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Examination of Isotopic Signals to Determine Trophic Dynamics and Diet of Gulf of Maine Mysticetes Prior to an Oceanographic Regime Shift

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Abstract

Stable isotope analysis (SIA) is a useful tool to assess the health and foraging habits of large marine predators, metabolic stress, pregnancy, and migration patterns. This study provides baseline SIA data for four Gulf of Maine mysticete species and serves as a benchmark for future assessments. SIA was conducted on skin biopsies collected in two time periods: 1988 to 1992 ($n = 15$) and 1999 to 2005 ($n = 187$). Samples were collected from humpback whales (*Megaptera novaeangliae*; $n = 116$), fin whales (*Balaenoptera physalus*; $n = 74$), minke whales (*Balaenoptera acutorostrata*; $n = 6$), and North Atlantic right whales (*Eubalaena glacialis*; $n = 6$). There were statistically significant differences in isotopic value among species, years, and regions sampled. By species, North Atlantic right whale $\delta^{13}C$ and $\delta^{15}N$ levels were significantly different than the other species analyzed. Additionally, humpback whales had a $\delta^{15}N$ value that was significantly higher than the value found in fin whales. By date, humpback whales showed significant difference in $\delta^{13}C$ in 2002 from the two previous years. For fin whales, 2002 showed significant difference in $\delta^{13}C$ for all other years' samples (2000 to 2003). By region, two regions that were the greatest distance apart (Bay of Fundy and Great South Channel) showed significant differences in $\delta^{13}C$ for humpback whales. Demographic analyses for humpback and fin whales found a significant difference between calves versus other age classes, presumably due to nursing. A decadal comparison of humpback whales at one site (Stellwagen Bank) found no significant difference between decades. This dataset provides a benchmark for stable isotope measurements in large baleen whales for this regional ecosystem.

Key Words: baleen whales, stable isotope, Gulf of Maine, nutrition, food/prey, trophic dynamics

Introduction

The Gulf of Maine (GoM) has traditionally been an area of high prey productivity. Cool temperatures coupled with nutrient-rich water, and both tidal and bathymetrically driven upwelling and mixing, provide an ideal environment for marine primary producers that, in turn, supports foraging for many marine species (Townsend et al., 2015). Baleen whales typically rely on regions with consistently high abundance of high-quality prey, such as have been found in the GoM—for example, copepods (*Calanus finmarchicus*) and forage fish such as Atlantic herring (*Clupea harengus*), Atlantic mackerel (*Scomber scombrus*), and sandlance (*Ammodytes* spp.)—for foraging and energetic accrual (Christiansen et al., 2013).

However, a warming trend over the past 15 to 20 y threatens the Gulf's productivity. Pershing et al. (2015) identified a northward shift in the Gulf Stream, reducing nutrient-rich cold water flowing south via the Labrador Current into the GoM. Average sea surface temperatures in the GoM have continued to steadily increase, punctuated by four specific marine heat waves: in 2012, 2016, 2022, and 2023 (Pershing et al., 2018; Fernandez et al., 2020; Gulf of Maine Research Institute [GOMRI], 2023; Lucey et al., 2023). In some cases, these changes correlate with anecdotal decreases in sightings of mysticete species. For example, summer sightings of the North Atlantic right whales (*Eubalaena glacialis*)—a critically endangered species—have decreased, possibly due to climate-induced shifts in prey sources and/or their abundance or calorific quality (Davis et al., 2017; Record et al., 2019;

King et al., 2021). The distribution and phenology of key prey species for lunge feeding baleen whales appears to have shifted in the last two to three decades (Nye et al., 2009; Henderson et al., 2017; Meyer-Gutbrod et al., 2021), but the individual and population health consequences to generalist marine mammals remain unknown. Effective species management and conservation depends on the ability to detect and predict impacts from warming ocean temperatures. To investigate prey quality and trophic relationships in a rapidly changing climate and their potential effects on cetacean species, we completed a stable isotope analysis (SIA) study which provides baseline data for four GoM mysticete species and serves as a benchmark for future assessments of warming on prey preferences/availability in baleen whales.

For many marine species, especially cetaceans, SIA of carbon-13 ($\delta^{13}C$) and nitrogen-15 ($\delta^{15}N$) is a useful tool for studying trophic ecology and habitat use (Milmann et al., 2020). SIA has become a standard in studies of habitat use (Schell et al., 1989; Hobson & Schell, 1998; Witteveen et al., 2009; Ryan et al., 2013; Eerkes-Medrano et al., 2021), and has proven useful in studying diet (Rowntree et al., 2008; Witteveen, 2011; Borrell et al., 2012; Ryan et al., 2014; Eisenmann et al., 2016), migration and population structure (Schell et al., 1989; Rowntree et al., 2001, 2008; Witteveen et al., 2009; Wright et al., 2015; Eisenmann et al., 2016; Silva et al., 2019), nutritional stress (Borrell et al., 2012; Aguilar et al., 2014), age (Gelippi et al., 2020), and pregnancy (Stegall et al., 2008; Habran et al., 2010; Borrell et al., 2016; Clark et al., 2016) in cetaceans and pinnipeds.

Isotopic carbon is typically used to identify nutrient sources within food chains (Park & Epstein, 1961; DeNiro & Epstein, 1978; Tieszen et al., 1983) because signals between nearshore and offshore marine ecosystems are distinct (Rau et al., 1983), and fractionation between predator and prey is minimal. Isotopic nitrogen has yielded insight regarding trophic relationships between predator and prey for several marine mammal species due to predictable fractionation between trophic levels (Hobson et al., 1996; Hobson & Schell, 1998; Caraveo-Patino et al., 2007; Niño-Torres et al., 2014). Both are expressed as ratios, or delta (δ) values, measured in parts per thousand (‰) relative to their more common periodic forms (Lajtha & Michener, 1994; del Rio et al., 2009).

Although SIA originated in the Earth Sciences, it has become a standard assay in ecological studies for marine mammal populations (Newsome et al., 2010). In marine mammals, isotopic carbon and nitrogen values vary between tissue types, species, trophic levels, and habitats. They behave in a semi-predictable manner within an ecosystem; values increase from primary producer to upper-level predators through the process of isotopic fractionation. The numerical increase in δ value per trophic level, termed an enrichment factor, reflects the increased retention of heavier isotopes over their lighter forms (Newsome et al., 2010). Enrichment factors vary based on the isotope investigated, environmental influences, species, geographic regions, and metabolic activity (Tieszen et al., 1983; Goericke & Fry, 1994; Lajtha & Michener, 1994). Many species- and tissue-specific enrichment factors are still unknown, but, in general, isotopic carbon increases ~1‰ per trophic level while isotopic nitrogen increases ~3‰ (Gannes et al., 1997; del Rio et al., 2009), permitting cautious trophic interpretations. If the isotopic signature of a prey species is sufficiently distinct, analysis can identify it in the diet of a consumer, particularly when multiple isotopic markers are used.

SIA is a particularly useful tool for studying marine mammals because it provides a method to examine trophic dynamics in an otherwise logistically challenging marine environment (Newsome et al., 2010). At its simplest, SIA requires only a small amount of tissue. In marine mammals, this tissue is most commonly skin (Todd et al., 1997), which can be collected from free-ranging animals through well-established remote-biopsy techniques (Palsbøll et al., 1991; Lambertsen et al., 1994). Such techniques are minimally invasive (Brown et al., 1991; Weinrich, 1991; Clapham & Mattila, 1993; Gauthier & Sears, 1999), allowing for directed sampling in the wild. In pinnipeds, single-point samples have been shown to be representative of the entire tissue pool of the animal (Todd et al., 2010).

In this study, we examined $\delta^{13}C$ and $\delta^{15}N$ levels in skin samples collected from four mysticete species in the GoM prior to the recent warming period there. We used a large sample dataset to examine isotopic variability across species, geographic regions, and over time. For humpback whales (*Megaptera novaeangliae*), data from longitudinal photo-identification studies allowed for a detailed examination of the effects of age class, sex, and calving status. This benchmark of isotopic-informed mysticete trophic ecology provides a basis for understanding the ecology of GoM baleen whales in a warmer, less productive ecosystem.

Methods

Sample Collection

We collected samples from humpback whales, fin whales (*Balaenoptera physalus*), minke whales (*Balaenoptera acutorostrata*), and North Atlantic right whales. Research programs of four organizations in the GoM collected the samples (Table 1).

Our work sampled the following GoM areas: the Great South Channel (GSC; *n* = 33), Georges Bank (GEO; *n* = 6), Stellwagen Bank (STB; *n* = 49), Jeffreys Ledge (JL; *n* = 4), Mount Desert Rock/Inner Schoodic Ridges (MDR; *n* = 87), and the Bay of Fundy/German Bank (BOF; *n* = 22). We collected samples using 150-lb (68 kg) draw crossbows and specialized darts equipped with a stainless-steel sampling tip (Palsbøll et al., 1991; Lambertsen et al., 1994). We paired our sampling with photo-identification techniques to link sampled individuals to demographic data (sex and age class) curated by long-term population research. Other data collected relevant to this study included the sampling date/time, species, sampling location, and the presence of a dependent calf. Depending on the research organization, we preserved our samples in brine, DMSO/salt solution, or stored frozen without chemical preservative.

Sample Processing

We prepared our samples according to protocols developed for SIA analysis of whale skin outlined in Todd et al. (1997). Specifically, we dried samples to a constant weight and ground them to a fine powder using a combination of a liquid nitrogen immersed mortar and pestle and a mechanical agitator. We then transferred the homogenized powder to a cellulose thimble and repeatedly washed within a Soxhlet apparatus for 8 h using an 87% chloroform to 13% methanol (by volume) mixture. This technique extracts any lipids from the sample and removes any DMSO preservative. Extracted samples were then dried at 35°C to a constant weight, removed from thimbles, and placed in secondary vials for transport to the analytical laboratory.

Stable Isotope Analysis

Samples collected in 1999 were analyzed for $\delta^{13}C$ and $\delta^{15}N$ at the Institution for Quaternary Studies at the University of Maine, Orono. All other samples were analyzed at the Department of Geological Studies at Michigan State University.

SIA analysis was accomplished at both locations using a Continuous Flow Isotope Ratio Mass Spectrometry employing a VG-Fisions SIRA Series II Mass Spectrometer fitted with a Fisions Carlo-Erba NA 1500 Elemental Analyzer. Isotopic ratios were calculated using the following equation:

$$\delta^{y}X \text{ (in ‰)} = [1 - (R_{sample}/R_{reference})] \times 10^{3}$$

where ${}^{y}X$ is ${}^{13}C$ or ${}^{15}N$, and R = ${}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$, respectively. Reference standards for $\delta^{13}C$ and $\delta^{15}N$ were PDB Belemnite and air, respectively. We frequently (every ~20 samples) checked analysis runs for measurement drift using a homogenized sample of known isotopic composition. In

Table 1. Summary of samples by year collected, sample count, and source institution

Species common name	Year	*n*	Source institution (sample size in parentheses)
Fin whale	2000	12	CCS (2), COA (10)
	2001	16	COA (16)
	2002	22	CCS (2), COA (20)
	2003	24	CCS (2), COA (22)
Humpback whale	1988	1	WCNE (1)
	1991	3	WCNE (3)
	1992	10	WCNE (10)
	1999	14	CCS (14)
	2000	20	CCS (15), COA (5)
	2001	8	CCS (7), COA (1)
	2002	14	CCS (6), COA (4), WCNE (4)
	2003	39	CCS (30), COA (9)
	2005	6	WCNE (6)
Minke whale	2003	6	CCS (6)
North Atlantic right whale	2002	6	NEFSC (6)

CCS = Center for Coastal Studies, COA = College of the Atlantic, NEFSC = NOAA Northeast Fisheries Science Center, and WCNE = Whale Center of New England. Not shown is one humpback whale sample collected in an unknown year prior to 1993 by CCS.

this way, we estimate machine accuracy at ±0.1‰ for either isotope.

Demographic Data

Individuals were photographed at the time of sampling and matched to catalogs from long-term population studies by the Center for Coastal Studies (CCS), the College of the Atlantic (COA), and the Whale Center of New England (WCNE). For humpback whales, sex was determined by molecular genetic techniques (Palsbøll et al., 1992; Bérubé & Palsbøll, 1996a, 1996b). We classified calves based on their size, stereotypical behaviors, and close, consistent association with a mature female (the mother). For other individuals, we assigned age class based on the exact or minimum years elapsed since birth. Humpback whales were considered to be juveniles if they were first seen as calves and known to be less than 5 y old at the time of sampling (Chittleborough, 1959; Clapham, 1992; Robbins, 2007). We classified individuals with a sighting history of at least 5 y as adults. We assumed an adult female humpback whale accompanied by a dependent calf to be lactating, although this was not directly observed. For fin whales, demographic analyses discriminated only between calves and non-calves.

Statistical Analysis of Sample Data

We conducted statistical analyses using general linear modeling generated in the programming language *R*, whereby we checked all model residuals using normal probability plots. We can confirm the appropriateness of parametric testing in all cases. For each analysis, we initially considered $\delta^{13}C$ and $\delta^{15}N$ values together as a multivariate combined isotopic signature (Pillai's Trace Test Statistic), and then $\delta^{13}C$ and $\delta^{15}N$ values separately as individual dependent variables using species, year, sex, reproductive status (if known), and geographic region as predictive variables. We used a rejection criterion of $\alpha = 0.05$; and we used Tukey's Honestly Significant Difference (Tukey HSD) to protect against Type I familywise error in *post hoc* analyses.

Results

Isotopic Analysis by Species

Overall, our study yielded data from humpback (n = 116), fin (n = 74), minke (n = 6), and North Atlantic right (n = 6) whales for a total of 202 samples analyzed. Average combined isotopic signals are shown by species in Table 2a. Bivariate species means were significantly different from each other (MANOVA: $\text{Pillai}_{6,396} = 0.70$; $p < 0.0001$) as a function of changes in both their $\delta^{13}C$ values (ANOVA: $F_{3,198} = 31.76$; $p < 0.0001$) as well as $\delta^{15}N$ values (ANOVA: $F_{3,198} = 46.68$; $p < 0.0001$), with species generally aggregating within their respective phyletic families. Table 2b and Figure 1 demonstrate the statistical nature of this grouping, with rorquals clearly separated from right whales. Within rorquals, humpback whales had a statistically higher mean $\delta^{15}N$ value (mean ± SE = 13.738 ± 0.0970) than fin whales (12.282 ± 0.1091).

Table 2a. Average $\delta^{13}C$ and $\delta^{15}N$ isotopic signals by species with associated standard errors (SE)

		$\delta^{13}C$		$\delta^{15}N$	
Species	*n*	Mean	SE	Mean	SE
Humpback whale	116	-18.165	0.0508	13.738	0.0970
Fin whale	74	-18.051	0.0616	12.282	0.1091
Minke whale	6	-18.218	0.1286	13.360	0.1534
North Atlantic right whale	6	-20.778	1.0188	10.347	0.6078

Table 2b. *P* values associated with Tukey HSD pairwise comparisons of mean species values; bolded values indicate a statistically significant result at $p < 0.05$.

	$\delta^{13}C$			$\delta^{15}N$		
Species	Humpback whale	Fin whale	Minke whale	Humpback whale	Fin whale	Minke whale
Fin whale	0.6522	--	--	**< 0.0001**	--	--
Minke whale	0.9975	0.9330	--	0.8074	0.0605	--
North Atlantic right whale	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**

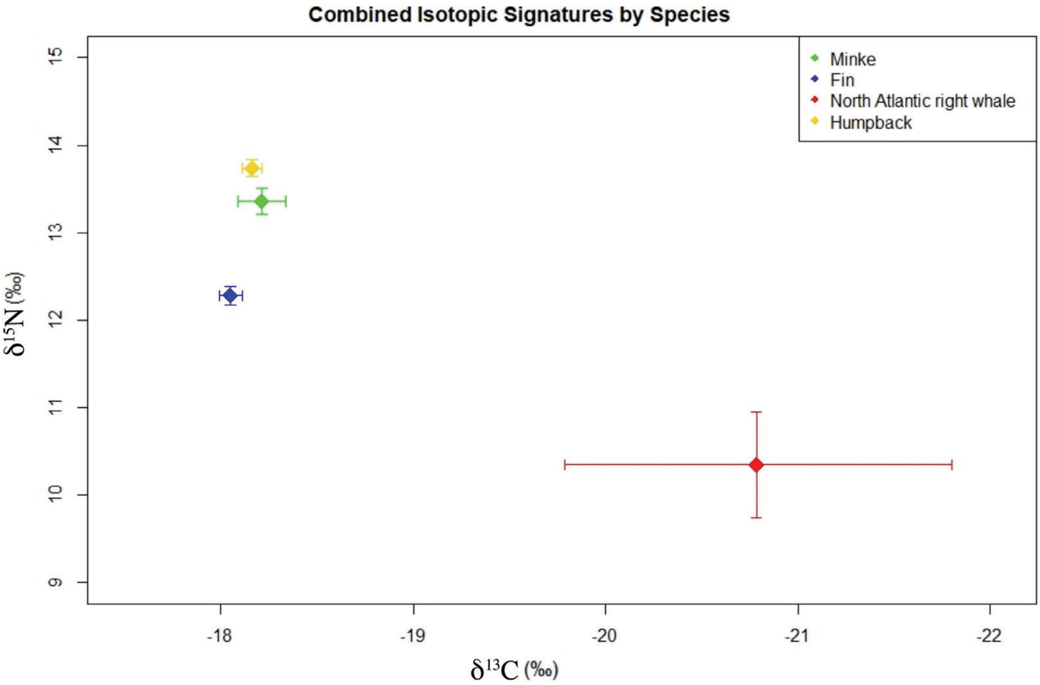

Figure 1. Combined isotopic bivariate signatures by species; error bars represent ± one standard error (SE).

Isotopic Signals over Time

Based on the samples available, we could only compare isotopic signals by year for humpback (MANOVA: $\text{Pillai}_{2,112} = 0.04$; $p < 0.1320$) and fin (MANOVA: $\text{Pillai}_{2,71} = 0.02$; $p < 0.5628$) whales (Table 3a).

For humpbacks, *post hoc* testing revealed δ^{13}C (ANOVA: $F_{8,106} = 2.88$; $p = 0.0060$) mean annual values in 2002 were statistically more negative compared to two prior years (Table 3b); we could not confirm a similar trend in δ^{15}N values as statistically significant (Table 3c).

For fin whales, δ^{13}C values also differed significantly by year (ANOVA: $F_{3,70} = 24.54$; $p < 0.0001$). *Post hoc* testing demonstrated that 2002 fin whale δ^{13}C values were significantly different to both prior and subsequent years (Table 3d), while δ^{15}N values did not change significantly by year (ANOVA: $F_{3,70} = 0.25$; $p = 0.8590$).

The longer span of humpback whale sampling at one site (STB) allowed for an additional, decadal comparison. Humpback combined isotopic signals did not change significantly between the periods 1988 to 1992 and 1999 to 2005 (MANOVA: $\text{Pillai}_{2,37} = 0.08$; $p = 0.2012$; Table 4a). *Post hoc* pairwise comparison between the two periods further indicated no significant difference in δ^{13}C ($p = 0.0970$) or δ^{15}N ($p = 0.1730$) (Table 4b).

Isotopic Signal by Geographic Region

Based on sufficient sample size for humpback whales, we conducted a multivariate analysis of isotopic signatures among the five geographic regions surveyed (Table 5a). We found a statistically significant regional effect (MANOVA: $\text{Pillai}_{10,218} = 0.224$; $p = 0.0033$) associated both with differences in δ^{13}C levels (ANOVA: $F_{5,109} = 2.85$; $p = 0.0186$) and δ^{15}N levels (ANOVA: $F_{5,109} = 3.01$; $p = 0.0139$) between regions. *Post hoc* analysis revealed significant variation in regional average δ^{13}C values between the GSC and BOF ($p = 0.0417$), and in the δ^{15}N values for GEO and STB ($p = 0.0350$) (Table 5b).

Sufficient data were available for a regional comparison of fin whale isotopic signatures between four geographic regions (Table 6a), although caution is recommended in the interpretation of these data given particular uneven sample sizes for each level of analysis. Multivariate testing results indicated that region was a significant predictor of combined isotopic signatures (MANOVA: $\text{Pillai}_{3,70} = 0.17$; $p = 0.0455$). Considered individually, mean δ^{13}C values were not significantly different by region (ANOVA: $F_{3,70} = 1.59$; $p = 0.1990$), but δ^{15}N values by region were significantly different (ANOVA: $F_{3,70} = 3.62$; $p = 0.0173$). *Post hoc* pairwise comparison of regional mean δ^{15}N values for fin whales (Table 6b) indicated a significant

Table 3a. Average isotopic signals by year and by species with associated SE

			$\delta^{13}C$		$\delta^{15}N$	
Species	Year	*n*	Mean	SE	Mean	SE
Humpback whale	1988	1	-18.320	—	13.360	—
	1991	3	-18.670	0.2654	13.207	0.1646
	1992	10	-18.340	0.2111	12.945	0.1925
	1999	14	-17.971	0.0940	14.042	0.2158
	2000	20	-17.915	0.1035	13.973	0.2133
	2001	8	-18.015	0.1402	13.988	0.2345
	2002	14	-18.629	0.1995	13.029	0.4490
	2003	39	-18.132	0.0675	13.955	0.1513
	2005	6	-18.254	0.1894	13.635	0.2367
Fin whale	2000	12	-17.761	0.1261	12.476	0.3270
	2001	16	-18.063	0.0457	12.315	0.2859
	2002	22	-18.591	0.0716	12.252	0.1369
	2003	24	-17.693	0.0955	12.190	0.1963

Table 3b. *P* values associated with Tukey HSD pairwise comparisons of $\delta^{13}C$ mean by year for humpback whales (M*egaptera novaeangliae*); bolded values indicate a statistically significant result at $p < 0.05$.

	$\delta^{13}C$							
Year	1988	1991	1992	1999	2000	2001	2002	2003
1988	--	--	--	--	--	--	--	--
1991	0.9996	--	--	--	--	--	--	--
1992	1.0000	0.9877	--	--	--	--	--	--
1999	0.9992	0.4609	0.7302	--	--	--	--	--
2000	0.9975	0.3157	0.4618	1.0000	--	--	--	--
2001	0.9998	0.6327	0.9209	1.0000	1.0000	--	--	--
2002	0.9997	1.0000	0.9134	**0.0281**	**0.0041**	0.1671	--	--
2003	1.0000	0.7204	0.9670	0.9854	0.8404	0.9997	0.0618	--
2005	1.0000	0.9667	1.0000	0.9695	0.8911	0.9946	0.8594	0.9998

Table 3c. *P* values associated with Tukey HSD pairwise comparisons of $\delta^{15}N$ mean by year for humpback whales

	$\delta^{15}N$							
Year	1988	1991	1992	1999	2000	2001	2002	2003
1988	--	--	--	--	--	--	--	--
1991	1.0000	--	--	--	--	--	--	--
1992	1.0000	1.0000	--	--	--	--	--	--
1999	0.9991	0.9239	0.1757	--	--	--	--	--
2000	0.9996	0.9453	0.1745	1.0000	--	--	--	--
2001	0.9996	0.9635	0.4100	1.0000	1.0000	--	--	--
2002	1.0000	1.0000	1.0000	0.1638	0.1541	0.4320	--	--
2003	0.9996	0.9423	0.1110	1.0000	1.0000	1.0000	0.0815	--
2005	1.0000	0.9995	0.9165	0.9954	0.9983	0.9992	0.9438	0.9982

Table 3d. *P* values associated with Tukey HSD pairwise comparisons of $\delta^{13}C$ and $\delta^{15}N$ mean values by year for fin whales (*Balaenoptera physalus*); bolded values indicate a statistically significant result at $p < 0.05$.

	$\delta^{13}C$			$\delta^{15}N$		
Year	2000	2001	2002	2000	2001	2002
2001	0.1666	--	--	0.9710	--	--
2002	**< 0.0001**	**0.0004**	--	0.9141	0.9971	--
2003	0.9562	**0.0175**	**< 0.0001**	0.8314	0.9772	0.9961

Table 4a. Mean isotopic signals by decade for humpback whales sampled at Stellwagen Bank with associated SE

		$\delta^{13}C$		$\delta^{15}N$	
Year range	*n*	Mean	SE	Mean	SE
1988-1992	14	-18.512	0.1574	12.963	0.1893
1999-2005	101	-18.180	0.0100	13.527	0.2244

Table 4b. *P* values associated with ANOVA pairwise comparisons of humpback whale $\delta^{13}C$ and $\delta^{15}N$ mean values

	$\delta^{13}C$		$\delta^{15}N$	
Year range	1988-1992	1999-2005	1988-1992	1999-2005
1988-1992	--	--	--	--
1999-2005	0.0970	--	0.1730	--

Table 5a. Humpback whale mean combined isotopic signals by area with associated SE

		$\delta^{13}C$		$\delta^{15}N$	
Area	*n*	Mean	SE	Mean	SE
BOF	20	-17.846	0.1064	13.914	0.1221
GEO	6	-17.777	0.0979	14.715	0.2309
GSC	26	-18.312	0.0973	13.692	0.2342
MDR	19	-18.233	0.1310	14.106	0.2199
STB	49	-18.263	0.0867	13.386	0.1780

Table 5b. *P* values associated with Tukey HSD pairwise comparisons of humpback whale $\delta^{13}C$ and $\delta^{15}N$ mean values by region; bolded values indicate statistical significance at $p < 0.05$.

	$\delta^{13}C$				$\delta^{15}N$			
Area	BOF	GEO	GSC	MDR	BOF	GEO	GSC	MDR
BOF	--	--	--	--	--	--	--	--
GEO	0.9998	--	--	--	0.5227	--	--	--
GSC	**0.0417**	0.2296	--	--	0.9758	0.2218	--	--
MDR	0.2082	0.4429	0.9962	--	0.9909	0.7855	0.7448	--
STB	0.0524	0.2945	0.9152	0.9999	0.3120	**0.0350**	0.8286	0.1104

difference between STB and MDR ($p = 0.0290$); all other regional comparisons were not significant ($p > 0.05$ for all other cases).

Isotopic Signal by Age Class

For both humpback (MANOVA: $\text{Pillai}_{4,198} = 0.29$; $p < 0.0001$) and fin (MANOVA: $\text{Pillai}_{2,12} = 0.47$; $p = 0.0226$) whales, the combined isotopic signals of calves were significantly higher than other age classes (Table 7a). Humpback samples varied significantly with age class in both $\delta^{15}N$ values (ANOVA: $F_{2,99} = 8.06$; $p = 0.0006$) and $\delta^{13}C$ values (ANOVA: $F_{2,99} = 6.59$; $p = 0.0021$). *Post hoc* pairwise testing indicated that humpback calves had higher $\delta^{15}N$ values than juveniles or adults who were not significantly different from each other (see Table 7b). Fin whale calves had significantly higher $\delta^{15}N$ values compared to non-calves (ANOVA: $F_{1,13} = 5.13$; $p = 0.0413$) with no significant difference in their $\delta^{13}C$ values (ANOVA: $F_{1,13} = 0.18$; $p = 0.6820$) (Table 7c).

Table 6a. Fin whale mean combined isotopic signals by area with associated SE

		$\delta^{13}C$		$\delta^{15}N$	
Area	*n*	Mean	SE	Mean	SE
GB	2	-18.240	0.0900	13.285	0.7850
GSC	1	-17.820	--	12.600	--
MDR	68	-18.076	0.0649	12.186	0.1080
STB	3	-17.433	0.0533	13.683	0.04736

Table 6b. *P* values associated with Tukey HSD pairwise comparisons of fin whale $\delta^{13}C$ and $\delta^{15}N$ mean values by region; bolded value indicates statistical significance at $p < 0.05$.

	$\delta^{13}C$			$\delta^{15}N$		
Area	GB	GSC	MDR	GB	GSC	MDR
GB	--	--	--	--	--	--
GSC	0.9136	--	--	0.9231	--	--
MDR	0.9719	0.9622	--	0.3226	0.9673	--
STB	0.3384	0.9190	0.1701	0.9613	0.7198	**0.0290**

Table 7a. Mean isotopic signals by species and age class with associated SE

			$\delta^{13}C$		$\delta^{15}N$	
Species	Class	*n*	Mean	SE	Mean	SE
Humpback whale	Calf	12	-18.359	0.1337	14.896	0.1011
	Juvenile	17	-18.562	0.1242	13.364	0.2572
	Adult	83	-18.069	0.0581	13.809	0.0930
Fin whale	Calf	5	-18.024	0.1960	13.432	0.4297
	Adult	10	-17.9435	0.1149	12.173	0.3283

Table 7b. *P* values associated with Tukey HSD pairwise comparisons of mean humpback whale $\delta^{13}C$ and $\delta^{15}N$ values by age class; bolded values indicate statistical significance at $p < 0.05$.

	$\delta^{13}C$		$\delta^{15}N$	
Class	Calf	Juvenile	Calf	Juvenile
Calf	--	--	--	--
Juvenile	0.6549	--	**0.0003**	--
Adult	0.3171	**0.0022**	**0.0034**	0.1460

Table 7c. *P* values associated with Tukey HSD pairwise comparisons of mean fin whale δ^{13}C and δ^{15}N values by age class; bolded value indicates statistical significance at $p < 0.05$.

	δ^{13}C		δ^{15}N	
Fin	Calf	Juvenile	Calf	Juvenile
Calf	--	--	--	--
Non-calf	0.6822	N/A	**0.0413**	N/A

Table 8a. Mean humpback isotopic carbon and nitrogen values, with associated SE, by sex and reproductive class

		δ^{13}C		δ^{15}N	
Class	*n*	Mean	SE	Mean	SE
Male	57	-18.218	0.0782	13.773	0.1540
Mother	13	-18.183	0.1451	14.079	0.2513
Other female	42	-18.115	0.0684	13.536	0.1393

Table 8b. *P* levels for Tukey-HSD pairwise comparisons of humpback mean δ^{13}C and δ^{15}N values by sex

	δ^{13}C		δ^{15}N	
Class	Male	Female	Male	Female
Male	--	--	--	--
Mother	0.9749	0.9137	0.5604	0.1850
Other female	0.6058	--	0.4525	--

Isotopic Signal by Sex and Calving Status

Based on available samples, we limited our analyses of the effects of sex and calving status to humpback whales. We initially excluded samples from mothers due to the potential chemical uniqueness of isotopic signals during lactation. With those 13 samples removed, there was no difference in combined isotopic signals of males and females (MANOVA: Pillai$_{2,96}$ = 0.04; p = 0.1335). When mothers were added as a third class of animal, there was still no significant difference in terms of mean bivariate signal (MANOVA: Pillai$_{4,218}$ = 0.06; p = 0.1466; Table 8a). *Post hoc* ANOVA *p* values further confirmed no significant variation among the humpback mean isotopic signals of these classes (Table 8b).

Discussion

The GoM is undergoing rapid oceanographic change, including general thermal shifts (Pershing et al., 2015; Friedland et al., 2020; Balch et al., 2022), specific rapid increases in surface and bottom temperature (Thomas et al., 2017), marine heat waves (Mills et al., 2013; Pershing et al., 2018; Fernandez et al., 2020; Lucey et al., 2023), and changes to ocean current circulation and strength (Caesar et al., 2018; Thornalley et al., 2018). The resulting impacts to the ecosystem could include decreases in quantity and quality of key prey species (Davis et al., 2017; Record et al., 2019), phenology and stock changes in commercial fish species (Sherman et al., 2007; Pershing et al., 2015; Henderson et al., 2017), and marine mammal distribution shifts (Davis et al., 2017; Meyer-Gutbrod et al., 2021; Thorne & Nye, 2021). The data reported in this study represent a comprehensive assessment of stable isotope-derived trophic ecology for baleen whales prior to many of these changes.

To our knowledge, this study provides the first and the largest isotopic dataset for mysticetes in this region (Milmann et al., 2020). We suggest that this dataset will be essential as a benchmark for future assessments of the impact of climate change on baleen whale trophic dynamics in the GoM, especially as the current trend of warming appears likely to continue (Pershing et al., 2021).

As expected, based on their δ^{15}N signals, North Atlantic right whales were trophically lower than other GoM mysticetes (Figure 1).

These findings correlate well with documented feeding behaviors for these species within the GoM. North Atlantic right whales feed almost exclusively on dense patches of herbivorous *Calanus* and other copepod species (Jiang et al., 2007; Sorochan et al., 2023), while humpback, fin, and minke whales target dense patches of schooling fish, including sand lance (Hain et al., 1982; Staudinger et al., 2020) and herring (Hain et al., 1982). Humpback whales in our study exhibited higher δ^{15}N signals than fin whales, although the specific cause of this difference is not known as there have been no systematic dietary studies of these species in the GoM. Watkins & Schevill (1979) observed fin whales feeding on patches of schooling fish that tended to be smaller in size than the fish targeted by humpback and minke whales. It is conceivable that our results were affected by the differential regional distribution of fin and humpback whale samples in this study as 92% of fin whales were sampled at Mount Desert Rock, whereas only 16.4% of humpbacks were sampled in this area. However, our findings are similar to the results from studies in other areas. For example, Borobia et al. (1995) recorded a slightly lower δ^{15}N for fin whales sampled in the Gulf of St. Lawrence (Canada) when compared to humpback whales, despite sympatric association between these two species when feeding. Gavrilchuk et al. (2014) also demonstrate isotopic separation in the Gulf of St. Lawrence, with blue whales at the lowest trophic position, followed by fin whales, minke whales, and finally humpback whales at the highest trophic position. Todd (1997) documented humpback whales as having significantly higher δ^{15}N values than fin whales further north, off Newfoundland, Canada. Finally, Witteveen & Wynne (2016) show a similar isotopically derived hierarchy among sympatric North Pacific humpback and fin whales. While we found no significant difference between minke whales and other rorquals, the small number of minke whale samples in our study may have reduced the statistical power to detect small differences.

Considered together, these data infer that humpback whales—having greater δ^{15}N values—feed on a trophically higher positioned prey than that of fin whales, assuming enrichment factors are similar between species (Gannes et al., 1997; del Rio et al., 2009; Newsome et al., 2010). Our data suggest that despite the sympatric association between humpback and fin whales, resource partitioning may still occur either through direct selection of different prey or through indirect selection via differing foraging strategies, or both. It is possible the rorqual species sampled in this study may avoid direct competition over resources, thus allowing these different species to successfully forage and co-exist within the same location.

Isotopic Signals over Time for Humpback and Fin Whales

For the most part, this study also recorded consistent δ^{13}C isotopic values in humpback and fin whales across years, suggestive of temporally consistent prey preferences. However, in 2002, humpback δ^{13}C values decreased nonsignificantly while fin whale δ^{13}C values decreased significantly, with their δ^{15}N values remaining similar to other years. Supporting this finding, field scientists from the organizations involved in this research reported observations of unusually frequent krill swarms in 2002, as well as increased sightings of uncommon species in the GoM such as sei (*Balaenoptera borealis*) and blue (*Balaenoptera musculus*) whales. In marine applications of SIA, more negative δ^{13}C values can, among other factors, be associated with sources of carbon that are located further offshore (Newsome et al., 2010). Combined with field observations, our 2002 results suggest nutrient sources attributable to a more offshore-based prey than in previous years, suggesting that humpback whales—and perhaps fin whales—may have relied more on krill or on a trophically intermediate prey that fed on the krill. Smith et al. (2012) reported that a regime shift in shelf water input into the GoM likely occurred sometime between 2000 and 2004, resulting in less nutrient-rich water entering the GoM. While the nutritional source might have been different, the lack of change in humpback and fin whale δ^{15}N values in 2002 suggests that the trophic positions of these two species did not change within that sampling period. In 2003, both species' isotopic signals returned to previous levels, suggesting that these species were able to take advantage of different prey sources on a year-to-year basis. However, as potential prey sources were not studied here, the interpretation of these data are limited.

Other SIA-based studies of yearly variation in diet have mixed results. Silva et al. (2019) recorded blue whales sampled within the Azores displaying no significant variation in isotopic signals between season or years; fin whales sampled in this same study did not display any significant difference within seasons but did between years. By contrast, sei whale isotopic signals within the Azores varied more between seasons than between years (Silva et al., 2019).

Considered in sum, our data and others support the hypothesis that humpback and fin whales might switch prey sources between years when a preferred prey is either not present or in low density.

Isotopic Signals and Geographic Region

For humpback whales, sufficient data were collected to permit a multivariate analysis across five regions: the Bay of Fundy, Mount Desert Rock, Stellwagen Bank, the Great South Channel, and Georges Bank. All these regions are known to be biologically productive areas that routinely host humpback whale aggregations. Our analyses showed that there was greater variation in humpback whale $\delta^{13}C$ values with distance between areas, suggesting that regions spaced further apart were likely to be attributed to isotopically different carbon sources. We found $\delta^{15}N$ varied significantly only between two regions: Georges Bank (offshore) and Stellwagen Bank (inshore) for humpbacks, albeit the sample sizes for Georges Bank were small as compared to those from Stellwagen Bank. Fin whale $\delta^{15}N$ values from Mount Desert Rock were significantly different from those sampled on Stellwagen Bank, although, similarly, caution in interpreting these results may be advisable due to uneven sample sizes (fewer samples were collected from Stellwagen Bank). Nonetheless, this finding may suggest that fin whales at Mount Desert Rock may have had a different dietary composition to those at Stellwagen Bank.

Our findings are supported by available literature. Depending on spatial scale, there is conflicting evidence as to whether marine $\delta^{15}N$ levels vary with latitude. For example, Takai et al. (2000) did not find global-scale latitudinal variation in $\delta^{15}N$ within squid, a potential prey item for marine mammals. However, in cases where feeding habitats are reasonably different—as is the case with Stellwagen Bank, having a strong sand lance density (Suca et al., 2022)—gradients in $\delta^{15}N$ may be observed. McMahon et al. (2013) further include localized nitrogen cycling and temporal variations as factors determining geographic $\delta^{15}N$ gradients. Rau et al. (1989) reasoned that cold temperatures encourage solubility of CO_2 in the natural environment, thus colder water is richer in CO_2, upon which productivity is based. Higher CO_2 concentrations encourage greater utilization of ^{12}C, resulting in a decrease in $\delta^{13}C$ in colder waters; thus, Rau et al. proposed a mechanism that explains a range of $\delta^{13}C$ values that varies with latitude, a hypothesis that was later supported by Goericke & Fry (1994). Ocean warming will doubtless impact the amount of dissolved CO_2 available for productivity and, thus, could impact baseline $\delta^{13}C$ values. Further, $\delta^{13}C$ values vary according to the source of carbon, with more productive, well-mixed inshore waters having higher levels of $\delta^{13}C$ in comparison to offshore waters (Hobson et al., 1993; Hobson, 1999; Gendron et al., 2001; Newsome et al., 2010). Based on the geographic scope of this study, variations in $\delta^{13}C$ seen in the GoM likely reflect an inshore-offshore gradient.

Isotopic Signal and Decadal Variation at Stellwagen Bank

A comparison of humpback whale samples from Stellwagen Bank between decades—1988 to 1992 and 1999 to 2005—indicated no significant change in either $\delta^{13}C$ or $\delta^{15}N$ values. This suggests that while changes occur on a yearly basis, there was no significant change in combined isotopic signals and, thus, no major prey shift over a longer time period. However, caution is advised due to the smaller sample size for the early decade; humpback whale plasticity in diet might allow them to take advantage of abundant prey sources from year to year, allowing them stability over time.

Recent work done by Forbes et al. (2023) examined North Atlantic right whale baleen recorded changes in $\delta^{13}C$ and $\delta^{15}N$ between two distinct time periods: 1992 to 2005 and 2016 to 2019. Right whales have a lower range of plasticity in diet, making them sensitive to changes within the marine system carbon flow. Within this context, our work illustrates the importance of a multispecies analysis between decades for understating how marine species are reacting to current environmental pressures that may not have been present in historical record periods. While these changes may not be recorded as statistically significant, understanding how the isotopic signal has changed in recent years provides insight to how current marine species are behaving and/or adjusting to current environmental pressures. This can then be used to further implement protective management for species conservation.

Isotopic Signals and Age Class

Our results show isotopic signals differ between calves and other age classes for both humpback and fin whales. As a calf is weaned and gains skills to forage on more evasive prey, a change in diet, and thus perhaps a change in isotopic values, can be expected. In our study, $\delta^{15}N$ values decreased after the calf's first year, a shift we believe can be accounted for by weaning.

Similar results have been reported between age classes for a number of marine wildlife species, albeit some are not mysticetes. Ames et al. (1996) found that the strongest shift in Florida manatee (*Trichechus manatus latirostris*) calf $\delta^{13}C$ values occurred during weaning to a vegetarian diet. In bowhead whales (*Balaena mysticetus*; Lee et al., 2005), striped dolphins (*Stenella coeruleoalba*; Gómez-Campos et al., 2011), bottlenose dolphins (*Tursiops truncatus*; Knoff et al., 2008), and California sea lions (*Zalophus californianus*; Orr et al., 2008), isotopic values decrease with maturity. Borrell et al. (2016) demonstrate higher $\delta^{15}N$ and $\delta^{13}C$ values for fin whale fetuses when compared to their mother. Therefore, it would appear that *in utero* and during nursing, when the calf is dependent, it would be positioned trophically higher than the mother, an expectation that is supported by our data. The subsequent lack of variation between juveniles and adults shown in our data suggests that diet selection may not drastically change once weaned. However, there were only 17 samples in this study from non-calf juveniles, and this may have reduced the ability to detect subtle differences in diet.

Isotopic Signals in Mothers, Other Females, and Males

A lack of variation between males and nonlactating female humpback whale isotopic signals suggests that both sexes are positioned similarly trophically and have similar prey preferences. A lack of isotopic variation between males and females without dependent calves has also been recorded in the Gulf of St. Lawrence's blue and humpback whales (Gavrilchuk et al., 2014), Pacific humpback whales (Clark et al., 2016), bowhead whales (Lee et al., 2005), bottlenose dolphins (Knoff et al., 2008), California sea lions (Drago et al., 2009), and striped dolphins (Gómez-Campos et al., 2011). However, sex differences have been reported in fin and minke whales (Gavrilchuk et al., 2014). Considered in sum, this suggests that the effect of biological sex on isotopic signals is not clear, although we might expect similarities in species where males and females have similar diets.

In our study, lactating females exhibited nonsignificant elevated $\delta^{15}N$ values from other females, perhaps suggesting that the stress-derived physiology of milk production influences how nutrient resources are metabolized and utilized during lactation. However, it is worth noting that the number of mothers in this study was relatively low and that might have affected the power to detect differences. It remains largely unclear how pregnancy and lactation affect stable isotopic signals in marine mammals (Newsome et al., 2010), with limited data available for large whales, although Todd (1997) provides anecdotal observations of two humpback whales that had unusually low $\delta^{13}C$ values and were later determined to be pregnant. Habran et al. (2010) found no changes in mother or pup blood, pup serum, or milk for northern elephant seals (*Mirounga angustirostris*) during lactation. Other studies have noted variation in values for pregnant or lactating females. For example, Borrell et al. (2016) found significantly lower $\delta^{13}C$ values in lactating fin whale females taken off northwestern Spain. Clark et al. (2016) found pregnant humpback whales off California had significantly lower $\delta^{13}C$ and $\delta^{15}N$ values in one year but not in the subsequent year.

While these studies suggest that $\delta^{13}C$ and $\delta^{15}N$ levels may be different in lactating mothers and pregnant females of various species, there is no clear trend; more research is needed in this area. The use of baleen plates *postmortem* as a source for simultaneous SIA and progesterone analyses (Lysiak et al., 2018; Lowe et al., 2021) may provide a more informed understanding.

Implications for Future Research

Since the time samples were collected for this study, the GoM has increased in average sea surface temperature. Our data provide a precedent-setting benchmark for both current and future studies that measure the trophic consequences of climate change impact. Three of the species studied are either endangered (fin whales), critically endangered (North Atlantic right whales), or recently delisted in the United States (humpback whales), and all are federally protected. The potential impact of climate change on these species has clear implications to their conservation and management.

In 2018, response to the GoM's warming trend and a change in recent whale sighting abundance and distributions, we initiated a follow-up isotopic examination of the GoM to compare with the benchmark data established in this study. Initial evaluations of those data collected by Pastor (2020) suggest that humpback and fin whale distributions are changing in response to a shift in their prey distributions, and, as a consequence, isotopic values are shifting. That study uses the same sampling methodology as described herein and re-examines isotopic signals of GoM rorquals and their potential prey over a 5-y period. We anticipate that this work will increase sample sizes for many analyses as well as allow an assessment of whether GoM trophic dynamics have shifted within the past 20 y as a function of climate change.

Conclusion

This study represents an important multispecies assessment of stable isotopic behavior in mysticetes in the GoM. As such, it captures the trophic dynamics of four species that are important predators in the GoM ecosystem and provides insight into variation in isotopic signals based on age class, sex, calving status, year, and location. There is minimal understanding of large whale diet compositions in this region. Though baleen whales in the GoM have historically exhibited strong side fidelity—remaining in nearby regions throughout the foraging season (Katona & Beard, 1990; Clapham et al., 1993; Stevick et al., 2006; Lubansky, 2015), and returning to the same foraging regions between years (Clapham et al., 1993)—recent northeastern shifts in baleen whale species' distributions have been modeled across the Northeast U.S. continental shelf (Chavez-Rosales et al., 2022), and recent observations in the GoM have indicated shifts in the presence or absence of individuals from traditional feeding grounds or former areas of site fidelity (Lubansky, 2015). The long-term utility of these data and prey changes captured within the GoM supply benchmark datasets for future studies and in advance of the imminent pressure of offshore wind energy development. Management policies by necessity require ongoing and updated current data on species presence and behavior.

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