Feeding by grey seals in the Gulf of St. Lawrence and around Newfoundland

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ABSTRACT

Diet composition of grey seals in the Gulf of St. Lawrence (Gulf) and around the coast of Newfoundland, Canada, was examined using identification of otoliths recovered from digestive tracts. Prey were recovered from 632 animals. Twenty-nine different prey taxa were identified. Grey seals sampled in the northern Gulf of St. Lawrence fed mainly on capelin, mackerel, wolffish and lumpfish during the spring, but consumed more cod, sandlance and winter flounder during late summer. Overall, the southern Gulf diet was more diverse, with sandlance, Atlantic cod, cunner, white hake and Atlantic herring dominating the diet. Capelin and winter flounder were the dominant prey in grey seals sampled from the east coast of Newfoundland, while Atlantic cod, flatfish and capelin were the most important prey from the south coast. Animals consumed prey with an average length of 20.4 cm (Range 4.2-99.2 cm). Capelin were the shortest prey (Mean = 13.9 cm, SE = 0.08, N = 1126), while wolffish were the longest with the largest fish having an estimated length of 99.2 cm (Mean = 59.4, SE = 2.8, N = 63). In the early 1990s most cod fisheries in Atlantic Canada were closed because of the collapse of the stocks. Since then they have shown limited sign of recovery. Diet samples from the west coast of Newfoundland indicate a decline in the contribution of cod to the diet from the pre-collapse to the post-collapse period, while samples from the southern Gulf indicate little change in the contribution of cod.

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INTRODUCTION

Marine mammals are often considered as important consumers because of their large size and abundance, which may lead to their having an important influence on the structure and function of marine ecosystems (Bowen 1997, Savenkoff *et al.* 2004a, Morissette *et al.* 2006). Furthermore, the consumption of commercially valuable species, by marine mammals, has the potential to reduce their commercial yield (Bogstad *et al.* 1997) and in areas where commercial stocks are quite low, predation by seals may slow their recovery (Bundy 2001, Chouinard *et al.* 2005). Evaluating this impact is complex because information is needed on both predator and prey populations as well as the functional relationships between them (Hammill and Stenson 2000, Yodzis 1994). Feeding is a major link between organisms and their environment and an understanding of feeding ecology of the various species is needed to understand ecosystem dynamics (Härkönen and Heide-Jørgensen 1991, Savenkoff *et al.* 2004a, Yodzis 1994). However, obtaining quantitative diet information is not a trivial problem. Several studies have shown strong temporal and spatial patterns in diet composition and the uncertainties associated with diet composition are among the most sensitive variables affecting estimates of consumption (Benoit and Bowen 1990a,b; Bowen *et al.* 1993, Beck *et al.* 1993, Bowen and Harrison 1994, Lawson *et al.* 1995, Shelton *et al.* 1997).

Studies of diet of marine mammals have been conducted over several decades using a variety of techniques (Andersen *et al.* 2004), which have included the use of serological methods, stable isotopes, fatty acid profiles and identification of hard parts from gastro-intestinal contents or scats (Olesiuk *et al.* 1990; Pierce *et al.* 1991, 1993; Lesage *et al.* 2001; Iverson *et al.* 2004; Hammill *et al.* 2005). The most frequently used techniques have involved the recovery, identification and measurement of hard parts from scats at haul-out sites or from digestive tract contents from harvested animals (Murie and Lavigne 1985, 1986, 1992; Jobling 1987; Jobling and Breiby 1986; Hammond *et al.* 1994; Olesiuk *et al.* 1990; Bowen *et al.* 1993; Bowen and Harrison 1994). All methods have certain limitations and associated biases with the result that no single method appears to be ideal (Jobling and Breiby 1986, Jobling 1987, Lesage *et al.* 2001, Bowen 2000, Hammond and Rothery 1996, Grahl-Nielsen *et al.* 2004, Thiemann *et al.* 2004, Hammill *et al.* 2005).

The Northwest Atlantic grey seal (*Halichoerus grypus*) occurs along the Atlantic seaboard from the northeastern United States to the northern tip of Labrador, and throughout the Gulf of St. Lawrence (Mansfield and Beck 1977, Lesage and Hammill 2001). Although rare early in this century (Lavigueur and Hammill 1993), their numbers have increased from around 30,300 animals in 1970 to approximately 246,500 animals in 2000 (Hammill *et al.* 2007). Early studies into grey seal diet composition were largely qualitative (Fisher and McKenzie 1955; Mansfield and Beck 1977; Benoît and Bowen 1990a), but in recent years much effort has been directed towards obtaining quantitative information in order to obtain a better understanding of variability in diet composition (Benoît and Bowen 1990b; Murie and Lavigne 1992; Bowen *et al.* 1993; Bowen and Harrison 1994). Some quantitative information data are available for the northern Gulf (Benoit and Bowen 1990b; Murie and Lavigne 1992), but little information was available for the southern Gulf of St. Lawrence and waters surrounding Newfoundland.

Here we examine diet composition of grey seals collected from Anticosti Island area in the northern Gulf of St. Lawrence, the coasts around Newfoundland and the southern Gulf coastal areas of New Brunswick, Prince Edward Island and Nova Scotia between 1985 and 2004.

MATERIALS AND METHODS

Stomach and intestinal contents were obtained by Department of Fisheries and Oceans employees or from contract hunters as part of normal programs to monitor pinniped diets. Animals were sampled in the Gulf of St. Lawrence (Gulf), the south coast of Newfoundland and the east coasts of Newfoundland and Labrador (Fig.1). Stomachs and digestive tracts were removed in the field, and frozen at –20°C, until analysis. Stomachs were opened along the external curve and were classified as "containing food" if food remnants, including otoliths and other hard parts, were present. Contents were weighed sorted using a sieve with 0.45 mm mesh. Invertebrates were identified to order; cephalopods were identified using beak identification guides (Clarke 1986). Fish were identified using otoliths and less frequently from whole fish found in the stomach.

Scientific names for all identified species are listed in Appendix 1. Otoliths and other hard parts were sorted manually and conserved dry for later identification. Fish were identified to species when possible, using reference collections (Fisheries & Oceans Canada, Mont-Joli, Québec) and an identification guide (Härkönen 1986). The number of fish in each stomach was determined by pairing left and right otoliths and counting the total number of paired and unique specimens.

Otoliths were sorted, visually, into 3 different classes depending on their degradation state: class D1, including perfectly conserved otoliths (generally found in intact skulls or whole fish in seal stomach); class D2, otoliths with very few degradation marks, but margins showing some signs of erosion; class D3, very eroded otoliths, with dorsal and ventral margins and internal and external areas showing advanced digestion marks. Only D1 and D2 otoliths were used to determine total fish length. If a large number of otoliths of a single species were present in a stomach, a random subsample of 30 otoliths was measured.

Otolith-fish metric and energy density relationships were developed from samples collected during Department of Fisheries and Oceans research missions in the Gulf of St. Lawrence and off the east coast of Newfoundland, or using values from the literature (e.g. Härkönen 1986, Lawson *et al.* 1995, Proust 1996, D. Chabot, Dept. of Fisheries and Oceans, Mont-Joli, QC, unpublished data)(Appendix A). Otoliths not measured were identified to species and it was assumed that their weight and energy density were equivalent to the mean size and energy density of the measured otoliths for that species in the sample. Otoliths that could not be identified to species were assumed to have size and energy density equivalent to the mean of all measured otoliths. In the case of invertebrates, total mass and energy contribution were determined by multiplying the number of identified individuals by the mean weight and species energy density. In some cases, only eyes or telson were present. The contribution of this material to the diet was determined by multiplying the number of individuals determined from the number of eyes and telson times a mean mass and a mean energy density using all identified invertebrates. Diets were reconstructed for each seal, using the seal as the sampling unit.

Diet composition is expressed as follows: Frequency of occurrence$_i$ (FO_i) =(S_i /S_t) •100, where S_i is the number of stomachs containing species *i* and S_t is the total number of stomachs; Numerical abundance $_i$ (NA_i) =(N_i /N_t) •100 , where N_i is the number of individuals of species i and N_t is the total number of individuals of all prey. % wet weight= (w_i/w_t) •100, where w_i is the reconstructed weight of species i in a digestive tract, and w_t is reconstructed weight of all prey found in an individual digestive tract. % gross energy= (e_i/e_t) •100,
where e_i is the reconstructed energy content (kj/g) of species i in a digestive tract, and e_t is reconstructed energy content (kj/g) of all prey found in an individual digestive tract.

Diet diversity was examined using species richness and calculating a Shannon index (*H*'). Species richness is the number of different species in the sample collection. The Shannon index is a measure of species diversity, taking into account the number of individuals examined, and was calculated using:
$H' = -\Sigma\{ pi*\log(pi)\}$, where pi is the proportion of species x in the sample (Legendre and Legendre 1998).

Owing to the small sample sizes and individual variation, standard deviations around the means were expected to be quite large. To reduce this variability, simulated data sets of total energy and total mass consumed were created using a bootstrapping technique (Hammill *et al.* 2005; Resampling Stats, Arlington VA, USA 1999). Each digestive tract was treated as a unit for resampling purposes. This process was repeated 1000 times to generate estimates of total mass and total energy, from which proportions contributed by each prey group were calculated. Differences in energy density between regions were examined by ANOVA, followed by Tukey's least squared difference test using SAS (SAS Institute Inc., Cary, NC).

RESULTS

A total of 1,118 animals were collected between 1985 and 2004. The largest sample was obtained from Anticosti Island in 1988 and 1992 (*N* = 506), followed by the southern Gulf of St. Lawrence, between 1994 and 2003 (*N* = 414) and the coast around Newfoundland between 1985 and 2004 (*N* = 198). Prey were recovered from 632 animals. Only stomach contents were examined in samples from Anticosti Island, and Newfoundland. Complete digestive tracts were examined in samples from the southern Gulf.

In samples obtained from both Anticosti Island and Newfoundland, a greater number of stomachs obtained during May-July contained food than stomachs obtained during August to October (Table 1) ($\chi^2_{Anticosti} = 121$, df = 1; $\chi^2_{Newfoundland} = 17.2$, df = 2 ($\chi^2$, P<0.05). Among samples collected between May and July, 114 of 256 (45%) stomachs contained prey remains. Overall, a larger proportion of samples obtained from the southern Gulf, contained prey remains because the complete digestive tract, not just the stomach, was examined for identifiable prey. With the exception of animals collected in late November and December, and in February, 68-100% of the digestive tracts contained some identifiable prey (Table 1).

Table 1. Number of animals collected (N), number of animals with food in digestive tracts (Ns), average reconstructed mass (g) in tract and average energy density (kj/g), with standard deviations in parentheses. Samples from Newfoundland, the northern Gulf and southern Gulf (Feb 2000, Nov-Dec 2003) examined stomachs only. The remaining samples from the southern Gulf examined complete digestive tracts.

		N	Ns (%)		Mass	(s)	Energy Density (s)
Stomachs							
Nfld.	West coast	111	78	(70)	1,403.4	(308.6)	4.42 (0.06)
	East coast/Labrador	52	25	(48)	2,092.3	(920.5)	4.52 (0.09)
	South coast	35	24	(69)	508.0	(133.4)	4.39 (0.09)
Northern Gulf	Anticosti 88 (May-July	256	114	(45)	1,839.5	(282.6)	6.16 (0.31)
	Anticosti 92 (Aug-Sept)	250	69	(28)	4,391.3	(960.7)	6.61 (0.33)
Southern Gulf							
	2000 (Feb)	17	6	(35)	6,267.5	(3,361.2)	5.27 (0.47)
	2003 (Nov-Dec)	37	10	(27)	2,978.1	(953.3)	5.40 (0.56)
Stomachs and Intestines							
Southern Gulf	1994 (May-July)	12	12	(100)	2,595.7	(647.4)	4.34 (0.14)
	1995 (Aug-Sept)	4	4	(100)	3,119.3	(1,356.0)	4.31 (0.46)
	1998 (Sept)	20	19	(95)	4,900.1	(1,969.9)	5.35 (0.13)
	1999 (Sept-Oct)	41	37	(90)	3,197.8	(732.6)	5.33 (0.17)
	1999 (Nov-Dec)	32	31	(97)	6,591.6	(1,473.6)	5.68 (0.19)
	2000 (June)	25	25	(100)	3,393.9	(1,028.8)	5.38 (0.14)
	2000 (Aug-Oct)	48	39	(81)	4,491.8	(680.3)	5.01 (0.12)
	2000 (Nov-Dec)	4	4	(100)	3,806.6	(1,623.6)	5.61 (0.12)
	2001 (June)	18	18	(100)	3,006.2	(672.0)	5.73 (0.90)
	2001 (Oct)	21	16	(76)	4,369.2	(2,494.0)	5.36 (0.23)
	2002 (June-July)	39	32	(82)	3,299.1	(831.0)	4.95 (0.12)
	2002 (Aug-Oct)	44	28	(64)	2,072.3	(714.6)	5.10 (0.12)
	2002 (Nov-Dec)	24	22	(92)	4,175.6	(891.3)	5.17 (0.09)
	2003 (Sept-Oct)	28	19	(68)	2,150.7	(354.6)	5.05 (0.17)
	Total/Average	**1,118**	**632**	**(73)**	**3,496.2**	**(1,595.9)**	**5.20 (0.58)**

No difference was observed between samples in reconstructed prey mass recovered from stomachs or complete digestive tracts. Significant differences in energy density (kJ/g) were observed between the Anticosti Island, the southern Gulf and Newfoundland samples (ANOVA: $F_{2,623}$ = 39.6, P<0.0001). The energy density of diets from Anticosti Island samples (Mean = 6.33 kJ/g, SD = 3.10, *N* = 183) was significantly higher than the energy density of diets from the southern Gulf (Mean = 5.22 kJ/g, SD = 1.18, *N* = 323) and from Newfoundland (Mean = 4.42 kJ/g, SD = 1.49, *N* = 120), while the energy density of the southern Gulf diet was significantly higher than reconstructed diets from Newfoundland. (Tukey's test, *P*<0.05) (Table 1).

Twenty-nine different prey or taxa, including 8 invertebrate taxa were identified in the food containing stomachs/digestive tracts. A wider range of prey species was consumed by grey seals from the southern Gulf and the south coast of Newfoundland (species richness = 9-35, Shannon index = 1.46-2.43), compared to grey seals collected from Anticosti Island and east coast of Newfoundland (Species richness = 8-18, Shannon index = 0.28-1.71)(Table 2).

Table 2. Species richness and Shannon indices for grey seal diet samples from Newfoundland, Anticosti Island and the southern Gulf.

Region	N	Species Richness	Shannon index
Newfoundland			
East coast	25	16	1.08
West coast	78	18	0.91
South coast	24	11	1.64
Anticosti Island			
May-July	114	8	0.28
August-September	69	13	1.71
Southern Gulf			
May-July	90	35	1.84
August-October	171	32	1.66
November-December	71	29	2.43
February	17	9	1.46

At Anticosti Island, Atlantic cod, capelin, mackerel, herring, wolffish, and lumpfish dominated the diet in terms of weight and energy, while sand lance was also important in terms of frequency of occurrence or relative abundance (Tables 3, 4). Noticeable differences were observed between the May-July 1988 sample, and the August-September 1992 sample. In the former, lumpfish, capelin, wolffish and mackerel were the 4 most important prey, accounting for almost 90% of the diet (Table 3). In the August-September 1992 Anticosti Island sample, Atlantic cod, wolffish, mackerel, winter flounder, and herring were the 5 most important prey species accounting for over 90% of the diet by weight and energy. Capelin and sand lance were not important in terms of mass or energy, but were important in frequency of occurrence and numbers of individuals (Table 4).

In the southern Gulf, cunner, white hake, sand lance, Atlantic cod, and herring, were the 5 most important prey accounting for 68% of the diet by weight and 74% of energy (Table 5). In the southern Gulf, cunner was the most important prey in February accounting for 88.7% of the diet by weight. During May-July, a more diverse diet was consumed, with sand lance, pleuronectids (flatfish), cunner, Atlantic cod, and Atlantic herring, accounting for 81.4% of the diet by weight (Table 6). Little change in diet composition was observed between May-July and August-October. The importance of Atlantic cod to the diet increased slightly from 12.8% to 17.3% and Atlantic herring increased from 10.9% to 13.3%. Little change was observed in the contribution of cunner, while the contribution by sand lance declined slightly (Table 6). Considerable interannual variation occurred in sampling effort. To compare between years, only samples collected in September and October were examined (Table 7). The contribution of different prey varied among the 7 years. Using only

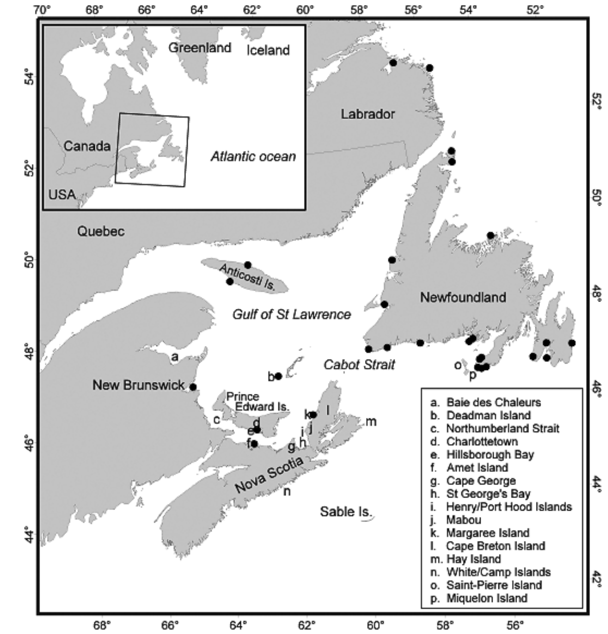

Fig. 1. *Map showing region where grey seals were collected. The dots represent locations where animals were collected.*

Table 3. Diet composition of 114 seals collected at Anticosti Island during May-July 1988. Frequency of occurrence and % frequency of occurrence in parentheses, numerical abundance with relative percent in parentheses, percent (%) mass and energy contribution to the diet with standard deviation in parentheses.

	Frequency of Occurrence (*s*)		Numerical Abundance (*s*)		% Mass Avg. (*s*)		% Energy Avg. (*s*)	
Atlantic Cod (*Gadus morhua*)	11	(9.5)	29	(0.7)	5.3	(1.4)	5.0	(1.4)
Atlantic herring (*Clupea harengus L.*)	7	(6.0)	35	(0.9)	1.0	(0.5)	2.2	(1.0)
Capelin (*Mallotus villosus*)	82	(70.7)	3,857	(94.4)	18.2	(3.3)	34.5	(5.7)
Haddock (*Melanogrammus aeglefinus*)	2	(1.7)	2	(0.0)	0.0	(0.0)	0.0	(0.0)
Mackerel (*Scomber scombrus*)	4	(3.4)	31	(0.8)	13.8	(5.1)	26.9	(8.3)
Wolffish (*Anarhichas lupus*)	10	(8.6)	15	(0.4)	16.8	(5.8)	14.7	(5.4)
Sculpin (*Cottidae*)	1	(0.9)	1	(0.0)	0.0	(0.0)	0.0	(0.0)
Lumpfish (*Cyclopterus lumpus*)	37	(31.9)	100	(2.4)	40.8	(5.4)	12.2	(2.3)
Unidentified	14	(12.1)	14	(0.3)	4.1	(0.8)	4.4	(1.0)
Total	**114**		**4,084**		**100.0**		**100.0**	

Table 4. Diet composition of 69 seals collected at Anticosti Island August-September 1992. Frequency of occurrence and % frequency of occurrence in parentheses, numerical abundance with relative percent in parentheses, and percent (%) mass and energy contribution to the diet with standard deviation in parentheses.

	Frequency of Occurrence		Numerical Abundance		% Mass Avg. (*s*)		% Energy Avg. (*s*)	
Atlantic Cod (*Gadus morhua*)	36.0	(52.2)	239.0	(21.0)	46.4	(6.8)	38.3	(6.7)
Atlantic herring (*Clupea harengus L.*)	21.0	(30.4)	122.0	(10.7)	9.0	(2.5)	14.0	(3.5)
Capelin (*Mallotus villosus*)	25.0	(36.2)	369.0	(32.4)	0.7	(0.3)	0.7	(0.3)
Mackerel (*Scomber scombrus*)	15.0	(21.7)	42.0	(3.7)	11.5	(3.7)	21.4	(5.9)
Eel Pout (*Lycodes spp.*)	5.0	(7.2)	11.0	(1.0)	0.5	(0.2)	0.6	(0.3)
Sandlance (*Ammodytes spp.*)	10.0	(14.5)	271.0	(23.8)	0.3	(0.1)	0.9	(0.5)
Winter flounder (*Pseudopleuronectes americanus*)	14.0	(20.4)	61.0	(5.4)	11.6	(2.7)	8.4	(2.1)
Redfish (*Sebastes spp.*)	1.0	(1.4)	3.0	(0.3)	0.2	(0.1)	0.2	(0.2)
Wolffish (*Anarhichas lupus*)	4.0	(5.8)	9.0	(0.8)	14.0	(7.8)	11.0	(6.7)
Sculpin (*Cottidae*)	4.0	(5.8)	6.0	(0.5)	4.4	(1.7)	3.3	(1.7)
Lumpfish (*Cyclopterus lumpus*)	1.0	(1.4)	1.0	(0.1)	0.3	(0.2)	0.1	(0.1)
Hake (*Urophysis tenuis*)	2.0	(2.9)	3.0	(0.3)	0.3	(0.2)	0.3	(0.2)
Unidentified fish	3.0	(4.3)	3.0	(0.3)	0.8	(0.5)	0.6	(0.3)
Total	**69**		**1,140.0**		**100**		**100**	

prey that made a 5% or greater contribution to the diet, winter flounder was an important prey in all years, followed by sandlance in 5/7 years, herring 4/7 years, cod for 3/7 years, cunner for 2/7 years and hake in 1 year only (Table 7).

Samples from Newfoundland were separated by coast, but were not analysed on a seasonal basis because of small sample sizes. A total of 25 food-containing stomachs were obtained from the east coast of Newfoundland and southern Labrador. Most of these samples (76%) were obtained between August and October. Capelin, gadoids and winter flounder were the most important prey by weight and energy in this area (Table 8). Along the south coast of Newfoundland, 88% of the

Table 5. Diet composition of 322 seals collected from the southern Gulf of St. Lawrence between 1994 and 2003. Frequency of occurrence and % frequency of occurrence in parentheses, numerical abundance with relative percent in parentheses, and percent (%) mass and energy contribution to the diet with standard deviation in parentheses.

	Frequency of Occurrence (%)		Numerical Abundance (%)		% Mass Avg. (s)		% Energy Avg. (*s*)	
Atlantic Cod (*Gadus morhua*)	58	(16.7)	214	(1.1)	12.8	(1.8)	11.9	(1.7)
Gadoids	28	(8.1)	82	(0.4)	2.0	(0.4)	1.8	(0.4)
Atlantic herring (*Clupea harengus* L.)	73	(21.0)	590	(2.9)	7.9	(1.2)	8.3	(1.3)
Capelin (*Mallotus villosus*)	2	(0.6)	10	(0.0)	<0.1		<0.1	
Mackerel (S*comber scombrus*)	10	(2.9)	30	(0.1)	0.7	(0.2)	1.4	(0.4)
Vahl's eelpout (*Lycodes gracilis*)	2	(0.6)	2	(0.0)	<0.1		<0.1	
Eelpout (*Lycodes spp.*)	19	(5.5)	46	(0.2)	0.1	(0.0)	<0.1	
Ocean pout (*Zoarces americanus*)	19	(5.5)	30	(0.1)	0.2	(0.1)	0.2	(0.0)
Sandlance (*Ammodytes spp.*)	127	(36.6)	10,932	(53.7)	14.7	(1.9)	15.0	(2.1)
American plaice (*Hippoglossoides platessoides*)	18	(5.2)	148	(0.7)	3.8	(1.1)	2.8	(0.8)
Yellowtail flounder (*Limanda ferruginea*)	19	(5.5)	96	(0.5)	3.1	(1.1)	2.5	(0.9)
Winter flounder (*Pseudopleuronectes americanus*)	87	(25.1)	1,077	(5.3)	4.7	(0.7)	3.1	(0.5)
Windowpane (*Scophthalmus aquosus*)	53	(15.3)	286	(1.4)	0.8	(0.2)	0.5	(0.1)
Righteye flounder	112	(32.3)	1,070	(5.3)	7.8	(1.1)	5.2	(0.8)
Cunner (*Tautogolabrus adspersus*)	25	(7.2)	338	(1.7)	17.8	(5.5)	22.2	(6.3)
White hake (*Urophysis tenuis*)	116	(33.4)	851	(4.2)	15.2	(1.9)	17.0	(2.3)
Atlantic hookear sculpin (*Artediellus atlanticus*)	1	(0.3)	1	(0.0)	<0.1		<0.1	
Sculpin (*Cottidae*)	20	(5.8)	73	(0.4)	<0.1		<0.1	
Wrymouth (*Cryptacanthodes maculatus*)	20	(5.8)	128	(0.6)	1.9	(0.9)	1.5	(0.7)
Fourbeard rockling (*Enchelyopus cimbrius*)	10	(2.9)	36	(0.2)	<0.1		<0.1	
Fourline snakeblenny (*Eumesogrammus praecisus*)	1	(0.3)	1	(0.0)	<0.1		<0.1	
Sea raven (*Hemitripterus americanus*)	1	(0.3)	1	(0.0)	0.0	(0.0)	0.0	(0.0)
Blenny/shanny	41	(11.8)	1,115	(5.5)	0.9	(0.3)	1.0	(0.3)
Haddock (*Melanogrammus aeglefinus*)	1	(0.3)	1	(0.0	<0.1		<0.1	
Horned sculpin (*Myoxocephalus scorpius*)	33	(9.5)	124	(0.6)	1.2	(0.2)	1.2	(0.2)
Smelt	29	(8.4)	74	(0.4)	0.2	(0.1)	0.1	(0.1)
Butterfish (*Perprilus triacanthus*)	29	(8.4)	156	(0.8)	0.9	(0.2)	0.8	(0.2)
Redfish (*Sebastes spp.*)	2	(0.6)	2	(0.0)	<0.1		<0.1	
Pricklebacks/Blenny	1	(0.3)	63	(0.3)	<0.1		<0.1	
Arctic shanny (*Stichaeus punctatus punctatus*)	2	(0.6)	11	(0.1)	<0.1		<0.1	
Moustache sculpin (*Triglops murrayi*)	1	(0.3)	1	(0.0)	<0.1		<0.1	
Unidentified fish	96	(27.7)	327	(1.6)	2.6	(0.3)	2.8	(0.3)
Cephalopoda	36	(10.4)	495	(2.4)	<0.1		<0.1	
Cumacea	7	(2.0)	12	(0.1)	<0.1		<0.1	
Decapoda	3	(0.9)	8	(0.0)	<0.1		<0.1	
Euphausiacae	59	(17.0)	1,506	(7.4)	0.4	(0.1)	0.4	(0.1)
Gasteropoda	3	(0.9)	17	(0.1)	<0.1		<0.1	
Isopoda	2	(0.6)	2	(0.0)	<0.1		<0.1	
Mollusca	5	(1.4)	36	(0.2)	<0.1		<0.1	
Nebaliacae	6	(1.7)	355	(1.7)	0.1	(0.1)	0.1	(0.0)
Total	**322**		**20,347**		**100**		**100**	

Table 6. Percent mass contribution of different prey by season to grey seal diets from animals collected in the Southern Gulf of St. Lawrence between 1994 and 2003. Samples include all years combined. Average with standard deviation in parentheses.

	February Avg. (*s*)		May-July Avg. (*s*)		August-October Avg. (*s*)		November-December Avg. (*s*)	
Atlantic cod (*Gadus morhua*)	3.1	(5.2)	12.8	(2.1)	17.3	(3.1)	17.3	(2.4)
Gadoids			0.7	(0.2)	0.9	(0.2)	6.3	(1.6)
Herring (*Clupea harengus L.*)			10.9	(1.6)	13.3	(2.3)	3.9	(1.4)
Mackerel (*Scomber scombrus*)			0.6	(0.2)	0.7	(0.4)	1.4	(0.5)
Vahl's eelpout (*Lycodes gracilis*)							<0.1	
Ocean pout (*Zoarces americanus*)			0.4	(0.1)	0.2	(0.0)	<0.1	
Pout	0.1	(0.1)	0.1	(0.0)	<0.1		<0.1	
Sandlance (*Ammodytes spp.*)			19.0	(2.4)	17.3	(2.8)	9.0	(3.6)
American plaice (*Hippoglossoides platessoides*)			3.6	(1.2)	3.4	(1.4)	5.4	(2.7)
Yellowtail flounder (*Limanda ferruginea*)			4.4	(1.6)	2.1	(0.9)	1.0	(0.6)
Winter flounder (*Pseudopleuronectes americanus*)	0.8	(1.9)	6.8	(1.0)	6.8	(1.4)	0.2	(0.1)
Pleuronectidae	2.4	(4.1)	9.3	(1.4)	7.1	(1.5)	7.1	(1.6)
Windowpane (*Scophthalmus aquosus*)			1.3	(0.3)	1.6	(0.4)		
Cunner (*Tautogolabrus adspersus*)	88.7		13.3	(3.8)	14.4	(5.7)		
White hake (*Urophysis tenuis*)			6.9	(1.1)	8.8	(1.6)	42.2	(3.9)
Wrymouth (*Cryptacanthodes maculatus*)			3.0	(1.4)	0.3	(0.1)	0.1	(0.1)
Fourbeard rockling (*Enchelyopus cimbrius*)			<0.1				<0.1	
Blenny/shanny			1.5	(0.4)	0.2	(0.1)		
Daubed shanny (*Leptoclinus maculatus*)			<0.1				<0.1	
Haddock (*Melanogrammus aeglefinus*)			<0.1					
Horned sculpin (*Myoxocephalus scorpius*)	1.4	(0.5)	1.4	(0.3)	1.7	(0.4)	0.2	(0.1)
Sculpin	0.1	(0.0)	0.1	(0.0)	0.1	(0.1)		
Smelt	0.1	(0.1)	0.1	(0.0)	0.1	(0.02)		
Butterfish (*Perprilus triacanthus*)			0.1	(0.03)	0.0	(0.01)	3.5	(0.8)
Redfish (*Sebastes spp.*)			<0.1		<0.1			
Pricklebacks/Blenny			<0.1					
Unidentified fish	3.4	(1.8)	2.8	(0.5)	2.9	(0.6)	2.0	(0.5)
Amphipoda					<0.1		<0.1	
Cephalopoda			<0.1		<0.1		<0.1	
Decapoda			0.6	(0.1)	0.7	(0.2)	0.1	(0.0)
Number of samples	**17**		**257**		**164**		**67**	

24 stomachs examined were collected between May and July. Atlantic cod, capelin, *Gadus spp*., pleuronectids and herring were the most important prey by weight and energy, while sand lance and shrimp were also important in terms of relative abundance (Table 9). Seventy-eight samples from the west coast of Newfoundland, were collected primarily between April and July (81%). Atlantic cod, *Gadus spp*., winter flounder, sand lance, lumpfish and mackerel were the most important prey, accounting for 80% of the diet by weight and 84% by energy. (Table 10). Capelin, Atlantic herring, mackerel, shrimp and smelt were also important using relative abundance.

The estimated overall mean length of prey eaten by grey seals was 20.4 cm (SE = 0.16, *N* = 4330, Range 4.2-99.2 cm) (Table 11, Fig. 2). The smallest fish consumed were capelin with a mean length of 13.9 cm (SE = 0.08; N = 1126,

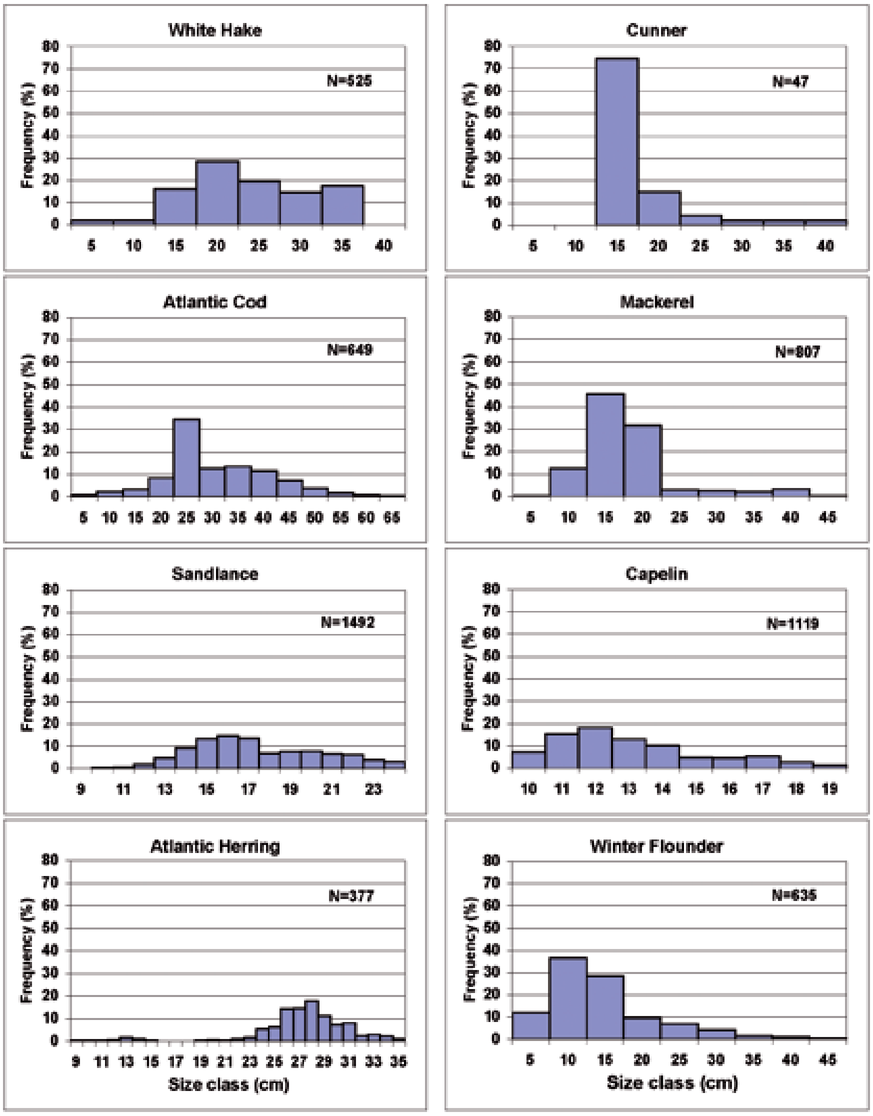

***Fig. 2.** Frequency distribution (%) of estimated lengths (cm) of prey consumed by grey seals in the Gulf of St. Lawrence and around Newfoundland between 1985 and 2004.*

Range 4.2-20.2). The largest fish consumed were wolffish (*Anarhichus spp*.), with a mean length of 59.4 cm (SE = 2.8, *N* = 63; Range 4.8-99.2 cm). Some regional differences in prey size were observed. The mean length of Atlantic cod consumed in the northern Gulf, which included Anticosti Island and western Newfoundland, was significantly greater (37.9 cm, SE = 0.6, *N* = 342, $F_{3,648} = 73.3$, $P<0.0001$) than cod consumed in the southern Gulf (27.6 cm, SE = 0.6, *N* = 268), along the south coast of Newfoundland (28.2 cm, SE = 2.3, *N* = 19) and on the east coast of Newfoundland (31.5 cm, SE = 2.6, N = 20). Mackerel consumed in the northern Gulf were significantly longer (38.9 cm, SE = 0.5, N = 58, $F_{2,809} = 991$, $P<0.0001$) than mackerel consumed in the southern Gulf (18.8 cm, SE = 0.1, *N* = 744) and from eastern Newfoundland (32.4 cm, SE = 0.9, *N* = 10). Sandlance consumed in the northern Gulf and along the southern Newfoundland coast were significantly smaller (NG = 16.1 cm, SE = 0.1, *N* = 713, $F_{2,778} = 66.6$, $P<0.0001$; SG = 17.6 cm, SE = 0.7, *N* = 14) than sandlance consumed along the east coast of Newfoundland (20.4 cm, SE = 0.5, *N* = 54). Winter flounder consumed in the northern Gulf were significantly longer (32.6 cm, SE = 1.2, *N* = 46, $F_{2,632} = 937$, $P<0.0001$) than winter flounder consumed in the southern Gulf (14.8 cm, SE = 0.2, *N* = 555) and eastern Newfoundland (28.1 cm, SE = 0.9, *N* = 34).

Table 7. Annual changes in diet composition (percent mass) of grey seals collected in the southern Gulf of St. Lawrence between 1995 and 2003. Only samples collected between September and October included in table. Average with standard deviation in parentheses. Latin binomial names are as in Table 6.

	1995 Avg. (*s*)		1998 Avg. (*s*)		1999 Avg. (*s*)		2000 Avg. (*s*)		2001 Avg. (*s*)		2002 Avg. (*s*)		2003 Avg. (*s*)	
Atlantic cod					17.9	(31.0)	11.7	(23.7)			12.9	(29.9)		
Gadus spp.							0.56	(3.4)	0.5	(2.1)	8.2	(17.2)	1.5	(3.6)
Herring			30.0	(37.6)	0.5	(1.6)	20.8	(31.6)	3.3	(11.9)	7.1	(17.6)	12.3	(26.0)
Mackerel					4.1	(18.2)								
Ocean pout	0.6	(1.3)	0.1	(0.3)	0.1	(0.5)	0.2	(0.8)	0	(0.2)	0.1	(0.3)		
Sandlance			25.2	(39.2)	14.3	(25.5)	6.1	(22.4)	16.8	(34.5)	8.5	(27.8)	34.8	(39.0)
American plaice					1.4	(5.3)	3.1	(12.0)						
Yellowtail flounder	1.9	(2.4)							1.7	(6.7)	6.7	(22.1)		
Winter flounder	37.6	(20.9)	8.9	(16.1)	6.5	(17.6)	5.2	(16.7)	4.3	(8.8)	1.0	(1.7)	7.2	(12.1)
Pleuronectidae spp.					7.1	(17.4)	13.2	(23.2)	13.2	(25.4)	21.7	(26.5)	11	(19.4)
Windowpane	12.2	(11.2)	1.2	(3.6)	0.3	(1.1)	2.4	(6.4)	4.1	(11.7)	0	(0.2)	1.8	(5.8)
Cunner	16.0		5.0	(22.0)	5.5	(15.5)	2.4		6.0	(24.1)	<0.1			
White hake	0.1		4.7	(7.8)	8.4	(20.4)	14.8		14.2		1.6	(5.4)	0.3	(1.3)
Wrymouth	1.8	(3.5)	1.8	(7.8)	0.4	(2.2)	0.1	(0.5)	0.4	(1.8)				
Snakeblenny	2.9	(5.1)	0	(0.1)	0.6	(3.5)			0.1	(0.3)				
Daube shanny							0	(0.2)	0	(0.1)				
Longhorn sculpin	2.0	(4.0)	0.1	(0.5)	2.6	(9.1)	0.3	(1.5)	7.2	(14.5)	1.5	(4.8)	3.2	(10.7)
Sculpin	4.6	(6.6)												
Smelt			0.3	(1.2)	0.2	(0.8)	0.0	(0.1)	0.6	(2.2)	0	(0.2)	0	(0.1)
Butterfish							0.1	(0.6)						
Redfish											0.2	(0.8)	0.4	(1.9)
Unidentified fish	0.51		0.7	(2.4)	9.6	(25.0)	8.3				12.6	(19.0)	1.3	(3.2)
Amphipods					0	(0.2)			<0.1					
Cephalopod	0.3		<0.1		0	(0.1)	0.2		<0.1					
Decapod	3.8		0.8	(3.0)	0.1	(0.4)	1.0		2.0	(4.5)	<0.1		0.3	(1.4)
Number of samples	**4**		**19**		**37**		**37**		**16**		**11**		**19**	

Table 8. Diet composition of 25 seals collected from the east coast of Newfoundland and southeastern coast of Labrador between 1985 and 2004. Frequency of occurrence and % frequency of occurrence in parentheses, numerical abundance with relative percent in parentheses, and percent (%) mass and energy contribution to the diet, average with standard deviation in parentheses.

	Frequency of Occurrence (%)		Numerical Abundance (%)		% Mass Contribution Avg. (*s*)		% Energy Contribution Avg. (*s*)	
Atlantic Cod	4	(16)	12	(1.7)	4.2	(3.64)	4.0	(3.4)
Gadus spp.	7	(28)	41	(5.6)	23.8	(15.2)	23.2	(14.1)
Rock Cod	1	(4)	2	(0.3)	0.3	(0.3)	0.2	(0.3)
Arctic Cod	1	(4)	1	(0.1)	<0.1		<0.1	
Atlantic Herring	1	(4)	2	(0.3)	<0.1		<0.1	
Capelin	8	(32)	531	(73.0)	29.8	(16.7)	32.1	(16.8)
Eelpout	1	(4)	1	(0.1)	0.3	(0.3)	0.2	(0.2)
Sand Lance	3	(12)	6	(0.8)	<0.1		<0.1	
Winter flounder	3	(12)	73	(10.0)	39.9	(26.5)	39.0	(25.2)
Pleuronectidae	1	(4)	1	(0.1)	<0.1		<0.1	
Sculpin	3	(12)	7	(1.0)	0.9	(0.9)	0.8	(0.75)
Redfish	0		<0.1		<0.1		<0.1	
Other Fish	1	(4)	3	(0.4)	0.6	(0.7)	0.3	(0.4)
Unidentified fish	2	(8)	2	(0.3)	<0.1		<0.1	
Squid	1	(4)	1	(0.1)	<0.1		<0.1	
Shrimp	2	(8)	18	(2.5)	<0.1		<0.1	
Snow Crab	1	(4)	1	(0.1)	<0.1		<0.1	
Other Inverts	1	(4)	25	(3.4)	<0.1		<0.1	
Total	**25**		**727**		**100.0**		**100.0**	

DISCUSSION

Major limitations to the hard part / reconstruction approach to quantify diet composition include the failure to find hard parts in the sample and under-estimating hard part size due to erosion while in the stomach (Jobling and Breiby 1986, Tollit *et al.* 2003, Christiansen *et al.* 2005). The degree to which these problems occur is affected by foraging behaviour, species composition of the diet, activity levels of the animal and meal size (Murie and Lavigne 1985, Jobling and Breiby 1986, Jobling 1987, Lawson *et al.* 1995, Tollit *et al.* 1997, Marcus *et al.* 1998). The impact of variability in otolith erosion rates, including complete otolith digestion on diet reconstructions, has been examined in captive studies and some solutions have been proposed (Tollit *et al.* 1997, 2003). We did not measure eroded otoliths because suggested correction factors to adjust otolith lengths to account for partial digestion are quite variable (reviewed by Bowen 2000) and when this variability is taken into account, considerable uncertainty to estimates of diet composition is added (Hammond and Rothery 1996).

In the Northwest Atlantic grey seal population reproduction occurs from late December until mid-February (Mansfield and Beck 1977). Little feeding occurs at that time. After moulting, animals forage intensively from the early spring (April-June) until July, after which a decrease in foraging bouts are observed until early autumn (October), when foraging activity again intensifies (Beck *et al.* 2003). The greater number of food-containing stomachs in samples obtained during the spring compared to late summer samples reflects this seasonal change. Little difference was observed between regions and seasons in estimated mean meal size, but samples obtained from Anticosti Island had a higher energy density than samples obtained from other regions, reflecting in part the importance of high energy species such as capelin and mackerel in the diet of grey seals from this area.

Table 9. Diet composition of 24 seals collected from the south coast of Newfoundland between 1985 and 2004. Frequency of occurrence and % frequency of occurrence in parentheses, numerical abundance with relative percent in parenthesis, and percent (%) mass and energy contribution to the diet with average and standard deviation in parentheses.

	Frequency of Ocurrence (%)		Numerical Abundance (%)		% Mass contribution Avg. (s)		% Energy contribution Avg. (s)	
Atlantic Cod	6	(25.0)	22	(12.4)	43.5	(16.3)	43.8	(16.7)
Gadus spp.	3	(12.5)	3	(1.7)	11.8	(8.4)	12.2	(8.7)
Atlantic Herring	2	(8.3)	2	(1.1)	5.4	(4.2)	6.2	(4.7)
Capelin	4	(16.7)	59	(33.1)	8.5	(7.9)	9.6	(8.6)
Eelpout	1	(4.2)	2	(1.1)	0.2	(0.2)	0.1	(0.1)
Sandlance	8	(33.4)	17	(9.6)	2.3	(1.5)	2.5	(1.7)
Pleuronectidae	5	(20.8)	7	(3.9)	15.9	(8.1)	13.2	(7.0)
Redfish	1	(4.2)	1	(0.6)	0.3	(0.3)	0.3	(0.4)
Unidentified fish	4	(16.7)	4	(2.2)	10.9	(7.3)	10.8	(7.4)
Shrimp	4	(16.7)	58	(32.6)	1.2	(1.0)	1.2	(1.0)
Amphipods	2	(8.3)	3	(1.7)	<0.1		<0.1	
Total	**24**		**178**		**100.0**		**100.0**	

Table 10. Diet composition of 78 seals collected from the west coast of Newfoundland between 1985 and 2004. Frequency of occurrence and % frequency of occurrence in parentheses, numerical abundance with relative percent in parenthesis, and percent (%) mass and energy contribution to the diet with average and standard deviation in parentheses.

	Frequency of Occurrence		Numerical Abundance (%)		% Mass contribution Avg. (s)		% Energy contribution Avg. (s)	
Atlantic Cod	14	(17.9)	91	(4.6)	28.4	(10.8)	29.0	(10.6)
Gadus spp.	13	(16.7)	51	(2.6)	13.5	(8.9)	13.2	(8.7)
Atlantic Herring	6	(7.7)	22	(1.1)	3.5	(1.8)	4.0	(2.0)
Capelin	9	(11.5)	59	(3.0)	0.6	(0.6)	0.8	(0.7)
Mackerel	2	(2.6)	11	(0.6)	4.5	(3.4)	4.5	(3.4)
Sandlance	28	(35.9)	1,588	(80.6)	15.4	(5.0)	17.6	(5.4)
American Plaice	1	(1.3)	1	(0.0)	0.1	(0.1)	0.1	(0.1)
Winter Flounder	5	(6.4)	55	(2.8)	23.1	(9.9)	24.0	(10.2)
Pleuronectidae	4	(5.1)	6	(0.3)	1.0	(0.7)	0.8	(0.5)
Lumpfish	3	(3.8)	6	(0.3)	5.9	(4.1)	2.4	(1.8)
Sculpin	5	(6.4)	5	(0.3)	0.7	(0.7)	0.7	(0.7)
Redfish.	6	(7.7)	8	(0.4)	0.5	(0.5)	0.5	(0.5)
Smelt	1	(1.3)	12	(0.6)	<0.1		<0.1	
Other Fish	4	(5.1)	4	(0.2)	1.2	(0.9)	0.8	(0.6)
Unidentified fish	15	(19.2)	15	(0.8)	1.5	(0.7)	1.5	(0.6)
Squid	3	(3.8)	7	(0.4)	<0.1		<0.1	
Shrimp	7	(9.0)	17	(0.9)	<0.1		<0.1	
Amphipods	4	(5.1)	10	(0.5)	<0.1		<0.1	
Other Inverts	1	(1.3)	1	(0.0)	<0.1		<0.1	
Total	**78**		**1,969**		**100**		**100**	

Table 11. Number of measured otoliths (N), average prey length (cm), with standard deviation in parentheses and range of prey lengths (cm) consumed by grey seals in samples collected from the Gulf of St. Lawrence and around Newfoundland between 1985 and 2004. Latin binomial names as in Table 6.

Species	N	Average	SD	Range
Atlantic cod	649	33.2	0.40	8.3 - 66.7
Atlantic herring	378	27.3	0.2	9.1 - 35.8
Capelin	1,126	13.9	0.1	4.2 - 20.2
Sandlance	1,525	17.6	0.1	6.3 – 26.0
Atlantic mackerel	807	20.3	0.1	8.3 - 45.0
Winter flounder	635	16.8	0.3	4.5 - 55.5
White hake	144	26.0	0.6	8.8 - 40.0
Wolffish	63	59.4	2.8	4.8 - 99.2

Grey seals are primarily piscivorous, with invertebrates accounting for only a very small fraction of their diet (Benoît and Bowen 1990a,b; Murie and Lavigne 1992; Bowen *et al.* 1993). Although a wide range of species were consumed, only about 3 to 5 species accounted for over 80% of the diet of grey seals in the northern Gulf of St. Lawrence and waters around Newfoundland. Grey seals from the southern Gulf of St. Lawrence had a more diverse diet, with up to 8 species accounting for about 80% of the diet composition. Major prey items included cunner, white hake, winter flounder, herring, cod, capelin, lumpfish and sand lance, which have also been reported as important prey elsewhere (Benoit and Bowen 1990a,b; Bowen *et al.* 1993; Bowen and Harrison 1994). We also identified wolffish as an important prey species in samples from the northern Gulf. Diet composition of samples from the southern Gulf of St. Lawrence had a higher species richness and Shannon Index than diets from the northern Gulf of St. Lawrence and the coasts of Newfoundland, which likely reflect ecosystem differences between the 2 regions. The northern Gulf is characterized by 2 deep channels (Laurentian and Esquiman), with an average depth of 420 m. Zooplankton biomass is high, while species diversity is low (De Lafontaine *et al.* 1991). Capelin, redfish, cod and sand lance are important species in the fish community (Savenkoff *et al.* 2004a). In contrast, the southern Gulf is characterized by a large relatively shallow area with an average depth of 50 m, called the Magdalen Shallows (De Lafontaine *et al.* 1991). Compared to the northern Gulf, zooplankton biomass is lower, but diversity is higher (De Lafontaine *et al.* 1991). Major species in the fish community include cod, white hake, mackerel, herring, shanny, cunner and flatfish such as flounders (Savenkoff *et al.* 2004b).

Substantial seasonal and inter-annual variation in the contribution of different prey was also observed. In the northern Gulf, lumpfish, capelin, mackerel and wolffish were the dominant prey in the early summer diet. The importance of capelin and lumpfish was also reported by Benoit and Bowen (1990b) and probably reflects the concentration and inshore movement of these species to spawn (Jangaard 1974, Scott and Scott 1988). Later in the season, cod, herring, mackerel and wolffish become dominant prey, which with the exception of wolffish, is similar to what was observed by Benoit and Bowen (1990b). This seasonal change also points to a change in diet from energy rich species consumed in early summer when foraging activity is more intensive to a less energy rich prey during the fall (Benoit and Bowen 1990b, Beck *et al.* 2003). However, similar changes in composition were not observed in the southern Gulf. In that area, sandlance, Atlantic herring, Atlantic cod, and white hake were the 4 most important prey species in both early summer and late summer-fall periods.

Grey seals consumed prey with a mean length of 20.4 cm. Capelin were the smallest prey consumed (mean = 13.9 cm), while wolffish were the largest (mean = 59.4 cm). Overall, mean prey size was similar to what has been reported elsewhere in Atlantic Canada and the Northeast Atlantic (Bowen *et al.* 1993, Hammond *et al.* 1994, Mikkelsen *et al.* 2002). The largest fish consumed, a wolffish with an estimated length of 99 cm, was longer than any fish previously reported consumed by grey seals in Atlantic Canada. Although the majority of fish were less than 35 cm long, predation on larger fish by grey seals has been documented elsewhere, particularly wolffish (catfish in NE Atlantic, *Anarhichas lupus*; Mikkelsen *et al.* 2002). A 13.6 kg wolffish was found beside a ringed seal hauled out on the ice in Arctic Canada, and saithe (*Pollachius virens* L.) and ling (*Molva molva L.*) with estimated lengths of around 90 cm have been reported for grey seal diets in the

United Kingdom (Hammond *et al.* 1994, Smith 1977). At the same time, detection of otoliths from such large wolffish in the stomachs of grey seals does not guarantee that the entire fish was consumed. There are some indications that seals may only consume soft parts of fish, leaving the heads behind (Lunneryd 2001). Perhaps in instances where seals attempt to take potentially aggressive prey such as the wolffish, seals might only have consumed the head and little else.

In the early 1990s, a moratorium on fishing for Atlantic cod was declared after several eastern Canadian cod fisheries had collapsed. Almost a decade later, evidence of marked changes in ecosystem structure are still evident, with almost all of these stocks showing no or very limited signs of recovery (Rice and Rivard 2003). In samples examined during 1986 and 1987, by Benoit and Bowen (1990b), just prior to the collapse, Atlantic cod made up 41.5% of the diet by weight which is similar to the 46.4% we observed in samples obtained at about the time of the collapse. Unfortunately no data are available from the Anticosti Island region since the collapse of the northern Gulf cod stock. Although samples are small, data from the west coast of Newfoundland suggest that the contribution of cod to the diet has declined from 32.5% (SD = 14.5, N = 11) between 1988 and 1992, just prior to the collapse of the cod, to 14.6% (SD = 4.7, N = 51) in samples obtained between 1995 and 2004, well after the stock had collapsed. In the southern Gulf, Benoit and Bowen (1990a) examined diet samples obtained during the mid-1980s, prior to the collapse. Expressed as frequency of occurrence, cod accounted for 13.5% of the diet, which is very similar to our 16.7%, suggesting that, in spite of major changes in cod biomass, there has been little change in the contribution of cod to the diet of grey seals in the southern Gulf of St. Lawrence in the areas we sampled. The contrasting inferences between the pre and post collapse diets from western Newfoundland, and the southern Gulf of St. Lawrence point to the dilemma in understanding foraging patterns in marine mammals. On the one hand, larger spatial scale commercial fish surveys point to the decline in cod biomass, while samples from individual grey seals reflect local prey choice which will be influenced by a much smaller spatial scale of local prey abundance, energy value and energy cost to obtain that prey.

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