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Biomarkers reveal dietary flexibility in northern bottlenose whales, *Hyperoodon ampullatus*, with implications for fisheries and resource management

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ABSTRACT

Beaked whales, including northern bottlenose whales (*Hyperoodon ampullatus*), are widely considered deep-diving squid specialists. In Canada, where northern bottlenose whales are of conservation concern following historical depletion, resolving diet composition is critical for understanding differences in population recovery and evaluating risks from overlap with regional fisheries. Here, we analyse stable isotopes (δ^{13}C, δ^{15}N; Bayesian mixing models) from skin ($n = 141$ samples) and fatty acids from blubber (quantitative fatty acid signature analysis,

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QFASA
Fisheries interactions

QFASA; $n = 96$ samples) from northern bottlenose whales, alongside a large library of potential prey (19 species) collected across the western North Atlantic (42–74 °N). Stable isotope data suggested that females in both Arctic and Scotian Shelf populations exhibited broader ecological niches than males. However, diet composition differed between regions, mirroring known genetic structure. In Arctic whales, squids' contribution was low, while diets were predominantly fish-based, with contributions from grenadiers (family *Macrouridae*), redfish (*Sebastes* spp.), and Greenland halibut (*Reinhardtius hippoglossoides*). Scotian Shelf whales consumed both demersal fish (redfish) and squid (*Gonatus fabricii*). Both biomarkers indicate substantial reliance on demersal fish, consistent with flexible foraging strategies and suggesting a broader diet than the obligate squid specialist view. These findings underscore the need to consider diverse prey fields and potential fisheries interactions in conservation and recovery efforts.

1. Introduction

Northern bottlenose whales (*Hyperoodon ampullatus*) are deep-diving cetaceans inhabiting the continental slope and deep waters of the sub-Arctic and North Atlantic-Arctic (Whitehead and Hooker, 2012). Like most beaked whale species, they have long been considered squid specialists, due to their deep benthic diving capacity (Neubarth et al., 2025; Hooker and Baird, 1999), habitat overlap with squid spawning areas (Bjørke, 2001), and the prevalence of squid beaks, particularly *Gonatus fabricii*, in the stomachs of stranded or commercially whaled individuals (Fernández et al., 2014; Santos et al., 2001; MacLeod et al., 2003; Lick and Piatkowski, 1998; Benjaminsen and Christensen., 1979). Early studies from the Scotian Shelf also suggested similarity in dietary marker profiles between whales and squids (Hooker et al., 2001). However, most of this evidence comes from a limited number of individuals and regions, which may not capture the full scope of northern bottlenose whale foraging behaviour across their range.

In Canadian waters, northern bottlenose whales are recognized as comprising at least two genetically distinct populations: the Scotian Shelf population off Nova Scotia, and the Davis-Strait-Baffin Bay-Labrador population in the eastern Arctic (hereafter referred to as the Arctic population) (Feyrer et al., 2019; de Greef et al., 2022). Historically, this species was heavily targeted by commercial whaling throughout the 20th century and is currently listed as Near Threatened by the IUCN Red List (Whitehead et al., 2021), with both populations in Canadian waters remaining of conservation concern (Whitehead and Hooker, 2012; Feyrer et al., 2019). The Scotian Shelf population is listed as Endangered under Canada's *Species at Risk Act* (*SARA*). The Arctic population has been assessed by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) as Special Concern but is not listed under *SARA*. Although northern bottlenose whales are relatively well studied compared to other beaked whale species, monitoring efforts remain challenging due to their offshore distribution and deep diving behavior (Whitehead and Hooker, 2012; Hooker et al., 2019), limiting our ability to effectively assess population status and inform conservation actions.

Recent genetic, telemetry, and photo identification studies have revealed intriguing patterns of habitat use and residency between the two populations. For example, despite genomic structure suggesting that populations are distinct and relatively isolated (de Greef et al., 2022), at least some Arctic individuals make long-distance excursions further south (>7000 km round-trip from 63 to 40 °N); these movements are potentially shaped by seasonal prey pulses, skin maintenance (Lefort et al., 2025), and sea ice constraints. In contrast, whales on the Scotian Shelf show long-term, year-round site fidelity (>30 years) to a relatively small slope edge area characterized by submarine canyons (Feyrer et al., 2021; 2024). These contrasting residency patterns likely reflect different prey landscapes: the Arctic offers episodic, ice constrained foraging opportunities, while the Scotian Shelf's canyon–slope setting provides a more predictable, locally anchored prey field. This ecological context highlights the potential for population-level differences in foraging strategy and dietary specialization.

Marked differences in prey communities across the species' range suggest the Arctic and Scotian Shelf populations draw on different prey bases. The Arctic demersal fish community is dominated by cold-adapted species such as polar cod (*Boreogadus saida*), Greenland halibut (*Reinhardtius hippoglossoides*), Arctic cod (*Arctogadus glacialis*), and redfish (*Sebastes* spp.) (Jorgensen et al., 2011; Hop and Gjøsæter, 2013). Cephalopod diversity is limited in this area (Xavier et al., 2018), with the squid *G. fabricii* present, but potentially less abundant than it is in the Nordic Basin (Gardiner and Dick, 2010; Bjørke, 2001). The demersal fish community across the Scotian Shelf–Newfoundland region includes redfish, Atlantic Cod (*Gadus morhua*), Atlantic halibut (*Hippoglossus hippoglossus*), Greenland halibut, and haddock (*Melanogrammus aeglefinus*) (Mahon and Smith, 1989). The northern shortfin squid (*Illex illecebrosus*) has been a commercially important cephalopod in the Canadian Atlantic (Amaratunga, 1981; Hurley, 1980), while the longfin squid (*Doryteuthis pealeii*) is present, but occurs at relatively lower abundances (Dawe et al., 1990, 2007). Deepwater species *G. fabricii* and *G. steenstrupi* have also been recorded in the area (Vecchione and Pohle, 2002; Taite et al., 2020). However, because most available ecosystem data focus on commercially targeted species, these patterns may not fully capture the broader prey community available to each population.

Despite the potential for ecological differences, direct evidence of northern bottlenose whale diet remains scarce. Traditional methods, such as visual observation or stomach content analyses from stranded animals, are limited, logistically challenging, and often biased toward recently consumed prey or those with indigestible hard parts like squid beaks (Bowen and Iverson, 2013). Diet inference is also shaped by observations from accessible, better-monitored areas, with limited coverage of remote Arctic habitats. To overcome these constraints and gain additional insight into long-term dietary patterns, biochemical tracers such as stable isotopes and fatty acids measured in the tissues of both consumers and their prey can be used.

Stable nitrogen isotopes (δ^{15}N) indicate consumers' trophic positions (Peterson and Fry, 1987; Hussey et al., 2014; Post, 2002), while the relative contributions of prey-derived carbon (δ^{13}C) can be linked to dietary sources and their habitats (Marcoux et al., 2012; Monteiro et al., 2015; Ryan et al., 2014; Peterson and Fry, 1987). The spread of δ^{13}C and δ^{15}N values (i.e., isotopic space) can be used to model an organism's isotopic niche breadth, offering insights into trophic variability, specialization, and overlap or segregation by sexes or genetically defined populations. Together, they provide valuable information on species' ecological interactions, resource utilization, and niche partitioning (Giménez et al., 2018; Yurkowski et al., 2018; Troina et al., 2020). Furthermore, stable isotope values of primary producers vary spatially due to environmental factors such as temperature, nutrient availability, and oceanographic conditions (McMahon et al., 2013; Magozzi et al., 2017). This spatial variability allows differentiation of foraging habitats where animals reside. For example, in the western North Atlantic, zooplankton δ^{15}N values increase from ~ 6‰ in the Davis Strait to ~ 8‰ in the Scotian Shelf-Newfoundland region (Espinasse et al., 2022; McMahon et al., 2013), a difference that persists across seasons (Espinasse et al., 2022). This shift in baseline isotope values is expected to propagate up the food web, resulting in distinct δ^{15}N values in predators that consistently forage within each region.

Fatty acid profiles in blubber tissue provide a second, independent biomarker line of evidence for investigating diet and trophic pathways in marine mammals (Budge et al., 2008; Iverson et al., 2004; Iverson, 2009). Many fatty acids are synthesised by organisms at the base of the food webs, such as phytoplankton and herbivorous zooplankton (Dalsgaard et al., 2003), and are transferred through the food chain via prey with minimal biochemical modification. At the same time, consumer species exhibit distinctive fatty acid profiles shaped by their diet and metabolism. Consequently, the relative composition of fatty acids in predator blubber tissue largely reflects that of their prey, with predictable modifications, making this approach a powerful tool for both qualitative and quantitative assessments of diet (Iverson et al., 1997; 2007; Iverson, 2009; Budge et al., 2006). Recently, quantitative fatty acid signature analysis (QFASA) has been validated and applied to cetaceans across the North Atlantic, enabling the identification of distinct feeding strategies and trophic niches among populations (Remili et al., 2022, 2023).

In this study, we combined stable isotope (δ^{13}C and δ^{15}N) and fatty acid analyses of skin and blubber samples, respectively, from northern bottlenose whales (1997–2024) and associated prey species (1990–2024) collected across the Arctic, Scotian Shelf, and Newfoundland regions. Our objectives were to: (1) examine regional variation in diet; (2) test for evidence of dietary specialization across populations and sexes; and (3) assess temporal trends in foraging over multiple years. The data presented here provide new insights into the trophic ecology of northern bottlenose whales, for which key dietary aspects remain poorly resolved, enabling formal

Table 1

Stable isotope values (sample size, *n*, mean and standard deviation, SD) of carbon (δ^{13}C) and nitrogen (δ^{15}N) in northern bottlenose whale (*Hyperoodon ampullatus*) by location, season, year, and sex (females ♀, males ♂). δ^{13}C values are corrected for the Suess effect. CN values are the ratio of particulate carbon to particulate nitrogen in the sample. ND = no data available.

Season	Sample year	Sex	*n*	δ^{13}C		δ^{13}C'		δ^{15}N		CN	
				Mean	SD	Mean	SD	Mean	SD	Mean	SD
Arctic											
Fall	2017	♂	1	-17.5	-	-17.0	-	15.7	-	3.1	-
Fall	2018	♀	2	-18.4	0.4	-17.9	0.4	15.3	0.5	3.3	0.2
Fall	2018	♂	7	-18.2	0.2	-17.7	0.2	15.6	0.4	3.1	0.0
Fall	2021	♀	3	-17.9	0.2	-17.3	0.2	16.1	0.2	3.2	0.1
Fall	2021	♂	2	-18.3	0.0	-17.7	0.0	15.0	0.2	3.3	0.0
Fall	2022	♀	3	-17.8	0.1	-17.1	0.1	14.4	0.6	3.0	0.0
Fall	2022	♂	16	-17.9	0.2	-17.2	0.2	14.7	0.3	3.0	0.1
Fall	2024	♀	5	-18.3	0.2	-17.6	0.2	15.2	0.5	3.1	0.1
Fall	2024	♂	5	-18.3	0.3	-17.5	0.3	15.2	0.3	3.1	0.1
Fall	2023	♀	4	-18.6	0.2	-17.9	0.2	14.7	0.4	3.2	0.0
Fall	2023	♂	2	-18.2	0.1	-17.5	0.1	15.1	0.5	3.2	0.0
Spring-summer	2019	♀	3	-18.0	1.1	-17.4	1.1	15.0	0.2	3.0	0.4
Spring-summer	2019	♂	16	-17.7	0.5	-17.1	0.5	15.6	0.3	3.2	0.2
Newfoundland											
Spring-summer	2016	♀	4	-18.1	0.6	-17.6	0.6	15.5	0.6	3.1	0.0
Spring-summer	2019	♀	1	-18.6	-	-18.1	-	14.3	-	3.8	-
Spring-summer	2021	♀	1	-19.0	-	-18.4	-	14.3	-	3.5	-
Spring-summer	2024	♂	1	-18.5	-	-17.8	-	15.1	-	3.1	-
Scotian Shelf											
Spring-summer	1997	♀	12	-17.3	0.4	-17.3	0.4	15.1	0.3	ND	ND
Spring-summer	1997	♂	4	-17.5	0.4	-17.5	0.4	15.5	0.1	ND	ND
Spring-summer	2013	♀	2	-17.0	0.5	-16.6	0.5	15.3	0.2	3.2	0.1
Spring-summer	2013	♂	4	-16.9	0.8	-16.6	0.8	15.4	0.2	3.2	0.1
Spring-summer	2015	♀	4	-16.5	1.3	-16.0	1.3	15.7	1.2	3.0	0.2
Spring-summer	2015	♂	3	-17.2	0.5	-16.8	0.5	15.4	0.1	3.1	0.0
Spring-summer	2016	♀	5	-17.2	0.5	-16.7	0.5	15.6	0.2	3.1	0.0
Spring-summer	2016	♂	6	-17.1	0.8	-16.6	0.8	15.6	0.3	3.1	0.1
Spring-summer	2019	♀	7	-19.5	0.8	-19.0	0.8	14.7	0.2	4.7	0.6
Spring-summer	2024	♀	6	-17.9	0.4	-17.1	0.4	15.3	0.3	3.1	0.0
Spring-summer	2024	♂	4	-17.4	0.4	-16.7	0.4	15.2	0.3	3.1	0.0
Spring-summer	2025	♀	5	-18.3	0.3	-17.5	0.3	14.9	0.2	3.3	0.0
Spring-summer	2025	♂	3	-18.1	0.2	-17.3	0.2	15.2	0.1	3.3	0.0

testing of long-held assumptions on prey preferences and informing conservation strategies for populations facing distinct ecological pressures in changing marine ecosystems.

2. Methods

2.1. Sample Collection

Blubber and skin samples from northern bottlenose whales were collected across multiple years and locations across the eastern Canadian Arctic, Scotian Shelf, and Newfoundland and Labrador. In the Arctic, biopsies ($n = 69$) were obtained between 2017 and 2024 (Table 1) during multi-species research surveys conducted from July to November (Fig. 1). On the Scotian Shelf, biopsies ($n = 65$) were collected during surveys for cetaceans (June to September) between 1997–2024 (Table 1). Off Newfoundland, biopsies ($n = 5$) were obtained during research cruises in 2016, 2017, and 2024. In addition, samples were collected from whales stranded in Newfoundland ($n = 2$) during necropsy in 2019 and 2021 (Table 1). Biopsies were collected from free-swimming whales through similar methods, typically using a crossbow fitted with a 4.0 cm × 0.6 cm stainless steel biopsy tip, targeting the flank adjacent to the dorsal fin. Field sampling was approved by Animal Care Committees at the Fisheries and Oceans Canada Freshwater Institute and

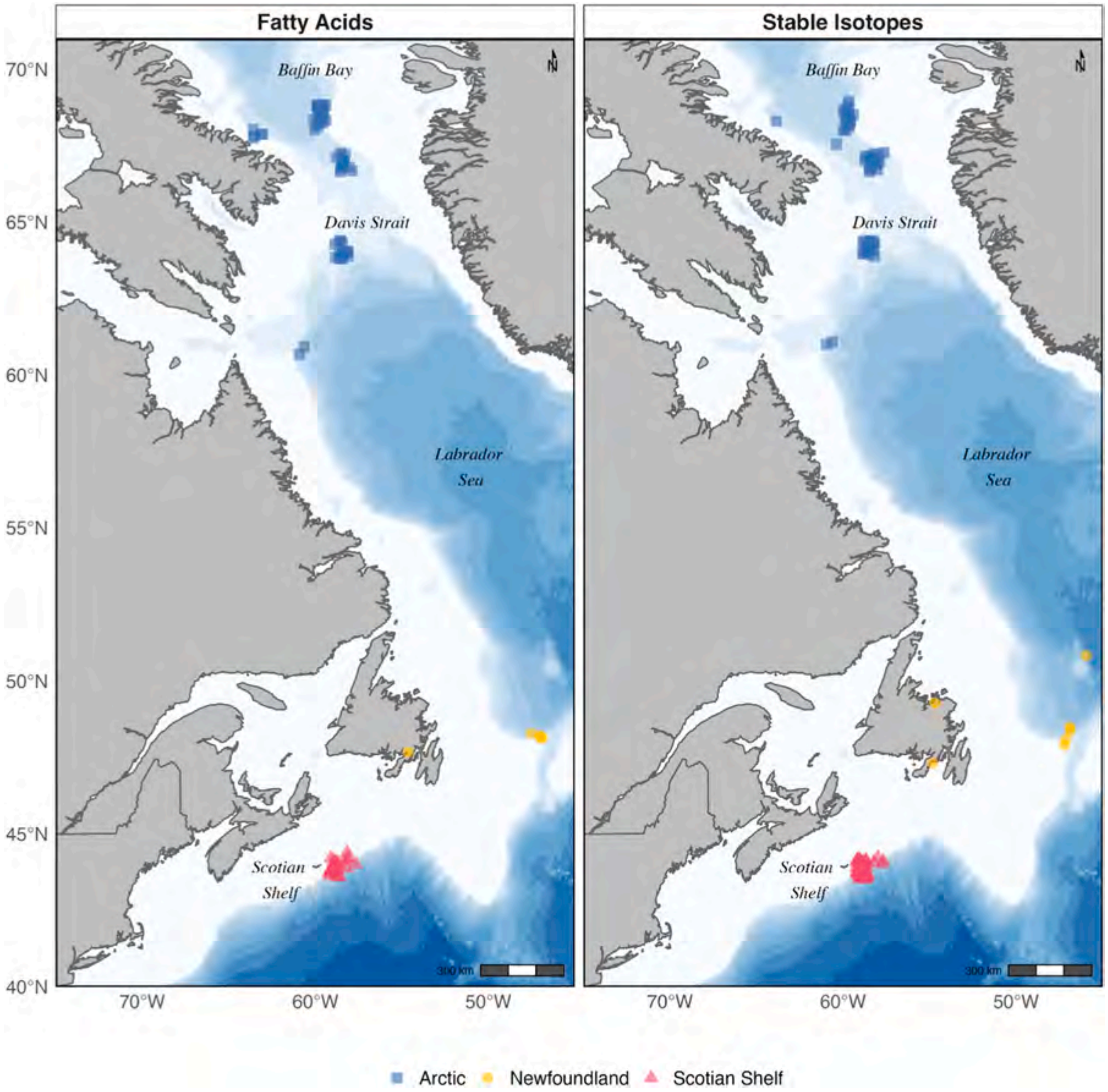

Fig. 1. Map of sampling locations of northern bottlenose whale tissue analysed for fatty acids (left) and stable isotopes (right) across the study area. Population location: red triangles (Scotian Shelf), yellow circles (Newfoundland), and blue squares (Arctic). Note: Newfoundland samples were not included in primary analysis due to small sample size.

Dalhousie University and authorized under scientific licenses and *Species at Risk* Permits issued by Fisheries and Oceans Canada (DFO) in each region. All samples were frozen in the field and stored at −80 °C until prepared for laboratory analysis.

Samples of potential prey (fish, cephalopods, and crustaceans) were collected during scientific trawl surveys and opportunistic sampling across regions (Table S1, S2). Species were selected based on their relative abundance in the respective ecosystems and stomach contents reported for northern bottlenose whales (see references in Table S3). All specimens were preserved at −80 °C for dietary marker analysis. Prey species were identified by morphology and, for a subset of cephalopods, confirmed genetically (Supplementary analysis SA1).

2.2. Stable isotope analysis

Wet tissue samples of northern bottlenose whale skin (Arctic, $n = 69$; Scotian Shelf, $n = 65$; Newfoundland, $n = 7$), fish (muscle or whole), and cephalopod (mantle, Tables S1, S4), were lyophilized at −48 °C and 133×10^3 mbar for 48 hr then homogenized into a fine powder by hand using a mortar and pestle or dissection scissors. Lipids were extracted using a 2:1 chloroform: methanol mixture incubated for 24 h at 30 °C, with the process repeated to ensure complete lipid extraction. Samples were then dried in a fume hood for 24 h, weighed into tin cups to a final mass of 400–600 µg, and analyzed for δ^{13}C and δ^{15}N in the GLIER Chemical Tracers Laboratory or McGill University's Ecological Tracers Lab. Instrumentation included a Delta V Advantage coupled to a 4010 Elemental Combustion System (Costech Instruments, Valencia, CA, USA) at GLIER lab; or a Delta V Plus Thermo Scientific Continuous Flow isotope Ratio Mass Spectrometer (Thermo Scientific, Bremen, Germany) coupled to a Thermo Scientific EA Isolink Flash Elemental Analyzer with a ramped gas chromatography oven at McGill University. Precision of four laboratory standards (NIST 1577c, tilapia muscle, USGS 40 and Urea [$n = 8$ for each]), were run every 12 samples and were < 0.14‰ for both δ^{13}C and δ^{15}N. Instrumentation accuracy was based on NIST standards 8573, 8547 and 8574 for δ^{15}N and 8542, 8573 and 8574 for δ^{13}C ($n = 10$ for all). The mean difference from the certified values were 0.00, −0.01, −0.02‰ for δ^{15}N and −0.15, −0.14 and 0.11‰ for δ^{13}C respectively.

2.3. Fatty acid analysis

Blubber biopsies from northern bottlenose whales (Arctic: $n = 59$; Scotian Shelf, $n = 32$; Newfoundland, $n = 5$) and tissue samples from cephalopod and fish prey (Tables S2, S5) were analyzed for fatty acid composition. Lipids were extracted using a modified Folch method (Folch et al., 1957; Budge et al., 2006), involving 2:1 chloroform:methanol, a saltwater wash, drying over anhydrous sodium sulfate, and evaporation under nitrogen.

Fatty acid methyl esters (FAMEs) were prepared from all lipid extracts using sulfuric acid in methanol (Budge et al., 2006). For whale samples, FAMEs were then isolated from fatty alcohols using thin-layer chromatography with 70:30:1 hexane:diethyl ether: acetic acid (Budge et al., 2006). FAMEs were analyzed in duplicate using temperature-programmed gas-liquid chromatography on a Perkin Elmer Autosystem II GC with flame ionization detection and a DB-23 capillary column (30 m, 0.25 mm ID, 0.25 µm film thickness; Agilent Technologies). Helium was used as the carrier gas, and an oxygen scrubber was installed on the gas line. Up to 66 fatty acids were identified as outlined in Budge et al. (2006) and are reported as mass percent of total fatty acids. Fatty acids are named using the shorthand A:Bn-X, where A is the number of carbon atoms, B the number of double bonds, and X the position of the double bond nearest the terminal methyl group.

2.4. Identification of northern bottlenose whale sex

The sex of individual whales was determined using established genetic methods targeting sex-linked markers in DNA extracted from biopsy tissue (Konrad et al., 2017; Gilson et al., 1998).

2.5. Data analysis

2.5.1. Stable isotope data

First, prey and northern bottlenose whale δ^{13}C values were corrected for the influence of increasing fossil fuel-derived atmospheric CO_2 on δ^{13}C values over time (i.e., Suess effect) using the SuessR package (Clark et al., 2021). Welch ANOVA was then applied to test the differences in absolute δ^{1} ^{3}C and δ^{1} ^{5}N values between northern bottlenose whale populations (Arctic, Scotian Shelf, and Newfoundland), sex (males and females), and season for Arctic whales (fall: September–October; and spring-summer: April–August). A non-parametric permutation analysis was applied to assess the null hypothesis of no differences in whale δ^{13}C and δ^{1} ^{5}N values across years due to non-normally distributed data. First, we calculated the absolute differences in mean δ^{13}C and δ^{15}N values between each pair of years. A total of 10,000 permutations were performed to generate a distribution of mean differences under the null hypothesis. In each iteration, the year labels were randomly shuffled while keeping the isotope values fixed. For each permutation, the mean isotope values were recalculated for each year, and the absolute differences between all possible pairs of years were computed. The *p*-value was then calculated by determining the proportion of permuted differences that were greater than or equal to the observed mean difference. A *p*-value less than 0.05 was used as a threshold to indicate that the observed difference between each pair of years was significant.

Isotope Mixing Models: Due to the small sample size in Newfoundland whales ($n = 7$, Table 1), diet was estimated for Arctic and Scotian Shelf whales only. Stable isotope mixing models were used to estimate diet composition using the simmr package (Govan et al., 2023), which implements a Bayesian framework. These models rely on prior knowledge of the isotopic values and variability among potential prey, as well as on estimates of the isotopic shift that occurs between prey and consumer tissues—typically described as *trophic discrimination factors (TDF)* or *trophic enrichment factors*. These are not fixed values but approximations based on controlled feeding studies, and may vary depending on species, tissue type, diet quality, and metabolic pathways (Stephens et al., 2023). We tested four models with distinct prey groupings (Fig. 2): (1) dominant demersal prey species in the ecosystem; (2) prey identified in dietary studies, either from stomach content analysis or visual observations (Table S3); (3) combining isotopically similar prey species

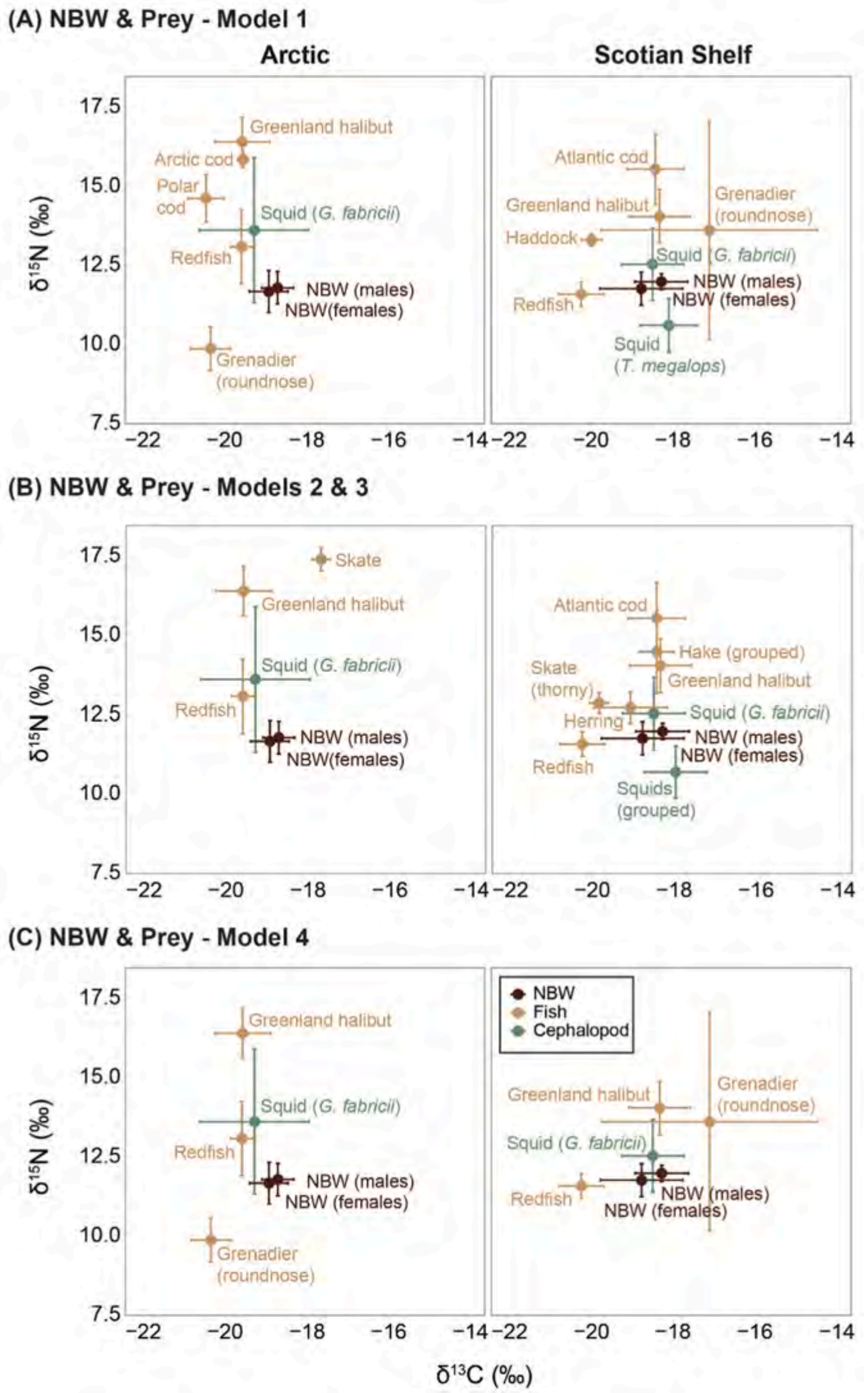

Fig. 2. Biplots of mean ± standard deviation (error bars) δ^{13}C and δ^{15}N values for northern bottlenose whales (NBW) and associated prey species from the Arctic and Scotian Shelf. δ^{13}C values have been corrected for the Suess Effect. Prey species shown for each model used in the stable isotope mixing models (details in Fig. S1 & S5). Prey species' common and scientific names are shown in Table S4. Trophic discrimination values estimated in SIDER for NBW muscle tissue were applied to NBW δ^{13}C and δ^{15}N values for easier comparison between whale and prey.

identified in the diet; (4) a final model combining the output prey in the ecosystem-dominant model (model 1) and those identified in dietary studies (Figure S1; Table S4). For each prey grouping, we evaluated three sets of TDFs (Figure S1): captive killer whale (*Orcinus orca*) skin (Caut et al., 2011), captive bottlenose dolphin (*Tursiops truncatus*) skin (Giménez et al., 2016), and TDF estimated for northern bottlenose whale muscle using SIDER package for R (Healy et al., 2018). Prior to running mixing models, we performed mixing polygon analyses (Smith et al., 2013) to assess whether whale isotope values fell within the isospace defined by each prey set and TDF combination. The TDF set that best encompassed the whale data was selected for subsequent mixing model runs. This process was repeated independently for Arctic and Scotian Shelf whales using region-specific prey data (Figure S1). The mixing models were run with 200,000 interactions, 5 chains, 5000 burn-in, and discarding every 5th sample (thinning).

Isotopic Niche: Stable Isotope Bayesian Ellipses in R (SIBER, Jackson et al., 2011) were applied to model the isotope niche area and assess the overlap between sexes within and across northern bottlenose whale populations. We calculated the standard ellipse area corrected for small sample size (SEA_C) and the Bayesian standard ellipse area (SEA_B). Isotopic niche area was estimated based on the standard ellipses that encompass 40% of the bivariate $\delta^{13}C$–$\delta^{15}N$ data. The *maxLikOverlap* function was used to calculate the overlap between the corresponding 40% prediction ellipses, with the degree of overlap expressed as the proportion of the non-overlapping area between each pair of ellipses.

2.5.2. *Fatty acid data*

Fatty acid composition of northern bottlenose whale tissue was analysed using a set of 18 fatty acids primarily derived from dietary sources (Iverson et al., 2004) and that contributed over 0.1% to the overall fatty acid profile. Proportions were normalized to sum to one, and data were centred log-ratio (clr) transformed. A distance matrix was then calculated based on Euclidean dissimilarity using the vegdist() function from the vegan package in R. A Permutational Multivariate Analysis of Variance (PERMANOVA) was performed using the adonis2() function in the vegan package to evaluate the effects of sex, location (whale population), and year on the variation in fatty acid composition. The model was run with 9999 permutations to assess the significance of the main effects and their interactions. Pairwise statistical differences between significant factors were tested using the function pairwise.adonis2() (9999 permutations) using the pairwiseAdonis package in R (Martinez, 2020). A PERMANOVA was also applied to compare the fatty acid profiles among prey species, location, and year, following the same approach. Differences in individual fatty acids among whale populations, sexes, and years were assessed using multi-factor ANOVA, with sex and year treated as factors nested within population. Analyses were conducted on clr-transformed data, and pairwise comparisons of significant effects were assessed using Tukey's HSD test.

We applied two multivariate approaches to reduce the dimensionality of the fatty acid dataset: non-metric multidimensional scaling (nMDS) and principal component analysis (PCA). nMDS was applied to evaluate overall similarity in fatty acid profiles among whale populations and sexes, based on the Euclidean distance matrix. The envfit function was applied to overlay fatty acid vectors on the nMDS plots, allowing assessment of the relationship between individual fatty acids and the first two nMDS axes (nMDS1 and nMDS2). The resulting nMDS scores were extracted and incorporated into SIBER models to estimate the niche area and overlap between populations, and to compare fatty acid-based niches with isotopic niches. These nMDS scores, representing the relative positions of each group in the multidimensional space, were also used to calculate the Euclidean distance between population/sex centroids, with smaller distances indicating greater similarity in fatty acid profiles.

PCA was performed on clr-transformed fatty acid data to identify the contribution of individual fatty acids to overall variance. Together, these multivariate methods provide complementary perspectives: PCA helps to identify which fatty acids drive variation (particularly relevant for whale-prey comparison), while nMDS helps to visualize similarity patterns among samples (sex, location, year) without being constrained by linear assumptions. For comparisons between whales and their prey (PCA), the analysis was restricted to eight dietary fatty acids (details of stepwise procedure for fatty acid selection is provided in the supplementary analysis SA2). These fatty acids had calibration coefficients estimated for killer whale blubber (Remili et al., 2022). Prior to analysis, full blubber-derived calibration coefficients were applied to adjust northern bottlenose whale fatty acid profiles to prey items.

Lastly, Quantitative Fatty Acid Signature Analysis (QFASA, Iverson et al., 2004) was applied to explore the diet composition of northern bottlenose whales. QFASA is a statistical method that estimates predators' diet by comparing fatty acid signatures in their tissue with those of potential prey species. The analysis was conducted using the QFASAR package (Bromaghin et al., 2017) in R (R Core Team 2023). Details on the method are provided in the supplementary analysis SA2. Differences in fatty acid stratification across blubber depth between delphinids and ziphiids (Koopman, 2007) make killer whale calibration coefficients an imperfect match for northern bottlenose whales, increasing uncertainty in absolute prey proportions. We therefore emphasize dominant prey signals and between group comparisons, rather than treating estimates of prey proportion as exact.

3. Results

3.1. *Stable Isotope Variability*

Absolute $\delta^{13}C$ or $\delta^{15}N$ isotope values were not statistically different between northern bottlenose whale populations (Table 1; $\delta^{13}C$: $F_{(2,\,16.4)} = 3.21$; $\delta^{15}N$: $F_{(2,\,16)} = 0.62$; $p > 0.05$). Nevertheless, distinct sex, annual, and seasonal patterns in stable isotopes were present within each population. Both $\delta^{13}C$ and $\delta^{15}N$ values were significantly higher in males than in females from the Scotian Shelf population ($\delta^{13}C$: $F(_{1,\,62.1}) = 5.65$; $\delta^{15}N$: $F(_{1,\,61.3}) = 5.14$; $p < 0.05$). Sex differences in Arctic whales were significant only in spring-summer, when males had higher $\delta^{15}N$ values than females ($F(_{1,\,3.3}) = 15.43$; $p < 0.05$). Arctic males also showed clear seasonal shifts in both isotopes, with higher values in spring-summer than in fall: $\delta^{13}C$ - $F(_{1,\,20.5}) = 4.92, p < 0.05$; $\delta^{15}N$ - $F(_{1,\,46.9}) = 21.93, p < 0.001$. In Arctic females,

δ^{15}N tended to be higher in fall, while δ^{13}C values were higher in spring-summer, but neither seasonal pattern was statistically significant. Seasonal differences could not be evaluated for Scotian Shelf whales because all samples were collected in summer.

Interannual analysis also revealed different trends in δ^{13}C and δ^{15}N values between Arctic and Scotian Shelf populations. Specifically, Arctic whales sampled between 2019 and 2022 had generally higher δ^{13}C values than those sampled in the other years (Fig. 3 A), while δ^{15}N values were lower in 2022 in comparison to whales sampled in the other years (Fig. 3 C). In the Scotian Shelf, δ^{13}C and δ^{15}N values were ~ 2‰ and ~1‰, respectively, lower in whales sampled in 2019 in comparison to whales sampled in the other years (Fig. 3B-D). Significant comparisons are indicated in Fig. 3.

Female northern bottlenose whales in both regions exhibited greater variability in δ^{13}C and δ^{15}N values, and broader isotopic niches than males (Fig. 4; Table 2, Table S6). There was large isotopic niche overlap (41%, Table 2) between females from both regions, but lower overlap between males (23%, Table 2). Between-sex niche overlap was greater in the Arctic (47%) than in Scotian Shelf whales (37%). Scotian Shelf males had greater niche partitioning with Arctic (both sexes), while Scotian Shelf females had greater niche overlap with Arctic whales (both sexes, Table 2, Table S7).

3.2. Fatty Acid Profiles

Fatty acid profiles revealed a clear distinction between Arctic and Scotian Shelf northern bottlenose whale populations. PERMANOVA analyses identified population (location), sex, and sampling year as significant factors influencing fatty acid composition. Sex and location accounted for 6% ($F = 13.8$, $p < 0.001$) and 15% ($F = 34.5$, $p < 0.001$) of the variation, respectively, while sampling year explained the largest proportion (44%, $F = 14.7$, $p < 0.001$). No significant differences in fatty acid profiles were observed between sexes in either Arctic or Scotian Shelf populations (Table S8, Figure S2). However, fatty acid profiles were significantly different between and within sexes across populations (Table S8). There were significant differences across years, with samples collected in 1997 different from all other years, and significant interannual differences between samples collected in the 2000s (Table S9).

At the individual fatty acid level, location was a major factor with all fatty acids varying significantly between populations, except for 18:2n-6 (Table S10). Of the 18 fatty acids considered, those contributing most to the variability between populations (highest *F*-values) were 18:3n-4, 20:5n-3, and 16:4n-3 (Table S10). Similarly, all fatty acids except 18:1n-13, 20:4n-6, and 22:5n-3, showed significant differences across sampling years (Table S10). Here too, 18:3n-4 contributed to the highest between year variability, followed by 18:2n-6 and 20:1n-9 (Table S10). Sex differences were less common, but significant for some fatty acids, including 18:3n-4, 22:1n-9, and 18:3n-3 (Table S10).

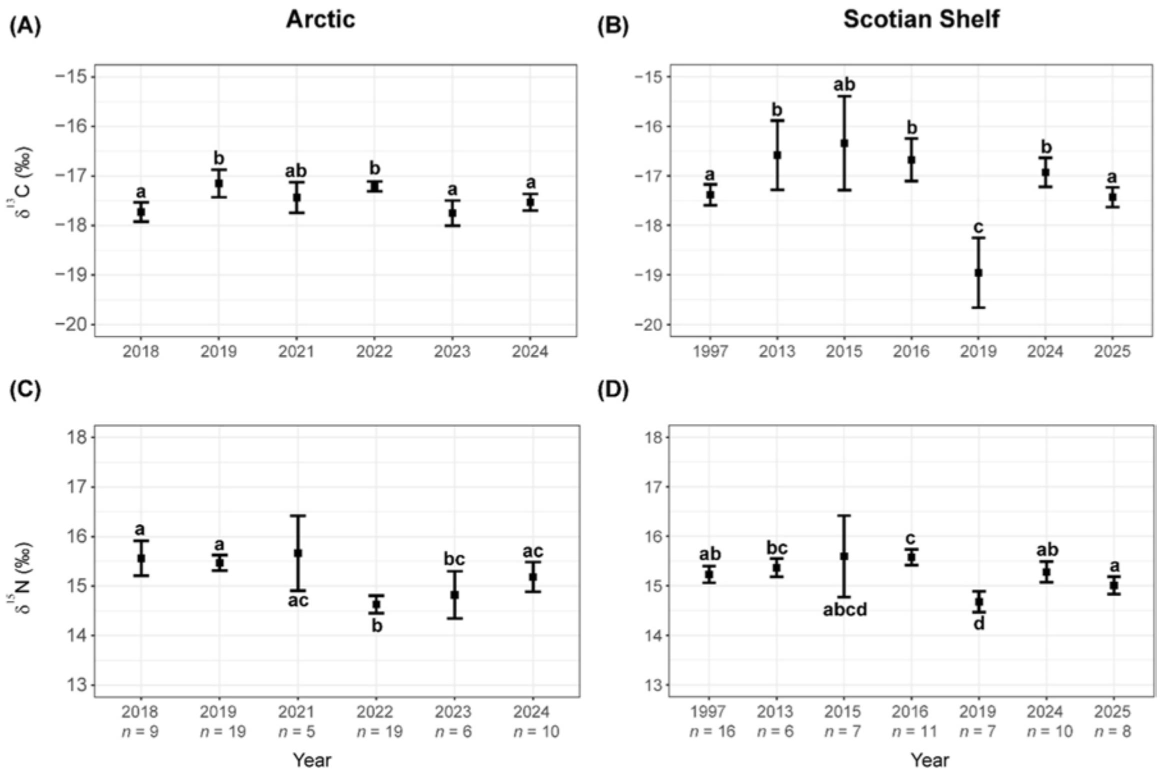

Fig. 3. Mean δ^{13}C and δ^{15}N in northern bottlenose whales (*Hyperoodon ampullatus*) from Arctic (A and C) and Scotian Shelf (B and D) by year, with 95% confidence intervals (error bars). Arctic 2017 ($n = 1$) and Scotian Shelf samples from 2021 ($n = 1$) were excluded from these comparisons due to low sample size. Lowercase letters around bars indicate statistically significant differences among years ($p < 0.05$).

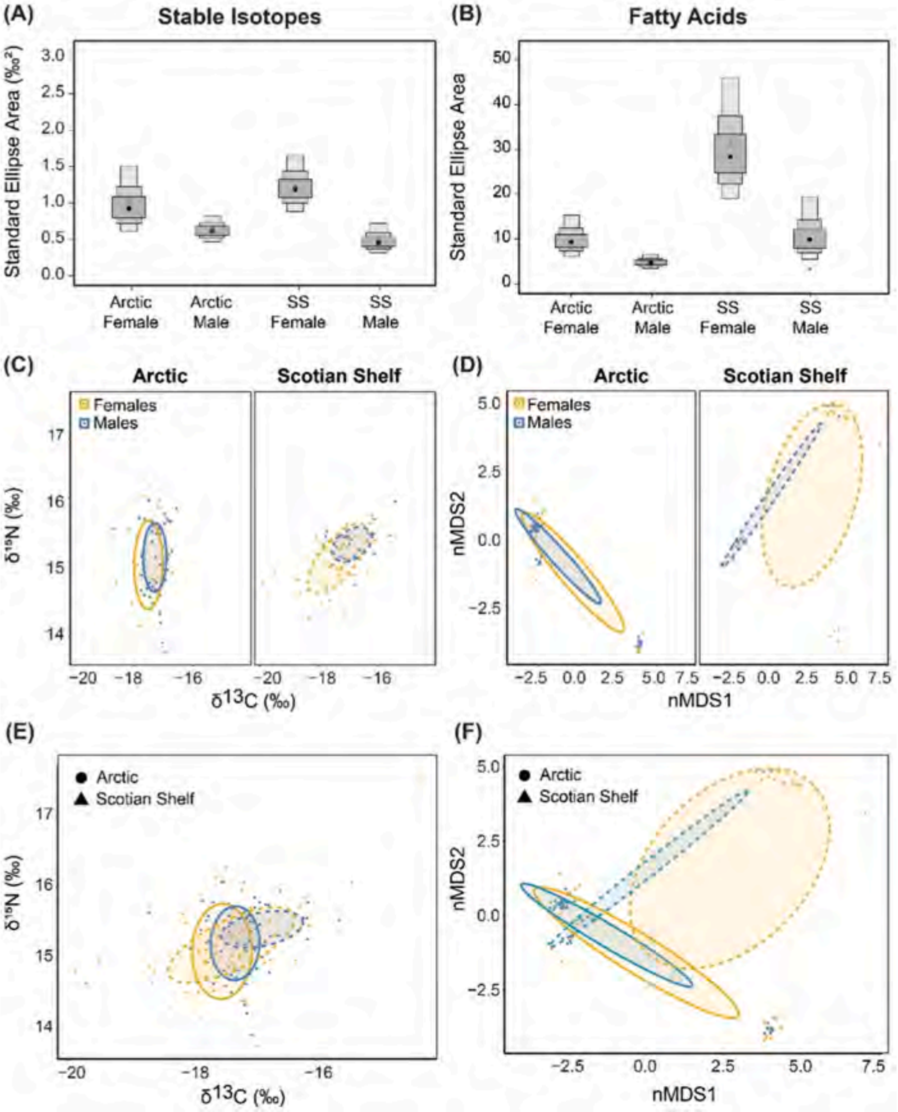

Fig. 4. Bayesian standard ellipse area (‰^{2}) mode (black dot) and maximum likelihood standard ellipses area corrected for sample size (SEAc, red X), with 50%, 75% and 95% credible intervals by sex in Arctic and Scotian Shelf northern bottlenose whales (*Hyperoodon ampullatus*) based on (A) carbon and nitrogen stable isotope data and (B) dietary fatty acid data; (C, E) SEAc by sex based on stable isotope and (D, F) dietary fatty acid data. Continuous lines represent Arctic whale ellipses, dashed lines represent Scotian Shelf whale ellipses.

Table 2

Stable isotope and fatty acid niche overlap (%) between northern bottlenose whale (*Hyperoodon ampullatus*) populations (Arctic; Scotian Shelf - SS) by sex, and probability (%) of posterior distributions being larger in the x group than in the y group (x > y). Overlap was calculated based on the maximum likelihood standard ellipse area corrected for small sample size (SEA$_C$), estimated based on the 40% prediction ellipses, and is expressed as the proportion of the non-overlapping area between each pair of ellipses. A detailed matrix showing the unidirectional percentage of isotope niche overlap is provided in Supplementary Table S7.

x	y	Stable Isotope		Fatty Acid	
		Overlap	x > y	Overlap	x > y
Arctic - Females	Arctic - Males	47%	96%	44%	100%
Arctic - Females	SS - Females	41%	22%	3%	0%
Arctic - Females	SS - Males	11%	99%	4%	41%
Arctic - Males	SS - Females	39%	0%	1%	0%
Arctic - Males	SS - Males	23%	84%	4%	1%
SS - Females	SS - Males	37%	100%	6%	99%

The nMDS ordination (stress = 0.07) provided a good two-dimensional representation of fatty acid profile dissimilarities among whale groups. The envfit analysis revealed significant correlations between several fatty acids and the ordination axes ($p < 0.05$). The fatty acid that best aligned with nMDS1 was 18:3n-3 (nMDS1 = −0.996, $r^2 = 0.88$, $p < 0.001$). Multiple fatty acids strongly aligned with nMDS2, including 18:3n-4 (nMDS2 = −0.943, $r^2 = 0.95$, $p < 0.001$), 20:1n-7 (nMDS2 = −0.936, $r^2 = 0.67$, $p < 0.001$), and 20:3n-6 (nMDS2 = −0.995, $r^2 = 0.67$, $p < 0.001$). Similar to the PERMANOVA analysis, Euclidean distances between northern bottlenose whale nMDS centroids separated Arctic and Scotian Shelf populations, but not sexes within populations (Figure S2). Niche area and overlap using fatty acid (nMDS scores) and isotope data revealed similar trends between sexes in both populations (Table 2), with females occupying a larger niche than males (Table S6), and males' niche falling mostly within that of females (Fig. 4). PCA results of northern bottlenose whale dietary fatty acids are provided in the supplementary analysis SA3).

PERMANOVA analyses comparing fatty acid profiles among prey species were significant for location, species, and year. However, year and location accounted for only 6% ($F = 12.7$, $p < 0.001$) and < 1% ($F = 8.5$, $p < 0.001$) of the variation, respectively, while species-specific differences in fatty acid profiles explained the largest proportion (51%, $F = 59.15$, $p < 0.001$, Table S11). The first principal component (PC1) of the PCA, which included dietary fatty acids from northern bottlenose whales and prey species, explained 47.1% of the total variability, while PC2 and PC3 accounted for 18.1% and 16.6%, respectively (Fig. 5). Together, the first three components accounted for 81.7% of the total variance. The most important fatty acids contributing to the variability in PC1 were 22:1n-11 (22.7%), 20:1n-9 (21.8%), and 22:1n-9 (19.6%), all with positive loadings, while 20:4n-6 contributed 13.7% and had a negative loading. Fatty acid contributions to PC2 were strong for 20:1n-7 and 16:2n-4 (37.8% and 20.4%, respectively), both with

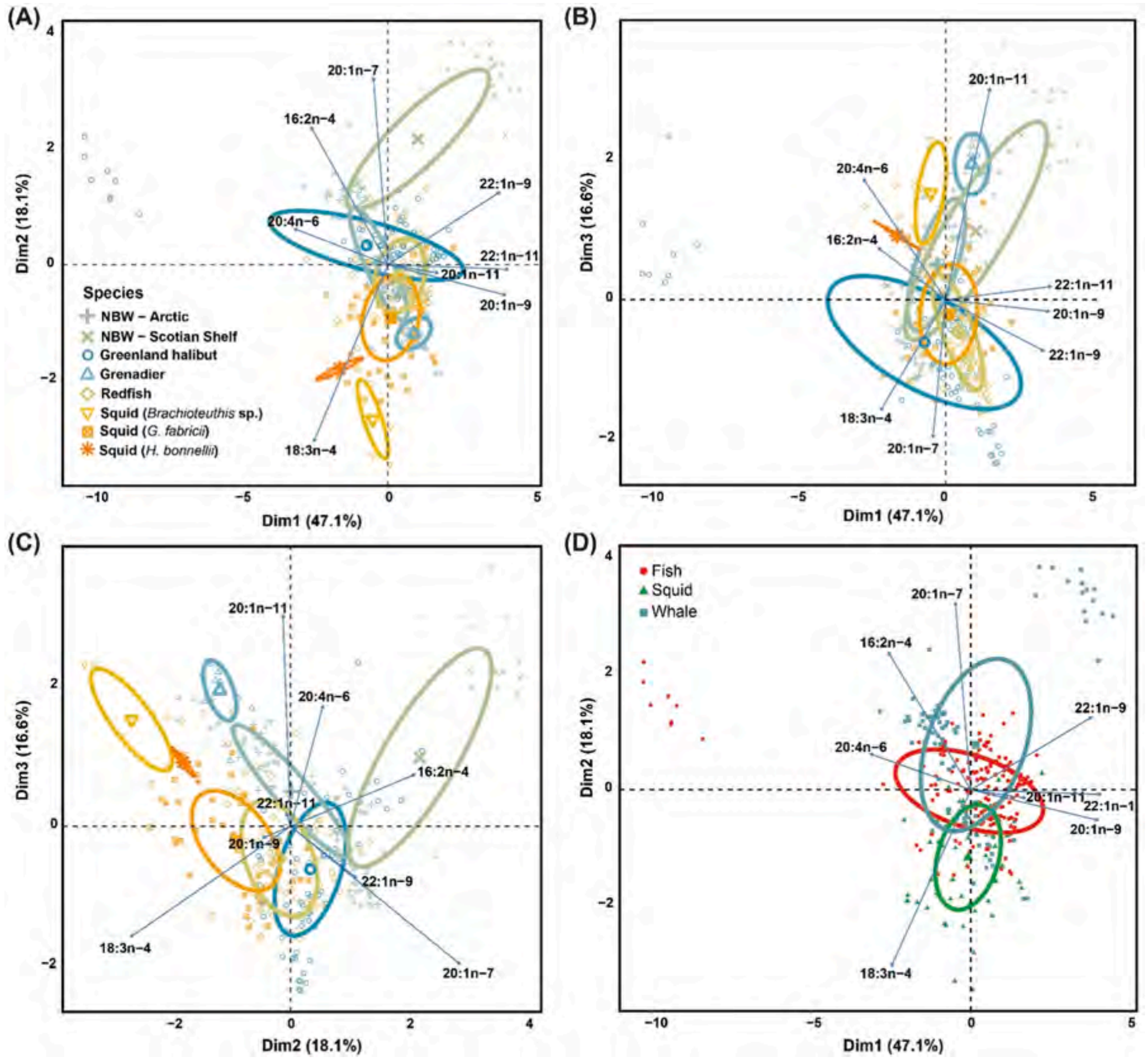

Fig. 5. Principal component analysis (PCA) biplots of northern bottlenose whale (NBW) and prey species dietary fatty acids. Whale fatty acid profiles were adjusted using killer whale calibration coefficients to enable direct comparison with prey data. Axes represent the three principal components (Dim1 = 47.1%, Dim2 = 18.1%, Dim3 = 16.6% of variance explained). Ellipses highlight individual prey species and NBW populations (A-C); or prey type (fish, squid) and whales (D). Vectors indicate fatty acids contributing to each dimension.

positive loadings, while 18:3n-4 (33.7%) had a strong contribution with a negative loading. The fatty acids that contributed most to PC3 were 20:1n-11 (46.4%, positive loading), 20:1n-7 (19.8%, negative loading), and 20:4n-6 (15.1%, positive loading). Northern bottlenose whale fatty acid profiles overlapped mostly with fish prey (Fig. 5D), especially Greenland halibut and redfish, although Arctic whales also showed a small overlap with the squid *G. fabricii* (Fig. 5A-C).

3.3. *Northern bottlenose whale diet*

Mixing polygon analyses compared candidate TDF-prey combinations and identified SIDER-based muscle TDFs as the best-fitting option for both Arctic and Scotian Shelf whales (δ^{13}C-TDF: 1.36 ± 1.96; δ^{15}N-TDF: 3.4 ± 1.6; Figures S3–S5). Across models, Arctic whales showed a fish-based diet, with grenadier as the dominant prey (45–50%) for both sexes (Fig. 6 A, Table S12). Seasonal models showed a 10% increase in grenadier in the fall relative to spring (both sexes), while redfish remained secondary (Table S13). On the Scotian Shelf, mixing models indicated higher cephalopod contributions (33–35%) alongside substantial redfish contributions (35–46%; Fig. 6B, Table S14). Isotope mixing models and QFASA converged on demersal fishes as a major prey group in both populations but differed in prey-specific rankings. Isotope mixing models emphasized grenadier as the dominant prey in the Arctic and redfish as the dominant prey on the Scotian Shelf, whereas QFASA ranked Greenland halibut highest overall, followed by redfish and grenadier (Fig. 7). The Leave-one-prey-out (LOPO) analysis revealed that fatty acid profiles in most prey species used in QFASA were well discriminated, but redfish and *Gonatus fabricii* showed weaker self-classification and higher misclassification rates than other prey (Figure S6).

4. Discussion

Stable isotopes and fatty acids independently indicate that demersal fishes are major prey for northern bottlenose whales across the

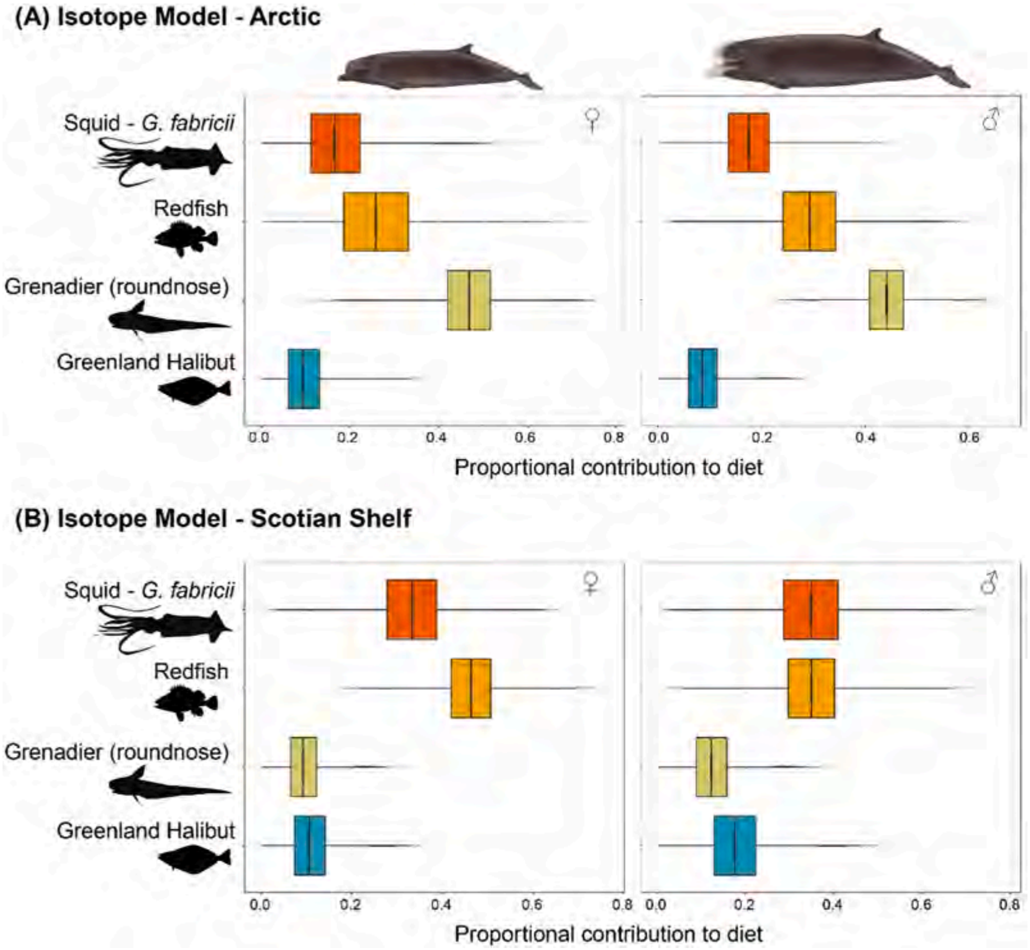

Fig. 6. Posterior distributions of proportional contributions of prey items to the diet of female (left) and male (right) northern bottlenose whales (*Hyperoodon ampullatus*) from (A) Arctic and (B) Scotian Shelf based on stable isotope mixing models. Box plots indicate the median, 25%, and 75% interquartile ranges.

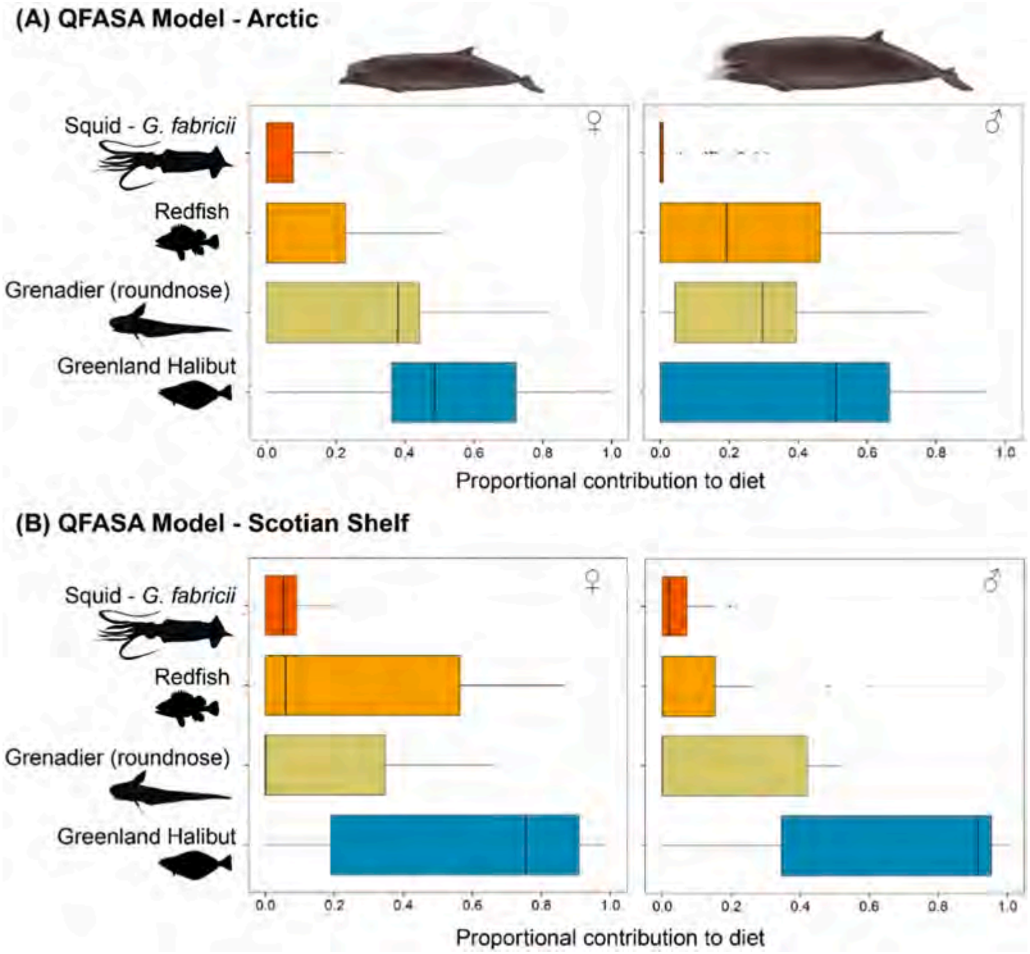

Fig. 7. Percentage contribution of prey species to the diet of female (left) and male (right) northern bottlenose whales (*Hyperoodon ampullatus)* from (A) Arctic and (B) Scotian Shelf, based on quantitative fatty acid signature analysis (QFASA). Box plots indicate the median, 25%, and 75% interquartile ranges.

western North Atlantic, suggesting that squids contribute less to their diet than previously thought. Stable isotope values did not consistently separate populations, but they captured meaningful within-population structure, including seasonal variation in Arctic whales, and sex and interannual trends in both regions. Isotope mixing models aligned with these patterns, emphasizing grenadier and redfish as important prey in the Arctic, with redfish and cephalopods as the main prey on the Scotian Shelf. Fatty acids provided additional discriminatory power between populations and across years, with Greenland halibut emerging as the top prey in QFASA. Together, both biomarker approaches converge on the same ecological signal and indicate broad reliance on demersal fishes, with population-level differences in prey composition.

4.1. *Revisiting the squid specialist paradigm*

Across regions and sexes, our stable isotope and fatty acid results do not align with the long-standing characterization of northern bottlenose whales as obligate squid specialists (Hooker et al., 2001; Santos et al., 2001; Fernández et al., 2014). Instead, both biomarker approaches indicate substantial contributions from demersal fishes, with squids making a comparatively minor contribution for Arctic whales. Squids appear more important to the diet on the Scotian Shelf, pointing to population-specific differences in prey use rather than a single diet archetype across the western North Atlantic.

Our findings help contextualize earlier work that emphasized consumption of squids, mainly *G. fabricii* (Bloch et al., 1996; Hooker et al., 2001; MacLeod et al., 2003). In the eastern Canadian Arctic, stomach contents from whaled individuals indicated a substantial contribution of fish (54%) (Benjaminsen and Christensen, 1979), broadly consistent with our inference that Arctic whales have a diet higher in fish than the Scotian Shelf population. In contrast, several eastern North Atlantic studies based on stranded whales have reported primarily squid consumption (e.g., Fernández et al., 2014; Santos et al., 2001; Lick and Piatkowski, 1998), which may reflect genuine regional level differences, variability in sampling context, or both.

Most diet evidence for northern bottlenose whales in the western North Atlantic is now several decades old, which raises the possibility that contemporary diets differ from those historically reported. The Northwest Atlantic experienced a major ecosystem change following the early-1990s groundfish collapse (Myers et al., 1997), which could have led to a shift in the distribution, abundance, and size structure of demersal and benthic prey, and may contribute to temporal variability in inferred diet signals.

Differences between biomarker-based inferences and stomach content studies may also reflect the scope of the available stomach content record. Many stomach content datasets are from studies on opportunistically sampled stranded specimens with small sample sizes ($n \leq 10$ whales) from the eastern Atlantic (Clarke and Kristensen, 1980; Lick and Piatkowski, 1998; Santos et al., 2001; Spitz et al., 2011; Fernández et al., 2014). Stomach contents capture only the most recent feeding events and can be influenced by differential digestion and retention: indigestible structures such as cephalopod beaks persist and are readily counted, whereas soft-bodied or rapidly digested prey, including many fishes, may be underrepresented (Bowen and Iverson, 2013). In addition, stranded animals may not reflect typical foraging conditions or behavior prior to death. Together these factors can make stomach contents reconstructions overrepresent cephalopods relative to integrated biomarker approaches.

Stable isotope and fatty acid biomarkers assimilate dominant dietary signals over periods of weeks to months and can complement stomach content evidence when evaluating population-level patterns. These biomarkers were previously applied to northern bottlenose whales in the western North Atlantic, and results at that time suggested a predominantly cephalopod-based diet (Hooker et al., 2001). However, Hooker et al. (2001) study did not apply QFASA or correct whale biomarkers for direct comparison with prey (i.e., applying calibration coefficient). Interpretation in that study was further constrained by a small sample size of whales, a limited fish prey library (only redfish and herring), and *Gonatus* specimens collected outside the whales' inferred foraging region. Hooker et al. (2001) reported similarity in fatty acid profiles between northern bottlenose whales and adult female *Gonatus*, but not with juvenile *Gonatus* or the fish species sampled, highlighting that prey life stage can also influence dietary interpretation. Some life stages, including reproductive *Gonatus* females, remain difficult to sample and are poorly represented in trophic baselines (Hooker et al., 2001; Golikov et al., 2018). Here, we reanalyzed Hooker et al. (2001) whale samples together with expanded dataset, used QFASA, calibrated whale data to prey, and used a broader prey library, providing a more robust, quantitative assessment than the earlier qualitative study and leveraging a larger sample size. These gaps and sampling limitations should be treated as explicit source of uncertainty when revisiting the degree of reliance on cephalopods.

In the present study, despite some differences between stable isotope- and fatty acid-based estimates in the identity of dominant prey between regions, both biomarkers converge on a benthic, demersal-fish foraging strategy, with cephalopods also contributing to the diet of Scotian Shelf whales. This pattern does not align with previous suggestions of prey specialization, but it also does not indicate a generalized, opportunistic predator. A more consistent interpretation is contextual specialization: a persistent focus on demersal prey, coupled with flexibility in which taxa dominate regionally or seasonally as availability changes. This pattern reflects a specialized foraging strategy with adaptive prey use, pointing to a more nuanced ecological role than previously understood. Such flexibility may be shaped in part by learning or social transmission of foraging behaviors. Records of northern bottlenose whale depredation and feeding in association with Greenland halibut fisheries in the Arctic and off Newfoundland provide observational evidence of fish consumption and a plausible mechanism whereby repeated exposure to fisheries could reinforce or influence prey preferences in some areas (Feyrer et al., 2025; Oyarbide et al., 2023; Smith et al., 2021).

Taken together, our results indicate that northern bottlenose whales in the western North Atlantic rely heavily on demersal fish, with regional variation in prey composition that likely reflects local prey availability, seasonal access, and potential overlap with fisheries, rather than fixed dietary preferences. Although fatty acids and isotopic models differed in the dominant prey inferred, both supported a demersal foraging strategy and a more limited contribution of squid, at least in the Arctic. Overall, our results refine current understanding of northern bottlenose whale trophic ecology and show the value of combining biomarkers to resolve population-specific patterns and longer-term dietary signals.

4.2. *Spatial, temporal and sex-based differences in foraging ecology*

Regional and temporal differences in stable isotope and fatty acid profiles were more pronounced than sex-based effects, consistent with foraging patterns shaped by spatial variation in prey communities. Arctic and Scotian Shelf whales exhibited distinct fatty acid signatures, supporting region-specific foraging patterns and providing evidence of ecological differentiation of the two populations, which has largely been defined using genetic (de Greef et al., 2022) as well as behavioural and morphological data (COSEWIC, 2024). Similar ecological structuring has been reported in other apex predators, including regionally distinct subpopulations of white sharks with divergent ontogenetic-specific habitat use (Burke et al., 2025), underscoring the management relevance of fine-scale ecological differences.

Comparing stable isotope values across regions typically requires baseline correction, but applying such a correction implicitly assumes that whales feed exclusively in their sampled region and would, by design, accentuate separation given the ~2‰ baseline $\delta^{15}N$ difference between regions (Espinasse et al., 2022; McMahon et al., 2013). To avoid embedding that assumption, we used uncorrected isotope values in our analysis. Under this conservative approach, stable isotopes alone did not detect significant differences between populations, but fatty acids consistently separated the two groups and diet models indicated differences in prey composition, providing strong evidence for ecological separation. If baseline correction were applied, apparent isotopic differences would be expected to increase, further supporting habitat segregation.

Arctic northern bottlenose whales showed clear seasonal structure in stable isotope values, with the strongest signal in males. Seasonality could not be evaluated on the Scotian Shelf because sampling there was limited to summer. Given a skin isotope turnover time of approximately two to four months (Giménez et al., 2016), isotope values measured in spring largely reflect winter foraging, whereas fall values integrate summer diets. The absence of sex differences in $\delta^{15}N$ or $\delta^{13}C$ in fall is consistent with broadly similar summer diets, while higher male δ^{15}N in spring suggests sex-specific differences in winter foraging. These patterns could reflect seasonal divergence in diet, foraging location, or both. Winter constraints on prey availability and habitat access due to low Arctic productivity and extensive sea ice (Carroll and Carroll., 2003; Daase et al., 2021) could increase competition and favour sex-specific diet partitioning. Alternatively, spatial differences in foraging areas between sexes may also contribute to the observed patterns. Seasonal movements into southern regions would be expected to increase δ^{15}N values irrespective of trophic level, due to the 2‰ rise in plankton-δ^{15}N from Davis Strait to the Scotian Shelf and Newfoundland (Espinasse et al., 2022; McMahon et al., 2013). Satellite telemetry supports the plausibility of such seasonal shifts, with Arctic-tagged northern bottlenose whales ranging widely across deployments (approximately 40.8–71.1°N; Feyrer et al., 2024; Lefort et al., 2025), which could contribute to the observed isotope patterns.

Interannual variation in Scotian Shelf whales' stable isotope values may reflect baseline isotope variability rather than shifts in prey composition, particularly when there is little evidence of major changes in the fish prey community (Bowlby et al., 2023). Evidence from the nearby Gulf of Maine shows that climate-driven circulation changes can restructure lower trophic level organisms and alter whale foraging behaviour (Record et al., 2019), highlighting how variability at the base of the food web – linked to gradients in oceanographic conditions – could plausibly drive year-to-year isotopic differences on the Scotian Shelf. The lower δ^{13}C and δ^{15}N values observed in 2019 are consistent with such baseline-driven processes. While the Scotian Shelf has generally experienced increasing bottom-water temperatures since 2016, anomalously cold conditions occurred in 2018 and 2019 (Bernier et al., 2023). Cooler water temperatures are typically associated with higher dissolved inorganic carbon (DIC) concentrations (Key et al., 2004), which can enhance isotopic discrimination during photosynthesis (Laws et al., 1995; Rau et al., 1996). Additionally, bottom waters tend to have inherently lower DIC-δ^{13}C values (McNichol and Druffel, 1992). Elevated nitrate concentrations observed in 2019–2020, likely resulting from enhanced wind-driven mixing (Bernier et al., 2023), suggest that vertical mixing may have transported both nutrient-rich and δ^{13}C-depleted DIC from deeper waters to the surface. These processes may have intensified isotopic discrimination in primary producers, lowering baseline δ^{13}C and δ^{15}N values. Such shifts likely propagated through the food web, contributing to the lower δ^{13}C and δ^{15}N values observed in whale tissue in 2019.

4.3. Ecological and Conservation Implications

Our findings reveal greater dietary flexibility in northern bottlenose whales than previously recognized. This foraging plasticity likely reflects an adaptation to regional prey availability and may offer energetic advantages. While Gonatidae squids yield approximately 101 kcal per 100 g (4.2 kJ/g, Chen et al., 2022), demersal fish such as Greenland halibut and redfish offer higher energy densities, up to 170 kcal and 127 kcal per 100 g (5.3 kJ/g) of muscle tissue, respectively (Seafood from Canada 2025; Rodrigues et al., 2025). To meet an estimated daily energy requirement of ~110,000 kcal (Hooker et al., 2002), a whale would need to consume ~110 kg of squid, compared to ~86 kg of redfish or ~65 kg of Greenland halibut, and less if consuming energy-dense tissues such as liver (240 kcal/100 g; 10.05 kJ/g).

Foraging on demersal fish may require different tactics than hunting squid, including deeper or longer dives, increased search effort, or more complex prey handling. These costs likely vary by region with prey patchiness and capture difficulty. In the Arctic, for example, Greenland halibut can be abundant and may increase in availability alongside fisheries (e.g., as escapees or discards) (Johnson et al., 2021), and their bottom-associated distribution may make them easier to capture than squids, which can require more effort to locate and handle. Together, these factors suggest that fish consumption may improve foraging efficiency and reduce daily energy expenditure. While trade-offs between prey types remain poorly understood, the ability to switch prey likely helps northern bottlenose whales meet energetic demands under variable conditions.

Dietary flexibility has direct management implications where diets overlap with commercial fisheries targeting demersal species. For the Scotian Shelf population, demersal fish appear to make up over 65% of their diet, so overlap with commercial fisheries may affect whale energetics and population recovery (Feyrer et al., 2025). Direct effects include risks from gear interactions (e.g., injury, disturbance, collision) (Feyrer et al., 2021, 2025; Luck et al., 2025), but also low-cost access to prey via depredation or discards (Tixier et al., 2017). Additional direct effects include removal of shared prey (exploitative competition), which may operate over longer timescales and reinforces the need to account for whale energetic requirements in an ecosystem-based approach to quota setting. The scope for fishery-related impacts on diet likely varies by region. On the Scotian Shelf, the Unit 3 redfish stock appears relatively stable and is concentrated in areas of northern bottlenose whale habitat (e.g., the shelf slope), making redfish a plausible and consistently available prey (DFO, 2021). In NAFO Subarea 0, redfish abundance has been more variable and there is no directed commercial redfish fishery, so any redfish subsidy would be less predictable and more dependent on bycatch and local availability (DFO, 2023). In the Arctic, the presence of Greenland halibut in the diet, as suggested by the fatty acids, is corroborated by observations of depredation and opportunistic foraging around longlines, gillnets, and trawl gear (Feyrer et al., 2025; Oyarbide et al., 2023; Smith et al., 2021). As Arctic fisheries expand seasonally and spatially, the consequences of whale-fishery interactions should be evaluated to determine whether mitigation is warranted. Management will also need to address prey limitation, not just harmful interactions, by ensuring the daily energetic demand of northern bottlenose whales (e.g., 65 kg of fish per individual per day) is considered within any ecosystem-based approaches to quotas to maintain viable fisheries without eroding stock biomass.

Across both regions, effective management will require integrating new ecological evidence into decisions, with clear triggers for review when overlap or interaction metrics rise. This depends on spatial monitoring of seasonal overlap among whales, key prey, and fishing effort, and on harvest strategies for demersal stocks that account for prey needs and energetic constraints. Canada's *Species at Risk Act*, the Marine Mammal Regulations under the *Fisheries Act*, and existing fisheries frameworks provide mechanisms to act, but outcomes will hinge on applying them proactively to address direct interactions (entanglement, bycatch, depredation, disturbance) and resource-mediated effects (changes in prey availability and prey fields) in both regions.

4.4. Limitations and future directions

Stable isotopes and fatty acids are powerful tools for investigating the feeding ecology of wild marine predators, but inference depends on key assumptions and robust reference data. Controlled feeding experiments are not feasible for northern bottlenose whales, so species- and tissue-specific TDFs and calibration coefficients are unlikely to ever be available. We addressed this uncertainty by evaluating a range of plausible TDF values (Figure S1) and applying estimates from taxonomically informed models (Healy et al., 2018), along with fatty acid calibration coefficients derived for killer whales (Remili et al., 2022). Even so, differences in metabolism between species, variation in individual physiology, and tissue biochemistry introduce uncertainty and likely contributed to differences between QFASA and isotope mixing model estimates (Stephens et al., 2023; Martínez Del Rio et al., 2009; Remili et al., 2022). In fatty acid analyses, several whales fell outside the prey convex-hull (pred-beyond-prey = 28%, SA2) indicating that the prey library and calibration coefficients may not fully capture the fatty acid signatures available to consumers. QFASA estimates should therefore be interpreted cautiously. By contrast, whale isotope data showed better support in diagnostics (Figure S3, S4) suggesting more robust isotope-based inference under the current parameterization.

Interpretation is also sensitive to tissue integration windows. Turnover rates differ between skin and blubber tissues (e.g., Wild et al., 2018; Busquets-Vass et al., 2017; Giménez et al., 2016; Choy et al., 2019), and variation in sample thickness can affect fatty acid profiles because blubber is typically stratified (Koopman et al., 1996). As a result, it is not always clear how far back in time skin isotopes and outer-blubber fatty acids reflect consumer diet. Uncertainty is further increased by mismatches between whale sampling and prey collections across space, season, or year. Prey libraries built from limited temporal sampling may miss interannual variability and shifts in isotopic baselines. Ideally, prey samples spanning the same temporal window as whale tissues would better capture species-specific temporal variation, which can bias interpretation of temporal trends in predator tissues (Johnson and Davoren, 2021). In addition, incomplete representation of the potential prey (e.g., missing taxa or age and sex classes) can affect both stable isotope and fatty acid baselines, given well-documented ontogenetic shifts (Chouvelon et al., 2011; Golikov et al., 2018; 2022). That said, this study compiles the largest prey biomarker library assembled to date for the deep waters of the western North Atlantic (n samples stable isotopes = 283, fatty acids = 795; n species = 19). Through iterative model evaluation and sensitivity checks, we consider it a robust approximation of the prey profiles available to northern bottlenose whales, and a reusable reference that can be expanded and re-analysed as new prey data, calibration techniques and models become available. Furthermore, the biomarker results for Newfoundland whales and prey taxa not included in the final dietary models were retained as a baseline for future synthesis as sampling, calibration, and prey coverage improve.

Despite the limitations and species-level discrepancies, both stable isotope and fatty acid models agreed on fish-dominated diets, reinforcing our inference of foraging patterns centered on demersal fish. At the same time, variation among isotope mixing models illustrates how assumptions about TDFs, prey grouping, and model structure can influence dietary estimates. Priorities for future work include ongoing improvement of predator and prey sampling across seasons and years (e.g., Arctic female whales in spring) and improved prey taxonomic and life-stage coverage (e.g., for demersal fish and cephalopods). Higher-resolution biomarker approaches should also help. For example, compound-specific isotope analysis can separate trophic position from baseline variation and sharpen regional and seasonal interpretation (Brault et al., 2019; Matthews et al., 2021; Troina et al., 2021). Comparable biomarker libraries in the eastern North Atlantic would enable direct cross-basin comparisons to test whether northern bottlenose whale diets reflect regional prey fields or differences in sampling and inference. Complementary approaches, such as photo-identification, morphometrics, environmental DNA (eDNA), and animal-borne tags could better link whale movements and habitat use to prey fields. Together, these approaches would improve inference about prey availability and spatiotemporal foraging dynamics and ground truth indirect diet estimation approaches, i.e., based on stable isotopes and fatty acids.

5. Conclusion

This study presents the first multi-year, multi-region assessment of northern bottlenose whale diet using both stable isotope and fatty acid tracers. Rather than obligate squid specialists, our findings indicate that northern bottlenose whales feed on demersal fish across their western range. In the Arctic, this reliance overlaps with prey species targeted by bottom-contact fisheries, raising the likelihood that fisheries can shape diet both through prey removal and through altered access to prey (e.g., via depredation or discards). This revised understanding has direct implications for identifying critical habitats, evaluating overlap with bottom-contact fisheries, such as those targeting Greenland halibut or redfish, and advancing an ecosystem approach to marine management. Region-specific foraging strategies, including stronger evidence of sex-based differences in the Arctic, provide ecological support for the current management approach that treats these as distinct populations, which has largely been based on genetic evidence. Together, these insights provide a clearer picture of northern bottlenose whale trophic ecology and demonstrate the value of combining dietary tracers to inform conservation, stock assessment, and recovery planning under Canada's *SARA* and the International Union for Conservation of Nature (IUCN) monitoring frameworks.

CRediT authorship contribution statement

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Laura J. Feyrer: Conceptualization; Methodology; Investigation; Formal analysis; Data curation; Validation; Funding Acquisition, Visualization; Project administration; Writing – original draft; Writing – review & editing
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Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2026.e04242.

Data availability

The data supporting the findings of this study are publicly available at the Open Science Framework: https://doi.org/10.17605/OSF.IO/BVZF3.

References

Amaratunga, T., 1981. 'The Short-Finned Squid (Illex illecebrosus) Fishery in Eastern Canada'. J. Shellfish Res. 1 (2), 143–152.
Benjaminsen, Terje, Christensen, Ivar, 1979. The Natural History of the Bottlenose Whale, *Hyperoodon ampullatus* (Forster). In: Winn, Howard E., Olla., Bori L. (Eds.), Behavior of Marine Animals: Current Perspectives in Research. Springer US. https://doi.org/10.1007/978-1-4684-2985-5_5.
Bernier, Renée Y., Jamieson, Robyn E., Kelly, Noreen E., Lafleur, Caroline, Moore, Andrea M. (eds.) 2023. State of the Atlantic Ocean Synthesis Report. Can. Tech. Rep. Fish. Aquat. Sci. 3544: v + 219 p.
Bjørke, Herman, 2001. Predators of the Squid Gonatus fabricii (Lichtenstein) in the Norwegian Sea. Fish. Res. 52 (1–2), 113–120. https://doi.org/10.1016/s0165-7836(01)00235-1.
Bloch, D., Desportes, G., Zachariassen, M., Christensen, I., 1996. The Northern Bottlenose Whale in the Faroe Islands, 1584-1993. J. Zool. 239 (1), 123–140. https://doi.org/10.1111/j.1469-7998.1996.tb05441.x.
Bowen, W.D., Iverson, S.J., 2013. Methods of estimating marine mammal diets: a review of validation experiments and sources of bias and uncertainty. Mar. Mammal. Sci. 29 (4), 719–754. https://doi.org/10.1111/j.1748-7692.2012.00604.x.
Bowlby, Heather D., Christina Bourne, Cindy Breau, et al. 2023. 'Marine and Diadromous Fish'. In *STATE OF THE ATLANTIC OCEAN SYNTHESIS REPORT*, Renée Y. Bernier, Robyn E. Jamieson, Noreen E. Kelly, Caroline Lafleur, and Andrea M. Moore.
Brault, Ek, Koch, Pl, Costa, Dp, et al., 2019. Trophic Position and Foraging Ecology of Ross, Weddell, and Crabeater Seals Revealed by Compound-Specific Isotope Analysis. Mar. Ecol. Prog. Ser. 611 (February), 1–18. https://doi.org/10.3354/meps12856.

Bromaghin, Jeffrey F., Budge, Suzanne M., Thiemann, Gregory W., Rode, Karyn D., 2017. Simultaneous Estimation of Diet Composition and Calibration Coefficients with Fatty Acid Signature Data. Ecol. Evol. 7 (16), 6103–6113. https://doi.org/10.1002/ece3.3179.

Budge, S.M., Springer, A.M., Iverson, S.J., Sheffield, G., Rosa, C., 2008. Blubber fatty acid composition of Bowhead Whales, Balaena mysticetus: implications for diet assessment and ecosystem monitoring. J. Exp. Mar. Biol. Ecol. 359 (1), 40–46. https://doi.org/10.1016/j.jembe.2008.02.014.

Budge, Suzanne M., Iverson, Sara J., Koopman, Heather N., 2006. Studying trophic ecology in marine ecosystems using fatty acids: a primer on analysis and interpretation. Mar. Mammal. Sci. 22 (4), 759–801. https://doi.org/10.1111/j.1748-7692.2006.00079.x.

Burke, T.G., Huveneers, C., Meyer, L., et al., 2025. Evidence for an ecological two population model for White Sharks (Carcharodon carcharias) in Australian waters'. Wildl. Res. 52 (3), WR24132. https://doi.org/10.1071/WR24132.

Busquets-Vass, Geraldine, Newsome, Seth D., Calambokidis, John, et al., 2017. Estimating Blue Whale Skin Isotopic Incorporation Rates and Baleen Growth Rates: Implications for Assessing Diet and Movement Patterns in Mysticetes. PLOS ONE 12 (5), e0177880. https://doi.org/10.1371/journal.pone.0177880.

Carroll, M.L., Carroll, J., 2003. 'The Arctic Seas'. Biogeochemistry of Marine Systems, 1st ed. Blackwell. https://doi.org/10.1201/9780367812423.

Caut, Stéphane, Laran, Sophie, Garcia-Hartmann, Emmanuel, Das, Krishna, 2011. Stable isotopes of captive cetaceans (killer whales and bottlenose dolphins). J. Exp. Biol. 214 (4), 538–545. https://doi.org/10.1242/jeb.045104.

Chen, Rachel S., Portner, Elan J., Choy, C.Anela, 2022. Gelatinous Cephalopods as Important Prey for a Deep-Sea Fish Predator. Mar. Biol. 169 (12). https://doi.org/10.1007/s00227-022-04116-w.

Chouvelon, T., Spitz, J., Cherel, Y., et al., 2011. Inter-Specific and Ontogenic Differences in δ13C and δ15N Values and Hg and Cd Concentrations in Cephalopods. Mar. Ecol. Prog. Ser. 433 (July), 107–120. https://doi.org/10.3354/meps09159.

Choy, Emily S., Sheehan, Brian, Haulena, Martin, Rosenberg, Bruno, Roth, James D., Loseto, Lisa L., 2019. A Comparison of Diet Estimates of Captive Beluga Whales Using Fatty Acid Mixing Models with Their True Diets. J. Exp. Mar. Biol. Ecol. 516 (July), 132–139. https://doi.org/10.1016/j.jembe.2019.05.005.

Clark, Casey T., Cape, Mattias R., Shapley, Mark D., Mueter, Franz J., Finney, Bruce P., Misarti, Nicole, 2021. SuessR: Regional Corrections for the Effects of Anthropogenic CO_2 on δ^{13} C Data from Marine Organisms. Methods Ecol. Evol. 12 (8), 1508–1520. https://doi.org/10.1111/2041-210X.13622.

Clarke, Malcolm R., Kristensen, Thomas K., 1980. Cephalopod Beaks from the Stomachs of Two Northern Bottlenosed Whales (*Hyperoodon ampullatus*). J. Mar. Biol. Assoc. U. Kingd. 60 (1), 151–156. https://doi.org/10.1017/S002531540002419X.

COSEWIC. 2024. *COSEWIC Assessment and Status Report on the Northern Bottlenose Whale Hyperoodon ampullatus, Davis Strait-Baffin Bay-Labrador Sea Population and Scotian Shelf Population, in Canada.* Committee on the Status of Endangered Wildlife in Canada. Ottawa.

Daase, Malin, Berge, Jørgen, Søreide, Janne E., Falk-Petersen, Stig, 2021. Ecology of Arctic Pelagic Communities. In: Thomas, David N. (Ed.), Arctic Ecology, 1st ed. Wiley. https://doi.org/10.1002/9781118846582.ch9.

Dalsgaard, Johanne, St. John, Michael, Kattner, Gerhard, Müller-Navarra, Dörthe, Hagen, Wilhelm, 2003. Fatty Acid Trophic Markers in the Pelagic Marine Environment. In: Advances in Marine Biology, 46. Elsevier. https://doi.org/10.1016/S0065-2881(03)46005-7.

Dawe, E.G., Hendrickson, L.C., Colbourne, E.B., Drinkwater, K.F., Showell, M.A., 2007. Ocean Climate Effects on the Relative Abundance of Short-finned (*Illex illecebrosus*) and Long-finned (*Loligo pealeii*) Squid in the Northwest Atlantic Ocean. Fish. Oceanogr. 16 (4), 303–316. https://doi.org/10.1111/j.1365-2419.2007.00431.x.

Dawe, E.G., Shears, J.C., Balch, N.E., O'Dor, R.K., 1990. Occurrence, Size, and Sexual Maturity of Long-Finned Squid (*Loligo Pealei*) at Nova Scotia and Newfoundland, Canada. Can. J. Fish. Aquat. Sci. 47 (9), 1830–1835. https://doi.org/10.1139/f90-208.

DFO. 2021. Stock Status Update of Unit 3 Redfish for 2020. DFO Can. Sci. Advis. Sec. Sci. Resp. 2021/026. Fisheries and Oceans Canada.

DFO. 2023. Stock Status of Redfish in Northwest Atlantic Fisheries Organization (NAFO) Subarea 0, and Subarea 2 + Division 3 K. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2023/004. Fisheries and Oceans Canada.

Espinasse, Boris, Sturbois, Anthony, Basedow, Sünnje L., et al., 2022. Temporal Dynamics in Zooplankton δ13C and δ15N Isoscapes for the North Atlantic Ocean: Decadal Cycles, Seasonality, and Implications for Predator Ecology. Front. Ecol. Evol. 10 (October), 986082. https://doi.org/10.3389/fevo.2022.986082.

Fernández, Ruth, Pierce, Graham J., MacLeod, Colin D., et al., 2014. Strandings of Northern Bottlenose Whales, *Hyperoodon ampullatus*, in the North-East Atlantic: Seasonality and Diet. J. Mar. Biol. Assoc. U. Kingd. 94 (6), 1109–1116. https://doi.org/10.1017/S002531541300180X.

Feyrer, L.J., Stanistreet, J.E., Gomez, C., et al., 2024. Identifying Important Habitat for Northern Bottlenose and Sowerby's Beaked Whales in the Western North Atlantic. Aquat. Conserv. Mar. Freshw. Ecosyst. 34 (1), e4064. https://doi.org/10.1002/aqc.4064.

Feyrer, Laura, Walmsley, Sam F., Stewart, Madison A., MacNeil, M.Aaron, Whitehead, Hal, 2025. Reversing Decline: The Impact of Spatial Conservation on Endangered Northern Bottlenose Whales (ahead of print). J. Appl. Ecol.. https://doi.org/10.1111/1365-2664.70122.

Feyrer, Laura J., Colbourne, Natalie, Lawson, Jack W., Moors-Murphy, Hilary B., Ferguson, Steven H., 2025. Three decades of observer records rveal ongoing risks of marine mammal depredation and entanglement in Canada's Atlantic fisheries. ICES J. Mar. Sci. 82, 8.

Feyrer, Laura Joan, Bentzen, Paul, Whitehead, Hal, Paterson, Ian G., Einfeldt, Anthony, 2019. Evolutionary Impacts Differ between Two Exploited Populations of Northern Bottlenose Whale (*Hyperoodon ampullatus*). Ecol. Evol. 9 (23), 13567–13584. https://doi.org/10.1002/ece3.5813.

Feyrer, Laura Joan, Stewart, Madison, Yeung, Jas, Soulier, Colette, Whitehead, Hal, 2021. Origin and Persistence of Markings in a Long-Term Photo-Identification Dataset Reveal the Threat of Entanglement for Endangered Northern Bottlenose Whales (Hyperoodon ampullatus). Front. Mar. Sci. 8 (May), 620804. https://doi.org/10.3389/fmars.2021.620804.

Folch, Jordi, Lees, M., Stanley, G.H. Sloane, 1957. A SIMPLE METHOD FOR THE ISOLATION AND PURIFICATION OF TOTAL LIPIDES FROM ANIMAL TISSUES. J. Biol. Chem. 226 (1), 497–509. https://doi.org/10.1016/S0021-9258(18)64849-5.

Gardiner, Kathleen, Dick, Terry A., 2010. Arctic Cephalopod Distributions and Their Associated Predators. Polar Res. 29 (2), 209–227. https://doi.org/10.1111/j.1751-8369.2010.00146.x.

Gilson, A., Syvanen, M., Levine, K., Banks, J., 1998. Deer Gender Determination by Polymerase Chain Reaction: Validation Study and Application to Tissues, Bloodstains, and Hair Forensic Samples from California'. Calif. Fish. Game 84 (4), 159–169.

Giménez, Joan, Cañadas, Ana, Ramírez, Francisco, et al., 2018. Living Apart Together: Niche Partitioning among Alboran Sea Cetaceans. Ecol. Indic. 95 (December), 32–40. https://doi.org/10.1016/j.ecolind.2018.07.020.

Giménez, Joan, Ramírez, Francisco, Almunia, Javier, G. Forero, Manuela, De Stephanis, Renaud, 2016. From the Pool to the Sea: Applicable Isotope Turnover Rates and Diet to Skin Discrimination Factors for Bottlenose Dolphins (Tursiops truncatus). J. Exp. Mar. Biol. Ecol. 475 (February), 54–61. https://doi.org/10.1016/j.jembe.2015.11.001.

Golikov, Alexey V., Ceia, Filipe R., Hoving, Hendrik J.T., et al., 2022. Life history of the Arctic Squid Gonatus fabricii (Cephalopoda: Oegopsida) reconstructed by analysis of individual ontogenetic stable isotopic trajectories. Animals 12 (24), 3548. https://doi.org/10.3390/ani12243548.

Golikov, Av, Ceia, Fr, Sabirov, Rm, et al., 2018. Ontogenetic Changes in Stable Isotope (δ13C and δ15N) Values in Squid Gonatus fabricii (Cephalopoda) Reveal Its Important Ecological Role in the Arctic. Mar. Ecol. Prog. Ser. 606 (ember), 65–78. https://doi.org/10.3354/meps12767.

Govan, Emma, Andrew L. Jackson, Richard Inger, Stuart Bearhop, and Andrew C. Parnell. 2023. 'Simmr: A Package for Fitting Stable Isotope Mixing Models in R'. arXiv:2306.07817. Preprint, arXiv, June 13. https://doi.org/10.48550/arXiv.2306.07817.

Greef, Evelien de, Einfeldt, Anthony L., Miller, Patrick J.O., et al., 2022. Genomics Reveal Population Structure, Evolutionary History, and Signatures of Selection in the Northern Bottlenose Whale, *Hyperoodon ampullatus*. Mol. Ecol. 31 (19), 4919–4931. https://doi.org/10.1111/mec.16643.

Healy, Kevin, Guillerme, Thomas, Kelly, Sean B.A., Inger, Richard, Bearhop, Stuart, Jackson, Andrew L., 2018. SIDER: An R Package for Predicting Trophic Discrimination Factors of Consumers Based on Their Ecology and Phylogenetic Relatedness. Ecography 41 (8), 1393–1400. https://doi.org/10.1111/ecog.03371.

Hooker, Sascha K., Baird, Robin W., 1999. Deep–Diving Behaviour of the Northern Bottlenose Whale, *Hyperoodon ampullatus* (Cetacea: Ziphiidae). Proc. R. Soc. Lond. Ser. B Biol. Sci. 266 (1420), 671–676. https://doi.org/10.1098/rspb.1999.0688.

Hooker, Sascha K., De Soto, Natacha Aguilar, Baird, Robin W., et al., 2019. Future Directions in Research on Beaked Whales. Front. Mar. Sci. 5 (January), 514. https://doi.org/10.3389/fmars.2018.00514.

Hooker, Sascha K., Iverson, Sara J., Ostrom, Peggy, Smith, Sean C., 2001. Diet of northern bottlenose whales inferred from fatty-acid and stable-isotope analyses of biopsy samples. Can. J. Zool. 79 (8), 1442–1454. https://doi.org/10.1139/z01-096.

Hooker, Sascha K., Whitehead, Hal, Gowans, Shannon, 2002. Ecosystem Consideration in Conservation Planning: Energy Demand of Foraging Bottlenose Whales (Hyperoodon ampullatus) in a Marine Protected Area. Biol. Conserv. 104 (1), 51–58. https://doi.org/10.1016/S0006-3207(01)00153-7.

Hop, Haakon, Gjøsæter, Harald, 2013. Polar Cod (*Boreogadus saida*) and Capelin (*Mallotus villosus*) as Key Species in Marine Food Webs of the Arctic and the Barents Sea. Mar. Biol. Res. 9 (9), 878–894. https://doi.org/10.1080/17451000.2013.775458.

Hurley, Geoffrey V, 1980. 'Recent Developments in the Squid, Illex Illecebrosus, Fishery of Newfoundland, Canada'. Mar. Fish. Rev. 42 (7–8), 15–22.

Hussey, Nigel E., MacNeil, M.Aaron, McMeans, Bailey C., et al., 2014. Rescaling the Trophic Structure of Marine Food Webs. Ecol. Lett. 17 (2), 239–250. https://doi.org/10.1111/ele.12226.

Iverson, Sara J., 2009. Tracing Aquatic Food Webs Using Fatty Acids: From Qualitative Indicators to Quantitative Determination. In: Kainz, Martin, Brett, Michael T., Arts., Michael T. (Eds.), Lipids in Aquatic Ecosystems. Springer New York. https://doi.org/10.1007/978-0-387-89366-2_12.

Iverson, Sara J., Field, Chris, Don Bowen, W., Blanchard, Wade, 2004. QUANTITATIVE FATTY ACID SIGNATURE ANALYSIS: A NEW METHOD OF ESTIMATING PREDATOR DIETS. Ecol. Monogr. 74 (2), 211–235. https://doi.org/10.1890/02-4105.

Iverson, Sara J., Frost, Kathryn J., Lowry, Lloyd F., 1997. Fatty Acid Signatures Reveal Fine Scale Structure of Foraging Distribution of Harbor Seals and Their Prey in Prince William Sound, Alaska. Mar. Ecol. Prog. Ser. 151, 255–271.

Iverson, Sj, Springer, Am, Kitaysky, As, 2007. Seabirds as Indicators of Food Web Structure and Ecosystem Variability: Qualitative and Quantitative Diet Analyses Using Fatty Acids. Mar. Ecol. Prog. Ser. 352 (December), 235–244. https://doi.org/10.3354/meps07073.

Jackson, Andrew L., Inger, Richard, Parnell, Andrew C., Bearhop, Stuart, 2011. Comparing Isotopic Niche Widths among and within Communities: SIBER - Stable Isotope Bayesian Ellipses in R: Bayesian Isotopic Niche Metrics'. J. Anim. Ecol. 80 (3), 595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x.

Johnson, Kelsey F., Davoren, Gail K., 2021. Stable Isotope Analysis Reveals That Humpback Whales (*Megaptera novaeangliae*) Primarily Consume Capelin (*Mallotus villosus*) in Coastal Newfoundland, Canada. Can. J. Zool. 99 (7), 564–572. https://doi.org/10.1139/cjz-2020-0257.

Johnson, Kelsey F., Hussey, Nigel E., Ferguson, Steven H., 2021. Observation of Marine Mammal and Bird Interactions Focused around a Commercial Fishing Vessel in Central Baffin Bay, Nunavut. Arct. Sci. 7 (2), 567–574. https://doi.org/10.1139/as-2020-0014.

Jorgensen, O.A., Hvingel, C., Treble, M.A., 2011. Identification and Mapping of Bottom Fish Assemblages in Northern Baffin Bay. J. Northwest Atl. Fish. Sci. 43 (March), 65–79. https://doi.org/10.2960/J.v43.m666.

Key, R.M., Kozyr, A., Sabine, C.L., et al., 2004. A Global Ocean Carbon Climatology: Results from Global Data Analysis Project (GLODAP). Glob. Biogeochem. Cycles 18 (4), 2004GB002247. https://doi.org/10.1029/2004GB002247.

Konrad, Christine M., Dupuis, Alysha, Gero, Shane, Frasier, Timothy, 2017. A Sexing Technique for Highly Degraded Cetacean DNA. Aquat. Mamm. 43 (6), 655–660. https://doi.org/10.1578/AM.43.6.2017.655.

Koopman, H.N., Iverson, S.J., Gaskin, D.E., 1996. Stratification and Age-Related Differences in Blubber Fatty Acids of the Male Harbour Porpoise (Phocoena phocoena). J. Comp. Physiol. B 165 (8), 628–639. https://doi.org/10.1007/BF00301131.

Koopman, Heather N., 2007. Phylogenetic, Ecological, and Ontogenetic Factors Influencing the Biochemical Structure of the Blubber of Odontocetes. Mar. Biol. 151 (1), 277–291. https://doi.org/10.1007/s00227-006-0489-8.

Laws, Edward A., Popp, Brian N., Bidigare, Robert R., Kennicutt, Mahlon C., Macko, Stephen A., 1995. Dependence of Phytoplankton Carbon Isotopic Composition on Growth Rate and [CO2)Aq: Theoretical Considerations and Experimental Results. Geochim. Et. Cosmochim. Acta 59 (6), 1131–1138. https://doi.org/10.1016/0016-7037(95)00030-4.

Lefort, K.J., Storrie, L., Hussey, N.E., Ferguson, S.H., 2025. Aseasonal Migration of a Northern Bottlenose Whale Provides Support for the Skin Molt Migration Hypothesis. Ecol. Evol. 15 (2), e70921. https://doi.org/10.1002/ece3.70921.

Lick, Roland, Piatkowski, Uwe, 1998. Stomach Contents of a Northern Bottlenose Whale (*Hyperoodon ampullatus*) Stranded at Hiddensee, Baltic Sea. J. Mar. Biol. Assoc. U. Kingd. 78 (2), 643–650. https://doi.org/10.1017/S0025315400041679.

Luck, Emma, Myers, Hannah, Criddle, Keith R., 2025. A Global Review of Operational Fishery Interactions with Killer Whales (Orcinus orca): Dynamics, Impacts, and Management Strategies. Front. Mar. Sci. 12 (September), 1629516. https://doi.org/10.3389/fmars.2025.1629516.

MacLeod, C.D., Santos, M.B., Pierce, G.J., 2003. Review of Data on Diets of Beaked Whales: Evidence of Niche Separation and Geographic Segregation. J. Mar. Biol. Assoc. U. Kingd. 83 (3), 651–665. https://doi.org/10.1017/S0025315403007616h.

Magozzi, S., Yool, A., Vander Zanden, H.B., Wunder, M.B., Trueman, C.N., 2017. Using Ocean Models to Predict Spatial and Temporal Variation in Marine Carbon Isotopes. Ecosphere 8 (5), e01763. https://doi.org/10.1002/ecs2.1763.

Mahon, Robin, Smith, Robert W., 1989. Demersal Fish Assemblages on the Scotian Shelf, Northwest Atlantic: Spatial Distribution and Persistence. Can. J. Fish. Aquat. Sci. 46 (S1), s134–s152. https://doi.org/10.1139/f89-285.

Marcoux, M., McMeans, Bc, Fisk, At, Ferguson, Sh, 2012. Composition and Temporal Variation in the Diet of Beluga Whales, Derived from Stable Isotopes. Mar. Ecol. Prog. Ser. 471 (December), 283–291. https://doi.org/10.3354/meps10029.

Martinez, Arbizu P. 2020. pairwiseAdonis: Pairwise Multilevel Comparison Using Adonis. Version 0.4. R Package. Released.

Martínez Del Rio, Carlos, Wolf, Nathan, Carleton, Scott A., Gannes, Leonard Z., 2009. Isotopic Ecology Ten Years after a Call for More Laboratory Experiments. Biol. Rev. 84 (1), 91–111. https://doi.org/10.1111/j.1469-185X.2008.00064.x.

Matthews, Cory J.D., Lawson, Jack W., Ferguson, Steven H., 2021. Amino Acid δ15N differences consistent with killer whale ecotypes in the Arctic and Northwest Atlantic. PLOS ONE 16 (4), e0249641. https://doi.org/10.1371/journal.pone.0249641.

McMahon, Kelton W., Hamady, Li. Ling, Thorrold, Simon R., 2013. A Review of Ecogeochemistry Approaches to Estimating Movements of Marine Animals. Limnol. Oceanogr. 58 (2), 697–714. https://doi.org/10.4319/lo.2013.58.2.0697.

McNichol, Ann P., Druffel, Ellen R.M., 1992. Variability of the δ13C of Dissolved Inorganic Carbon at a Site in the North Pacific Ocean. Geochim. Et. Cosmochim. Acta 56, 3589–3592.

Monteiro, Sílvia, Ferreira, Marisa, Vingada, José V., López, Alfredo, Brownlow, Andrew, Méndez-Fernandez, Paula, 2015. Application of Stable Isotopes to Assess the Feeding Ecology of Long-Finned Pilot Whale (Globicephala melas) in the Northeast Atlantic Ocean. J. Exp. Mar. Biol. Ecol. 465 (April), 56–63. https://doi.org/10.1016/j.jembe.2015.01.007.

Myers, Ransom A., Jeffrey, A.Hutchings, Nicholas, J.Barrowman, 1997. 'Why Do Fish Stocks Collapse? The Example of Cod in Atlantic Canada.'. Ecol. Appl. 7 (1), 91–106. https://doi.org/10.1890/1051-0761(1997)007[0091:WDFSCT]2.0.CO;2.

Neubarth, Barbara K., Miller, Patrick J.O., Roland, Rune, Kleivane, Lars, Wensveen, Paul J., 2025. Long-Term Depth Records of Satellite-Tagged Northern Bottlenose Whales Reveal Extraordinary Dive Capabilities. Ecol. Evol. 15 (8), e71862. https://doi.org/10.1002/ece3.71862.

Oyarbide, Usua, Feyrer, Laura Joan, Gordon, Jonathan, 2023. Sperm and Northern Bottlenose Whale Interactions with Deep-Water Trawlers in the Western North Atlantic. PLOS ONE 18 (8), e0289626. https://doi.org/10.1371/journal.pone.0289626.

Peterson, Bruce J., Fry, Brian, 1987. Stable isotopes in ecosystem studies. Annu. Rev. Ecol. Syst. 18, 293–320. https://doi.org/10.1146/annurev.es.18.110187.001453.

Post, David M., 2002. 'Using stable isotopes to estimate trophic position: models, methods, and assumptions'. Ecology 83 (3), 703–718. https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2.

Rau, Gh, Riebesell, U., Wolf-Gladrow, D., 1996. A model of photosynthetic 13C fractionation by marine phytoplankton based on diffusive molecular CO2 uptake. Mar. Ecol. Prog. Ser. 133, 275–285. https://doi.org/10.3354/meps133275.

Record, Nicholas, Runge, Jeffrey, Pendleton, Daniel, et al., 2019. Rapid climate-driven circulation changes threaten conservation of endangered North Atlantic Right Whales. Oceanography 32 (2). https://doi.org/10.5670/oceanog.2019.201.

Remili, Anaïs, Dietz, Rune, Sonne, Christian, et al., 2022. Validation of Quantitative Fatty Acid Signature Analysis for Estimating the Diet Composition of Free-Ranging Killer Whales. Sci. Rep. 12 (1), 7938. https://doi.org/10.1038/s41598-022-11660-4.

Remili, Anaïs, Dietz, Rune, Sonne, Christian, et al., 2023. Quantitative Fatty Acid Signature Analysis Reveals a High Level of Dietary Specialization in Killer Whales across the North Atlantic. J. Anim. Ecol. 92 (6), 1216–1229. https://doi.org/10.1111/1365-2656.13920.

Rodrigues, Karina A., Leonarduzzi, Ezequiel, Militelli, María I., Macchi, Gustavo J., 2025. Condition and Energy Allocation during the Reproductive Cycle of the Patagonian Redfish Sebastes oculatus from the Argentine Continental Shelf. Mar. Fish. Sci. (MAFIS) 38 (4). https://doi.org/10.47193/mafis.3842025011002.

Ryan, Conor, Berrow, Simon D., McHugh, Brendan, O'Donnell, Ciarán, Trueman, Clive N., O'Connor, Ian, 2014. Prey Preferences of Sympatric Fin (*Balaenoptera physalus*) and Humpback (*Megaptera novaeangliae*) Whales Revealed by Stable Isotope Mixing Models. Mar. Mammal. Sci. 30 (1), 242–258. https://doi.org/10.1111/mms.12034.

Santos, M.B., Pierce, G.J., Smeenk, C., et al., 2001. Stomach Contents of Northern Bottlenose Whales *Hyperoodon ampullatus* Stranded in the North Sea. J. Mar. Biol. Assoc. U. Kingd. 81 (1), 143–150. https://doi.org/10.1017/S0025315401003484.

Smith, James A., Mazumder, Debashish, Suthers, Iain M., Taylor, Matthew D., 2013. To Fit or Not to Fit: Evaluating Stable Isotope Mixing Models Using Simulated Mixing Polygons. Methods Ecol. Evol. 4 (7), 612–618. https://doi.org/10.1111/2041-210X.12048.

Smith, Kerri J., Trueman, Clive N., France, Christine A.M., et al., 2021. Stable Isotope Analysis of Specimens of Opportunity Reveals Ocean-Scale Site Fidelity in an Elusive Whale Species. Front. Conserv. Sci. 2 (May), 653766. https://doi.org/10.3389/fcosc.2021.653766.

Spitz, Jérôme, Cherel, Yves, Bertin, Stéphane, Kiszka, Jeremy, Dewez, Alexandre, Ridoux, Vincent, 2011. Prey Preferences among the Community of Deep-Diving Odontocetes from the Bay of Biscay, Northeast Atlantic. Deep Sea Res. Part I Oceanogr. Res. Pap. 58 (3), 273–282. https://doi.org/10.1016/j.dsr.2010.12.009.

Stephens, Ryan B., Shipley, Oliver N., Moll, Remington J., 2023. Meta-analysis and Critical Review of Trophic Discrimination Factors (Δ^{1}3C and Δ^{15} N): Importance of Tissue, Trophic Level and Diet Source'. Funct. Ecol. 37 (9), 2535–2548. https://doi.org/10.1111/1365-2435.14403.

Taite, Morag, Vecchione, Michael, Fennell, Sheena, Allcock, Louise A., 2020. Paralarval and Juvenile Cephalopods within Warm-Core Eddies in the North Atlantic. Bull. Mar. Sci. 96 (2), 235–262. https://doi.org/10.5343/bms.2019.0042.

Tixier, Paul, Barbraud, Christophe, Pardo, Deborah, Gasco, Nicolas, Duhamel, Guy, Guinet, Christophe, 2017. Demographic Consequences of Fisheries Interaction within a Killer Whale (Orcinus orca) Population. Mar. Biol. 164 (8), 170. https://doi.org/10.1007/s00227-017-3195-9.

Troina, Genyffer C., Riekenberg, Philip, Van Der Meer, Marcel T.J., Botta, Silvina, Dehairs, Frank, Secchi, Eduardo R., 2021. Combining Isotopic Analysis of Bulk-Skin and Individual Amino Acids to Investigate the Trophic Position and Foraging Areas of Multiple Cetacean Species in the Western South Atlantic. Environ. Res. 201 (October), 111610. https://doi.org/10.1016/j.envres.2021.111610.

Troina, Genyffer Cibele, Botta, Silvina, Dehairs, Frank, Di Tullio, Juliana Couto, Elskens, Marc, Secchi, Eduardo Resende, 2020. Skin δ13C and δ15N Reveal Spatial and Temporal Patterns of Habitat and Resource Use by Free-Ranging Odontocetes from the Southwestern Atlantic Ocean. Mar. Biol. 167 (12), 186. https://doi.org/10.1007/s00227-020-03805-8.

Vecchione, M., Pohle, G., 2002. Midwater Cephalopods in the Western North Atlantic Ocean off Nova Scotia'. Bull. Mar. Sci. 71 (2).

Whitehead, H., Hooker, Sk, 2012. Uncertain Status of the Northern Bottlenose Whale Hyperoodon ampullatus: Population Fragmentation, Legacy of Whaling and Current Threats. Endanger. Species Res. 19 (1), 47–61. https://doi.org/10.3354/esr00458.

Whitehead, H., R. Reeves, L.J. Feyrer, and R.L. Brownell Jr. 2021. Hyperoodon ampullatus. E. T10707A50357742. The IUCN Red List of Threatened Species 2021. International Union for Conservation of Nature. ⟨https://www.iucnredlist.org/species/10707/50357742⟩.

Wild, Lauren A., Chenoweth, Ellen M., Mueter, Franz J., Straley, Janice M., 2018. Evidence for Dietary Time Series in Layers of Cetacean Skin Using Stable Carbon and Nitrogen Isotope Ratios. Rapid Commun. Mass Spectrom. 32 (16), 1425–1438. https://doi.org/10.1002/rcm.8168.

Xavier, José C., Cherel, Yves, Allcock, Louise, et al., 2018. A Review on the biodiversity, distribution and trophic role of cephalopods in the Arctic and Antarctic Marine Ecosystems under a changing ocean. Mar. Biol. 165 (5), 93. https://doi.org/10.1007/s00227-018-3352-9.

Yurkowski, David J., Hussey, Nigel E., Ferguson, Steven H., Fisk, Aaron T., 2018. A temporal shift in trophic diversity among a predator assemblage in a warming Arctic. R. Soc. Open Sci. 5 (10), 180259. https://doi.org/10.1098/rsos.180259.