



Trophic niche partitioning among sympatric baleen whale species following the collapse of groundfish stocks in the Northwest Atlantic

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ABSTRACT: Ecologically similar species may coexist when resource partitioning over time and space reduces interspecific competition. Understanding resource use within these species assemblages may help predict how species relative abundance might influence ecosystem functioning. In the Gulf of St. Lawrence, Canada, 4 species of rorqual whales (blue *Balaenoptera musculus*, fin *B. physalus*, minke *B. acutorostrata* and humpback *Megaptera novaeangliae*) coexist during the summer feeding period. They can be observed within hundreds of meters of one another, suggesting an overlap in ecological niches; yet fine-scale habitat use analyses suggest some resource partitioning. While major ecological changes have been observed in marine ecosystems, including the Gulf of St. Lawrence, we have little understanding of how the removal of predatory fish might cascade through ecosystems. Here, we take advantage of a 19 yr tissue collection subsequent to a fishery collapse (which occurred in 1992) to investigate trophic niche partitioning within a guild of rorqual whales following the loss of a key ecosystem component, groundfish. We analyzed stable isotope ratios for 626 rorqual individuals sampled between 1992 and 2010. Using Bayesian isotopic mixing models, we demonstrated that the 4 rorqual species segregated trophically by consuming different proportions of shared prey. An overall increase in $\delta^{15}\text{N}$ values over the study period (post groundfish collapse), particularly for fin and humpback whales, suggested a progressive use of higher-trophic level prey, such as small pelagic fish, whereas the stability of blue whale diet over time confirmed their specialized feeding behaviour. This study provides the first long-term assessment of trophic ecology among rorqual populations on this Northwest Atlantic feeding ground, and evidence for differential resource use among large marine predators following ecosystem change.

KEY WORDS: Trophic niche · Interspecific · Stable isotopes · $\delta^{13}\text{C}$ · $\delta^{15}\text{N}$ · Rorqual · Ecosystem change

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INTRODUCTION

The coexistence of species within ecological communities often requires trophic, spatial or temporal segregation to avoid competitive exclusion (Gause

1934, Hutchinson 1957, Pianka 1973). Therefore, it is intriguing to find closely related and ecologically similar species living in sympatry, as the struggle for existence should be greater (Harper et al. 1961). Competition among conspecifics for shared resour-

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ces is equally prevalent, and intrapopulation variation in resource use can profoundly influence population ecology (Bolnick et al. 2003). A comparison of the ecological niches of potentially interacting species is thus fundamental to evaluate underlying mechanisms of coexistence, and to eventually predict consequences of ecosystem change on animal communities (Chase & Leibold 2003).

Four species of baleen whales co-occur seasonally in one of the most productive marine ecosystems in Canada, the Gulf of St. Lawrence (Dickie & Trites 1983). These whales belong to the same family (commonly known as rorquals) and are characterized by a unique set of morphological traits (ventral pleats and baleen) and specialized lunge feeding behaviour, making them particularly adapted to exploit small, aggregating prey (Pivorunas 1979). Blue whales *Balaenoptera musculus* are recognized worldwide as stenophagous predators (selective consumers), foraging exclusively on a few species of euphausiid zooplankton (Kawamura 1980, Gaskin 1982, Yochem & Leatherwood 1985), whereas fin *B. physalus*, minke *B. acutorostrata* and humpback *Megaptera novaeangliae* whales have more varied diets including zooplankton and small schooling fish (Jonsgård 1966, Mitchell 1975, Whitehead & Carscadden 1985, Piatt et al. 1989). Until now, there has only been one rigorous attempt to determine whether these closely related species segregate their ecological niche within the Gulf of St. Lawrence in eastern Canada. Doniol-Valcroze (2008) characterized rorqual habitat selection by combining a long-term observation dataset with static and dynamic environmental parameters. They determined that despite large-scale spatial overlap, each rorqual species differed in its association with dynamic oceanographic features, particularly thermal fronts. Such a fine-scale spatial segregation may indicate differences in feeding strategies among and perhaps within species, leading to new questions about ecological requirements and mechanisms of coexistence in these understudied cetacean species.

Moreover, it is poorly known how major oceanographic and ecological shifts influence rorqual trophic ecology. In the early 1990s, the abundance of several commercial groundfish populations (mainly Atlantic cod *Gadus morhua*) declined to historically low levels in the Northwest Atlantic (CSAS 1994, Hutchings & Myers 1995, Myers et al. 1996, 1997). At around the same time, the physical environment of the Northwest Atlantic underwent prolonged below-average sea temperatures (Mann & Drinkwater 1994), impacting fish productivity and potentially cod

recovery (Parsons & Lear 2001). A combination of human-mediated and environmental factors may have resulted in the observed changes in stock abundance (Lilly et al. 1999, Carscadden et al. 2001). Collapse of these important groundfish stocks coincided with an increase in their benthic invertebrate prey (northern shrimp *Pandalus borealis*, snow crab *Chionocetes opilio*, American lobster *Homarus americanus*) in several regions of the Northwest Atlantic (Myers et al. 1996, Worm & Myers 2003). Although less well documented, a decline in groundfish stocks potentially released small forage fish from predation pressure, thereby indirectly influencing prey availability for other consumers such as baleen whales (Frank et al. 2005, Savenkoff et al. 2007, Heithaus et al. 2008). For example, in the northern Gulf of St. Lawrence, mass-balance ecosystem models indicated that a trophic community formerly dominated by large predatory fish and small forage fish (1980s) shifted to one largely dominated by small forage fish (1990s and 2000s) following the decline of cod stocks (Savenkoff et al. 2007). These models also predicted that marine mammals (seals and cetaceans) occupied a strong predatory role on forage fish (particularly capelin *Mallotus villosus*) from the mid-1980s to the early 2000s (Savenkoff et al. 2007). However, dietary data for large baleen whales during this period is lacking, making it problematic to identify their trophic role after the cod collapse. Densities of blue whales (krill specialists) may have declined in some areas of the northern Gulf of St. Lawrence during the 1990s (Ramp & Sears 2013), while those of humpback whales (generalist foragers) increased (Comtois 2009), which may reflect a response to prey distribution and/or availability during this period. Unfortunately, changes in biomass of euphausiid zooplankton and forage fish coincident with the decline of groundfish populations, as well as changes in densities of some of the rorqual species in the Gulf of St. Lawrence remain unclear (McQuinn 2009). Therefore, there is need for an alternative approach, such as a retrospective analysis of rorqual trophic ecology subsequent to the cod collapse, to better understand trophic interactions between large cetacean predators and their prey in this changing ecosystem.

Traditional methods to study animal trophic ecology have relied on gut or fecal samples or direct observation of feeding (Reynolds & Aebischer 1991, Deb 1997). Despite being informative, these methods are impractical and challenging with large, oceanic predators and may not capture the extent of exploited food sources (Deb 1997). The analysis of biochemical trophic markers (i.e. stable isotopes)

within consumer tissue is often better suited for such cases (Newsome et al. 2010). This tool has the advantage of reflecting assimilated (not just ingested) diet over various time frames depending on the tissue sampled (Peterson & Fry 1987, Hobson 1999, Kelly 2000). Stable isotope analysis can be used to gain insight into the trophic niche; however, the technique remains indirect, and findings should be referred to as the 'isotopic niche' of an animal (Newsome et al. 2007). By combining isotopic niche metrics with diet reconstruction techniques, we can apply a quantitative framework to evaluate isotopic niche partitioning and dietary trends among wild populations over time (Bearhop et al. 2004, Layman et al. 2007, Jackson et al. 2011, Newsome et al. 2012). In this study, we assess diet using the stable isotope ratios of 4 rorqual species in the Gulf of St. Lawrence over a 19 yr period to evaluate intra- and interspecific trophic partitioning. This retrospective study also enables the investigation of long-term patterns in dietary resource use in these marine predators following the collapse of groundfish populations in this region.

MATERIALS AND METHODS

Sample collection

Skin samples were collected from 626 free-ranging rorqual individuals (143 blue, 195 fin, 207 humpback and 81 minke whales). Sampling occurred from May to October of 1992 to 2010 in the Estuary, Jacques-Cartier Passage and Gaspé region of the Gulf of St. Lawrence, Québec, Canada (49° 36' N, 64° 20' W), with the majority of samples (~85%) collected in July, August and September. Biopsies were collected from rigid-hulled, inflatable boats using a crossbow and hollow-tipped (40 mm in length and 8 mm in diameter) arrow system (Palsbøll et al. 1991, Borobia et al. 1995). The pigmented layer of the skin (epidermis) was separated from the dermis and underlying fat using a sterile scalpel. All samples were stored in plastic vials and on ice immediately after collection, and subsequently at -20°C until analyses. Samples taken from 1992 to 2005 were originally destined for genetic analyses and preserved in a 20% v/v dimethyl sulfoxide (DMSO) solution of deionized water saturated with NaCl (Amos & Hoelzel 1991). Thereafter, samples were stored in sea water (2006 through 2008) or without solution (2009 through 2010). The effect of DMSO on carbon and nitrogen isotope ratios of balaenopterid skin has been assessed and is pre-

dictable (Lesage et al. 2010). Since the effect of sea water on isotope ratios was less certain, any potential bias was evaluated by comparing isotope ratios between skin aliquots preserved for 10 to 33 weeks in sea water and those stored without solution.

All sampled individuals, except minke whales, were photo-identified using pigmentation patterns, scars, and size and shape of the dorsal fin (Katona & Whitehead 1981, Agler et al. 1990, Sears et al. 1990). Since rorquals exhibit weak sexual dimorphism, gender determination in the field is unreliable. Gender was thus determined genetically for all individuals using standard polymerase chain reaction methods (PCR; Saiki et al. 1988) targeting sex-specific gene regions (Palsbøll et al. 1992, Bérubé & Palsbøll 1996). Age class of humpback whales (the species with the most complete dataset) was determined using photo-identification and individual sighting history. Calves (<1 yr old) were identified by their unambiguous dependence on a mother; juveniles (1 to 5 yr old) were individuals seen in the previous 5 years as calves; adults (≥ 6 yr old) were those with sighting periods extending over 5 yr (Chittleborough 1965, Clapham & Mayo 1990). Reproductive state of mature females was inferred by the presence of a calf (lactating). We assumed pregnancy in the preceding year and 'resting' in the year following lactation (Chittleborough 1958). There have been reports of female humpbacks becoming pregnant immediately following lactation (Clapham & Mayo 1990), however this has not yet been observed in the Gulf of St. Lawrence (Ramp 2008).

Potential prey species were selected based on rorqual stomach and fecal contents (Nemoto 1959, 1970, Croll et al. 1998) and direct observation of feeding behaviour (Watkins & Schevill 1979). Prey were collected primarily from May to September of 1995, 1996, 2001–2004 and 2010 following methods outlined in Lesage et al. (2001). Briefly, zooplankton was collected by vertically towing Bongo nets (1 m diameter \times 3 m length) with a 333 μm mesh size, and kept alive overnight to allow gut clearance. Muscle tissue was excised from prey specimens (including all species of zooplankton except copepods), lipid-extracted and analyzed for stable isotope values. In addition, particulate organic matter (POM, used to represent primary producers) and euphausiid zooplankton were sampled weekly from May to September in 2001 at a fixed station in the St. Lawrence Estuary to monitor seasonal isotopic shifts and assist the interpretation of rorqual isotopic signatures. POM was collected with 4 l Niskin bottles at a depth of maximum chlorophyll production (10 to 24 m) and

obtained by filtering water through pre-combusted Whatman GF/C glass microfiber filters (Lesage et al. 2001). All samples were stored at -20°C until further analyses.

Rorqual skin preserved in sea water or without solution was rinsed 3 times with deionized water, cut into small pieces, transferred into aluminum cups and freeze-dried at -40°C to a constant mass. Dried samples (ca. 20 mg) were then homogenized to a fine powder and transferred into inert plastic or glass vials. Since variable lipid content within and between individuals can alter the carbon isotope ratio of bulk tissue (DeNiro & Epstein 1977, Focken & Becker 1998), a subset of samples preserved without solution was halved to assess the effect of lipid-extraction on isotope ratios; 1 aliquot was analysed without further treatment whereas the second aliquot was analysed following lipid-extraction. All samples stored in DMSO were also rinsed 3 times and lipid-extracted, as this procedure has the potential to completely remove DMSO from skin tissue (Lesage et al. 2010). Lipids were extracted from freeze-dried, homogenized samples with a 2:1 chloroform:methanol solution following a modified Bligh & Dyer (1959) procedure. Samples were analyzed for carbon and nitrogen isotope ratios using a Thermo Finnigan DELTA plus XL Continuous Flow Stable Isotope Mass Spectrometer coupled to a Carlo Erba Elemental Analyzer (CHN EA1110; Isotope Tracer Technologies). The ratio of heavy to light isotope is presented in delta notation (δ) relative to reference standards (PeeDee Belemnite for carbon and atmospheric N_2 for nitrogen), such that $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ (‰) = $[(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where R_{sample} is the $^{13}\text{C}:^{12}\text{C}$ or $^{15}\text{N}:^{14}\text{N}$ ratio of the sample and R_{standard} is the ratio of the appropriate standard. Duplicate isotopic measurements were made on a subset of samples ($n = 115$) to quantify repeatability, and yielded an average absolute difference of $0.1 \pm 0.2\%$ for $\delta^{13}\text{C}$ and $0.2 \pm 0.3\%$ for $\delta^{15}\text{N}$. Element-specific laboratory standards were run every 10 samples to calibrate the system and compensate for any drift in isotope readings.

Data analyses

Preservative and lipid-extraction effects

The effect of DMSO solution on isotope values of balaenopterid skin has been quantified (Lesage et al. 2010), thus we applied these correction factors to our DMSO samples post-lipid removal (see the Supple-

ment at www.int-res.com/articles/suppl/m497p285_supp.pdf). The effect of sea water on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values was assessed by comparing isotope values of samples stored in sea water with those stored without solution using paired Student's t -tests ($\alpha = 0.05$) and linear regressions. Levene's test of homogeneity was used to examine the effect of preservation method on sample variance. All subsequent analyses considered lipid-extracted $\delta^{13}\text{C}$ and non-lipid-extracted $\delta^{15}\text{N}$ (bulk) as the true or reference isotope values for tissues (Sotiropoulos et al. 2004, Sweeting et al. 2006, Mintenbeck et al. 2008).

Interspecific isotopic niche variation

Isotopic turnover rate for epidermal tissue is unknown for baleen whales, but is estimated at 70 to 75 d for belugas *Delphinapterus leucas* (St. Aubin et al. 1990) and bottlenose dolphins *Tursiops truncatus* (Hicks et al. 1985). Since accurate turnover rates are not available for baleen whales, we assumed that turnover time in baleen whale skin is at least 75 d, and possibly longer due to their lower metabolic rates compared to delphinids (Ruiz-Cooley et al. 2004, Lockyer 2007). Thus, by August, most rorquals in the Gulf of St. Lawrence should have integrated summer diet within their epidermal tissue.

Levene's tests were used to test for equality of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variances among the 4 rorqual species. Niche location and width for each rorqual species was determined using metrics based on the position, and Euclidean distance between isotope data points in bivariate space (Cornwell et al. 2006, Layman et al. 2007, Turner et al. 2010, Jackson et al. 2011). The location of the centroid (LOC), or the bivariate $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ mean, representing the average niche position, was first compared among species. Next, to measure the average degree of trophic diversity within each species and the trophic similarity between individuals, the mean Euclidean distance to centroid (CD) and the mean nearest-neighbour Euclidean distance (NND) were calculated, respectively. Niche width of 'typical' members of the species was estimated using a Bayesian approach based on multivariate ellipse metrics (Jackson et al. 2011). This method of inference is desirable when comparing niche widths of populations with different sample sizes since it takes into account uncertainty related to the data and incorporates error arising from the sampling process, propagating it through to the niche width estimations (Jackson et al. 2011). These area-based metrics were not baseline-corrected as we

assumed all 4 species belong to the same food web and have access to the same resources.

Since minke whales were only sampled from 2007 to 2010, interspecific comparisons of isotopic niche and diet were made during this time period. We tested for differences in the LOC using a multivariate Hotelling's T^2 test, appropriate for pair-wise comparisons of means (Hotelling 1931). Differences in CD and NND were tested by generating null distributions from residual permutation procedures in order to evaluate probabilities associated with test statistics (Turner et al. 2010). The LOC, CD and NND metrics between any 2 species were considered significantly different if the difference between them was statistically greater than zero (Turner et al. 2010). All metrics were determined using the SIAR package (Parnell et al. 2008, 2010) available from the Comprehensive R Archive Network (<http://cran.r-project.org/>).

Diet inference

Diet composition of each rorqual species was estimated using SIAR (a multi-source, multi-isotope Bayesian mixing model; Parnell et al. 2010). This model explicitly accounts for uncertainty in input parameters, such as isotopic variation of dietary sources and discrimination factors, and estimates probability distributions of source contributions (Parnell et al. 2010). An important prerequisite for any isotope mixing model is that relevant dietary sources must be isotopically distinct (Phillips 2001). In this study, prey sources were pooled if their isotope signatures were not statistically different (ANOVA and Tukey's HSD tests) and if the sources in question were functionally related. Sources were combined *a posteriori* by summing their respective posterior contributions for each model iteration. Isotope mixing models also require trophic discrimination factors (TDFs) between consumer tissue and diet (i.e. the shift in isotope ratio associated with the conversion of diet into consumer tissue). True TDFs (also expressed as $\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$) can only be established from controlled feeding experiments where the isotopic discrepancy between consumer and diet can be quantified (DeNiro & Epstein 1978, 1981, Tieszen et al. 1983). TDFs are undefined for baleen whales; however, there appears to be a relatively predictable relationship between the C:N ratio of a dietary protein source and the ^{15}N enrichment from prey to consumer, which can be used to estimate the true TDF (Caut et al. 2008). Prey sources in this study have C:N

ratios between 4 and 5, thus we would expect a $\Delta^{15}\text{N}$ of approximately 1.5 to 2.0‰ (Caut et al. 2008). This appears to be consistent with Gendron et al. (2001)'s TDFs for blue whale skin relative to euphausiid diet (1.3‰ for $\Delta^{13}\text{C}$ and 1.7 to 1.9‰ for $\Delta^{15}\text{N}$). Borrell et al. (2012) report equivalent $\Delta^{13}\text{C}$ values (1.3‰) for fin whales also feeding on euphausiids; however, their $\Delta^{15}\text{N}$ values are higher compared to blue whales (2.8‰). As the most feasible TDFs for our system, we used a value of 0.5‰ for $\Delta^{13}\text{C}$ and of 1.7‰ for $\Delta^{15}\text{N}$, each with a standard deviation of $\pm 0.5\%$, which seems realistic for baleen whale skin-prey isotopic discrimination.

Temporal and intraspecific effects

To examine interannual variation of trophic niche width, a standard ellipse area was computed for each rorqual species and each year for which more than 5 samples were available. Regression splines were then used to assess intra- and interannual patterns in rorqual $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Hastie & Tibshirani 1986, 1990). We applied penalized cubic regression splines to temporal variables for the best possible fit incorporating the least amount of error (Wood 2006). The optimal degree of smoothing, resulting in minimal residual deviance and maximal parsimony (lowest possible effective degrees of freedom; Hastie & Tibshirani 1986, 1990, Wood 2006) was determined using a robust cross-validation method to estimate the smoothing parameters (R package 'mgcv'). Due to the limited number of years over which minke whale biopsies were collected, interannual effects were examined using general linear models (GLMs). Seasonal isotope trends for blue, fin and humpback whales were examined for years when POM and zooplankton species were sampled at regular intervals throughout the season to verify whether seasonal isotope variation in lower trophic levels is reflected in rorqual tissues. The effect of sex (for all species), age class (calf, juvenile, adult; for humpbacks) and reproductive status (pregnant, lactating, resting; for humpbacks) on isotope ratios was tested using a random effects model to control for interannual variability. For years in which calves and their mothers were both biopsied, their isotope ratios were directly compared using paired Student's *t*-tests to assess mother-offspring trophic relationships. Significance level was set at $\alpha = 0.05$ and results are presented as 95% confidence intervals unless otherwise stated.

RESULTS

Interspecific isotopic niche variation

The effect of seawater on isotope and C:N ratios in rorqual tissue was negligible, but we nevertheless corrected for this. Lipid extraction enriched both ^{13}C and ^{15}N , and homogenized C:N ratios (Tables S1 & S2 in the Supplement). All 4 rorqual species had similar $\delta^{13}\text{C}$ values (blue: $-18.7 \pm 0.4\text{‰}$; $n = 22$; fin: $-18.6 \pm 0.4\text{‰}$; $n = 69$; minke: $-18.6 \pm 0.4\text{‰}$; $n = 53$; humpback: $-18.7 \pm 0.4\text{‰}$; $n = 97$). However, blue whales had the lowest mean $\delta^{15}\text{N}$ values ($9.9 \pm 1.4\text{‰}$), followed by fin ($12.4 \pm 1.3\text{‰}$), minke ($13.0 \pm 1.4\text{‰}$), and humpback whales ($14.3 \pm 0.6\text{‰}$). The 4 species had comparable $\delta^{13}\text{C}$ variances about the mean (Levene's $F_{3,250} = 0.27$, $p = 0.84$), however differed significantly in their $\delta^{15}\text{N}$ variance (Levene's $F_{3,240} = 9.94$, $p < 0.001$).

There were several indications of isotopic niche partitioning among the 4 rorqual species, despite some overlap. The LOC differed significantly among rorqual species, whereby blue whales occupied the lowest position in isotope space, followed by fin, minke and humpback whales (Hotelling's T^2 , all pair-wise comparisons: $p < 0.007$; Fig. 1). The blue whale niche (standard ellipse area; SEA) overlapped slightly with fin whales, but not with minke or humpbacks whales (Fig. 1). Fin whales occupied nearly half of the minke whale isotope niche, while minke

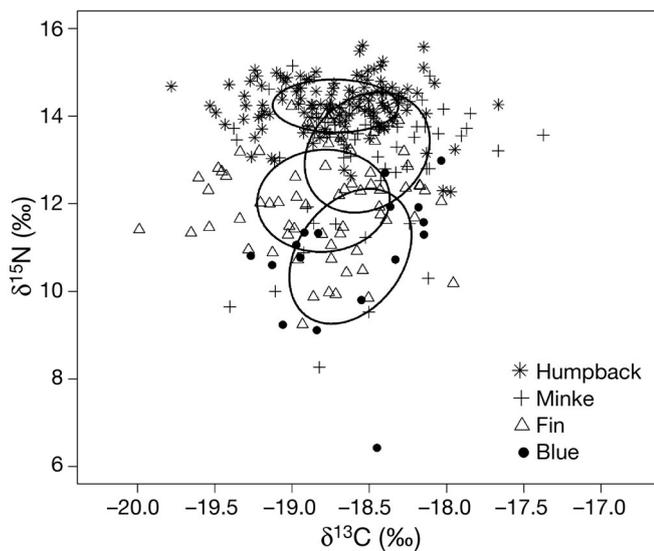


Fig. 1. Core isotopic niches of blue *Balaenoptera musculus* ($n = 17$), fin *B. physalus* ($n = 68$), humpback *Megaptera novaeangliae* ($n = 132$) and minke *B. acutorostrata* whales ($n = 64$) from 2007 to 2010, represented by standard ellipse areas. The order of the legend corresponds to the ellipse order (on the $\delta^{15}\text{N}$ scale)

Table 1. Isotope niche metrics for blue whales *Balaenoptera musculus*, fin whales *B. physalus*, humpback whales *Megaptera novaeangliae* and minke whales *B. acutorostrata* from 2007 to 2010. The location of the centroid (LOC) indicates where the niche is centered in isotope space; the mean distance to centroid (CD) and the mean nearest-neighbour distance (NND) are proxies of intrapopulation trophic diversity, and the core isotope niche width is represented by the standard ellipse area (SEA; non-corrected for low sample size, with 95 % confidence intervals)

Rorqual	n	LOC	CD	NND	SEA
Blue	17	-18.6,10.8	1.2	0.4	2.5 (1.6–4.0)
Fin	68	-18.8,12.1	1.1	0.2	1.7 (1.4–2.2)
Humpback	132	-18.7,14.2	0.6	0.1	0.8 (0.7–1.0)
Minke	64	-18.5,13.2	1.1	0.2	1.9 (1.5–2.4)

whales overlapped close to half of the humpback whale isotope niche (Fig. 1). The niche width of humpbacks was the smallest relative to the other 3 rorqual species (SEA; Table 1). CD for humpbacks was also significantly shorter, and approximately half that of other species (Table 1). NND was comparable among the 4 rorqual species, although also the shortest for humpbacks (Table 1).

Six prey species were used to estimate rorqual diet using isotope mixing models. However, due to the isotopic similarity of certain prey (Fig. 2), we delin-

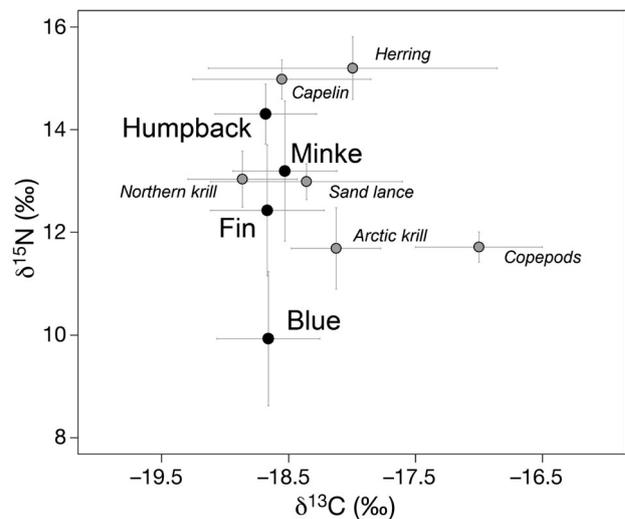


Fig. 2. Mean (\pm SD) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of blue *Balaenoptera musculus*, fin *B. physalus*, minke *B. acutorostrata*, humpback *Megaptera novaeangliae* whales and 6 potential prey sources (copepods *Calanus* sp., Arctic krill *Thysanoessa raschii*, northern krill *Meganyctiphanes norvegica*, American sand lance *Ammodytes americanus*, capelin *Mallotus villosus* and Atlantic herring *Clupea harengus*) sampled between 1992 and 2010 in the Gulf of St. Lawrence. Prey species are corrected for trophic discrimination values of 0.5‰ and 1.7‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively

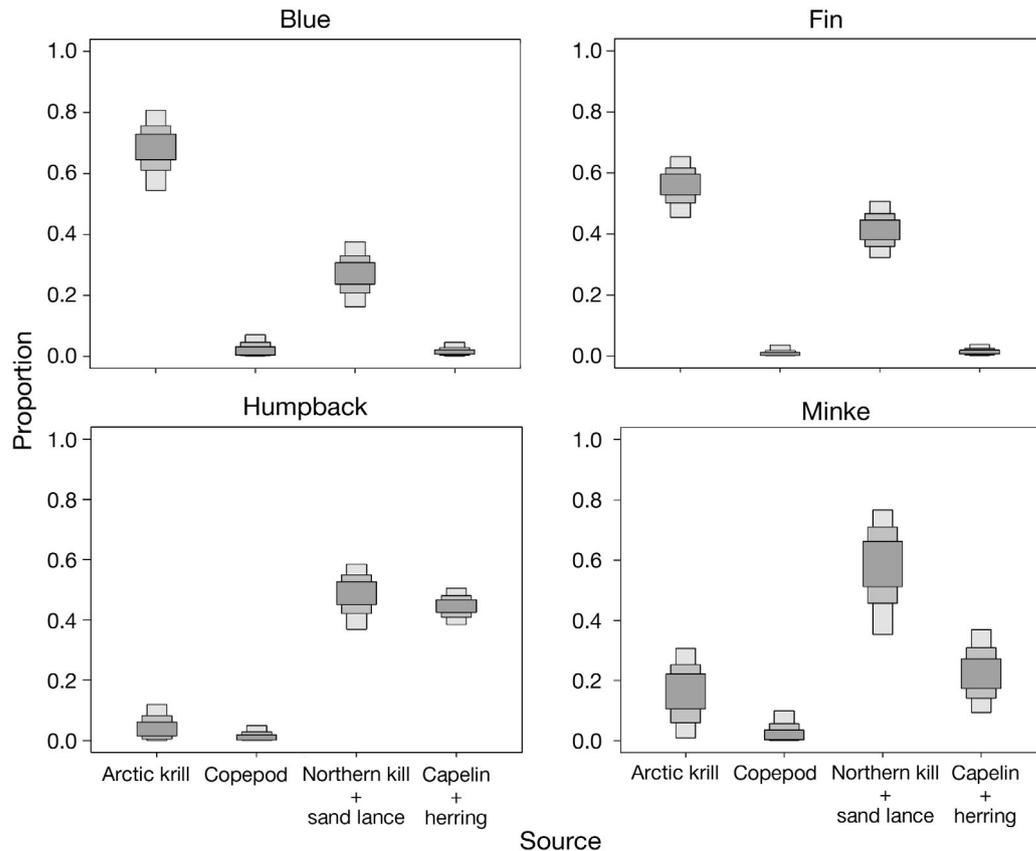


Fig. 3. Overall diet composition estimated for blue whales *Balaenoptera musculus* and humpback whales *Megaptera novaeangliae* from 1995 to 2010, for fin whales *B. physalus* from 1992 to 2010, and for minke whales *B. acutorostrata* from 2007 to 2010 in the Gulf of St. Lawrence. The proportion of Arctic krill, copepods, northern krill + sand lance and capelin + herring are presented as 50% (inner box), 75%, and 95% (outer box) credibility intervals

eated 4 dietary sources; 2 groups of primary consumers: (1) *Calanus* copepods and (2) Arctic krill *Thysanoessa raschii*; and 2 groups of secondary consumers: (3) northern krill *Meganyctiphanes norvegica* and American sand lance *Ammodytes americanus* and (4) capelin *Mallotus villosus* and Atlantic herring *Clupea harengus*.

Overall, the proportion of each potential dietary source varied among rorqual species (Fig. 3). The dietary contribution of copepods was low (<10%) for all species. Arctic krill formed the bulk of blue whale (70%) and fin whale (56%) diet, but was much less important to minke (16%) and humpback (10%) whale diets. Northern krill + sand lance were the second most important prey to blue whales (26%; despite the isotopic overlap, we assume blue whales target krill and not sand lance). This group was also the second most important in fin whale diet (40%), and the most important to minke (57%) and humpback (48%) diets. Capelin + herring contributed to less than 10% of the diet of fin whales; however, they

were an important component in minke (22%) and humpback whale (44%) diet (Fig. 3). Four prey sources were used to estimate blue whale overall diet. However, given the very low proportion of capelin + herring in their diet (0.02 [0.00–0.04]), and the unlikelihood that capelin + herring are food sources, this prey group was removed from the long-term diet analysis for blue whales.

Temporal effects

Isotopic niche area was relatively stable over the study period for humpback whales, and slightly more variable for blue and fin whales (Fig. 4). No trend in isotope niche width was discernible for minke whales, although a slight increase was observed in 2010 (Fig. 4). The average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values varied between years for all species. However, an overall trend toward more depleted carbon isotope values was observed in all species, whereas stability or an

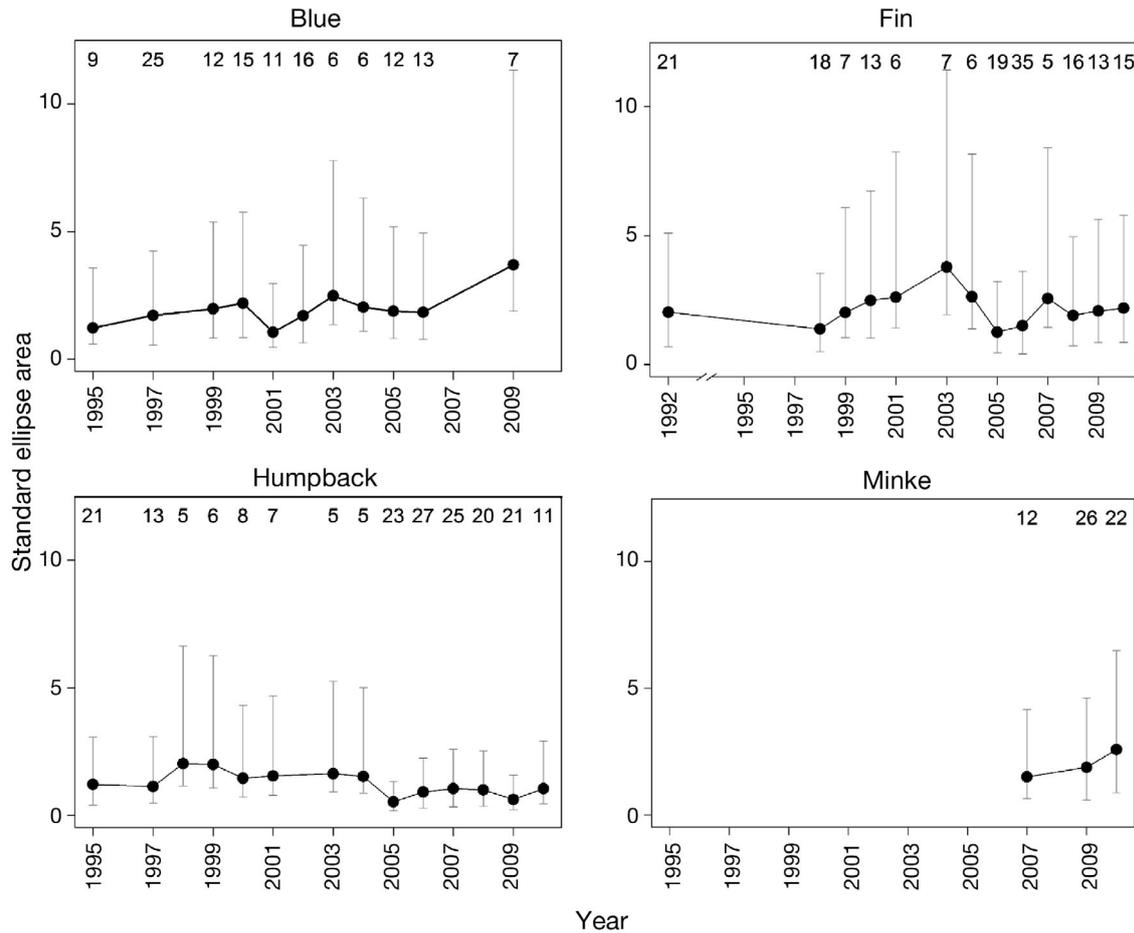


Fig. 4. Mean and 95 % credibility intervals of the isotopic niche width (standard ellipse area) for blue whales *Balaenoptera musculus* and humpback whales *Megaptera novaeangliae* from 1995 to 2010, for fin whales *B. physalus* from 1992 to 2010, and for minke whales *B. acutorostrata* from 2007 to 2010 in the Gulf of St. Lawrence. Sample sizes are indicated above each year

overall increase was observed for $\delta^{15}\text{N}$ values. Blue and fin whales showed a similar and significant decline in $\delta^{13}\text{C}$ values from 1992/1995 to 2010 (Fig. 5; blue whale effective degrees of freedom [edf] = 1.0, $F = 44.69$, $p < 0.001$; fin whale edf = 2.4, $F = 8.44$, $p < 0.001$), as well as minke whales over the 2007 to 2010 period (Fig. 5; $F_{3,61} = 6.55$, $p < 0.001$). Humpback whale $\delta^{13}\text{C}$ values varied more widely over time, but also declined over the study period (Fig. 5; edf = 8.2, $F = 14.86$, $p < 0.001$). Interannual $\delta^{15}\text{N}$ patterns differed among the 4 rorqual species, and were towards an overall mean increase in fin (edf = 5.8, $F = 11.90$, $p < 0.001$) and humpback whales (edf = 7.7, $F = 14.08$, $p < 0.001$) over the study period (Fig. 6), and no overall change in blue whales (edf = 1.0, $F = 3.13$, $p = 0.08$) and minke whales (Fig. 6; $F_{3,61} = 0.51$, $p = 0.676$), although the time series was short (4 yr) for the latter species.

An increase in the contribution of the northern krill + sand lance group for blue and fin whales, and of

capelin + herring for humpback whales, appeared to be responsible for the progressive increase in $\delta^{15}\text{N}$ observed over the study period (Fig. 7). Arctic krill was a stable contributor to blue whale diet over time; however, the importance of northern krill gradually increased after 2001. For fin whales, contributions of Arctic krill and the capelin + herring group were variable over time and only the northern krill + sand lance exhibited an increasing trend over time (Fig. 7). Humpbacks also exhibited dietary variability over time with the major constituents always being either the northern krill + sand lance or capelin + herring group. However, capelin + herring became more important in their diet after 2003. In the case of minke whales, the northern krill + sand lance group increased in importance over the period 2007 to 2010, while the contribution capelin + herring decreased (Fig. 7).

No within-season trends in isotopic signatures were detected in any of the species, although a slight ^{15}N -depletion over the sampling season, not echoed

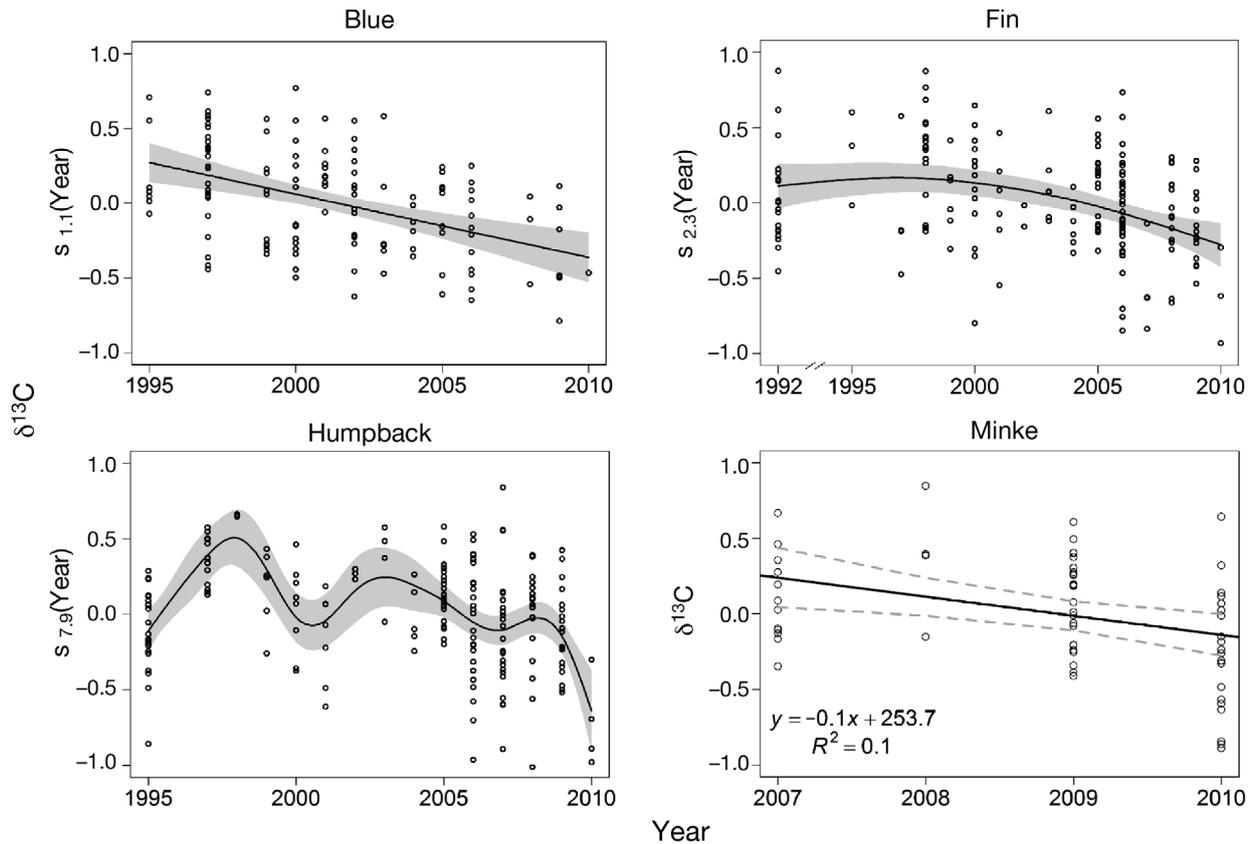


Fig. 5. Interannual $\delta^{13}\text{C}$ trends for blue whales *Balaenoptera musculus* and humpback whales *Megaptera novaeangliae* from 1995 to 2010, for fin whales *B. physalus* from 1992 to 2010, and for minke whales *B. acutorostrata* from 2007 to 2010 in the Gulf of St. Lawrence. The y-axis shows deviations from mean $\delta^{13}\text{C}$ values, and the 95% credibility interval is depicted by grey shading or dashed lines

in primary or secondary consumers, was observed in fin whales (Figs. S1 & S2 in the Supplement).

Intraspecific effects

Male and female blue and humpback whales had comparable isotopic signatures (Table 2). Fin whale males, however, were significantly enriched in both ^{13}C and ^{15}N relative to females (Table 2). Minke whale females had significantly higher $\delta^{15}\text{N}$ values than males, although similar $\delta^{13}\text{C}$ values (Table 2). There was no significant effect of age class (calf, juvenile, adult) on isotope ratios of humpback whales ($\delta^{13}\text{C}$: $F_{2,138} = 0.63$, $p = 0.59$, $\delta^{15}\text{N}$: $F_{2,138} = 0.77$, $p = 0.52$). Calves were on average ^{13}C -depleted ($0.08 \pm 0.15\text{‰}$) and ^{15}N -enriched ($0.73 \pm 0.86\text{‰}$) relative to their mothers, although non-significantly ($\delta^{13}\text{C}$: $t_5 = 1.30$, $p = 0.25$, $\delta^{15}\text{N}$: $t_5 = 2.10$, $p = 0.09$). Within mature female humpbacks, there was no significant effect of reproductive state (pregnant, lactating, resting) on isotope values ($\delta^{13}\text{C}$: $F_{2,18} = 0.72$, $p = 0.51$, $\delta^{15}\text{N}$: $F_{2,18} = 1.22$, $p = 0.34$).

DISCUSSION

Niche partitioning among species

Here we show that despite some trophic overlap, 4 sympatric and closely-related baleen whale species do appear to segregate their dietary niche. All species except blue whales fed on a mixture of macrozooplankton and forage fish; however, the proportion of each prey source in the diet varied among rorqual species (Fig. 3). Blue and fin whales derived a large proportion of their energy from Arctic krill; however, separation of their 'core' isotope niches suggests that potential competition between blue and fin whales might be dampened by the greater ability of fin whales to feed on fish prey. The isotopic niches of fin and minke whales showed the greatest overlap (Fig. 1), likely owing to similar contributions of northern krill + sand lance to their overall diet (Fig. 3). Similarly, minke whales appeared to reduce potential competition by including more capelin + herring into their diet than fin whales, placing their average trophic position higher than fin whales. Humpback

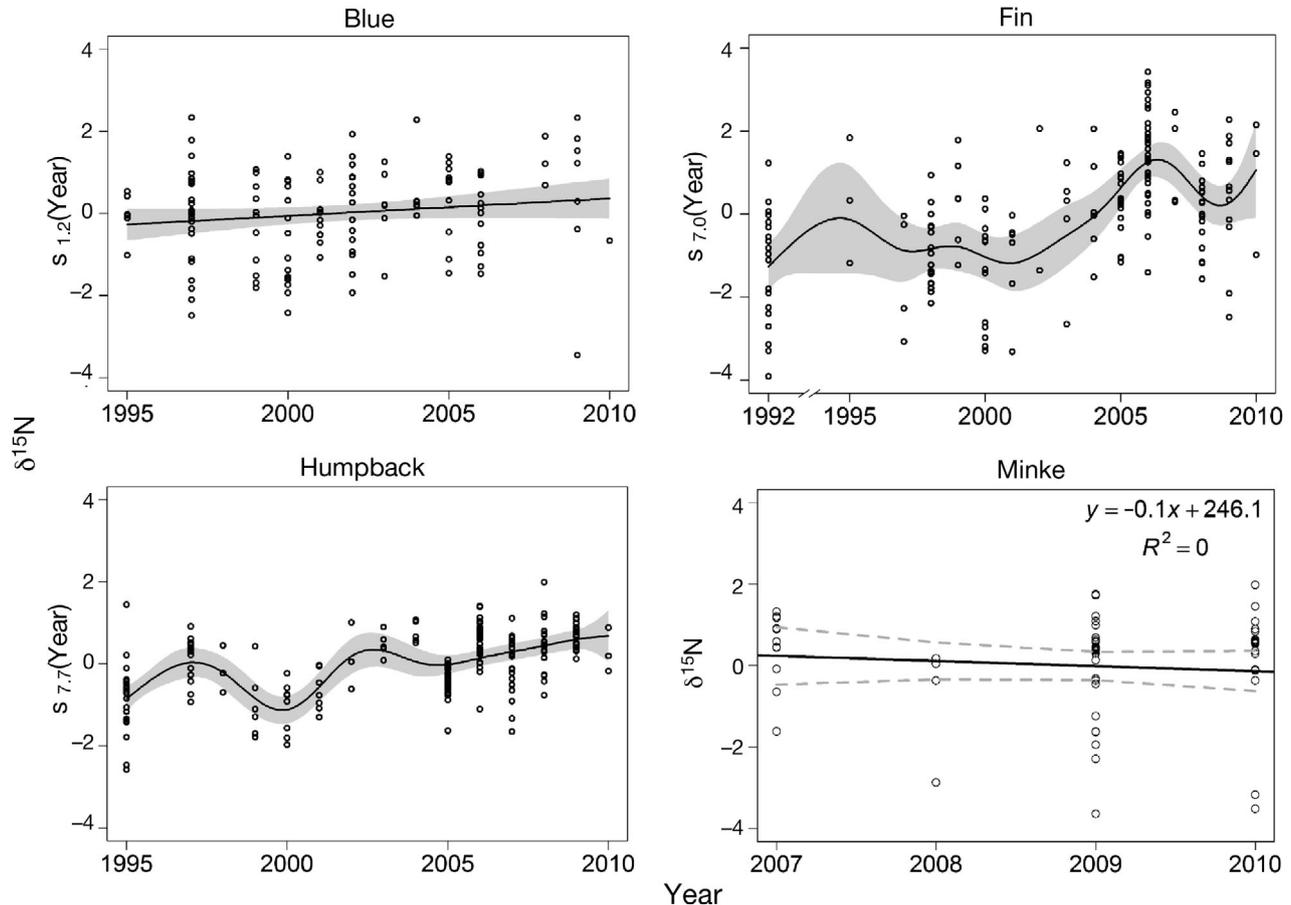


Fig. 6. Interannual $\delta^{15}\text{N}$ trends for blue whales *Balaenoptera musculus* and humpback whales *Megaptera novaeangliae* from 1995 to 2010, for fin whales *B. physalus* from 1992 to 2010, and for minke whales *B. acutorostrata* from 2007 to 2010 in the Gulf of St. Lawrence. The y-axis shows deviations from mean $\delta^{15}\text{N}$ values and the 95% credibility interval is depicted by grey shading or dashed lines

whales were likely the most piscivorous of the 4 species on this feeding ground, given their trophic position and the high proportion of capelin + herring in their diet (Figs. 1 & 3).

Interestingly, although our diet analyses indicate that humpback whales were generalist predators feeding on both zooplankton and fish, their isotopic niche area was the smallest among all rorqual species (Table 1). Likewise, humpbacks also had the shortest CD, as well as the shortest NND (Table 1). These observations suggest that individuals are more trophically similar to one another compared to blue, fin and minke whales. A narrow trophic niche had been expected for species such as blue whales, which specialize on a narrow range of zooplankton species. One hypothesis to explain the apparent ambiguity between isotopic niche area and degree of dietary specialization could be that isotopic variability within primary producers is progressively attenuated with trophic level, making a given prey more homogenous in isotopic values when found at

higher trophic positions (Cabana & Rasmussen 1996). Weekly sampling of POM and 2 species of zooplankton in the St. Lawrence Estuary provided support to an attenuation of the isotopic variability found at the base of the food web with increasing trophic position (Fig. S2 in the Supplement). However, given the trophic positions of potential prey for blue whales (i.e. the 2 species of euphausiid) and humpback whales (all species except copepods) were approximately equally distant isotopically, differences in niche width cannot be explained solely by the uneven isotopic spread of potential prey (Matthews & Mazumder 2004, Newsome et al. 2007). An alternative hypothesis to explain the smaller than expected niche width of humpbacks compared to blue whales could be that even though humpback diet consists of a mixture of different prey, this mixture is more uniform across individuals compared to blue whales or other rorqual species (Bearhop et al. 2004, Cummings et al. 2012). This scenario seems plausible judging by the narrower

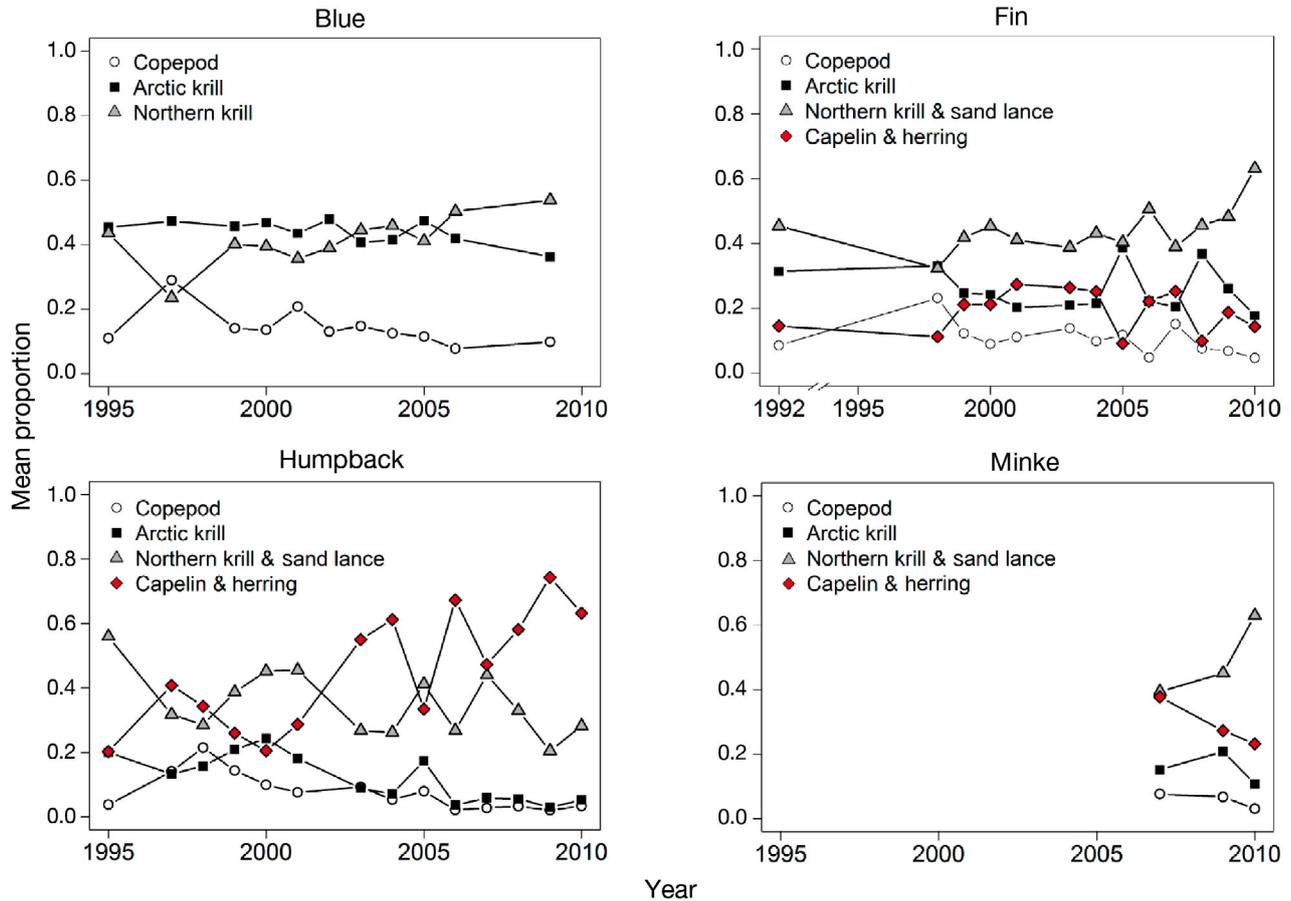


Fig. 7. Diet composition of blue whales *Balaenoptera musculus* and humpback whales *Megaptera novaeangliae* from 1995 to 2010, for fin whales *B. physalus* from 1992 to 2010, and for minke whales *B. acutorostrata* from 2007 to 2010 in the Gulf of St. Lawrence. The mean proportion of each dietary source is presented for each year, and credibility intervals have been removed for clarity

credible intervals around source proportion estimates for humpback diet (Fig. 3). This may also help explain the relatively stable niche width of humpback whales over time (Fig. 4). In contrast, some

blue whale individuals may preferentially forage on Arctic krill, others only on northern krill, and others on a mixture of euphausiid species; such a pattern would widen the credible intervals of dietary estimates at the population level and could lead to a greater variability in population niche width (Fig. 4).

Species with substantial isotopic overlap (e.g. fin and minke whales) may be segregating their ecological niche on a different axis, such as spatially or temporally. For instance, while minke whales can be found offshore, they tend to occupy more nearshore waters than fin whales in the northern Gulf of St. Lawrence (Doniol-Valcroze et al. 2007) and off the west coast of Newfoundland (Piatt et al. 1989). They may also segregate vertically when feeding within the same prey patch (Friedlaender et al.

Table 2. Mean (\pm SD) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (‰) for male and female blue whales *Balaenoptera musculus* (1995 to 2010), fin whales *B. physalus* (1992 to 2010), humpback whales *Megaptera novaeangliae* (1995 to 2010) and minke whales *B. acutorostrata* (2007 to 2010) in the Gulf of St. Lawrence. Significant differences between male and female isotope ratios are indicated in **bold**

		— Male —		— Female —		<i>F</i>	<i>p</i>
		Mean \pm SD	<i>n</i>	Mean \pm SD	<i>n</i>		
Blue	$\delta^{13}\text{C}$	-18.4 \pm 0.3	67	-18.4 \pm 0.4	69	0.31	0.580
	$\delta^{15}\text{N}$	9.9 \pm 1.2	67	9.7 \pm 1.0	69	2.04	0.160
Fin	$\delta^{13}\text{C}$	-18.4 \pm 0.4	102	-18.5 \pm 0.5	74	6.25	0.010
	$\delta^{15}\text{N}$	11.7 \pm 1.6	102	11.1 \pm 1.5	74	8.38	0.004
Humpback	$\delta^{13}\text{C}$	-18.5 \pm 0.4	64	-18.5 \pm 0.4	80	0.32	0.570
	$\delta^{15}\text{N}$	13.9 \pm 0.8	64	13.9 \pm 0.7	80	0.71	0.400
Minke	$\delta^{13}\text{C}$	-18.4 \pm 0.3	8	-18.4 \pm 0.4	40	0.02	0.880
	$\delta^{15}\text{N}$	12.2 \pm 1.0	8	13.4 \pm 1.3	40	7.75	0.010

2009), although this remains to be demonstrated for the Gulf of St. Lawrence.

Interannual isotope and diet trends

While isotopic niche characteristics prior to the groundfish collapse could not be examined using the current time series, diet composition appeared relatively stable over the post-collapse period for the 4 species, with some diet shifts towards higher trophic levels observed in recent years in fin and humpback whales. Two opposite long-term isotopic trends in blue, fin and humpback whales were observed: an overall increase in $\delta^{15}\text{N}$ and a concomitant decrease in $\delta^{13}\text{C}$ values. The progressive ^{15}N -enrichment in rorqual tissues over time could reflect an increase in $\delta^{15}\text{N}$ values at the base of the food web over time; however, to our knowledge such phenomenon has not been documented in the St. Lawrence. Alternatively, if the increase in $\delta^{15}\text{N}$ values is related to an increase in trophic position, then we would expect a similar change in $\delta^{13}\text{C}$ values, unless trophic ^{13}C -enrichment was near zero in our system. Conversely, a decrease in $\delta^{13}\text{C}$ values (blue: -0.74% , fin: -0.65% and humpback: -0.64%) was observed in the 3 rorqual species sampled over the 19 yr period, suggesting other phenomena (such as the Suess effect) might have contributed to the ^{13}C -depletion in rorqual tissues over time. The Suess effect transcends from long-term anthropogenic influences on the global environment causing a decrease in the $^{13}\text{C}/^{12}\text{C}$ ratio of atmospheric CO_2 (Friedli et al. 1986, Keeling et al. 1996), which has led to a progressive ^{13}C -depletion in the oceanic dissolved inorganic carbon (DIC) pool of approximately 0.1 to 0.2‰ per decade (Sonnerup et al. 1999). Körtzinger et al. (2003) reported a mean $\delta^{13}\text{C}$ decrease in DIC of the North Atlantic Ocean of approximately 0.03‰ per year, which would lead to a net depletion of 0.48‰ over 16 yr (for blue and humpback whales) and of 0.57‰ over 19 yr (for fin whales). Assuming there is no discernible trophic enrichment of $\delta^{13}\text{C}$ values from primary consumers to higher trophic levels in our system, then the Suess effect alone could account for a maximum of 60 to 80% of the observed ^{13}C -depletion in rorquals over time. However, given that a trophic enrichment in $\delta^{13}\text{C}$ of approximately 1.5‰ has been documented previously in the Gulf of St. Lawrence (Lesage et al. 2001), the proportion of the observed depletion attributed to the Suess effect is likely much less than 60%, although we cannot assess its relative magnitude in our system. Some of the ^{13}C -

depletion observed over time in the various rorqual species could reflect a progressive shift in foraging location towards more ^{13}C -depleted habitats (e.g. pelagic or offshore) for all 3 rorquals, since carbon isotope ratios also track primary productivity within marine systems (Fry & Sherr 1984). Although we cannot confirm whether a vertical habitat shift occurred, no systematic shift in horizontal spatial distribution was detected over the study period. An additional hypothesis to explain the rorqual ^{13}C -depletion trend would entail a decline in the photosynthetic rate and subsequent primary production of the Gulf of St. Lawrence, as recorded in the Bering Sea (Schell 2000). Long-term estimates of plankton biomass in the Gulf of St. Lawrence show interannual variations, but no sign of a long-term negative trend since the 1990s (Plourde et al. 2011). Therefore, the most likely causes for the overall decrease in $\delta^{13}\text{C}$ values in rorquals over time are a combination of the Suess effect and diet shifts. It will be important to monitor isotopic change at the base of the food web in the Gulf of St. Lawrence to further test mechanisms driving rorqual isotope trends.

The overall increase in $\delta^{15}\text{N}$ values over the study period in blue, fin and humpback whales (Fig. 6) could be attributed to a gradual shift towards consumption of higher trophic level prey (Fig. 7). This diet shift persisted even after rorqual $\delta^{13}\text{C}$ values were corrected using previously published Suess corrections for the North Atlantic (Körtzinger et al. 2003; results not shown). For blue whales, there appears to be a progressive increase of northern krill in their diet since the mid-1990s, possibly reflecting either an increase in the availability of this species, or a reduction in the abundance of what appears to be their preferred prey—the Arctic krill. There is evidence that euphausiid abundance has declined in certain areas of the Northwest Atlantic over the last 2 decades (Hanson & Chouinard 2002, Head & Sameoto 2007), but species-specific data is generally lacking, and it is unclear whether this trend also exists in the Gulf of St. Lawrence. Alternatively, blue whale occurrence patterns can be a valuable indicator of the state of their prey. Sightings of blue whales in some areas of the northern Gulf have decreased since the 1980s, suggesting these sectors have become progressively less attractive to this specialist feeder (Comtois 2009). Compared to the other generalist rorquals who appear capable of switching prey, blue whales would most likely be displaced from an area given a reduction in availability of their preferred prey (Schoenherr 1991, Croll et al. 1998, Sears & Calambokidis 2002, Croll et al. 2005).

In absence of long-term abundance trends for small pelagic fish (capelin, herring) and euphausiid zooplankton in the Gulf of St. Lawrence, we need to look at other lines of indirect evidence to understand the potential impact of the groundfish collapse on non-target species, such as large whales. When populations of cod collapsed across the North Atlantic in the early 1990s, a parallel increase in their benthic invertebrate prey was observed (Worm & Myers 2003). During this same period, an index of distribution showed a geographic expansion of capelin stocks (inferred from presence/absence in commercial fish bottom trawl surveys; DFO 2011). Since pelagic fish are also cod prey (Jackson et al. 2001), it is reasonable to suggest that pelagic fish stocks increased following the cod collapse. Thus, the observed increase in rorqual $\delta^{15}\text{N}$, particularly for humpbacks, could indeed reflect a progressive use of forage fish in the period subsequent to the cod decline. This is also in accordance with ecosystem models which predicted fish-eating cetaceans to exert a strong predatory role on capelin stocks in the late 1990s and early 2000s (Savenkoff et al. 2007).

While capelin + herring have apparently become a progressively important food source in humpback whale diet, we found no clear indication that this prey group gained significance in fin and minke whale diet (Fig. 7). On the contrary, fin and minke whales seem to be consuming more northern krill + sand lance over time. However, given the years over which minkes were sampled, dietary changes in relation to the cod collapse would be difficult to judge. Several non-exclusive hypotheses may explain such a finding. First, capelin and/or herring biomass may not have reached a sufficient level to represent a profitable food source to all 3 rorqual populations. Alternatively, humpback whales may be more efficient predators of these prey, and might be competitively excluding the other 2 rorquals. Finally, resource partitioning may be maintained over time, despite the increased availability of capelin. Humpback, fin and minke whales all appear capable of switching prey depending on availability. For instance, although we do not have abundance trends for all rorqual prey species in the Gulf of St. Lawrence, Fig. 7 suggests that 1995, 2000, 2005 and 2007 may have been years of lower capelin + herring availability in which humpbacks instead exploited the northern krill + sand lance group. We may expect interspecific competition between humpback, fin and minke whales to increase in years of low capelin + herring or Arctic krill abundance as the northern krill + sand lance prey group will be mutually ex-

ploited. All 3 generalists consume both northern krill and sand lance (Overholtz & Nicolas 1979, Hain et al. 1982, Haug et al. 1995, Stevick et al. 2008); however, it would be interesting to use a complementary chemical marker (e.g. fatty acid signatures) to tease apart specific contributions of different prey species to rorqual diet and further investigate resource partitioning.

Seasonal patterns

The seasonal isotopic variability in POM was not mirrored within primary (Arctic krill) and secondary (northern krill) consumers, supporting findings from previous studies suggesting that the slower integration time of consumers attenuates short-term isotope fluctuations in organisms at the base of food webs (Cabana & Rasmussen 1996). Similarly, no significant seasonal trends were detected among rorqual isotope ratios (Figs. S1 & S2 in the Supplement), suggesting no marked seasonal dietary shift.

Intrapopulation variation

Individuals within a species can reduce the impact of competition via partitioning of resources by gender, age class, reproductive state or simply through differences in individual preferences (Schoener 1974). The isotopic similarity between male and female blue and humpback whales, coupled with the lack of sexual spatial segregation (Doniol-Valcroze 2008) and weak sexual dimorphism (Chittleborough 1965, Friedli et al. 1986), suggests gender is not a factor influencing niche segregation within these species. In contrast, we did find isotopic differences related to gender in fin and minke whales. Minkes segregate spatially in northern latitudes, with females found in greater numbers than males at higher latitudes (Born et al. 2003). In the Gulf of St. Lawrence, there is a female-biased sex ratio (4.8:1) among minkes based on our biopsy samples, and our diet results suggest females incorporate 15% more capelin + herring in their diet, placing them at a slightly higher trophic position. Conversely, male fin whales fed at a slightly higher trophic position than females. However, sexual dimorphism is weak in fin whales, and there is no evidence of spatial segregation within the Gulf of St. Lawrence. Thus, mechanisms behind sexual trophic niche segregation may reflect social preferences or strong competitive pressure among individuals. This source of intrapop-

ulation diet variation may help explain why minke and fin whales have wider isotopic niche widths.

Although juvenile and adult humpback whales have been observed foraging in different areas within the northern Gulf of St. Lawrence (Mingan Island Cetacean Study unpubl. data), their isotopic similarity suggests trophic roles are comparable among age classes. While calves were not isotopically distinct from juveniles and adults, they occupied higher trophic positions when compared to their own mothers. This is consistent with the mother–offspring trophic enrichment reported for several other mammals (Jenkins et al. 2001, Polischuk et al. 2001), and most likely related to milk consumption. Lastly, reproductive state of adult female humpbacks appears to have no effect on isotopic niche. Thus, the trophic similarity among different gender, age classes and reproductive states within humpbacks might help explain their narrower niche width. The remaining trophic variation, although minor, could be a function of individual dietary preferences and should be examined by re-sampling known individuals over time.

In conclusion, despite some overlap of their isotopic niches, the 4 rorqual species of the Gulf of St. Lawrence differed in the proportional contribution of prey sources to diet, providing support for ecological niche segregation among these closely related and sympatric species. The observed trophic overlap may either imply that shared food sources are plentiful enough to support exploitation by different species, or that food sources are limited in general, and consequently, joint use of resources by different species is required for survival (Pianka 1974). Unfortunately, the lack of long-term data on abundance and density of macrozooplankton and forage fish prevents an in-depth analysis of the evolution of prey availability to rorquals and rationale for the observed food partitioning. Nevertheless, our results indicate that the effects on non-target species following the collapse of groundfish stocks in the early 1990s might be less favourable to species such as blue whales, which showed little long-term variation and a relatively narrow trophic niche, compared to baleen whales with generalist foraging strategies. In a warming climate, oceanographic conditions favourable to species such as Arctic krill (the preferred prey of blue whales) might be observed less frequently at our latitudes around 49° 36' N, 64° 20' W (Walther et al. 2002, Hays et al. 2005). How this will influence prey availability and distribution and survival of blue whales, an endangered species, remains uncertain and should be closely monitored.

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