal: pelagic open-water hyperphagy, benthic feeding over winter and spring fasting during molt. *Wildl. Res.* 40, 52–60. <https://doi.org/10.1071/WR12168>.
- Young, A., Tallman, R.F., Ogle, D.H., 2021. Life history variation in Arctic charr (*Salvelinus alpinus*) and the effects of diet and migration on the growth, condition, and body morphology of two Arctic charr populations in Cumberland Sound, Nunavut, Canada. *Arctic Sci.* 7, 436–453. <https://doi.org/10.1139/as-2019-0036>.
- Yunda-Guarin, G., Brown, T.A., Michel, L.N., Saint-Béat, B., Amiraux, R., Nozais, C., Archambault, P., 2020. Reliance of deep-sea benthic macrofauna on ice-derived organic matter highlighted by multiple trophic markers during spring in Baffin Bay, Canadian Arctic. *Elementa Sci. Anthropocene*. 8 (1): 047. <https://doi.org/10.1525/elementa.2020.047>.
- Yurkowski, D.J., Brown, T.A., Blanchfield, P.J., Ferguson, S.H. 2020. Atlantic walrus signal latitudinal differences in the long-term decline of sea ice-derived carbon to benthic fauna in the Canadian Arctic. *Proc. R. Soc. B*. 287: 20202126. <https://doi.org/10.1098/rspb.2020.2126>.
- Yurkowski, D.J., Hussey, N.E., Semeniuk, C., Ferguson, S.H., 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 Biol.* 38, 131–143. <https://doi.org/10.1007/s00300-014-1571-1>.
- Yurkowski, D.J., Ferguson, S.H., Semeniuk, C.A., Brown, T.M., Muir, D.C., Fisk, A.T., 2016. Spatial and temporal variation of an ice-adapted predator's feeding ecology in a changing Arctic marine ecosystem. *Oecologia* 180, 631–644. <https://doi.org/10.1007/s00442-015-3384-5>.