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Fueling phocids: Divergent exploitation of primary energy sources and parallel ontogenetic diet switches among three species of subarctic seals

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ABSTRACT

Determining how marine predators partition resources is hindered by the difficulty in obtaining information on diet and distribution. Stable isotopes (SI) of carbon ($^{13}C/^{12}C$, $\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$, $\delta^{15}N$) provide a two-dimensional estimate of the dietary space of consumers; an animal's isotopic composition is directly influenced by what they consume and where they feed. Harp (*Pagophilus groenlandicus*) and hooded (*Cystophora cristata*) seals are abundant phocid species found in the North Atlantic. We measured and contrasted SI values between seals sampled at nearshore and offshore sites to test for effects of sampling location, sex, age-class, and body size to gain insight into how these species partition space and prey resources. In addition we contrasted previously published results for gray seals (*Halichoerus grypus*). Isotope values differed significantly by age class and location in harp and hooded seals. We found significant differences in SI values (mean $\delta^{13}C$ and $\delta^{15}N$ ± SE) between all species. Hooded seals, a continental shelf-edge, deep-diving species, exhibited low SI values (juveniles: −20.9‰ ± 0.03‰, 13.36‰ ± 0.05‰; adults: −20.41‰ ± 0.03‰, 14.81‰ ± 0.04‰) characteristic of feeding on meso- to bathypelagic prey. Harp seals, which dive to moderate depths primarily on the shelf had intermediate SI values (juveniles: −20.53‰ ± 0.01‰, 13.91‰ ± 0.01‰; adults: −20.13‰ ± 0.01‰, 14.96‰ ± 0.01‰) characteristic of feeding on epipelagic prey, whereas gray seals, which feed on or near the sea floor in shallow shelf waters, had high SI values (juveniles: −19.74‰ ± 0.04‰, 17.51‰ ± 0.05‰; adults: −18.86‰ ± 0.01‰, 17.23‰ ± 0.02‰) characteristic of feeding on demersal prey. In all species, $\delta^{13}C$ values increased with body size and age in the same manner, indicating that seals exploit or forage in deeper habitats as they get larger

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and older. We hypothesize that the consistent ontogenetic shift in foraging niche, despite large differences between species in their diving behavior, geographic range and habitat use, not only reflects increased access to different prey due to increased diving capacity, but a progressive adjustment to balance energy budgets by reducing foraging costs.

Key words: seal diet, ontogenetic, habitat, stable isotopes, energetics.

Theoretical studies have emphasized the influence of competition for finite resources on the evolution of species and communities (Bolnick *et al.* 2003). Competition can be mitigated through resource (*i.e.*, niche) partitioning over varying spatial and temporal scales (Bolnick *et al.* 2003). Despite the importance of understanding how competition for resources may influence the evolution of species, studying resource partitioning, particularly in upper-trophic level marine predators, has been hindered by the difficulty in obtaining reliable estimates of diet and distribution (Bowen *et al.* 2002).

Body size is thought to be important in structuring trophic linkages within food webs (*e.g.* Carbone *et al.* 1999, 2007) and among terrestrial predators is thought to have evolved to reduce competition (Rosenzweig 1968). Body size of sympatric terrestrial carnivores is positively correlated with mass of their prey, as larger predators often consume larger prey items in order to satisfy larger absolute energy requirements (*e.g.* Carbone *et al.* 1999, 2007; Sinclair *et al.* 2003; Radloff and du Toit 2004; Owen-Smith and Mills 2008). Recent studies have also emphasized the energetic importance of diet shifts as well as food web structure for growth in freshwater fish and marine fish (Trudel *et al.* 2001; Pazzia *et al.* 2002; Sherwood *et al.* 2002, 2007; Rasmussen *et al.* 2008). Within-species, diet shifts toward progressively larger prey items as individuals grow are commonly observed (*e.g.*, Pazzia *et al.* 2002, Sherwood *et al.* 2002). These diet shifts may also require changes in feeding habitats. In many marine predator species, we know relatively little about diet shifts and therefore about how resource partitioning may change with changes in body size. Although obtaining reliable estimates of the diets of predators, such as marine mammals, continues to pose challenges (Bowen and Iverson, in press), our understanding of the spatial distribution of marine predators has increased dramatically (*e.g.*, Field *et al.* 2005, Breed *et al.* 2006, Bajzak *et al.* 2009, Bailleul *et al.* 2010). These studies have revealed sex and age-specific differences in habitat segregation at different spatial and temporal scales. Energy requirements and physiology are known to vary with reproductive status and ontogeny, which in turn may influence foraging behavior, habitat use and resource selection (*e.g.* Beck *et al.* 2003, 2007). To fully capitalize on this growing understanding of the spatial ecology of marine predators and to better understand niche partitioning and the role these predators might play in regulating food webs, we need better information on which habitats are important and what resources are exploited.

The analysis of stable nitrogen ($^{15}N/^{14}N$, $\delta^{15}N$) and stable carbon ($^{13}C/^{12}C$, $\delta^{13}C$) isotopes has proven useful in describing trophic interactions in food webs (Newsome *et al.* 2010). Essentially, stable isotopes (SI) provide a description of how various sources of primary production fuel higher order consumers and the subsequent links between them. Isotopes of nitrogen are enriched in consumers relative to diet by an average of 3‰–5‰ (Hobson and Welch 1992), thereby providing a measure of trophic position (TP). On the other hand, carbon isotopes are enriched by ~1‰ with trophic transfers. Variation in $\delta^{13}C$ occurs over both small and large scales due to differences in photosynthetic production and/or various physical-chemical processes (reviewed in Newsome *et al.* 2010) resulting in differences in signatures between primary producer communities; these differences are transferred throughout the food webs they fuel permitting, among others, inferences about where consumers forage (*e.g.*, Cherel and Hobson 2007). This allows for a geographical interpretation of carbon isotope values, which can be used to designate broad-scale foraging locations of animals in the marine environment. In marine environments, including the North Atlantic, differences in δ^{13}C signatures are observed with latitude, between nearshore and offshore systems and between demersal and pelagic communities (Sherwood and Rose 2005, Tucker *et al.* 2007, McMeans *et al.* 2010, Pinela *et al.* 2010); δ^{13}C is lower (more negative) in both offshore and pelagic food webs relative to nearshore and benthic food webs and decreases with increasing latitude.

Gray seals (*Halichoerus grypus)* are a wide-ranging and abundant species inhabiting the continental shelf of the Northwest Atlantic and diving to depths generally <100 m (Beck *et al.* 2003, Austin *et al.* 2004, Breed *et al.* 2006). Gray seals are sex-dimorphic, generalist predators consuming a mixture of both demersal and pelagic fishes, with males being about 50% heavier than females (Beck *et al.* 2007, Bowen and Harrison 2007). There is evidence of dietary niche segregation in gray seals with an increasing reliance on demersal prey in larger and older individuals and from females to males (Beck *et al.* 2007, Tucker *et al.* 2007). These differences were reflected in differences in foraging behavior at the level of individual dives, movement, and seasonal habitat use (Beck *et al.* 2003; Austin *et al.* 2004; Breed *et al.* 2006, 2009; Breed 2008). Moreover, there was a significant positive correlation between body size and both δ^{13}C and δ^{15}N, with overlap between sex and age groups, suggesting that diet shifts towards a larger fraction of both demersal and higher trophic level prey as seals grow (Tucker *et al.* 2007).

Like gray seals, harp (*Pagophilus groenlandicus*) and hooded (*Cystophora cristata*) seals are abundant phocids in the subarctic Atlantic Ocean (Stenson *et al.* 1997, 2003; Hammill and Stenson 2006). They exhibit interspecific differences in body size, distribution and diving patterns (Folkow *et al.* 1996, 2004). Hooded seals are size-dimorphic, with adult males being approximately 50% larger than females and 2.5 times larger than adult harps of either sex (Hammill and Stenson 2000). Harp seals are only slightly dimorphic with males being 10% larger than females (Chabot *et al.* 1996). Following moulting in April, harp seals gradually increase fat reserves over the summer and fall (Chabot *et al.* 1996). Both adult male and female harp seals reach peak body mass just prior to breeding in February. In hooded seals, most energy stores are accumulated between September and March just prior to breeding (Chabot *et al.* 2006). Although they are both wide ranging and exhibit long-distance seasonal migrations (>3,000 km), summering in Arctic waters of eastern Canada and west Greenland, and wintering off Newfoundland and in the Gulf of St. Lawrence, harp seals mainly inhabit the continental shelf (Stenson and Sjare 1997, Folkow *et al.* 2004), while hooded seals are more strongly associated with the continental shelf edge and the deep ocean (Folkow and Blix 1999, Anderson *et al.* 2009, Bajzak et al 2009). Most harp seal dives are <50m (Folkow *et al.* 2004; Nordøy *et al.* 2008; GBS, unpublished data). By contrast, hooded seals regularly dive >100 m and can exceed 1,500 m (Folkow and Blix 1999; GBS, unpublished data). Limited satellite tagging indicates that both species may co-occur throughout much of the year (Folkow *et al.* 1996, 2004; Anderson *et al.*

2009) and overlap with gray seals during the winter, particularly in the Gulf of St. Lawrence.

Differences in foraging among these species are reflected in what is known about diet. Harp seals primarily consume a mixed diet of pelagic fish and invertebrates such as capelin, *Mallotus villosus*, Arctic cod, *Boregadus saida*, herring, *Clupea harengus*, euphausiids, and amphipods (Lawson *et al.* 1995, Lawson and Stenson 1997, Lawson *et al.* 1998, Tucker *et al.* 2009). Hooded seal diets are typically a mixture of deeper-water pelagic and demersal species such as halibut (*Hippoglossus hippoglossus*), redfish (*Sebastes* sp.), and squid, with smaller quantities of herring, capelin, Atlantic cod (*Gadus morhua)*, and Arctic cod (Hammill and Stenson 2000; Haug *et al.* 2004, 2007; Tucker *et al.* 2009). Ontogenetic changes in diving and foraging behavior are poorly described for these species, although there is evidence of ontogenetic diet shifts in harp seals where the proportion of pelagic fish declines as the proportion of pelagic invertebrates increases in the diet as seals grow (Lawson *et al.* 1995, Lawson and Stenson 1997, Tucker *et al.* 2009). Similarly, juvenile hooded seals consume more pelagic fish than adults (Tucker *et al.* 2009). To date, diet studies on other pinniped species have generally documented an increase in consumption of benthic prey from postweaning to adulthood (*e.g.* Field *et al.* 2007, Drago *et al.* 2009, Newland *et al.* 2011, Jeglinski *et al.* 2012). This underlies the widespread suggestion that diet shifts are tied to improvements in diving skills.

Although we have estimates of the species composition of the diet and where these animals are generally foraging, we lack a comprehensive understanding of which food webs are exploited, how resources are partitioned within and among species, and how distribution and variation in prey availability and quality affect energy accumulation. Climate and oceanic regime change in the North Atlantic can result in major shifts in both the composition and abundance of primary producer, secondary and tertiary consumer communities, resulting in alternative pathways of energy flow to top consumers (Frank *et al.* 2005, Greene *et al.* 2008, Shackell *et al.* 2010) which may vary in complexity, quality and in efficiency of trophic transfers. Short-term impacts of such shifts in prey communities have been noted in various aspects of seal foraging behavior, diet and life history variables (*e.g.*, Bowen *et al.* 2006, Tucker *et al.* 2009), but the long-term consequences of changes on marine mammal and prey populations are poorly understood (*e.g.*, Bowen *et al.* 2006, Newsome *et al.* 2007).

In the current study, we measured SI signatures in harp and hooded seals and compared these data to our previously published gray seal results to test for effects of age-class and body size on niche segregation within and between these phocid species. Although these species are not sympatric in the classic sense, as in the case of various guilds of terrestrial predators (*e.g.*, Sinclair *et al.* 2003, Radloff and du Toit 2004, Owen-Smith and Mills 2008), the comparison among species should provide insight into how these similar species (from an evolutionary perspective) have partitioned space and prey resources.

Methods

Sampling of Seals

Harp and hooded seals were collected along the northeast coast of Newfoundland and southern Labrador between November and March from 1995 to 2004 by experienced seals hunters and scientific personnel from the Canadian Department of Fisheries and Oceans (178 harp, 51 hooded; Sjare and Stenson 2010) and during an offshore cruise in the winter of 2004 (Fig. 1). Seals were weighed to the nearest 0.5 kg and a muscle sample (approximately 0.5 kg) was taken from the posterior flank, placed in Whirlpaks, and frozen.

Seal ages were determined to the nearest year by sectioning a lower canine tooth and then counting dentine annuli (Bowen *et al*. 1983). Both species were divided into juveniles (1–4 yr) and adults ($\geq$5 yr) (Sjare and Stenson 2010) and grouped by sampling location: nearshore (defined as <30 km from shore; Lawson *et al*. 1995) and offshore (>30 km). The delineation and sampling locations generally correspond to the shelf-break (Fig. 1). Because of small sample sizes, seals were pooled across years.

Stable Isotope Analysis

Muscle samples were dried to constant weight (for 48 h at 80°C in a drying oven) and crushed to a fine powder using a mortar and pestle. Stable carbon and nitrogen isotope ratios were determined by the analysis of CO_2 and N_2 produced by combustion in a CE Elemental Analyzer followed by gas chromatograph separation and analysis with a Delta plus isotope ratio mass spectrometer (G. G. Hatch Isotope Laboratories, University of Ottawa, Ottawa, Ontario, Canada). Stable carbon and nitrogen ratios were expressed in delta (δ) notation, defined as the parts per thousand

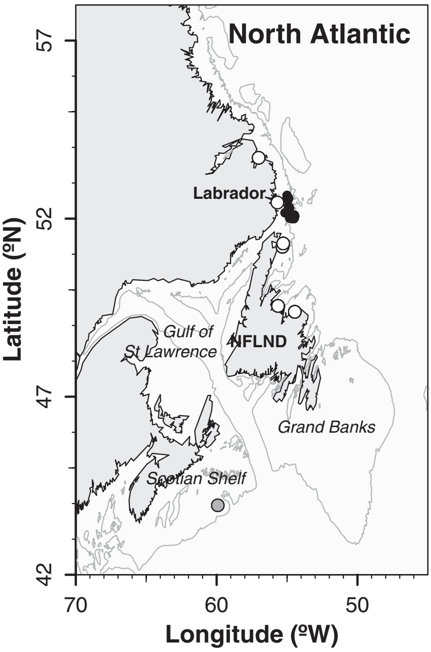

Figure 1. Map of sampling locations. Open circles represent inshore sampling locations in Newfoundland (NFLND) and Labrador; closed circles are offshore sampling locations (defined as >30 km from shore) for harp and hooded seals. The gray circle denotes the location of Sable Island where gray seals were sampled. The solid line delineating the margin of the continental shelf is the 200 m depth contour.

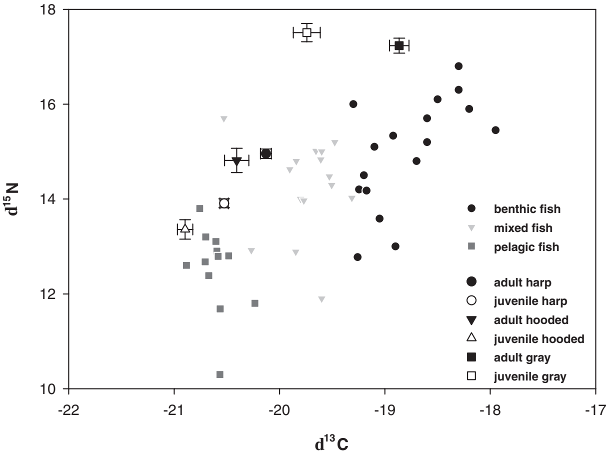

Figure 2. Isotope values for fish species (n = 40) sampled in the foraging range of harp, hooded, and gray seals in the Northwest Atlantic including the Gulf of St Lawrence (Lesage *et al.* 2001), the Scotian Shelf (Tucker *et al.* 2007; Trzcinski, unpublished data[4]) and the Grand Banks (Sherwood and Rose 2005). Fish diets were classified as pelagic, mixed, or benthic based on knowledge of feeding habits (Scott and Scott 1988, Sherwood and Rose 2005, Froese and Pauly 2011). Overlain are mean (± SE) isotope values for adult and juvenile harp, hooded, and gray seals (this study).

(‰) deviation from a standard material: δ^{13}C or δ^{15}N = ([$R_{\text{sample}}/R_{\text{standard}}$] −1) × 1,000; R = ^{13}C/^{12}C or ^{15}N/^{14}N). Standards used were PDB limestone for δ^{13}C and N_2 in air for δ^{15}N. A subsample (10%) was analyzed in duplicate; the average standard error of the mean for replicates was 0.05‰ for δ^{13}C and 0.07‰ for δ^{15}N. Lipid-normalized values of δ^{13}C were calculated from C:N ratios using the equations in McConnaughey and McRoy (1979). As muscle has an average protein half-life of ~12.5–83.3 d, isotope ratios likely reflect diets assimilated up to many months previous to collection (Kurle and Worthy 2002, Newsome *et al.* 2010), *i.e.*, over the prebreeding fattening period.

To illustrate the shift in stable isotope values between habitats (Fig. 2), we summarized the published data (available on request) for fish in the Northwest Atlantic including the Scotian Shelf (Tucker *et al.* 2007; Trzcinski, unpublished data[4]), the Grand Banks (Sherwood and Rose 2005) and the Gulf of St Lawrence (Lesage *et al.* 2001). Fish were classified as pelagic, mixed or benthic based on independent knowledge of feeding habits and distribution (Scott and Scott 1988, Sherwood and Rose 2005, Froese and Pauly 2011). Note that this data set is insufficient to estimate diets of seals as many common prey taxa are missing.

To compare gray seals to harp and hooded seals, we selected only prebreeding, winter samples (n = 75) from the previously published data (Tucker *et al.* 2007) for consistency. Briefly, gray seals were sampled on Sable Island (43°55'N, 60°00'W; approximately 300 km southeast of mainland Nova Scotia, Canada) from 1996 to 2001 (Tucker *et al.* 2007). Individuals were captured onshore using hand-held nets (see Bowen *et al.* 1992) and most animals were weighed to the nearest 0.5 kg. Skin

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[4] Personal communication from Kurtis M. Trzcinski, Fisheries and Oceans Canada, Bedford Institute of Oceanography, 1 Challenger Drive, Dartmouth, Nova Scotia B2Y 4A2, Canada, 19 April 2011.

samples (approximately 0.05–0.1 g) were taken from the rear flipper of known-aged adult male (n = 29) and female (n = 29) gray seals in January at the start of the breeding season. Seventeen juveniles (mostly yearlings; n = 7 male, n = 10 female) were sampled in January 2004. As gray seals were live-captured upon returning to Sable Island, foraging location of the animals sampled was not known, but results from satellite-telemetry tracking indicates that foraging prior to our sampling period occurs on the eastern Scotian Shelf (Breed *et al.* 2006, 2009). As skin and muscle display different fractionation coefficients for δ^{13}C, we corrected the harp and hooded seal muscle values by −1.3‰ and gray seal skin values by −2.8‰, respectively to make values directly comparable (Hobson *et al.* 1996).

Statistical Analyses

We used General Linear Models (GLMs) with Gaussian error distributions to test the following hypotheses for harp and hooded seals at a 0.05 significance level: do stable isotope values (δ^{13}C and δ^{15}N) vary between species with different diving behavior, do values change between age classes and sex, and is there an effect of sampling location. We had insufficient samples to examine interannual effects. To examine intraspecific differences in greater detail, we ran separate GLMs for harp and hooded seals, respectively. We then compared isotope values between all three species by running a separate GLM with species, age class, and sex as factors. In this analysis all individuals in a species were pooled, irrespective of sampling location to represent the broadest niche of each species. We fit linear regressions (LM) to evaluate the relationship between δ^{13}C and body size and δ^{15}N and body size using species as an independent factor. All possible models with two-way interactions were run and residuals were examined for lack of fit. GLM and LM models were fitted in R version 2.12.2 (R Development Core Team 2011). Means are reported throughout with standard error (SE).

RESULTS

In addition to the 75 prebreeding samples from our previously published gray seal data (58 adult, 17 juvenile), SI values where determined for 178 harp seals and 51 hooded seals (Table 1).

δ^{13}C values differed significantly by age class in harp seals ($F_{(1,177)}$ = 17.54, P < 0.001) and sampling area ($F_{(1,177)}$ = 11.20, P = 0.001; Table 1, 2). Sex was not significant ($F_{(1,177)}$ = 1.56, P = 0.213), nor were there significant interaction terms. δ^{15}N values differed significantly by age class ($F_{(1,177)}$ = 44.79, P < 0.001), but not for sampling area ($F_{(1,177)}$ = 0.80, P = 0.372) or sex ($F_{(1,177)}$ = 3.71, P = 0.057). Similarly, in hooded seals, δ^{13}C values differed significantly by age class ($F_{(1,50)}$ = 12.89, P = 0.001) and sampling area ($F_{(1,50)}$ = 12.32, P = 0.001, Table 1, 2), but not by sex ($F_{(1,50)}$ = 0.88, P = 0.355), nor were there significant interaction terms. δ^{15}N values differed significantly by age class ($F_{(1,50)}$ = 19.14, P < 0.001) and sampling area ($F_{(1,50)}$ = 11.13, P = 0.002), but not by sex ($F_{(1,50)}$ = 3.73, P = 0.06).

When entered as a main effect, harp and hooded seals (Fig. 3, Table 2) differed significantly in δ^{13}C values ($F_{(1,228)}$ = 4.27, P = 0.04). There were significant effects of age class ($F_{(1,228)}$ = 38.62, P < 0.001) and sampling area ($F_{(1,50)}$ = 30.33, P < 0.001), but there was also a marginally significant interaction between species and area ($F_{(1,228)}$ = 3.92, P = 0.049). For animals taken in the nearshore area, there

Table 1. Mean (± SE) body mass, $\delta^{13}C$ and $\delta^{15}N$ for adult and juvenile, male and female harp and hooded seals. Harp and hooded seals were sampled in nearshore and offshore (>30 km from shore) locations of the northwest Atlantic adjacent to Newfoundland and Labrador; gray seals were sampled on Sable Island, Nova Scotia (Fig. 1).

Species	Location	Age class	Sex	*n*	Mass (kg)	$\delta^{13}C$(‰)	$\delta^{15}N$(‰)
Harp	nearshore	adult	F	39	113.7 (5.2)	-20.02 (0.09)	14.91 (0.15)
			M	24	96.9 (5.8)	-20.0 (0.07)	14.94 (0.19)
		juvenile	F	38	43.7 (2.3)	-20.51 (0.06)	13.89 (0.16)
			M	42	47.9 (3)	-20.51 (0.06)	14.02 (0.13)
	offshore	adult	F	11	97.2 (10)	-20.55 (0.12)	14.57 (0.2)
			M	13	110.2 (5.2)	-20.33 (0.08)	15.45 (0.25)
		juvenile	F	6	29.7 (2.5)	-20.7 (0.11)	13.54 (0.37)
			M	5	31.4 (3.1)	-20.59 (0.04)	13.5 (0.05)
Hooded	nearshore	adult	F	3	184.3 (33.1)	-20.14 (0.2)	15.18 (0.29)
			M	8	199.3 (24.3)	-19.73 (0.18)	16.31 (0.43)
		juvenile	F	3	37.0 (5.5)	-20.66 (0.02)	13.75 (1)
			M	2	32.0 (8)	-20.74 (0.11)	14.21 (0.51)
	offshore	adult	F	12	149.4 (10.3)	-20.84 (0.14)	13.64 (0.21)
			M	8	218.5 (17.9)	-20.53 (0.15)	14.94 (0.42)
		juvenile	F	4	42.6 (2.6)	-20.88 (0.14)	13.37 (0.5)
			M	11	45.4 (2.8)	-20.99 (0.11)	13.09 (0.19)
Gray	Sable Island	adult	F	29	189.5 (31)	-19.14 (0.69)	16.68 (0.96)
			M	29	290.8 (42.1)	-18.59 (0.6)	17.79 (1.17)
		juvenile	F	10	56.4 (24.1)	-19.81 (0.64)	17.53 (0.91)
			M	7	45.6 (6.5)	-19.65 (0.35)	17.47 (0.63)

was no significant difference in $\delta^{13}C$ between harp and hooded seals ($F_{(1,158)} = 0.05$, $P = 0.823$). However, these species differed significantly in $\delta^{13}C$ values in samples taken offshore ($F_{(1,69)} = 8.47$, $P = 0.005$) with more negative values for hooded seals.

By contrast, we found no significant difference in $\delta^{15}N$ values between harp and hooded seals ($F_{(1,228)} = 0.24$, $P = 0.625$), but there were significant effects of age class ($F_{(1,228)} = 67.09$, $P < 0.001$) and sampling area ($F_{(1,50)} = 19.11$, $P < 0.001$). There was a significant interaction term between species and area ($F_{(1,228)} = 13.27$, $P < 0.001$) with nearshore samples not differing between species ($F_{(1,158)} = 2.93$, $P = 0.089$), whereas offshore samples did ($F_{(1,158)} = 6.39$, $P = 0.014$) with lower values for hooded seals.

Overall, the three species differed significantly in SI values (for $\delta^{13}C$: $F_{(2,303)} = 111.18$, $P < 0.001$; for $\delta^{15}N$: $F_{(2,303)} = 202.65$, $P < 0.001$; Fig. 4, Table 2). *Post hoc* testing indicated that gray seals had the most enriched $\delta^{13}C$ (mean ± SE: -19.1‰ ± 0.1) and elevated $\delta^{15}N$ (mean ± SE: 17.3‰ ± 0.1), while hooded seals had the most depleted $\delta^{13}C$ (mean: -20.6‰ ± 0.1) and lowest $\delta^{15}N$ (mean: 14.1‰ ± 0.2). Harp seals had intermediate $\delta^{13}C$ (mean: -20.2‰ ± 0.04) and $\delta^{15}N$ (mean: 14.4‰ ± 0.1) values. $\delta^{13}C$ values differed significantly by sex ($F_{(1,303)} = 15.49$, $P < 0.001$) and age class ($F_{(1,303)} = 67.45$, $P < 0.001$), but there were significant interactions among species and sex ($F_{(2,303)} = 5.53$, $P = 0.004$) and species and age class ($F_{(2,303)} = 3.84$, $P = 0.023$). Similarly, $\delta^{15}N$ values differed significantly by sex ($F_{(1,303)} = 25.97$, $P < 0.001$) and age class ($F_{(1,303)} = 25.49$, $P < 0.001$). Again, there were significant interactions among species and sex ($F_{(2,303)} = 4.49$, $P = 0.012$) and species and age class ($F_{(2,303)} = 13.82$, $P < 0.001$). The species-sex interaction was likely driven by gray seals, which exhibit strong sex-specific SI values (Tucker *et al.* 2007) not

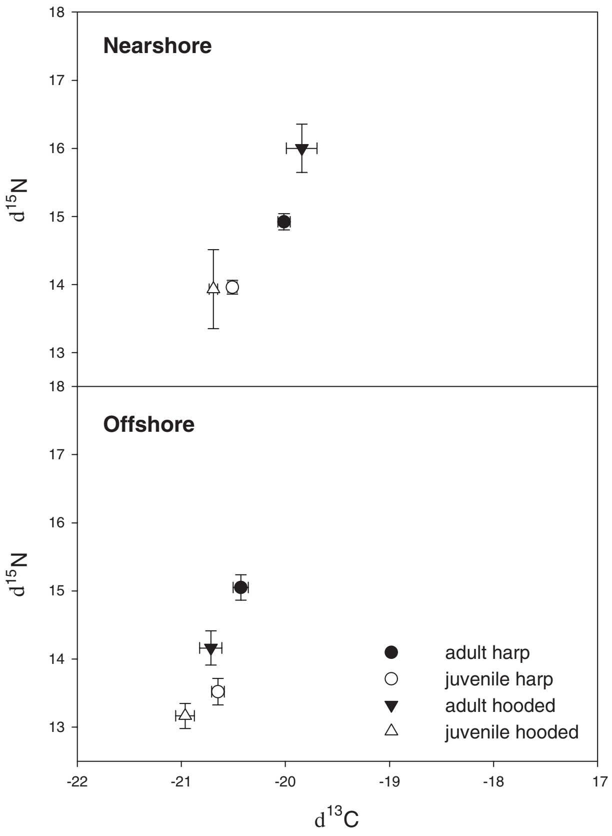

Figure 3. Mean (± SE) isotope values for adult and juvenile harp and hooded seals in nearshore and offshore sampling locations.

Table 2. Summary of main effects (age class, sex, sampling location, and species) for within and between seal species $\delta^{13}C$ and $\delta^{15}N$. Gray seals are included in all seals.

			$\delta^{13}C$		$\delta^{15}N$	
	Effect	df	*F*	*P*	*F*	*P*
Harp	age class	177	17.54	<0.001	44.79	<0.001
	sex	177	1.56	0.21	3.71	0.057
	location	177	11.20	0.001	0.80	0.372
Hooded	age class	50	12.89	0.001	19.14	<0.001
	sex	50	0.88	0.355	3.73	0.06
	location	50	12.32	0.001	11.13	0.002
Harp *vs.* hooded	species	228	4.27	0.04	0.24	0.625
	age class	228	38.62	<0.001	67.09	<0.001
	location	50	30.33	<0.001	19.11	<0.001
All seals	species	303	111.2	<0.001	202.65	<0.001

found in the other two species. The interaction with age-class implies species shifted diets in different ways. Again, gray seals demonstrated more complex differences between sex and age-classes and were likely driving this interaction (Tucker *et al.* 2007).

Body size ranged between 20 and 182 kg, 24 and 301 kg, and 38 and 381 kg in harp, hooded, and gray seals, respectively. There was a significant relationship between δ^{13}C and body size (LM $r^2 = 0.66$, $P < 0.001$) with a significant effect of species ($F_{(2,303)} = 16.87$, $P < 0.001$) indicating that intercepts differed (Fig. 5, Table 3). The interaction between body size and species was not significant ($F_{(2,303)} = 1.41$, $P = 0.246$) indicating that the slopes of the relationships did not differ significantly. Similarly, there was a significant relationship between δ^{15}N and body size (LM $r^2 = 0.66$, $P < 0.001$) with a significant effect of species (different intercepts; $F_{(2,303)} = 91.12$, $P < 0.001$). However, unlike δ^{13}C values, the interaction between body size and species was significant ($F_{(2,303)} = 24.53$, $P < 0.001$) suggesting δ^{15}N values changed differently with body size among species.

Table 3. Relationship between δ^{13}C, as a proxy for primary energy source, as well as δ^{15}N and body size (W, kg; SE_{est} is the standard error of the estimate) determined for three seal species. Standard error of the coefficients is given in parentheses. Note: the gray seal model for δ^{15}N is for adult animals only.

Species	Model	*n*	SE_{est}	r^2
Gray	$\delta^{13}C = -20.073(0.152) + 0.005(0.001)W$	75	0.576	0.43
	$\delta^{15}N = 15.31(0.58) + 0.008(0.001)W$	58	1.1	0.42
Harp	$\delta^{13}C = -20.752(0.063) + 0.006(0.001)W$	178	0.394	0.25
	$\delta^{15}N = 13.30(0.14) + 0.015(0.002)W$		0.87	0.32
Hooded	$\delta^{13}C = -21.070(0.131) + 0.004(0.001)W$	51	0.506	0.27
	$\delta^{15}N = 12.75(0.28) + 0.012(0.002)W$		1.08	0.45

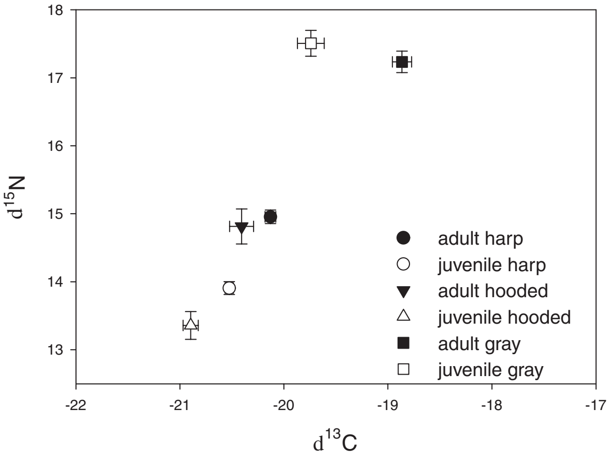

Figure 4. Mean (± SE) isotope values for adult and juvenile harp, hooded, and gray seals; all sampling locations combined.

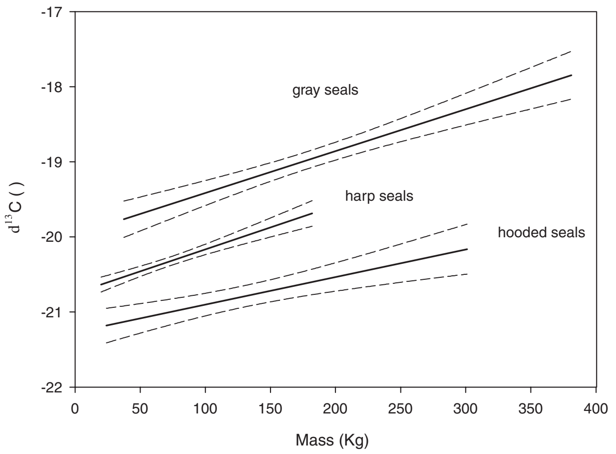

Figure 5. Regression (and 95% confidence intervals) of seal body mass (kg) *vs.* carbon isotope values for three species of seals. Regression equations provided in Table 3.

DISCUSSION

The key finding of our study was that each species displayed a similar ontogenetic diet shift characterized by a change in the main carbon source exploited, despite differences between species in SI values. δ^{13}C values of all three species increased with size and age, indicating that seals exploit or forage in deeper habitats as they get larger and older. We also found similar slopes among species in the regression of δ^{13}C against body mass suggesting that there is a common factor driving habitat shifts or dietary changes with body size despite species differences in diet, foraging behavior, habitat, and distribution.

Isotope data of potential prey in the North Atlantic are unfortunately scarce and scattered amongst different studies and do not permit an actual estimation of the diet of seals primarily because of the lack of isotope data for common prey taxa (*i.e.*, Hammill and Stenson 2000, Tucker *et al.* 2009). Instead, we have presented the data (Fig. 2) to characterize the general trends between benthic-pelagic systems of the North Atlantic. In the North Atlantic as in all marine systems, δ^{13}C becomes relatively lower further offshore and increases with depth along a vertical axis (Fig. 2; Sherwood and Rose 2005, Tucker *et al.* 2007, McMeans *et al.* 2010, Pinela *et al.* 2010). Therefore, δ^{13}C can be used as proxy for where seals are feeding in the water column relative to the bottom.

Harp, hooded, and gray seals displayed significant differences in δ^{13}C values (Fig. 2, 4). Gray seals, which feed over relatively shallower waters of the Scotian Shelf and often dive to the sea floor (Beck *et al.* 2003, Breed *et al.* 2009), had high δ^{13}C values characteristic of feeding on demersal prey (Tucker *et al.* 2007). Hooded seals, which are mainly a deep diving, shelf edge species (Folkow *et al.* 1999, Bajzak *et al.* 2009), had low δ^{13}C values, characteristic of feeding on meso- to bathypelagic prey (McMeans *et al.* 2010), whereas harp seals, which are moderate divers over the shelf both inshore and offshore (Folkow *et al.* 2004, Bajzak *et al.* 2009) displayed intermediate δ^{13}C values characteristic of feeding on epipelagic prey (McMeans *et al.* 2010, Pinela *et al.* 2010). Harp and hooded seal δ^{13}C values became lower in offshore samples for both adults and juveniles consistent with general expectations in baseline isotope values between these two habitats (Sherwood and Rose 2005, Tucker *et al.* 2007). Harp and hooded seal δ^{13}C overlapped in the nearshore but were divergent in offshore areas. However, diet differences between species are more pronounced in the offshore (Lawson *et al.* 1998, Hammill and Stenson 2000, Tucker *et al.* 2009).

Nitrogen increases with each trophic level, but baseline values vary among food webs. Pelagic communities typically have lower δ^{15}N values relative to shelf-based benthic communities (Sherwood and Rose 2005, Tucker *et al.* 2007, McMeans *et al.* 2010, Pinela *et al.* 2010). Therefore baseline nitrogen values change relative to the position on the carbon axis, such that overlap in δ^{15}N values of animals with different δ^{13}C values does not necessarily imply convergent trophic position or diet. Without explicit analysis of potential prey, it becomes difficult to estimate and interpret changes in trophic levels between animals residing in different habitats. We already have a good idea of trophic levels occupied by these seals given other quantitative descriptions of diet composition (*e.g.,* Hammill and Stenson 2000, Haug *et al.* 2004, Bowen and Harrison 2007). All three species consume a mix of invertebrates and fishes, making them to varying degrees, secondary and tertiary consumers. What is most revealing from the stable isotopes are the shifts in habitat. Both within and between species, our results show that δ^{15}N shifted with age and sampling location consistent with changes in δ^{13}C.

The lack of sex differences in stable isotope values, particularly for the size-dimorphic hooded seal, was somewhat unexpected. In a previous study using fatty acid analysis, we found sex differences in diets for both adult harp and hooded seals (Tucker *et al.* 2009). Adult male harp seals had higher proportions of pelagic amphipods in diets while females consumed higher proportions of epipelagic fish such as arctic cod and sand lance. In adult hooded seals, males consumed higher proportions of redfish while females consumed greater proportions of other meso- to bathypelagic fishes such as blue hake and white baraccudine. Failing to find a sex effect might be attributed to small sample size, but it is more likely a function of the overlap in where male and female seals forage coupled with the lower resolution of stable isotopes relative to fatty acids in delineating diets (Tucker *et al.* 2008).

Sex differences in foraging behavior are not as pronounced in harp and hooded seals as for other seal species. For example, although Folkow *et al.* (2004) and Nordøy *et al.* (2008) found that females dove significantly deeper than males in some areas of the White, Barents, and Greenland Seas this was not systematic, or consistent over the entire study area; in some cases males were actually diving slightly deeper than females. Bajzak *et al.* (2009) found that adult hooded seals display alternating seasonal differences in dive depths with males tending to make deeper dives than females preceding their postbreeding, northward migration but more shallow dives after migration. In addition, both species exhibit synchronous seasonal migrations during which female and male distributions overlap (Folkow *et al.* 2004, Nordøy *et al.* 2008, Andersen *et al.* 2009, Bajzak *et al.* 2009). Thus the different sexes appear to be exploiting similar carbon pools (habitats), and feeding at similar trophic levels even though the exact species compositions of the diets are different. This contrasts with the sexually size-dimorphic gray seal which shows pronounced differences between males and females in diving (Beck *et al.* 2003) and seasonal sex segregation in habitat use (Breed *et al.* 2006), presumably accounting for the large differences in stable isotope values (Tucker *et al.* 2007).

Each species displayed a similar ontogenetic diet shift characterized by a change in the main carbon source exploited as seals got older. δ^{13}C values increased with size and age, indicating that seals exploit/forage in deeper habitats as they get larger and older. Finding similar slopes among species suggests a common factor driving dietary changes with body size despite species differences in diet, foraging behavior, habitat, and distribution.

Following the retreat of pack ice in spring, both harp and hooded seals appear to follow a similar northward migration pattern each year spanning thousands of kilometers, irrespective of sex and age, and return south in winter. Granted, for both harp and hooded seals we have little information on ontogenetic differences in movement patterns, although all age classes of both sexes are observed over the entire range (*e.g.*, this study, Folkow *et al.* 2004). However, foraging range generally increases with age in pinnipeds (*e.g.*, Field *et al.* 2005). δ^{13}C becomes lower with increasing latitude (Newsome *et al.* 2010). Therefore, if adult seals systematically foraged in higher latitudes relative to juveniles, we might expect them to have lower δ^{13}C values, all else being equal. The opposite pattern was observed. Therefore, while a latitude effect may contribute to variation in carbon isotope values between individuals, as some individuals might range further north, it is likely not systematic between demographic groups (species, age-classes, and sex). Latitudinal range is far more restricted in gray seals (Breed 2006) and likely not a large effect on isotope values.

Another possible explanation for this ontogenetic shift in isotope values, without involving a change in diet, is the simple influence of growth on isotope fractionation. In tissues comprised primarily of protein, growth and nutritional status are more likely to impact δ^{15}N (Fuller *et al.* 2005); effects on δ^{13}C typically occur through changes in tissue lipid composition (Newsome *et al.* 2010). In a recent controlled feeding study of birds, there was no effect of growth on δ^{13}C values (Sears *et al.* 2009) consistent with other studies of food restriction (Fuller *et al.* 2005, Kempster *et al.* 2007). Growth affected nitrogen values by 0.37‰–0.55‰ (Sears *et al.* 2009) which is a small effect with respect to the differences noted here between adults and juveniles. As independent diet estimates also have shown ontogenetic diet shifts in all three species (*i.e.*, Lawson and Stenson 1997, Beck *et al.* 2007, Tucker *et al.* 2009), we strongly suspect that changes in seal δ^{13}C values reflect changes in diet concomitant with a change in primary habitat, rather than a growth effect or potential shift in baseline isotope values for the same dietary species. Moreover, we found the same pattern with age (data not shown).

Although classifying animals into demographic groups is a useful and common practice, body size is potentially a more ecologically integrative variable as many aspects related to foraging ability are related to body size (Peters 1983). Conventionally, it is hypothesized that an increase in size with age influences the ability of an individual to obtain prey and expand its foraging niche (*e.g.*, Field *et al.* 2005, 2007) since larger animals are physiologically capable of diving longer and deeper. Both dive duration and dive depth have been found to increase with body mass among marine mammals and birds (Halsey *et al.* 2006). Thus, it is possible that ontogenetic diet differences are a direct function of change in diving skill and behavior as older individuals that can remain at deeper depths longer have greater access to deeper dwelling species (*e.g.*, Field *et al.* 2005, 2007). Although small body size may constrain the diving capacity of juvenile seals ultimately limiting access to prey, it is not clear why adults would consistently switch from pelagic or epipelagic prey, simply because they have the diving capacity to reach more mesopelagic or benthic prey, particularly since pelagic prey tend to have higher energy density than benthic prey in these systems (Beck *et al.* 2007, Tucker *et al.* 2007) and older animals are likely competitively superior to younger, less experienced animals. Yet in all three species, these types of ontogenetic diet shifts have been found (Beck *et al.* 2007, Tucker *et al.* 2009). Thus size may be a proxy for something else, or size influences foraging efficiency.

The interaction between body size, foraging energetics, prey size, prey quality, and feeding behavior is better understood for terrestrial predators (Carbone *et al.* 1999, Sinclair *et al.* 2003, Carbone *et al.* 2007, Owen-Smith and Mills 2008) and for other upper-trophic level aquatic predators (Trudel *et al.* 2001, Pazzia *et al.* 2002, Sherwood *et al.* 2002, Rasmussen *et al.* 2008). In terrestrial animals, predator size often determines dietary overlap (*e.g.,* Radloff and du Toit 2004) and also both the prey size and the type of prey that can be consumed in order to efficiently satisfy energy requirements (Carbone *et al.* 1999). As a result, it is likely that there is an interaction between body size, energy requirements, prey size, and prey availability, as well as the overall efficiency with which prey can be consumed and digested, which drives consistent patterns in resource use and diet in terrestrial animals (Carbone *et al.* 1999, Sinclair *et al.* 2003, Radloff and du Toit 2004). Terrestrial carnivores do not appear to display the same degree of ontogenetic diet shifts as their marine counterparts. Perhaps this is due to longer weaning times and their more social hunting behavior (Sinclair *et al.* 2003). In contrast, phocids are typically weaned abruptly and begin independent foraging soon after birth (Bowen 1991). Ontogenetic diet shifts in fish are thought to reflect the increasing foraging cost of consuming increasingly relatively smaller prey (Piazza *et al.* 2002, Sherwood *et al.* 2002). Typically this diet switch is made in the direction of larger prey, but the underlying operative is decreased foraging costs (Rasmussen *et al.* 2008). Harbor seals (*Phoca vitulina*), fitted with an animal borne video system (Crittercam), used repeated, high-speed pursuit of schools and of individuals when foraging on conspicuous sand lance, but used a slower cruising or a digging tactic when foraging on cryptic sand lance and flounder in the bottom substrate (Bowen *et al.* 2002). Consequently, the estimated profitability (*i.e.*, net energy intake per unit time) of cryptic prey was higher than conspicuous prey. Thus these results suggest that diet selection, in particular as it relates to pursuit and handling costs, have important implications on the foraging energetics of pinnipeds in general.

We hypothesize that diet shifts reduce foraging costs since foraging costs are the largest fraction of the energy budget (Sparling and Fedak 2004), and are not simply a matter of increased access to different prey due to increased diving capacity, foraging range and altered behavior. Activity costs, which include such extraneous costs as swimming, foraging, and other behavioral activities, are typically estimated to be at least twice basal metabolic costs (*e.g.*, Hammill and Stenson 2000, Trzcinski *et al.* 2006). Thus, a progressive adjustment might be made by minimizing foraging costs since these are such a large component of the energy budget. As observed in the harbor seal example, foraging costs may be reduced on more sedentary, benthic prey, despite their lower quality. On the other hand, foraging costs on highly mobile prey for large bodied adults may be too large for them to be beneficial. Another feature of a diet based more on benthic prey species is that it may be relatively more predictable in time and space given the typically higher recruitment variability in small pelagics (Frank *et al.* 2005). This increased predictability may make benthic resource increasing attractive for large individuals with absolute greater food requirement compared to juveniles, despite having to forage at greater depths. Notwithstanding greater predictability of resources, higher relative costs related to growth or pregnancy might actually confine animals to feed within pelagic food webs given the higher energy return (Keiver *et al.* 1984, Costa *et al.* 1989, Martensson *et al.* 1994).

All seals are shifting the primary source of energy derivation as they grow. While there was a degree of overlap in stable isotope values, species differences were maintained over their lives. There is also overlap in body size among all species. In particular, gray seals are of a similar size range as hooded seals over their lifespan. Therefore, the general relationship between body size and dive depth does not always hold true between species (Halsey *et al.* 2006). Strictly from a body size perspective, either gray seals under-perform with respect to their dive performance, or hooded seals are over-achieving. Therefore, interspecific segregation in isotope values appears to be more aligned with differences in diving physiology and subsequent dive performance. Diving marine mammals and birds have a number of important physiological adaptations conferring greater mass-specific oxygen storage capacities than their terrestrial relatives (Halsey *et al.* 2006). Like other pinnipeds, both harp and hooded seals have achieved their large total body oxygen stores (TBO_2) stores by elevating both their blood and muscle oxygen stores. Burns *et al.* (2007) found that harp and hooded seal adults have large TBO_2 stores, due primarily to very high concentrations of muscle myoglobin (Mb); among the highest recorded in any marine mammal. Thus, the higher Mb in the major swimming muscles of hooded seals fits with their deep diving behavior (Folkow and Blix 1999). Harp seals might have elevated stores due to their more active locomotory patterns (Burns *et al.* 2007). For their size, gray seals have very moderate TBO_2 stores (Burns *et al.* 2007) due to relatively lower Mb in muscle (Noren *et al.* 2005). In marine mammal species and in particular amongst the pinnipeds studied to date, muscle myoglobin concentrations reaches adult values at some point soon after independent foraging has begun, including the three species under consideration here (Noren *et al.* 2005, Burns *et al.* 2007).

We have taken a comparative approach to explore niche partitioning both between and within three seal species. Even in the absence of explicit prey values, stable isotopes can be useful to indicate representative trophic relationships related more to functional patterns of feeding (*i.e.*, demersal-pelagic, inshore-offshore). Our results show that these species are segregated with respect to energy sources they exploit. This is reflected in species differences in dive behavior and dive physiology. Our results also reveal that over the course of their lives, these species systematically switch the primary prey source they exploit, relying more heavily on deeper prey. This appears to be a pattern observed in other pinniped species, as juveniles typically have lower carbon values than adults (*i.e.*, Holst *et al.* 2001, Zhao *et al.* 2004, Drago *et al.* 2009, Bailleul *et al.* 2010, Young *et al.* 2010, Zeppelin and Orr 2010). Given similar patterns among these three species, relative to body size, and evidence from several other species, we hypothesize such shifts may be widespread response to changes in foraging energetics, likely offsetting increasing energy demands with reduced foraging costs.

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Literature Cited

Andersen, J. M., Y. F. Wiersma, G. B. Stenson, M. O. Hammill and A. Rosing-Asvid. 2009. Movement patterns of hooded seals (*Cystophora cristata*) in the Northwest Atlantic Ocean during the post-moult and pre-breed seasons. Journal of Northwest Atlantic Fisheries Society 42:1–11.

Austin, D., W. D. Bowen and J. I. McMillan. 2004. Intraspecific variation in movement patterns: Modeling individual behaviour in a large marine predator. Oikos 150:15–30.

Bailleul, F., M. Authier, S. Ducatez, F. Roquet, J.-B. Charrassin, Y. Cherel and C. Guinet. 2010. Looking at the unseen: Combining animal bio-logging and stable isotopes to reveal a shift in the ecological niche of a deep diving predator. Ecography 33:709–719.

Bajzak, C. E., S. D Côte, M. O. Hammill and G. B. Stenson. 2009. Intersexual differences in the postbreeding foraging behavior of the Northwest Atlantic hooded seal. Marine Ecology Progress Series 385:285–294.

Beck, C. A., W. D. Bowen, J. I. McMillan and S. J. Iverson. 2003. Sex differences in the diving behaviour of a size-dimorphic capital breeder: The grey seal. Animal Behaviour 66:777–789.

Beck, C. A., S. J. Iverson, W. D. Bowen and W. Blanchard. 2007. Sex differences in grey seal diet reflect seasonal variation in foraging behaviour and reproductive expenditure: Evidence from quantitative fatty acid signature analysis. Journal of Animal Ecology 76:490–502.

Bolnick, D. I., R. Svanback, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey and M. L. Forister. 2003. The ecology of individuals: Incidence and implications of individual specialization. The American Naturalist 1:1–28.

Bowen, W. D. 1991. Behavioural ecology of pinniped neonates. Pages 66–127 *in* D. Renouf, ed. Behaviour of pinnipeds. Chapman and Hall, London, U.K.

Bowen, W. D., and G. Harrison. 2007. Seasonal and interannual variability in grey seal diets on Sable Island, eastern Scotian Shelf, p. 123–134. Nammco Scientific Publications, The North Atlantic Marine Mammal Commission, Tromso, NO.

Bowen, W. D., and S. J. Iverson. In press. Methods of estimating marine mammal diets: A review of validation experiments and sources of bias and uncertainty. Marine Mammal Science. doi:10.1111/j.1748-7692.2012.00604.x.

Bowen, W. D., D. E. Sergeant and T. Oritsland. 1983. Validation of age determination in the harp seal, *Phoca groenlandica*, using dentinal annuli. Canadian Journal of Fisheries and Aquatic Sciences 40:1430–1441.

Bowen, W. D., O. T. Oftedal and D. J. Boness. 1992. Mass and energy transfer during lactation in a small phocid, the harbor seal (*Phoca vitulina*). Physiological Zoology 65:844–866.

Bowen, W. D., D. Tully, D. J. Boness, B. M. Bulheier and G. J. Marshall. 2002. Prey-dependent foraging tactics and prey profitability in a marine mammal. Marine Ecology Progress Series 244:235–245.

Bowen, W. D., C. A. Beck, S. J. Iverson, D. Austin and J. I. McMillan. 2006. Linking predator foraging behaviour and diet with variability in continental shelf ecosystems: Grey seals of eastern Canada. Pages 63–89 *in* I. L. Boyd, S. Wanless and C. J. Camphuysen eds. Top predators in marine ecosystem. Cambridge University Press, Cambridge, U.K.

Breed, G. A. 2008. State-space analyses indicate experience, prey availability, competition, and reproductive status drive foraging behaviour in a top marine predator. Ph.D. dissertation, Dalhousie University, Halifax, Canada. 201 pp.

Breed, G. A., W. D. Bowen, J. I. McMillan and M. L. Leonard. 2006. Sexual segregation of seasonal foraging habitats in a non-migratory marine mammal. Proceedings of the Royal Society B 273:2319–2326.

Breed, G. A., I. D. Jonsen, R. A. Myers, W. D. Bowen and M. L. Leonard. 2009. Sex-specific, seasonal foraging tactics of adult grey seals (*Halichoerus grypus*) revealed by state–space analysis. Ecology 90:3209–3221.

Burns, J. M., K. C. Lestyk, L. P. Folkow, M. O. Hammill and A. S. Blix. 2007. Size and distribution of oxygen stores in harp and hooded seals from birth to maturity. Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology 177:687–700.

Carbone, C., G. M. Mace, S. G. Roberts and D. W. Macdonald. 1999. Energetic constraints on the diet of terrestrial carnivores. Nature 402:286–288.

Carbone, C., A. Teacher and J. M. Rowcliffe. 2007. The costs of carnivory. PLoS BIOLOGY 5:363–368.

Chabot, D., G. B. Stenson and N. G. Cadigan. 1996. Short- and Long-term Fluctuations in the Size and Condition of Harp Seal (*Phoca groenlandica*) in the Northwest Atlantic. NAFO Science Council Studies 26:15–32.

Chabot, D., M. J. Leblanc, G. B. Stenson, F. O. Kapel and C. Audet. 2006. Growth and condition of hooded seal (*Cystophora cristata*): Seasonal and density effects. Joint ICES/NAFO Working Group on Harp and Hooded Seals ICES HQ WPSEA-161. 37 pp.

Cherel, Y., and K. A. Hobson. 2007. Geographical variation in carbon stable isotope signatures of marine predators: A tool to investigate their foraging areas in the Southern Ocean. Marine Ecology Progress Series 329:281–287.

Costa, D. P., J. P. Croxall and C. D. Duck. 1989. Foraging energetics of antarctic fur seals in relation to changes in prey availability. Ecology 70:596–606.

Drago, M., L. Cardona, E. A. Crespo and A. Aguilar. 2009. Ontogenetic dietary changes in South American sea lions. Journal of Zoology 279:251–261.

Field, I. C., C. J. A. Bradshaw, H. R. Burton, M. D. Sumner and M. A. Hindell. 2005. Resource partitioning through oceanic segregation of foraging juvenile southern elephant seals (*Mirounga leonina*). Oecologia 142:127–135.

Field, I. C., C. J. A. Bradshaw, J. van den Hoff, H. R. Burton and M. A. Hindell. 2007. Age-related shifts in the diet composition of southern elephant seals expand overall foraging niche. Marine Biology 150:1441–1452.

Folkow, L. P., and A. S. Blix. 1999. Diving behaviour of hooded seals (*Cystophora cristata*) in the Greenland and Norwegian Seas. Polar Biology 22:61–74.

Folkow, L. P., P. Martensson and A. S. Blix. 1996. Annual distribution of hooded seals (*Cystophora cristata*) in the Greenland and Norwegian Seas. Polar Biology 16:179–189.

Folkow, L. P., E. S. Nordøy and A. S. Blix. 2004. Distribution and diving behaviour of harp seals (*Pagophilus groenlandicus*) from the Greenland Sea stock. Polar Biology 27:281–298.

Frank, K. T., B. Petrie, J. S. Choi and W. C. Leggett. 2005. Trophic cascades in a formerly cod-dominated ecosystem. Science 308:1621–1623.

Froese, R., and D. Pauly. 2011. FishBase, version (06/2011). Available at http://www.fishbase.org.

Fuller, B. T., J. L. Fuller, N. E. Sage, D. A. Harris, T. C. O'Connell and R. E. Hedges. 2005. Nitrogen balance and δ15N: Why you're not what you eat during nutritional stress. Rapid Communications in Mass Spectrometry 19:2497–2506.

Greene, C. H., A. J. Pershing, T. M. Cronin and N. Ceci. 2008. Arctic climate change and its impacts on the ecology of the North Atlantic. Ecology 89:S24–S38.

Halsey, L. G., T. M. Blackburn and P. J. Butler. 2006. A comparative analysis of the diving behaviour of birds and mammals. Functional Ecology 20:889–899.

Hammill, M. O., and G. B. Stenson. 2000. Estimated prey consumption by harp seals (*Phoca groenlandica*), hooded seals (*Cystophora cristata*), grey seals, (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) in Atlantic Canada. Journal of Northwest Atlantic Fishery Science 26:1–23.

Hammill, M. O., and G. B. Stenson. 2006. Abundance of Northwest Atlantic hooded seals (1960–2005). DFO Canada. Canadian Science Advisory Secretariat Research Document 2006/068. 19 pp. Available at http://www.dfo-mpo.gc.ca/csas/.

Haug, T., K. T. Nilssen and L. Lindblom. 2004. Feeding habits of harp and hooded seals in drift ice waters along the east coast of Greenland in summer and winter. Polar Research 23:35–42.

Haug, T., K. T. Nilssen, L. Lindblom and U. Lindstrøm. 2007. Diets of hooded seals (*Cystophora cristata*) in coastal waters and drift ice waters along the east coast of Greenland. Marine Biology Research 3:123–133.

Hobson, K. A., and H. E. Welch. 1992. Determination of trophic relationships within a high Arctic marine food web using δ^{13}C and δ^{15}N analysis. Marine Ecology Progress Series 84:9–18.

Hobson, K. A., D. M. Schell, D. Renouf, E. Noseworthy and E . 1996. Stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: Implications for dietary reconstructions involving marine mammals. Canadian Journal of Fisheries and Aquatic Sciences 53:528–533.

Holst, M., I. Stirling and K. A. Hobson. 2001. Diet of ringed seals (*Phoca hispida*) on the east and west sides of the north water polynya, northern Baffin Bay. Marine Mammal Science 17:888–908.

Jeglinski, J. W. E., C. Werner, P. W. Robinson, D. P. Costa and F. Trillmich. 2012. Age, body mass and environmental variation shape the foraging ontogeny of Galapagos sea lions. Marine Ecology Progress Series 453:279–296.

Keiver, K. M., K. Ronald and F. W. H. Beamish. 1984. Metabolizable energy requirements for maintenance and faecal and urinary losses of juvenile harp seals (*Phoca groenlandica*). Canadian Journal of Zoology 62:769–776.

Kempster, B., L. Zanette, F. J. Longstaffe, S. A. MacDougall-Shackleton, J. C. Wingfield and M. Clinchy. 2007. Do stable isotopes reflect nutritional stress? Results from a laboratory experiment on song sparrows. Oecologia 151:365–371.

Kurle, C. M., and G. A. J. Worthy. 2002. Stable nitrogen and carbon isotope ratios in multiple tissues of the northern fur seal *Callorhinus ursinus*: Implications for dietary and migratory reconstructions. Marine Ecology Progress Series 236:289–300.

Lawson, J. W., and G. B. Stenson. 1997. Diet of Northwest Atlantic harp seals (*Phoca groenlandica*) in offshore areas. Canadian Journal of Zoology 75:2095–2106.

Lawson, J. W., G. B. Stenson and D. G. McKinnon. 1995. Diet of harp seals (*Phoca groenlandica*) in nearshore waters of the northwest Atlantic during 1990–1993. Canadian Journal of Zoology 73:1805–1818.

Lawson, J. W., J. T. Anderson, E. L. Dalley and G. B. Stenson. 1998. Selective foraging by harp seals *Phoca groenlandica* in nearshore and offshore waters of Newfoundland, 1993 and 1994. Marine Ecology Progress Series 163:1–10.

Lesage, V., M. O. Hammill and K. M. Kovacs. 2001. Marine mammals and the community structure of the Estuary and Gulf of St Lawrence, Canada: Evidence from stable isotope analysis. Marine Ecology Progress Series 210:203–221.

Martensson, P. E., E. S. Nordøy and A. S. Blix. 1994. Digestibility of crustaceans and capelin in harp seals (*Phoca groenlandica*). Marine Mammal Science 10:325–331.

McConnaughey, T., and C. P. McRoy. 1979. Food web structure and the fractionation of carbon isotopes in the Bering Sea. Marine Biology 53:257–262.

McMeans, B. C., J. Svavarsson, S. Dennard and A. T. Fisk. 2010. Diet and resource use among Greenland sharks (*Somniosus microcephalus*) and teleosts sampled in Icelandic waters, using δ^{13}C, δ^{15}N, and mercury. Canadian Journal of Fisheries and Aquatic Sciences 67:1428–1438.

Newland, C., I. C. Field, Y. Cherel, C. Guinet, C. J. A. Bradshaw, C. R. McMahon and M. A. Hindell. 2011. Diet of juvenile southern elephant seals reappraised by stable isotopes in whiskers. Marine Ecology Progress Series 424:247–258.

Newsome, S. D., M. A. Etnier, C. M. Kurle, J. R. Waldbauer, C. P. Chamberlain and P. L. Koch. 2007. Historic decline in primary productivity in western Gulf of Alaska and eastern Bering Sea: Isotopic analysis of northern fur seal teeth. Marine Ecology Progress Series 332:211–224.

Newsome, S. D., M. R. Clementz and P. L. Koch. 2010. Using stable isotope biochemistry to study marine mammal ecology. Marine Mammal Science 26:509–572.

Nordøy, E. S., L. P. Folkow, V. Potelov, V. Prischemikhin and A. S. Blix. 2008. Seasonal distribution and dive behaviour of harp seals (*Pagophilus groenlandicus*) of the White Sea–Barents Sea stock. Polar Biology 31:1119–1135.

Noren, S. R., S. J. Iverson and D. J. Boness. 2005. Development of the blood and muscle oxygen stores in gray seals (*Halichoerus grypus*): Implications for juvenile diving capacity and the necessity of a terrestrial postweaning fast. Physiological and Biochemical Zoology 78:482–490.

Owen-Smith, N., and M. G. L. Mills. 2008. Predator–prey size relationships in an African large-mammal food web. Journal of Animal Ecology 77:173–183.

Pazzia, I., M. Trudel, M. Ridgway and J. B. Rasmussen. 2002. Influence of food web structure on the growth and bioenergetics of lake trout (*Salvelinus namaycush*). Canadian Journal of Fisheries and Aquatic Sciences 59:1593–1605.

Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge, U.K.

Pinela, A. M., A. Borrell, L. Cardona and A. Aguilar. 2010. Stable isotope analysis reveals habitat partitioning among marine mammals off the NW African coast and unique trophic niches for two globally threatened species. Marine Ecology Progress Series 416:295–306.

R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Radloff, F. G. T., and J. T. du Toit. 2004. Large predators and their prey in a southern African savanna: A predator's size determines its prey size range. Journal of Animal Ecology 73:410–423.

Rasmussen, J. B., J. M. Gunn, G. D. Sherwood, A. Iles, A. Gagnon, P. G. C. Campbell and A. Hontela. 2008. Direct and indirect (foodweb mediated) effects of metal exposure on the growth of yellow perch (*Perca flavescens*): Implications for ecological risk assessment. Human and Ecological Risk Assessment 14:317–350.

Rosenzweig, M. L. 1968. The strategy of body size in mammalian carnivores. American Midland Naturalist 80:299–315.

Scott, W. B., and M. G. Scott. 1988. Atlantic fishes of Canada. Canadian Bulletin of Fisheries and Aquatic Sciences 219. 731 pp.

Sears, J., S. A. Hatch and D. M. O'Brien. 2009. Disentangling effects of growth and nutritional status on seabird stable isotope ratios. Oecologia 159:41–48.

Shackell, N. L., K. T. Frank, J. A. D. Fisher, B. Petrie and W. C. Leggett. 2010. Decline in top predator body size and changing climate alter trophic structure in an oceanic ecosystem. Proceedings of the Royal Society B 277:1353–1360.

Sherwood, G. D., and G. A. Rose. 2005. Stable isotope analysis of some representative fish and invertebrates of the Newfoundland and Labrador continental shelf food web. Estuarine Coastal and Shelf Science 63:537–549.

Sherwood, G. D., I. Pazzia, A. Moeser, A. Hontela and J. B. Rasmussen. 2002. Shifting gears: Enzymatic evidence for the energetic advantage of switching diet in wild-living fish. Canadian Journal of Fisheries and Aquatic Science 59:229–241.

Sherwood, G. D., R. M. Rideout, S. B. Fudge and G. A. Rose. 2007. Influence of diet on growth, condition and reproductive capacity in Newfoundland and Labrador cod (*Gadus morhua*): Insights from stable carbon isotopes. Deep-Sea Research II 54: 2794–2809.

Sinclair, A. R. E., S. Mduma and J. S. Brashares. 2003. Patterns of predation in a diverse predator-prey system. Nature 425:288–290.

Sjare, B., and G. B. Stenson. 2010. Changes in the reproductive parameters of female harp seals (*Pagophilus groenlandicus*) in the Northwest Atlantic. ICES Journal of Marine Science 67:304–315.

Sparling, C. E., and M. A. Fedak. 2004. Metabolic rates of captive grey seals during voluntary diving. Journal of Experimental Biology 207:1615–1624.

Stenson, G. B., and B. Sjare. 1997. Seasonal distribution of harp seals, *Phoca groenlandica*, in the northwest Atlantic. ICES CM 1997/CC:10. ICES Copenhagen.

Stenson, G. B., R. A. Myers, I. N. Ni and W. G. Warren. 1997. Pup production and population growth of hooded seals (*Cystophora cristata*) near Newfoundland, Canada. Canadian Journal of Fisheries and Aquatic Sciences 54(Supplement 1):209–216.

Stenson, G. B., L.-P. Rivest, M. O. Hammill, J.-F. Gosselin and B. Sjare. 2003. Estimating pup production of harp seals, *Pagophilus groenlandicus*, in the Northwest Atlantic. Marine Mammal Science 19:141–160.

Trudel, M., A. Tremblay, R. Schetagne and J. B. Rasmussen. 2001. Why are dwarf fish so small? An energetic analysis of polymorphism in lake whitefish (*Coregonus clupeaformis).* Canadian Journal of Fisheries and Aquatic Sciences 58:394–405.

Trzcinski, M. K., R. Mohn and W. D. Bowen. 2006. Continued decline of an Atlantic cod population: How important is gray seal predation? Ecological Applications 16:2276–2292.

Tucker, S., W. D. Bowen and S. J. Iverson. 2007. Dimensions of diet segregation in grey seals *Halichoerus grypus* revealed through stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$). Marine Ecology Progress Series 339:271–282.

Tucker, S., W. D. Bowen and S. J. Iverson. 2008. Convergence of diet estimates derived from fatty acids and stable isotopes: Support for long-term integrators of natural diets within individual grey seals. Marine Ecology Progress Series 354:267–276.

Tucker, S., W. D. Bowen, S. J. Iverson, W. Blanchard and G. B. Stenson. 2009. Sources of variation in diets of harp and hooded seals estimated from quantitative fatty acid signature analysis (QFASA). Marine Ecology Progress Series 384:287–302.

Young, B. G., L. L. Loseto and S. H. Ferguson. 2010. Diet differences among age classes of Arctic seals: Evidence from stable isotope and mercury biomarkers. Polar Biology 33:153 –162.

Zeppelin, T. K., and A. J. Orr. 2010. Stable isotope and scat analyses indicate diet and habitat partitioning in northern fur seals *Callorhinus ursinus* across the eastern Pacific. Marine Ecology Progress Series 409:241–253.

Zhao, L., M. A. Castellini, T. L. Mau and S. J. Trumble. 2004. Trophic interactions of Antarctic seals as determined by stable isotope signatures. Polar Biology 27:368–373.

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