

Sex differences in grey seal diet reflect seasonal variation in foraging behaviour and reproductive expenditure: evidence from quantitative fatty acid signature analysis

CARRIE A. BECK, SARA J. IVERSON, W. DON BOWEN* and
WADE BLANCHARD†

Department of Biology, Dalhousie University, Halifax, Nova Scotia, B3H 4J1, Canada; *Marine Fish Division, Bedford Institute of Oceanography, Department of Fisheries and Oceans, Dartmouth, Nova Scotia, B2Y 4A2, Canada; and †Department of Mathematics and Statistics, Dalhousie University, Halifax, Nova Scotia, B3H 4J1, Canada

Summary

1. Intraspecific variation in diet can be an important component of a species niche breadth. We tested the hypothesis that sex differences in seasonal foraging behaviour and energy storage of sexually size dimorphic grey seals *Halichoerus grypus* (Fabricius 1971) are reflected in differences in the diet and niche breadth. Diet composition was estimated for 496 adult (226 males, 270 females) and 91 juvenile (46 males/45 females; all 6 months old) grey seals sampled between 1993 and 2000 using quantitative fatty acid signature analysis. Niche breadth and overlap were estimated using the Shannon–Weaver diversity index (H') and the Morisita–Horn index (C_H), respectively.

2. Sand lance *Ammodytes dubius* (Reinhardt 1837) and redfish *Sebastes* sp. (Cuvier 1829) accounted for a high proportion of the diet in both sexes and age groups. However, the diets of adult males were significantly more diverse across all seasons (H' : males 0.36 ± 0.007 vs. females 0.28 ± 0.007) and less energy dense in spring (male 5.3 ± 0.07 kJ g⁻¹ vs. females 5.6 ± 0.09 kJ g⁻¹) than those of adult females.

3. Season and sex explained most of the observed variation in adult diets, but there were significant sex–season interactions. These differences were most evident during the post-breeding (spring) foraging period when energy acquisition is important to female recovery of nutrient stores needed to support pregnancy. Females selected fewer and higher quality prey species in spring than males.

4. There were no sex differences in the diets of juvenile grey seals. Although many of the species overlapped with those eaten by adults, juvenile niche breadth (H' : 0.41 ± 0.014 , $n = 91$) was significantly broader than that of adults (H' : 0.30 ± 0.011 , $n = 115$). Juvenile diets were also of lower energy density (5.3 ± 0.04 kJ g⁻¹) than those of adults (5.6 ± 0.09 kJ g⁻¹), suggesting less selectivity in these young and relatively naïve predators.

5. Sex-specific seasonal changes in diet correspond to seasonal changes in diving behaviour and rate of body energy accumulation of adult males and females. Sex-specific reproductive requirements appear to be a primary factor generating the intraspecific variation in the seasonal foraging ecology of this large marine carnivore. However, sex differences in the breadth and energy content of diets also suggest the influence of body-size dimorphism as a factor shaping the diet of this species.

Key-words: diversity, niche breath, pinniped, size dimorphism.

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Introduction

An understanding of carnivore diets and the factors influencing what is consumed are central issues in determining how predation may impact prey populations. This is particularly important in evaluating predation effects on commercially harvested species (Mohn and Bowen 1996; Yodzis 1998) or those of conservation concern (Estes *et al.* 1998). However, for many carnivore species, our understanding of what is eaten, how diet is influenced by foraging behaviour, and the consequences of diet and foraging on predator body condition is often quite limited. This is partly due to the fact that predator diets are influenced by factors that are intrinsic to the individual (e.g. age, size) and those that are features of their environment (e.g. prey size, diversity and abundance in time and space), both of which are often difficult to measure.

Failure to account for within-species differences in diet can bias our understanding of predation effects by underestimating dietary niche breadth (Polis 1984; Forero *et al.* 2002). Sex is an intrinsic factor that is commonly associated with intraspecific differences in diet in a variety of taxa (e.g. birds, Weimerskirch *et al.* 1997; reptiles, Parmelee and Guyer 1995; invertebrates, Jormalainen *et al.* 2001; mammals, Clutton-Brock, Guinness and Albon 1982). Several, nonmutually exclusive hypotheses have been advanced to account for such sex differences. The reproductive decisions hypothesis attributes sex differences in foraging behaviour and the resulting diets to the differing trade-offs between foraging and other vital activities (e.g. predator avoidance, provisioning of young, mate acquisition) faced by each sex to maximize individual fitness (Clutton-Brock and Parker 1992; Jormalainen *et al.* 2001). This hypothesis does not generally make specific predictions about the diet of each sex, but evidence from the marine isopod, *Idotea baltica*, indicates that sex-specific fitness maximizing strategies may result in the sexes consuming different diets (Jormalainen *et al.* 2001). The sexual size-dimorphism hypothesis predicts that differences in energy requirements of males and females, based on differences in body size, can account for sex-specific foraging behaviour (Clutton-Brock, Iason and Guinness 1987; Nagy 1987; Mysterud 2000). Thus, in size-dimorphic species, the larger sex may consume more of the same foods eaten by the smaller sex or consume a different diet in order to satisfy its higher energy requirements (Clutton-Brock *et al.* 1982). Finally, the niche divergence hypothesis is based on the fitness benefit of reducing intraspecific competition by each sex foraging in different locations or on different prey species or both (Schoener 1970; Clarke *et al.* 1998).

Relatively little is known about sex differences in the diets of marine carnivores, even though clear sex differences in foraging behaviour have been reported in northern, *Mirounga augustirostris*, and southern, *M. leonina*, elephant seals (Slip, Hindell and Burton 1994; Le Boeuf *et al.* 2000) and in grey seals *Halichoerus grypus* (Beck *et al.* 2003a,b). The diets of these species are poorly known because prey are consumed at depth and at remote

locations where foraging cannot be observed. Furthermore, estimating diet in marine carnivores from the recovery of prey hard parts found in faecal samples or stomach contents often involve substantial biases due to rapid and differential digestion of prey (Jobling and Breiby 1986; Harvey 1989; Bowen 2000). Thus, in the case of wide-ranging species, the faecal or stomach sample obtained may not be representative of longer-term diet. By contrast, inferences about diet from fatty acids (FA) do not rely on the recovery of prey hard parts and reflect dietary intake over weeks or months (Rouvinen and Kiiskinen 1989; Kirsch, Iverson and Bowen 2000). The diverse array of FA in marine ecosystems (Ackman 1980) are deposited in predator adipose tissue in a predictable manner (Lhuillery *et al.* 1988; Summer *et al.* 2000; Iverson *et al.* 2004), such that the FA profile of a predator's lipid depots reflects that of the prey consumed (e.g. Pond *et al.* 1995; Raclot, Groscolas and Chérel 1998; Iverson, McDonald and Smith 2001a).

Multivariate analyses of predator FA signatures have been used to infer differences in the diets of pinnipeds (e.g. Iverson, Frost and Lowry 1997; Walton and Pomeroy 2003), cetaceans (Borobia *et al.* 1995), terrestrial carnivores (Pond *et al.* 1995; Iverson *et al.* 2001a), penguins (Raclot *et al.* 1998) and fish (Logan *et al.* 2000) without attempting to specify the prey species consumed. Although this is a useful approach, it falls short of providing an estimate of the prey species consumed and their relative contribution to the energy requirements of predators. Here we estimate the species composition of diet for adult male and female grey seals using quantitative FA signature analysis (QFASA, Iverson *et al.* 2004). This method provides estimates of diet by determining the weighted combination of prey FA signatures that best matches the FA composition of the predator.

Grey seals are size-dimorphic, marine carnivores in which adult males are approximately 50% heavier than adult females throughout the year (Beck, Bowen and Iverson 2003c). This size dimorphism is evident early in life with males being 8% heavier than females at weaning (Hall, McConnell and Barker 2001). They are a long-lived species with males living > 30 years and females > 40 years. Females are capital breeders, fasting during a 16-day lactation period during which they provision a single offspring with high-fat milk (Mellish, Iverson and Bowen 2000). Females leave the breeding colony having used 62–68% of their lipid stores (Mellish, Iverson and Bowen 1999; Beck *et al.* 2003c). Males also fast or substantially reduce feeding during the breeding season such that they too can be regarded as capital breeders (Lidgard *et al.* 2005). In the North-west Atlantic population, movement data from satellite tracking and geolocation tags indicate broad overlap in the foraging distributions of adult males and females during the summer and fall, but marked sex segregation during the several months before the breeding season and again during the post-breeding period (Beck 2002; Breed *et al.* 2006). During the 8 months between spring pelage moult and the January breeding season, males and females

also exhibit significantly different seasonal patterns of diving behaviour, energy storage (Beck *et al.* 2003a,b,c) and foraging tactics (Austin, Bowen and McMillan 2004).

These differences in behaviour and physiology suggest that the sexes exhibit quite different foraging strategies. Our objective here was to test the hypothesis that these seasonal sex differences in foraging behaviour and energy accumulation of adult grey seals were reflected in differences in diets and dietary niche breadth. We expected that males, the larger sex, would have a wider dietary niche than females because of their greater energetic requirements and physiological ability (larger breath-hold capacity) to exploit a greater range of habitats and prey quality (Ginnett and Demment 1997). We predicted that females would consume higher quality prey than males during the post-breeding period as females recover body condition early in the year to support pregnancy (Boyd 1984; Pitcher, Calkins and Pendleton 1998), whereas males do not. Finally, we predicted that the diets of males and females would be most similar during the several months leading up to the breeding season, when both sexes prepare for the high energetic expenditures associated with reproduction by storing energy in the form of blubber.

Intraspecific differences in diet can also arise as a result of ontogenetic changes (e.g. Polis 1984; Bundy, Lilly and Shelton 2000; Forero *et al.* 2002). Age structure can be an important component of total niche width in other taxa (Polis 1984), but has been rarely examined in a marine carnivore. We examined evidence for ontogenetic changes in grey seals by comparing the diet of adults with those of juveniles with only 6 months of foraging experience. We predicted that the diets of inexperienced juveniles would not differ significantly with sex, given that they are nonreproductive and that males are only about 5% heavier than females at this age ($n = 24$ males and 24 females; Cooper, Bowen and Iverson, unpublished). A similar lack of sex differences in foraging behaviour of juvenile southern elephant seals has been observed and attributed to the lack of reproductive expenses and sexual size dimorphism of individuals at this young age (Field *et al.* 2005). However, we did expect the diets of juvenile grey seals to be more diverse than those of adults (Polis 1984) on the assumption that they would exhibit less preference for prey than adults with many years of foraging experience (Smith and Metcalfe 1997; Forero *et al.* 2002).

Methods

FIELD SAMPLING

The study was carried out between May 1993 and January 2001 on Sable Island (43°55'N, 60°00'W), a crescent-shaped, vegetated sandbar 288 km south-east of Halifax, Nova Scotia, Canada. Sable Island supports the largest breeding colony of grey seals in the world (Bowen, McMillan and Mohn 2003) and large numbers of seals are present on the island and in the surrounding waters throughout the year.

Adult grey seals were captured on-shore using hand-held nets (Bowen, Oftedal and Boness 1992). Our sample of adults and juveniles was unselective; with the constraints that equal numbers of both sexes were caught and that only one blubber sample per identifiable animal (i.e. previously branded or tagged) was used for these analyses. Full-depth blubber biopsies were taken from individuals during the moult (May–June), in late fall (late September/early October) or early in the breeding season (late December/early January) following Kirschet *et al.* (2000). Prey FA are deposited in adipose tissue (i.e. blubber) over time (Cooper 2004; Iverson *et al.* 2004), such that the FA composition of grey seal blubber samples taken at the above times reflect the integration of diet consumed in spring, summer and fall/early winter, respectively. The spring diets of 6-month-old juveniles were estimated from blubber FA compositions sampled in June, using the same methods.

Biopsies were wrapped in aluminium foil and kept chilled for several hours until placed in a solution of 2 : 1 chloroform : methanol containing 0.01% 2,6-di-*tert*-butyl-4-methyl-phenol (BHT) and stored frozen until analysis.

LABORATORY PROCEDURES

Lipid was extracted from each blubber biopsy with chloroform (Iverson, Lang and Cooper 2001b). FA methyl esters (FAME) were prepared from *c.* 100 mg of the pure lipid (filtered and dried over anhydrous sodium sulphate) by transesterification using 1.5 mL 8% anhydrous boron trifluoride in methanol (v/v) and 1.5 mL of hexane, capped under nitrogen and heated for 1 h at 100 °C. FAME were then extracted into hexane, concentrated and brought up to volume (50 mg mL⁻¹) with high purity hexane.

FAME were analysed in duplicate using temperature-programmed gas liquid chromatography according to Iverson *et al.* (1997) and Budge, Cooper and Iverson (2004) on a Perkin Elmer Autosystem II Capillary FID gas chromatograph fitted with a 30 m by 0.25 mm i.d. column coated with 50% cyanopropyl poly siloxane (0.25 µm film thickness; J and W DB-23; Folsom, CA, USA) and linked to a computerized integration system (Turbochrom 4 software, PE Nelson, Woodbridge, Ontario, Canada). FA are expressed as mass percentage of total FA and are designated by the shorthand nomenclature of carbon chain length: number of double bonds and location ($n-x$) of the double bond nearest the terminal methyl group.

DIET ESTIMATION

The diet of each grey seal was estimated using QFASA (Iverson *et al.* 2004), following a two-step procedure. In the first step, a statistical model was used to estimate the mixture of prey FA signatures (FAS_p) that minimize the Kullback–Leibler distance between that mixture and the FA composition of each seal. We used 39 of the 67 quantified FA (Table 1) known to be derived solely or largely from diet (Iverson *et al.* 2004). In the second step, the estimated mixture of prey species was converted to

Table 1. Fatty acids used for diet estimation by quantitative fatty acid signature analysis. Values indicate the proportion that each fatty acid contributed to the average fatty acid profile of adult grey seals ($n = 485$). In total, 67 individuals FA identified and quantified in the FA profile of each grey seal, however, only these 39 dietary FA were used in the QFASA model

Fatty Acid	Mean \pm SE	Fatty Acid	Mean \pm SE
14:0	4.51 \pm 0.034	18:4n-1	0.21 \pm 0.004
16:0	9.00 \pm 0.074	20:1n-11	2.21 \pm 0.031
16:1n-11	0.45 \pm 0.003	20:1n-9	8.23 \pm 0.087
16:1n-9	0.36 \pm 0.005	20:1n-7	0.66 \pm 0.010
16:1n-7	13.06 \pm 0.075	20:2n-6	0.19 \pm 0.002
16:2n-6	0.75 \pm 0.001	20:3n-6	0.07 \pm 0.001
16:2n-4	0.28 \pm 0.003	20:4n-6	0.43 \pm 0.007
16:3n-6	0.51 \pm 0.006	20:3n-3	0.06 \pm 0.001
16:3n-4	0.32 \pm 0.005	20:4n-3	0.52 \pm 0.004
16:4n-1	0.60 \pm 0.014	20:5n-3	6.11 \pm 0.071
18:0	0.99 \pm 0.010	22:1n-11	3.67 \pm 0.080
18:1n-9	13.22 \pm 0.152	22:1n-9	0.63 \pm 0.012
18:1n-7	4.26 \pm 0.042	22:1n-7	0.09 \pm 0.002
18:1n-5	0.45 \pm 0.002	21:5n-3	0.45 \pm 0.003
18:2n-6	1.26 \pm 0.010	22:4n-6	0.14 \pm 0.003
18:2n-4	0.14 \pm 0.001	22:5n-6	0.19 \pm 0.003
18:3n-6	0.05 \pm 0.001	22:4n-3	0.11 \pm 0.001
18:3n-4	0.10 \pm 0.002	22:5n-3	5.49 \pm 0.033
18:3n-3	0.50 \pm 0.006	22:6n-3	11.63 \pm 0.099
18:4n-3	1.11 \pm 0.015		

Total = 92.32 \pm 0.057% of fatty acids identified.

an estimate of diet by weighting each prey species by its relative seasonal fat content (i.e. its FA contribution to the FA composition of the predator).

QFASA requires that a broad range of potential FAS_p be sampled, as species not included in the model cannot be estimated. We used a prey library comprising 2110 individual prey representing 28 species (≥ 12 individuals/prey species) of fishes and invertebrates that were collected throughout the grey seal range between 1993 and 2001 (Budge *et al.* 2002; Table 2). Among these species were those known to be eaten by grey seals based on previous stomach content and faecal analyses (e.g. Bowen, Lawson and Beck 1993; Bowen and Harrison 1994) or that were reasonably abundant and found at depths at which grey seals are known to forage (Beck *et al.* 2003a,b). Although prey lipid content can vary seasonally (Iverson, Frost and Lang 2002), there is little evidence that the FA composition of prey differs significantly by season (Iverson *et al.* 2002). Thus, although we accounted for seasonal variability in fat content, the average FAS_p for each species was used to estimate diet in all seasons. FAS_p used in this study are available in Appendix S1 (see Supplementary material).

FAS_p may vary as a function of body length, due mostly to ontogenetic changes in prey diet with size (Budge *et al.* 2002; Iverson *et al.* 2002). Thus, for prey species with ≥ 100 samples we compared the FAS_p of small and large individuals using MANOVA. Size-class cut-points were based on either median prey length in the database or on a length at which significant changes in diet were observed in stomach content data collected from research

trawl surveys and sentinel fisheries on the Scotian Shelf from 1995 to 1999 (A. Bundy pers. comm., Cannalejo *et al.* 1989; Martell and McClelland 1994; Bundy *et al.* 2000). Species whose FAS_p differed significantly by size were then divided into small and large size-classes to estimate the diet of grey seals (Table 2).

Standard errors of the estimated diet include variability within and between seals. Within-seal standard errors were estimated using a bootstrapping procedure that included within-species variability in FAS_p and fat content (Iverson *et al.* 2004). First, new mean FAS_p and mean fat contents were created by resampling with replacement within species and season. Bootstrapped mean FAS_p were then used to estimate the mixture of FAS_p that most closely resembled the FA profile of the individual predator. These estimates were then converted to diet by weighting each prey species by the new fat content. This bootstrapping procedure was performed 1000 times (Iverson *et al.* 2004). The average within-seal standard error for each prey type was calculated as:

$$SE_{wj} = \sqrt{\left(\sum_{i=1}^n SE_{wji}^2 \right) / n}$$

where SE_{wj} is the average within-seal standard error for prey type (j), SE_{wji} is the within standard error for prey type (j) for individual seal (i) using the bootstrapping procedure, and n is the number of seals. Total SE for each prey type (SE_j) was calculated using both the within- and between-seal standard error as follows:

$$\text{Total } SE_j = \sqrt{(SE_{wj}^2 + SE_{bj}^2) / n}$$

where SE_{bj} is the standard error of the mean percentage of the diet accounted for by prey type j between individual seals.

Owing to the effects of predator metabolism, the FA composition of the predator will never match that of the prey consumed (Cook 1991; Iverson *et al.* 2004). Nevertheless, individual FA are deposited in predator lipid stores in predictable ways (Lhuillery *et al.* 1988; Summer *et al.* 2000; Cooper 2004; Iverson *et al.* 2004) such that it is possible to correct for the effects of predator metabolism using calibration coefficients (Iverson *et al.* 2004). Calibration coefficients were determined empirically through experiments in which captive seals were fed diets of known FA composition. We used the average calibration coefficients from studies on grey seal adults and pups as well as juvenile harp seals *Phoca groenlandica* (Erxleben 1777), a closely related phocid species (see Iverson *et al.* 2004 for details). We averaged these data because each experiment involved relatively few individuals.

We used a randomization procedure (Efron and Tibshirani 1998) to compare the diet composition of grey seals by sex, age-class, and season. First, a two-way MANOVA was performed to generate test statistics for main effects and interactions. However, rather than compare test statistics to the normal theory distributions to compute significance levels, we randomly permuted the factor

Table 2. Prey species used to estimate diet composition of adult grey seals in the North-west Atlantic Ocean

Common name	Scientific name and authority	Size-class	<i>n</i>
Forage fish			
Butterfish	<i>Peprilus triacanthus</i> Peck 1804		35
Capelin	<i>Mallotus villosus</i> Müller 1776	Small (≤ 13.5 cm)	88
		Large (> 13.5 cm)	77
Herring	<i>Clupea harengus</i> Linnaeus 1758	Small (≤ 20 cm)	42
		Large (> 20 cm)	205
Mackerel	<i>Scomber scombrus</i> Linnaeus 1758		34
Northern sand lance	<i>Ammodytes dubius</i> Reinhardt 1837	Small (≤ 20 cm)	62
		Large (> 20 cm)	62
Snake blenny	<i>Lumpenus lumpretaeformis</i> Walbaum 1792		18
Gaspereau	<i>Alosa pseudoharengus</i> Wilson 1811		70
Gadids			
Cod	<i>Gadus morhua</i> Linnaeus 1758	Small (≤ 35 cm)	32
		Large (> 35 cm)	115
Haddock	<i>Melanogrammus aeglefinus</i> Linnaeus 1758	Small (≤ 26.5 cm)	69
		Large (> 26.5 cm)	79
Pollock	<i>Pollachius virens</i> Linnaeus 1758	Small (≤ 25 cm)	38
		Large (> 25 cm)	19
Red hake	<i>Urophycis chuss</i> Walbaum 1792		25
Silver hake	<i>Merluccius bilinearis</i> Mitchill 1814	Small (≤ 21.5 cm)	39
		Large (> 21.5 cm)	31
White hake	<i>Urophycis tenuis</i> Mitchill 1814		75
Flounders			
American plaice	<i>Hippoglossoides platessoides</i> Fabricius 1780	Small (≤ 25 cm)	70
		Large (> 25 cm)	78
Halibut	<i>Hippoglossus hippoglossus</i> Linnaeus 1758		13
Turbot	<i>Reinhardtius hippoglossides</i> Walbaum 1792		20
Winter flounder	<i>Pseudopleuronectes americanus</i> Walbaum 1792		90
Witch flounder	<i>Glyptocephalus cynoglossus</i> Linnaeus 1758		40
Yellowtail flounder	<i>Limanda ferruginea</i> Storer 1839		118
Skates			
Thorny skate	<i>Raja radiata</i> Donovan 1808		74
Winter skate	<i>Raja ocellata</i> Mitchill 1815		40
Other fish			
Longhorn sculpin	<i>Myoxocephalus</i>	Small (≤ 25 cm)	26
	<i>Octodecemspinus</i> Mitchill 1814	Large (> 25 cm)	44
Lumpfish	<i>Cyclopterus lumpus</i> Linnaeus 1758		22
Ocean pout	<i>Macrozoarces americanus</i> Bloch and Schneider 1801		31
Redfish	<i>Sebastes</i> sp. Cuvier 1829	Small (≤ 27 cm)	37
		Large (> 27 cm)	47
Invertebrates			
Lobster	<i>Homarus americanus</i> Edwards 1837		21
Shrimp	<i>Pandalus borealis</i> Krøyer 1838		122
Squid	<i>Illex illecebrosus</i> Lesueur 1821		18
Total			2110

labels, 9999 times, to build up a permutation distribution. Significance levels were then computed by calculating how many times the reference distribution gave a test statistic equal to or greater than the observed value. To determine where the significant differences occurred, post hoc tests (multivariate and univariate *t*-tests) were also compared with appropriate reference distributions.

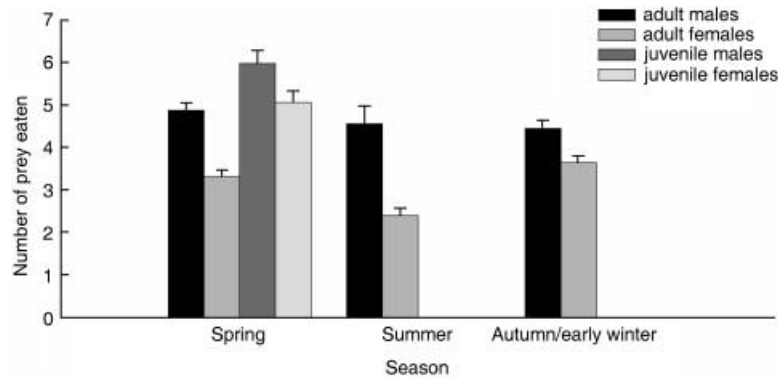
Energy density (kJ g⁻¹) of each seal's diet was calculated using the seasonal proximate composition of prey species (see Appendix S2 in Supplementary material). Diet diversity was calculated using a standardized Shannon–Weiner Index (Krebs 1989; Newton-Fisher 1999):

$$H' = \left(-\sum_s^j p_j \ln p_j \right) / \ln S$$

where H' is the standardized measure of diversity, p_j is the proportion of prey species j in the diet and S is the total number of prey species consumed by all individuals. General Linear Model ANOVAs were used to test for sex, age-class, and season differences on energy density, diet diversity, and the number of prey consumed. Energy density and the number of prey consumed were transformed using a natural log and square-root transformation, respectively, to meet the assumption of normal distribution. Akaike's information criterion (AIC), Delta AIC, and Akaike weights were calculated to determine the factors that best explained the variation in the data. Only the best predicted model for each analysis is reported below; however, all models tested and their associated AIC values are available in Appendix S3 (see Supplementary material).

Table 3. Number of male (M) and female (F) grey seals sampled by year, season, and age-class

Year	Adults							6 month olds		
	Spring		Summer		Fall/early winter		Total	Spring		Total
	M	F	M	F	M	F		M	F	
1993	10	7			15	28	60			
1994	16	16			18	20	70			
1995	4	9	2	4	3	24	46			
1996	13	11	5	6	6	16	57			
1997	11	14	4	4	9	6	48	10	10	20
1998	12	10			22	21	65	10	10	20
1999	24	25	11	11	18	18	107	16	15	31
2000	11	8	6	7	6	5	43	10	10	20
Total	101	100	28	32	97	138	496	46	45	91

**Fig. 1.** Mean number of prey species consumed during each season by grey seals in the western North Atlantic Ocean between 1993 and 2000. Error bars represent 1 SE. Sample size is shown in Table 3.

Dietary overlap between each sex/age-class group for each season was calculated using the simplified Morisita–Horn index (C_H ; Krebs 1989; Simpfendorfer, Goodreid and McAuley 2001):

$$C_H = \frac{2 \left(\sum_j p_{jk} p_{jl} \right)}{\left[\left(\sum_j p_{jk}^2 \right) + \left(\sum_j p_{jl}^2 \right) \right]}$$

where p_{jk} is the mean proportion that prey type j accounts for in the diet of group k , p_{jl} is the mean proportion that prey j accounts for in the diet of group l , and n is the total number of prey consumed by both groups. Degree of overlap is considered to be small, medium or high when C_H is between 0 and 0.29, 0.30–0.59, and > 0.60, respectively (Langton 1982).

Grey seal blubber samples were collected over a number of years. While there was some interannual variation in the diets, but there were no clear trends. As a result we felt justified in combining years to examine hypotheses relating to seasonal variation. Presently there is relative little information on the interannual abundance of many of the more frequently eaten prey, therefore we have chosen to present interannual changes in the diet of grey seals in a future paper.

Results

Blubber samples were obtained from 496 different adult grey seals (226 males, 270 females) over the eight years of

our study and from 91 juveniles (46 males, 45 females) between 1997 and 2000 (Table 3). Seventeen prey species accounted for > 1% of the diet in one or more sex and/or age-class (Table 4). Individual adult grey seals consumed between two and nine prey species. The number of species consumed differed significantly by sex (ANOVA: $F_{1,490} = 82.1$, $P < 0.001$) and season ($F_{2,490} = 5.0$, $P = 0.007$). However, there was also a significant sex \times season interaction ($F_{2,490} = 10.3$, $P < 0.001$) with adult females consuming fewer prey species in the summer than other seasons, whereas males exhibited little seasonal variation (Fig. 1). There was no significant difference in the number of species eaten by juvenile males and females ($F_{1,89} = 0.371$, $P = 0.554$). In spring, when both age-classes were sampled, the number of prey species eaten by juveniles was significantly greater than that consumed by adults ($F_{1,204} = 33.4$, $P < 0.001$; Fig. 1).

The dominant prey species consumed by seals differed by season, sex and age-class; however, sand lance *Ammodytes dubius* Reinhardt (1837), and redfish *Sebastes* sp. Cuvier (1829) together accounted for between 40 and 91% of the diet in all seasons, sexes and age-classes (Table 4). Pollock *Pollachius virens* Linnaeus 1758, and flounders (turbot *Reinhardtius hippoglossoides* Walbaum 1792; witch *Glyptocephalus cynoglossus* Linnaeus 1758; and yellow-tail *Limanda ferruginea* Storer 1839) accounted for $\geq 10\%$ of the diet in some seasonal demographic groups (Table 4).

Table 4. Seasonal diet of grey seals in the North-west Atlantic estimated using quantitative fatty acid signature analysis. Values are mean percentage of diet by wet weight \pm total SE (see text) for all prey species/size-classes that represented more than 1% of the diet in any one age-class/season group. Data from all years are combined

Prey species	Size-class (cm)	Spring			Summer		Fall/early winter	
		Males <i>n</i> = 100	Females <i>n</i> = 101	Juveniles <i>n</i> = 91	Males <i>n</i> = 28	Females <i>n</i> = 32	Males <i>n</i> = 97	Females <i>n</i> = 138
Forage fish								
Capelin	Small: ≤ 13.5	0.3 \pm 0.31	1.1 \pm 0.65	0.0 \pm 0.12	1.5 \pm 1.5	0.0 \pm 0.60	2.8 \pm 0.85	1.8 \pm 0.53
Herring	Large: > 20	3.2 \pm 0.29	5.1 \pm 0.38	0.3 \pm 0.11	8.6 \pm 1.06	0.0 \pm 0.21	3.5 \pm 0.33	1.0 \pm 0.16
Northern sand lance	Small: ≤ 20	2.3 \pm 0.21	5.6 \pm 0.43	9.8 \pm 0.37	4.5 \pm 0.64	4.5 \pm 0.68	4.0 \pm 0.28	7.7 \pm 0.37
Northern sand lance	Large: > 20	4.8 \pm 0.38	36.4 \pm 0.97	12.9 \pm 0.65	18.6 \pm 1.52	63.8 \pm 1.85	27.8 \pm 0.78	32.1 \pm 0.78
Snake blenny		0.3 \pm 0.13	0.4 \pm 0.07	1.9 \pm 0.24	0.0 \pm 0.19	2.5 \pm 0.36	1.0 \pm 0.16	0.8 \pm 0.15
Gadids								
Cod	Small ≤ 35	0.0 \pm 0.15	0.0 \pm 0.14	1.7 \pm 0.58	0.0 \pm 0.06	2.1 \pm 1.00	0.0 \pm 0.18	0.3 \pm 0.26
Cod	Large: > 35	0.4 \pm 0.15	0.4 \pm 0.18	6.9 \pm 0.71	0.0 \pm 0.10	2.4 \pm 0.91	1.0 \pm 0.25	1.3 \pm 0.25
Pollock	Small: ≤ 25	27.5 \pm 0.63	3.0 \pm 0.29	6.4 \pm 0.47	18.9 \pm 1.17	0.0 \pm 0.16	11.0 \pm 0.39	5.4 \pm 0.26
Pollock	Large: > 25	3.2 \pm 0.40	2.4 \pm 0.34	5.8 \pm 0.62	1.2 \pm 0.48	0.0 \pm 0.11	0.0 \pm 0.07	0.0 \pm 0.06
Silver hake	Large: > 21.5	1.8 \pm 0.56	0.7 \pm 0.37	1.2 \pm 0.52	0.2 \pm 0.50	0.0 \pm 0.08	0.0 \pm 0.05	0.0 \pm 0.01
White hake		6.4 \pm 0.73	1.4 \pm 0.30	2.0 \pm 0.37	4.1 \pm 1.10	0.0 \pm 0.00	0.3 \pm 0.25	0.0 \pm 0.02
Flounders								
Turbot		4.6 \pm 0.29	1.6 \pm 0.20	5.5 \pm 0.41	2.9 \pm 0.55	0.1 \pm 0.17	1.1 \pm 0.20	0.3 \pm 0.11
Witch flounder		2.4 \pm 0.17	1.1 \pm 0.09	3.6 \pm 0.27	2.9 \pm 0.42	0.0 \pm 0.01	4.7 \pm 0.22	4.3 \pm 0.17
Yellowtail flounder		0.0 \pm 0.02	0.0 \pm 0.00	1.3 \pm 0.26	0.0 \pm 0.00	0.0 \pm 0.00	0.0 \pm 0.00	0.0 \pm 0.01
Skates								
Thorny skate		3.4 \pm 0.33	0.2 \pm 0.13	5.8 \pm 0.51	1.8 \pm 0.55	0.0 \pm 0.01	1.9 \pm 0.30	0.2 \pm 0.10
Winter skate		0.6 \pm 0.18	0.2 \pm 0.08	0.3 \pm 0.12	0.3 \pm 0.34	0.0 \pm 0.00	2.0 \pm 0.20	0.1 \pm 0.05
Other								
Longhorn sculpin	Large > 25	0.3 \pm 0.16	0.1 \pm 0.14	3.2 \pm 0.62	0.2 \pm 0.25	0.2 \pm 0.21	0.0 \pm 0.05	0.1 \pm 0.07
Lumpfish		4.4 \pm 0.26	4.3 \pm 0.27	7.0 \pm 0.35	0.7 \pm 0.27	0.0 \pm 0.24	1.6 \pm 0.13	5.6 \pm 0.17
Redfish	Small ≤ 27	19.4 \pm 0.59	14.6 \pm 0.79	20.5 \pm 0.64	13.5 \pm 1.50	4.0 \pm 1.91	13.9 \pm 0.93	17.7 \pm 0.95
Redfish	Large > 27	13.0 \pm 0.45	20.2 \pm 0.61	1.8 \pm 0.29	18.0 \pm 1.48	19.4 \pm 1.51	21.3 \pm 0.77	20.0 \pm 0.71
Squid		0.0 \pm 0.06	0.2 \pm 0.04	0.4 \pm 0.12	1.3 \pm 0.32	0.3 \pm 0.25	0.9 \pm 0.18	0.5 \pm 0.12
No. of prey species/seal		4.9 \pm 0.17	3.3 \pm 0.14	5.5 \pm 0.21	4.6 \pm 0.16	2.4 \pm 0.16	4.5 \pm 0.19	3.7 \pm 0.13
Diet diversity		0.35 \pm 0.016	0.27 \pm 0.010	0.41 \pm 0.014	0.38 \pm 0.023	0.21 \pm 0.016	0.36 \pm 0.012	0.31 \pm 0.010
Energy density (kJ g ⁻¹)		5.3 \pm 0.07	5.6 \pm 0.09	5.3 \pm 0.04	5.4 \pm 0.08	5.2 \pm 0.04	5.5 \pm 0.04	5.5 \pm 0.03

The FA signature of some prey species differed significantly by length class. For those species, we could obtain coarse information on the size of prey eaten (Table 4). No consistent pattern was evident in the prey sizes eaten by adult males and females. Our estimates indicated that grey seals ate mainly large sand lance, herring and cod, but generally showed no strong tendency in the case of redfish. In contrast, small redfish and pollock were eaten principally by juveniles and adult males, respectively.

SEX DIFFERENCES – SEASONAL EFFECTS

Blubber samples collected in the spring and fall/early winter were used to examine the effects of sex and season on grey seal diet composition over the entire study period (Table 3). There were significant sex ($P < 0.001$), and season ($P < 0.001$) effects on diet composition and a significant sex \times season interaction ($P < 0.001$). Adult females consumed a higher percentage of sand lance ($P < 0.001$), but less pollock ($P < 0.001$), white hake *Urophycis tenuis* Mitchell 1814 ($P < 0.001$), thorny skate *Raja radiata* Donovan 1808 ($P < 0.001$), and turbot ($P < 0.001$) than adult males during spring (Fig. 2a). Diets of males and females had a medium degree of

overlap at this time of year ($C_H = 0.50$). Diets of the two sexes were more similar in the fall/early winter (Fig. 2c, $C_H = 0.97$); however, males consumed a higher percentage of pollock ($P = 0.003$) and winter skate *Raja ocellata* Mitchell 1815 ($P < 0.001$) compared with females.

We then conducted a second seasonal analysis on a subset of years (1995–97, 1999 and 2000) that also included samples collected from adult grey seals in the summer. As above, we found significant sex ($P < 0.001$), season ($P < 0.001$) and sex \times season ($P < 0.001$) effects. Sex differences in diet were evident in all three seasons; however, these differences were more pronounced in spring ($P < 0.001$) and summer ($P < 0.001$; $C_H = 0.55$) than in fall/early winter ($P = 0.001$; Fig. 2). During the summer, females consumed a greater proportion of sand lance ($P < 0.001$) and cod *Gadus morhua* Linnaeus 1758 ($P = 0.010$), but significantly less pollock ($P < 0.001$) and herring *Clupea harengus* Linnaeus 1758 ($P = 0.006$) than males (Fig. 2b).

In spring and fall/early winter, diet diversity differed significantly between sexes ($F_{1,432} = 49.8$, $P < 0.001$) and seasons ($F_{1,432} = 9.6$, $P = 0.002$) but there was a significant sex \times season interaction ($F_{1,432} = 5.6$, $P = 0.018$). Adult male diets were significantly more diverse and relatively uniform across seasons compared with the

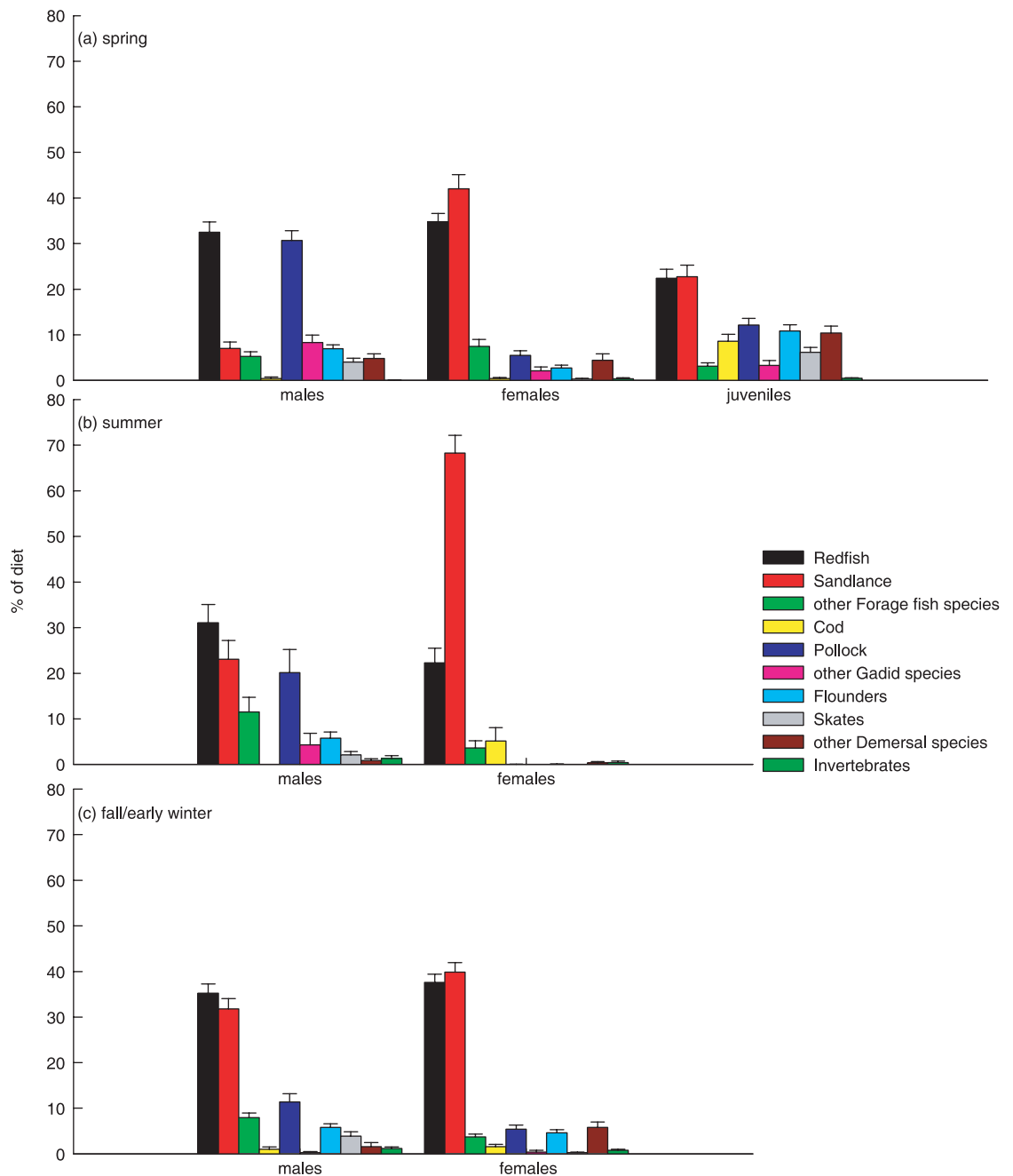


Fig. 2. Seasonal estimates of diet composition for adult grey seals in the western North Atlantic Ocean between 1993 and 2000 and spring diet composition of juveniles between 1997 and 2000. Sample sizes are shown in Table 3. Bars represent means with 1 SE.

diet of females whose diet was more diverse in fall/early winter compared with spring. Energy density of the diet also differed by sex (females > males; $F_{1,432} = 8.4$, $P = 0.004$), and season ($F_{1,432} = 4.9$, $P = 0.028$). However, there was a significant sex \times season interaction ($F_{1,432} = 5.9$, $P = 0.015$) with energy density increasing from spring to fall/early winter in males but not in females. Energy density of the diets just prior to the breeding season did not differ by sex (t -test: $t_{233} = -0.5$, $P = 0.596$).

When all three seasons were included for the subset of years indicated above, diet diversity still differed between males and females ($F_{1,295} = 79.8$, $P < 0.001$), but not by season ($F_{2,295} = 2.9$, $P = 0.059$), and there still was a

significant sex \times season interaction ($F_{2,295} = 10.2$, $P < 0.001$). Diversity was relatively constant across all seasons in males, but varied significantly in females (Fig. 3). Using this reduced data set, the model that best predicted energy density of diet included only sex as a factor (see Appendix S3 in Supplementary material). However, energy density of diet did not differ significantly by sex ($F_{1,299} = 2.2$, $P = 0.137$).

SEX AND AGE-CLASS DIFFERENCES

In the years when all age/sex-classes were sampled (1997–2000), spring diets differed significantly by age-class

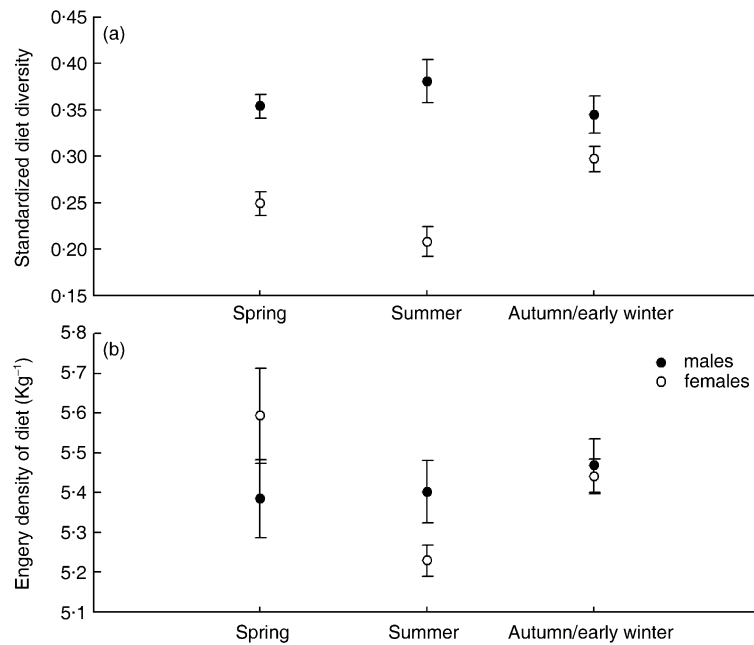


Fig. 3. Diet diversity (a) and energy density (b) of diets estimated for adult grey seals in the western North Atlantic Ocean in years when all three seasons were sampled (1995–97 and 1999–2000). Bars represent means with 1 SE.

($P < 0.001$) and sex ($P < 0.001$) and there was a significant sex \times age-class interaction ($P < 0.001$). Unlike adults, the diet composition of juveniles did not differ by sex ($P = 0.057$).

There was high overlap between the diets of juveniles and adult males ($C_H = 0.67$) and adult females ($C_H = 0.63$). However, juveniles ate less redfish and more cod, small sand lance, longhorned sculpin *Myoxocephalus octodecemspinosus* Mitchell 1814, and yellowtail flounder than adults (all P -values < 0.001 ; Fig. 2). Juveniles also consumed more snake blenny *Lumpenus lumpretaeformis* Walbaum 1972 ($P < 0.001$) and less pollock ($P < 0.001$) than adult males and a higher percentage of turbot, thorny skate and large herring, but less large sand lance than adult females (all P -values < 0.001 ; Fig. 2).

Diet diversity differed by sex ($F_{1,202} = 22.9$, $P < 0.001$) and age-class ($F_{1,202} = 36.0$, $P < 0.001$) and there was a sex \times age-class interaction ($F_{1,202} = 8.1$, $P = 0.005$) with the diversity of juvenile diets higher than that of adults (Table 4). By contrast, energy density of diets did not differ by sex ($F_{1,202} = 2.3$, $P = 0.135$), but showed a significant age-class effect ($F_{1,202} = 5.8$, $P = 0.017$) with adults having a spring diet with a higher energy density than juveniles (Table 4). The best predictive model for energy density did not include an interaction term (Appendix S3 in Supplementary material).

Discussion

We found that previously reported seasonal changes in diving/foraging behaviour (Beck *et al.* 2003a,b) and body energy storage (Beck *et al.* 2003c) of male and female grey seals were associated with seasonal changes in diet

estimated using quantitative FA signature analysis. Furthermore, those seasonal differences seem to reflect the influence of sex-specific differences in the timing and magnitude of energetic expenditures on reproduction. However, sex differences in diet diversity and energy density suggest that differential energy requirements resulting from body size dimorphism may also underlie sex differences in dietary niche breadth. The lack of sex differences in the diet of nonreproductive and less size-dimorphic (i.e. males only *c.* 5% heavier than females) juvenile grey seals lend support to this interpretation. Many other marine mammals, both pinnipeds and cetaceans, and seabirds are similarly size dimorphic, suggesting the ecological factors driving sex differences in grey seals may be widespread in marine ecosystems.

Grey seal females are capital breeders and males also rely, to a substantial extent, on body energy stores to fuel courtship and mating. During lactation, female grey seals lose about 40% of their body mass, depleting 62–68% of their lipid stores and 16% of their protein stores (Mellish *et al.* 1999; Beck *et al.* 2003c). Before returning to sea, females are mated and after about 3 months, the fertilized egg implants and begins to develop. Female body condition is positively correlated with successful implantation and pregnancy in several mammalian species, including pinnipeds (Mitchell, McCowen and Nicholson 1976; Boyd 1984; White, Rowell and Hauer 1997). Thus, to successfully support pregnancy, females must recover from their substantial loss of body protein and energy stores relatively quickly after the breeding season. During this time, female grey seals consumed predominantly sand lance and redfish, as well as other small pelagic fish species. These prey types tend to have high energy densities (Appendix S2 in Supplementary material) relative to

gadoids and other demersal prey species, which presumably enables females to more efficiently increase body energy nutrient stores.

In contrast, male grey seals consumed a more diverse diet with less emphasis on the higher energy small pelagic fish species. Although males deplete about 36% their body energy during the breeding season (Beck *et al.* 2003c), they do not appear to have direct costs associated with future reproduction immediately following the breeding season. Consistent with this, during the post-breeding foraging period males maintain body mass, but continue to lose total body energy (Beck *et al.* 2003c) suggesting that subsequent reproductive success in males is less sensitive to total body energy during this period. Data from other species (roe deer *Capreolus capreolus*, Hewison *et al.* 1996; muskrats *Ondatra zibethicus*, Virgl and Messier 1992) also indicate that females consume higher quality prey and increase their fat content more quickly following the breeding season than males suggesting that this difference between sexes may be rather common among taxa.

During the several months leading up to the winter breeding season, the diets of adult male and female grey seals were highly similar ($C_H = 0.97$). It is also during this period that both sexes exhibit the greatest level of foraging effort and energy deposition (Beck *et al.* 2003a,b,c). This increased dietary overlap results from females consuming a more diverse diet and males consuming a somewhat higher-quality diet. Similarly, in burrowing owls *Athene cunicularia*, both sexes increase their dietary niche breadth during the breeding season to meet the energetic requirements of reproduction and chick rearing (York, Rosenberg and Strum 2002).

Sexual body-size dimorphism and intraspecific competition can also lead to differences in foraging behaviour and diet (Schoener 1970; Clutton-Brock *et al.* 1987; Clarke *et al.* 1998; Mysterud 2000). In sexually size-dimorphic species, the larger sex requires a higher absolute energy intake than the smaller sex to meet metabolic requirements imposed by a larger body mass. Theoretically, this can be done in several ways. For example, by consuming a larger quantity of the same prey as the smaller sex, or the larger sex could consume different or additional prey species to increase energy intake. In size-dimorphic ungulate species, greater foraging time observed in females is thought to reflect the increased search time required to locate the higher quality foods eaten by females compared with males (Ginnett and Demment 1997; Perez-Barberia and Gordon 1999). We found that male grey seals consumed a broader range of prey species, particularly during the spring and summer compared with the more selective and somewhat higher energy-density diets of females, suggesting that body size dimorphism may also play a role in determining the diets of this marine carnivore. However, sexual size dimorphism cannot easily account for the seasonal component of dietary differences between male and female grey seals as males are about 1.5 times heavier than females throughout the year (Beck *et al.* 2003c). Given that the degree of sexual size dimor-

phism does not vary seasonally, other factors must be largely responsible for seasonal differences.

Niche divergence to reduce intraspecific competition has been advanced to explain sex differences in foraging behaviour and diet in several species (Kilham 1965; Ligon 1968; Schoener 1970). The foraging areas used by adult male and female grey seals overlap broadly throughout much of the year (Beck 2002; Bowen *et al.* 2006), however, when examined at a finer temporal scale, males and females exhibit rather marked spatial segregation during the post-reproduction foraging period (i.e. spring; Breed *et al.* 2006). It is during this period that the diets of the two sexes differ most and when the effects of intraspecific competition on female fitness may be greatest (see above). During the several months leading up to the breeding season, when the diets of males and females are most similar, spatial sexual segregation of adults is also evident, although to a lesser extent (Breed *et al.* 2006). Segregation at this time of year may provide a means of reducing intraspecific competition, while permitting males access to higher quality foods needed to prepare for the energetic costs of reproduction.

Our data provide compelling evidence of sex differences in the diets of adults. However, sex differences were not evident in the diet of juvenile grey seals suggesting that the factors driving sex differences in adults do not become influential until later in life. While some size dimorphism is evident at this young age (Hall *et al.* 2001), the degree of sexual dimorphism is considerably less than that found in adults. Additionally, juveniles do not have reproductive costs that might influence the quantity and types of foods that may enhance fitness. Currently, the spatial distribution of these young foragers is unknown; however, the lack of sex differences in diet suggest that intrasexual competition for resources has little influence on foraging behaviour at this age.

Ontogenetic niche differentiation was evident in grey seals and has been demonstrated in several other taxa (e.g. desert scorpion, Polis 1984; southern elephant seals, Field *et al.* 2005). The diet composition of 6-month-old grey seals differed significantly from that of adults during the spring. Juveniles consumed more prey species than adults, which may indicate more experimentation by these relatively inexperienced foragers. Additionally, juveniles are substantially smaller than adults, limiting both diving ability and perhaps the prey species that can be captured. Both of these factors probably contribute to the less selective and lower energy density of juvenile diets compared with those of adults.

Intraspecific variation in diet, whether as a result of sex differences or ontogenetic niche shift, broadens the niche breadth of a predator and must be considered when attempting to determine the functional role of a species in an ecosystem. The mechanisms underlying intraspecific diet variation are also of interest to ecosystem managers, particularly when they can be linked to the overall physiological and behavioural ecology of a species. In adult grey seals, sex-specific seasonal changes in diet correspond to seasonal sex-specific changes in diving behaviour and rate

of body energy accumulation. Sex-specific reproductive requirements appear to be a primary factor generating the intraspecific variation in the foraging ecology of this large marine carnivore, with the concomitant influence of body-size dimorphism.

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Supplementary material

The following supplementary material is available for this article.

Appendix S1. An Excel database of the fatty acid signatures from 2110 individual prey, representing 28 species of fishes and invertebrates, which were collected in the North-west Atlantic between 1993 and 2001 and used to estimate the diet of grey seals using quantitative fatty acid signature analysis.

Appendix S2. Percentage fat and energy density of each prey/size group used to estimate diet and diet characteristics in grey seals using quantitative fatty acid signature analysis.

Appendix S3. Akaike's information criterion (AIC) of the univariate general linear models for diet diversity and energy density of diets between sex, season and/or age-class.

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