ICES Journal of Marine Science

ICES CIEM International Council for the Exploration of the Sea Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science (2014), 71(6), 1332–1341. doi:10.1093/icesjms/fsu123

Contribution to the Symposium: 'Gadoid Fisheries: The Ecology of Management and Rebuilding'

Original Article

Feeding by grey seals on endangered stocks of Atlantic cod and white hake

M.O. Hammill[1]*, G.B. Stenson[2], D.P. Swain[3], and H.P. Benoît[3]

[1]*Department of Fisheries and Oceans, Maurice Lamontagne Institute, PO Box 1000, Mont-Joli, QC, Canada G5H 3Z4*
[2]*Department of Fisheries and Oceans, Northwest Atlantic Fisheries Centre, PO Box 5667, St John's, NL, Canada A1C 5X1*
[3]*Fisheries and Oceans Canada, Gulf Fisheries Centre, PO Box 5030, Moncton, NB, Canada E1C 9B6*

**Corresponding author: tel: +1 418 775 0580; fax: +1 418 775 0545; e-mail: mike.hammill@dfo-mpo.gc.ca*

Hammill, M.O., Stenson, G.B., Swain, D.P., and Benoît, H.P. Feeding by grey seals on endangered stocks of Atlantic cod and white hake. – ICES Journal of Marine Science, 71: 1332–1341.

Received 16 January 2014; revised 13 June 2014; accepted 22 June 2014; advance access publication 21 July 2014.

High natural mortality is preventing the recovery of collapsed stocks of Atlantic cod and white hake in the southern Gulf of St Lawrence, Canada. Predation by grey seals has been proposed as an important cause of this high mortality. We determined the contribution of cod and hake to the diet of grey seals collected along the west coast of Cape Breton Island and in the Cabot Strait, an area where overwintering cod aggregate. Along the coast of Cape Breton Island, the contribution of hake and cod to the diet was 30 and 17%, respectively, by weight using stomach contents and 13 and 9%, respectively, based on intestine contents. In the Cabot Strait, when overwintering aggregations of cod were present, cod accounted for 68% (range 57–80%) of the male diet from stomachs, and 46% (range: 31–64%) of the diet determined from intestines. Among females, cod represented 14% (range: 0–34%) and 9% (range: 3–54%) of the diet from stomachs and intestines, respectively. In Cabot Strait, white hake accounted for up to 17% of the diet by weight from stomachs, and up to 6% of the diet determined from intestines. The mean length of cod consumed by seals was 28 cm (SD = 8.6) along the coast of Cape Breton Island, and 39 cm (SD = 5.7) in Cabot Strait. The mean length of hake consumed by seals was 29 cm (SD = 7.0) along the coast of Cape Breton Island, and 35 cm (SD = 5.6) in Cabot Strait. Cod and hake are more important to the diet of males than that of females. The contribution of cod to the diet of grey seals foraging in the cod overwintering area is much greater than has been reported elsewhere.

Keywords: Atlantic cod, diet, gadoid, grey seal, predation, white hake.

Introduction

Northwest Atlantic ecosystems have undergone significant changes in recent decades, characterized by the collapse of several demersal fish stocks and a shift in ecosystem structure from one dominated by large demersal fish to ecosystems dominated by small pelagic fish and invertebrates (e.g. Bundy *et al.*, 2009). These collapses were largely due to overfishing (Myers *et al.*, 1997; Sinclair and Murawski, 1997). Twenty years later, most stocks have not recovered. A number of explanations have been considered, including increased natural mortality, and reduced recruitment rates, while in some cases continued fishing in directed and bycatch fisheries is also an important factor (Shelton *et al.*, 2006).

In the southern Gulf of St Lawrence (sGSL, NAFO fishing zone 4T), the collapsed stock of white hake (*Urophycis tenuis*) has shown no sign of recovery and the collapsed stock of Atlantic cod (*Gadus morhua*) continues to decline despite negligible fishing mortality (Swain and Chouinard, 2008). This lack of recovery is due to elevated natural mortality of large fish (Chouinard *et al.*, 2005; Swain and Chouinard, 2008; Swain *et al.*, 2012a,b). Because of their continued low abundance, these stocks have been designated as 'Endangered' by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC www.cosewic.gc.ca; Swain and Chouinard, 2008). While these stocks have declined, grey seals (*Halichoerus grypus*) have increased in abundance and it has been suggested that seal predation may be an important factor limiting their recovery (Chouinard *et al.*, 2005; Benoît and Swain, 2008; Benoît *et al.*, 2011). A difficulty with this hypothesis is that the failure of fish stocks in this area to recover is primarily due to high mortality among fish >35 cm long, while diet analyses suggest that species such as cod and hake are not major prey of grey seals and that grey seals consume smaller prey with an average length of 23–28 cm (Bowen *et al.*, 1993; Bowen and Harrison, 1994; Hammill *et al.*, 2007a,b). However, most diet studies have focused on nearshore or accessible beach areas, during summer and early autumn (June–October) (e.g. Benoît and Bowen, 1990, Bowen *et al.*, 1993; Hammill *et al.*, 2007a,b). At this time of the year, cod are widely dispersed, and the larger cod which occur further offshore maybe underrepresented in diet samples collected from these nearshore areas (Benoît *et al.*, 2011).

During November and early December, most commercially important groundfish in the sGSL migrate to overwinter in the Laurentian Channel (Figure 1) (Clay, 1991; Darbyson and Benoît, 2003). Many of these fish, particularly cod, are highly aggregated in winter. Surveys carried out during January, 1994–1997, showed that the entire spawning stock of southern sGSL cod overwinters along the southern slope of the Channel in the Cabot Strait area (NAFO fishing zone 4Vn), in particular off St Paul Island (Swain *et al.*, 1998, 2001). The timing of this change in the sGSL fish community coincides with movements of grey seals in late November from their more dispersed summer distribution throughout most of the sGSL and neighbouring areas, to a more aggregated distribution in the sGSL, Cabot Strait, and Scotian Shelf (Harvey *et al.*, 2008). The extended grey seal breeding season occurs from late-January to February in the sGSL (Hammill *et al.*, 2007a,b). As capital breeders, grey seals rely on stored energy reserves during the roughly 3-week haul-out period, then return to sea to forage. A recent study on the movements of satellite-transmitter equipped grey seals has shown that there can be a considerable overlap between grey seals, particularly males, and the overwintering aggregations of plaice, hake, redfish, herring, and cod, during November–March, and it has been suggested that grey seals are preying on cod and hake aggregations during this period (Harvey *et al.*, 2012). However, co-occurrence does not necessarily indicate predation and no previous studies have examined the diet of grey seals in this area at this time of year.

In this study, we used digestive tract contents from grey seals collected during autumn and winter around coastal Cape Breton Island, an area outside of the overwintering fish aggregations, as well as samples collected from the Cabot Strait area, where overwintering aggregations of demersal fish do occur, to determine whether grey seals feed on these aggregations of cod and hake.

Material and methods

Stomach and intestinal contents were obtained under scientific permit by contract hunters as part of ongoing research to monitor Northwest Atlantic grey seal diets. Animals were sampled in the Cabot Strait area near St Paul Island, and from the west coast of Cape Breton Island (Figure 1).

Stomachs and digestive tracts were removed in the field, and frozen at -20°C. In the laboratory, contents were thawed, washed, and sorted using a sieve with 0.425 mm mesh. All items were retained in a basin. Prey were identified to the lowest possible taxonomic level (Hammill *et al.*, 2007a,b). Otoliths and other hard parts were sorted manually and were identified using reference collections (Fisheries and Oceans Canada, Mont-Joli, QC and St John's NL) and an identification guide (Clarke, 1986; Härkönen 1986).

Otoliths were sorted, visually, into three 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 the total fish length. If a large number of otoliths of a single species were present in a stomach, a random subsample of 25 otoliths was measured. Unmeasured otoliths were identified to the lowest taxon possible.

The lengths and weights of consumed fish were estimated using otolith measurements and species-specific otolith size-body length and length–weight relationships developed from samples collected during Department of Fisheries and Oceans research surveys or using parameters from the literature (e.g. Lawson *et al.*, 1995; D. Chabot, Dept. of Fisheries and Oceans, Mont-Joli, QC, unpublished data; G. Stenson, unpublished data). Diets were reconstructed by estimating the species proportions from data pooled over all seals for a particular region, year, or sex. To correct for loss of prey items due to digestion, numerical correction factors (NCFs) were applied to otoliths from intestinal contents (Grellier and Hammond, 2006: Lundström *et al.*, 2007).

Diet composition is expressed as per cent wet mass, by digestive tract component (stomach or intestine), where % mass of species $A = 100 \times$ estimated mass of species A/estimated mass of all prey for the particular dataset.

Seasonal changes in the distribution of cod will affect the availability of cod to seals. Cod overwinter in Cabot Strait but disperse to their summer feeding areas in the sGSL in spring. Most of the Cabot Strait samples were collected when cod were in the Cabot Strait overwintering area. However, nine seals were collected on 30 April 2011, when cod would have been leaving or had left Cabot Strait, and 27 animals were collected 12–27 October 2011, when most cod would not yet have arrived in Cabot Strait (Comeau *et al.*, 2002). Animals collected on these dates were treated separately.

Diet composition may vary considerably between seals. Here sample means are presented, but because of small sample sizes and large variation among individuals, 95% confidence intervals were estimated using percentiles from bootstrapped distributions. One thousand bootstrapped samples of the observed sample sizes were generated by random sampling with replacement and the 2.5th and 97.5th percentiles were calculated for each prey group. The bootstrapping routine was written using the R programming language. Differences in species composition between samples were examined using a Cochran–Mantel–Haenszel (CMH) statistic (Agresti, 2007). Differences between samples in mean fish lengths and reconstructed diet mass were assessed using an analysis of variance (ANOVA) and post hoc comparisons were made using a Tukey–Kramer test for unequal group sizes. Reconstructed diet mass data were log-transformed to meet the homogeneity of variance assumption. All statistical analyses were completed using SAS software (SAS version 9.3; SAS Institute, Inc., Cary, NC, USA). Differences were considered significant at $p < 0.05$, unless otherwise stated.

Results

Digestive tracts were obtained from 169 grey seals (71 females (F), 98 males (M), age 1–33 years, mean = 7 years, SD = 6.6) collected along the west coast of Cape Breton Island, between September and January, 1996–2011, including 100 animals collected in 1999–2003 and presented in Hammill *et al.*, (2007a,b) (Figure 1). In the Cabot Strait area, digestive tracts were obtained from

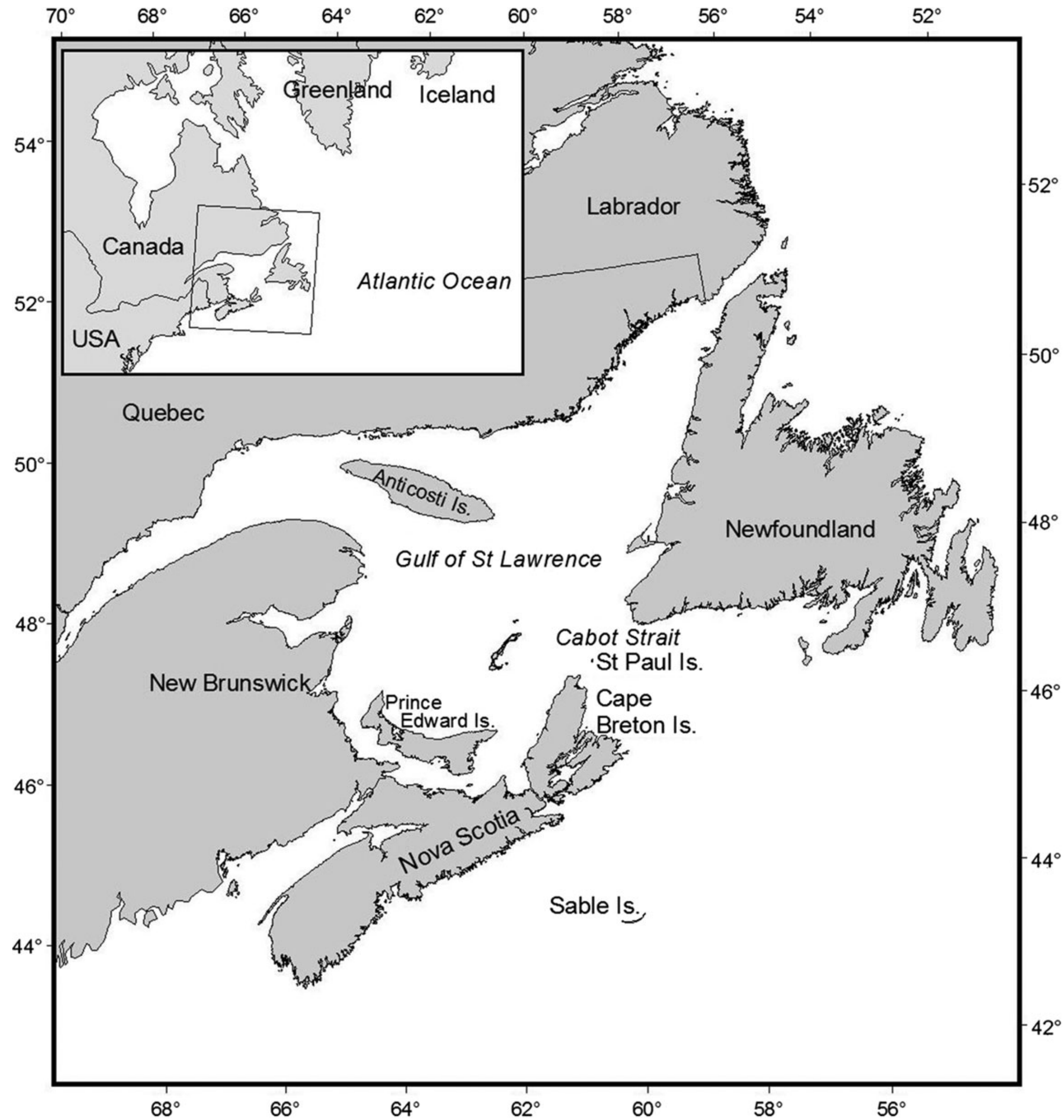

Figure 1. Map showing the study area. Samples were collected from west coast of Cape Breton Island and in Cabot Strait near St Paul Island.

74 grey seals (20F, 54M, age 1–29 years, mean = 10 years, SD = 6.0) collected between 25 October and 29 December 2008, 74 animals (7F, 67M, age 1–28 years, mean = 12 years, SD = 5.1) collected between 4 November 2010 and 6 January 2011 and 89 seals (18F, 71M, age 1–25 years, mean = 10 years, SD = 5.4) collected in April–December 2011. The latter collection included 9 males obtained on April 30, 27 animals collected October 12–24 and 53 animals collected between November 23 and December 13.

In total, 27 prey species were identified (Table 1). Atlantic cod (cod), Atlantic herring (herring), sandlance, mackerel, various species of flatfish (winter flounder, American plaice, yellow-tailed flounder, windowpane and Greenland halibut) and white hake accounted for over 90% of the diet in the Cabot Strait area and off the west coast of Cape Breton Island (Tables 2 and 3). Diets were more restricted in Cabot Strait with only three species: cod, flatfish (primarily American plaice), and sandlance accounting for ≥88% of the intestine-based diet, whereas from the west coast of Cape Breton Island, six species: cod, herring, flatfish (primarily winter flounder), sandlance, hake, and mackerel accounted for ≥85% of the intestine-based diet (Tables 2 and 3). Hake was a more important prey item in stomachs from Cape Breton Island (CMH statistic = 3.86, d.f. = 1, $N = 19$, $p = 0.049$), whereas cod was a more important prey item in samples from Cabot Strait among stomachs (CMH statistic = 4.23, d.f. = 1, $N = 19$, $p = 0.040$) and

Table 1. Species found in grey seal digestive tracts from Cabot Strait area and numerical correction factors ([1]Grellier and Hammond 2006; [2]Tollit *et al.*, 2007).

Common name	Scientific name	Rounded (NCF)	Source
Atlantic herring	*Clupea harengus*	2.9	1
Atlantic mackerel	*Scomber scombrus*	1.4	1
Sandeel	*Ammodytes marinus*	2.9	1
Atlantic cod	*Gadus morhua*	1.1	1
Haddock	*Melanogrammus aeglefinus*	1.1	1
White Hake	*Urophysis tenuis*	**1.1**	
Silver hake	*Merluccius bilinearis*	**1.1**	
Pollock	*Pollachius virens*	**1.1**	
Gadoids		1.1	
Fourberd rockling	*Enchelyopus cimbrius*	**1**	
Marlin spike	*Nezumia bairdi*	**1**	
Flatfish		1.3	
Greenland halibut	*Reinhardtius hippoglossoides*	**1.3**	
Winter flounder	*Psuedopleuronectes americanius*	**1.3**	
American Plaice	*Hippogloossides*	**1.3**	
Yellowtail flounder	*Limanda feruginea*	**1.3**	
Windowpane flounder	*Scophthalmus aquosus*	**1.3**	
Capelin	*Mallotus villous*	7.9	2
Wolffish	*Anarhichas lupus*	**2.9**	
Sculpin	Cottidae	**2.9**	
Sea raven	*Hemitripterus americanus*	**2.9**	
Morstack sculpin	*Tryglops murrayi*	**2.9**	
Lumpfish	*Cyclopterus lumpus*	**2.9**	
Eel pout	*Lycodes* sp.	**1.2**	
Cunner	*Tautagolabrus adspersus*	**2.9**	
Fourline snake blenny	*Eumesogrammus praecisus*	**1.3**	
Snailfish	*Liparis* sp.	**1**	
Redfish	*Sebastes* sp.	**1.1**	
Ocean pout	*Zoarces americanus*	**1.2**	

Bold are assumed NCF based on otolith size and robustness of similar species from Campana (2004) and Härkönen (1986).

intestines (CMH statistic = 4.94, d.f. = 1, $N = 19$, $p = 0.026$) after controlling for sex (Tables 2–5). No differences in reconstructed diet mass were observed between males and females in either the stomach or intestine based diets, but log-transformed reconstructed stomach diets were significantly heavier among males from Cabot Strait, than males from Cape Breton Island (ANOVA $F_{1,129} = 4.12$, $p = 0.044$). Reconstructed intestine-based diets were significantly heavier among animals from Cabot Strait than animals from Cape Breton Island ($F_{3,354} = 6.6$, $p < 0.002$).

Coastal Cape Breton Island

In samples from the west coast of Cape Breton Island, no differences were observed between animals ≤3 years of age ($N = 28$) and those 4 years and older ($p > 0.05$) in the stomachs or intestine-based diets. No differences were observed between years or between males and females in diet composition from stomachs among the main prey ($p > 0.05$). Hake was the most important prey (28.3 and 31.5% males and females, respectively), and along with sandlance, cod, herring, and flatfish accounted for 95% of the diet by weight (Tables 2 and 4). In the intestines, sandlance was the most important prey species (24.4 and 29.1% males and females, respectively), although hake remained an important prey (14.6 and 11.2% males and females, respectively) (Table 2). In the intestines, no differences were observed between sexes nor year for the contribution of sandlance, herring, flatfish, and hake to the diet, but males consumed more cod, than females, when controlling for year (Tables 2 and 5) (CMH statistic = 4.5, $p = 0.034$, d.f. = 1, $N = 18$).

Cabot Strait

The Cabot Strait sample was divided into three groups: November to early January 2008–2011, April 2011, and October 2011. Cod, herring, flatfish, sandlance, and hake accounted for 90% or more of the diet in both the stomachs and the intestines collected from November to early January (Table 3). Cod was the most important prey contributing up to 79.8% of the diet determined from stomachs and 63.6% of the diet determined using intestines among males (Tables 4 and 5). No differences were observed between years or between sexes in the contribution of sandlance, herring, flatfish, hake, and cod to the diet using stomach contents. However, samples sizes were small for the comparisons between years and sex (Tables 4 and 5), and the magnitude of the difference between males and females in the contribution to the diet was large for cod (68.4% for males, 14.3% for females) and for herring (3.6% for males and 49.3% for females (Tables 3 and 4). Based on intestine contents, hake was more important in the diet of males than in that of females (Chi-square = 3.86, d.f. = 1, $p = 0.0495$, $N = 6$). Similarly, the greater contribution of cod to the diet of males (46.5%) than females (9.4%) was marginally significant despite low statistical power (Chi-square = 3.0, $p = 0.083$, d.f. = 1, $N = 6$). The estimated contribution of sandlance to the diet was greater for females than males (13.8 and 2.0%, respectively, in stomachs and 30.3 and 3.3% in intestines), but these differences were not statistically significant (Tables 3 and 5).

For the nine males collected in April 2011, the diet reconstructed from stomach contents was comprised mainly of flatfish, capelin, white hake, wolffish, and cod, accounting for nearly 99% of the diet (Tables 6). Based on reconstruction of the intestine contents, flatfish, capelin, cod, and white hake accounted for almost 98% of the diet.

Twenty-seven animals were collected in the last week of October 2011 (Table 6). Based on stomachs, cod and flatfish were the main prey for males, while cod and sandlance were the most important prey for females. In the intestines, flatfish and cod accounted for 93% of the diet among males, while for females, the diet was dominated by flatfish, cod, and herring (80.6%).

Size of fish

Grey seals fed on cod ranging between 10 and 77 cm long. Significant differences were observed between samples in mean length of cod consumed (ANOVA $F = 50.5$, d.f. = 3,454, $p < 0.001$; Figure 2, Table 7). A post hoc Tukey test showed that seals consumed significantly longer cod in Cabot Strait ($p < 0.05$), and that fish consumed in Cabot Strait in 2010 and 2011 were significantly longer than fish consumed in 2008. Grey seals fed on white hake that ranged from 5 to 64 cm in length. Significant differences were observed between samples in mean length of white hake consumed (ANOVA $F = 10.5$, d.f. = 3,375, $p < 0.001$; Figure 2, Table 7). A post hoc Tukey test showed that seals consumed significantly longer hake in Cabot Strait in 2011 ($p < 0.05$) than in other years or off Cape Breton Island, but no differences were observed between the 2008 and 2010 Cabot Strait and Cape Breton Island samples. Herring consumed

Table 2. Reconstructed diet composition and 95% confidence limits in parentheses, average reconstructed mass and standard deviation (SD) and number of tracts examined (N) from stomach and intestine contents of grey seals collected from the west coast of Cape Breton Island Canada.

	Stomach		Intestine	
	Male	**Female**	**Male**	**Female**
Atlantic cod	11.1 (6.8 – 15.9)	26.5 (3.7 – 35.4)	10.8 (8.5 – 13.3)	6.4 (3.3 – 10.7)
Atlantic herring	16.9 (9.3 – 24.2)	6.4 (1.6 – 11.2)	14.7 (10.7 – 18.2)	5.2 (3.0 – 8.8)
Mackerel		1.1 (0 – 1.6)	6.2 (3.5 – 8.2)	0.7 (0 – 1.5)
Capelin		<0.1	<0.1	
Pouts, blennies		<0.1	0.1 (0 – 0.2)	
Flatfish	9.2 (3.8 – 13.1)	4.5 (2.0 – 7.4)	8.3 (5.1 – 10.5)	10.9 (6.6 – 16.5)
Winter flounder	3.2 (0.2 – 2.7)	10.3 (4.3 – 17.5)	6.5 (1.4 – 8.5)	23.8 (12.1 – 36.5)
American plaice	0.4 (0.1 – 0.6)	0.2 (0 – 0.3)	3.4 (0.9 – 4.4)	0.9 (0.4 – 1.5)
Yellow-tailed flounder	<0.1	2.0 (0.3 – 3.5)	0.8 (0.2 – 1.0)	0.9 (0.1 – 1.7)
Windowpane	1.7 (0.2 – 2.7)	0.1 (0 – 0.2)	0.6 (0.4 – 0.7)	0.8 (0.3 – 1.3)
Sandlance	22.9 (7.0 – 32.0)	7.3 (2.5 – 13.0)	24.4 (15.1 – 31.0)	29.1 (5.4 – 40.6)
Sculpins	0.6 (0 – 1.0)	0.3 (0.1 – 0.5)	2.2 (0.3 – 3.1)	1.5 (0 – 3.0)
Smelt			<0.1	<0.1
Redfish	<0.1		<0.1	0.5 (0 – 0.9)
White hake	28.3 (18.7 – 36.8)	31.5 (21.9 – 50.0)	14.6 (11.0 – 17.7)	11.2 (7.4 – 17.2)
Wrymouth	5.0 (0 – 9.7)	0.1 (0 – 0.2)	1.2 (0.2 – 2.3)	
Fourbeard rockling	<0.1	<0.1	<0.1	
Barracudina				
Butterfish	1.9 (0.7 – 2.8)	2.1 (1.0 – 3.6)	2.3 (0.9 – 3.0)	0.4 (0.2 – 0.8)
Cunner	0.3 (0 – 0.6)	0.2 (0 – 0.3)	0.1 (0 – 0.2)	0.8 (0 – 1.5)
unspecified	2.9 (1.1 – 4.5)	1.0 (0.3 – 1.8)	4.0 (2.9 – 5.0)	5.3 (2.6 – 8.9)
Average mass (SD)	3506 (3904)	3187 (5220)	3948 (5466)	3632 (7182)
N	54	40	98	71

Intestine samples have been adjusted by applying numerical correction factors.

Table 3. Reconstructed diet composition and 95% confidence limits in parentheses, average reconstructed mass and standard deviation (SD) and number of tracts examined (*N*) from stomach and intestine contents of grey seals collected from Cabot Strait, Canada.

	Stomach		Intestines	
	Male	**Female**	**Male**	**Female**
Atlantic Cod	68.4 (59.7 – 79.8)	14.3 (2.8 – 24.2)	46.5 (43.5 – 51.4)	9.4 (6.1 – 17.9)
Atlantic Herring	3.6 (1.5 – 5.4)	49.3 (22.6 – 64.6)	1.0 (0.7 – 1.2)	2.2 (0.7 – 4.7
Atlantic Mackerel	1.7 (0.6 – 2.6)	2.7 (0.8 – 4.6)	0.4 (0.1 – 0.5)	0.4 (0 – 1.2)
Capelin	0.2 (0 – 0.3)	1.2 (0 – 2.2)	1.1 (0.4 – 1.3)	1.4 (0.5 – 3.4)
Eelpouts		0.7 (0 – 1.2)	0.4 (0.2 – 0.45)	0.2 (0 – 0.5)
Flatfish	12.4 (4.8 – 17.6)	11.4 (0.19.4)	38.7 (32.6 – 41.6)	52.6 (15.1 – 68.1)
Winter Flounder				0.3 (0 – 0.4)
Am. Plaice	0.2 (0 – 0.3)		0.9 (0.6 – 1.0)	0.4 (0 – 1.0)
Y-t flounder				<0.1
Gr halibut	0.2 (0 – 0.4)			
Sandlance	2.0 (0.8 – 3.1)	13.8 (5.0 – 23.1)	3.3 (2.5 – 3.9)	30.3 (13.8 – 59.5)
Sculpin	<0.1	0.4 (0 – 0.8)	0.2 (0.1 – 0.31)	0.1 (0 – 0.3)
Smelt		0.1 (0 – 0.2)		
Redfish	<0.1	0.4 (0 – 0.8)	<0.1	0.1 (0 – 0.3)
White Hake	9.8 (6.8 – 12.9)	1.6 (0 – 3.1)	4.0 (3.2 – 4.6)	0.7 (0.2 – 0.9)
Silver Hake	0.3 (0 – 0.4)			
Cunner				0.1 (0 – 0.4)
Snailfish				<0.1
Unidentified Fish	1.0 (0.1 – 1.5)	3.8 (0.1 – 6.7)	3.3 (2.0 – 3.8)	1.5 (0.4 – 3.6)
Average mass (SD)	6687 (9554)	1657 (2534)	7462 (11418)	6162 (17133)
N	81	25	166	37

Intestine samples have been adjusted by applying numerical correction factors.

by seals varied from 10 to 35 cm in length. Significant differences were observed between samples in mean length of Atlantic herring consumed (ANOVA $F = 64.0$, d.f. = 2,221, $p < 0.0001$; Figure 2, Table 7). Seals consumed significantly shorter herring in Cabot Strait in 2008 (post hoc Tukey test: $p < 0.05$) than in 2011 or off Cape Breton. No herring were detected in the diet in 2010. The flatfish group was dominated by winter flounder off the west coast of Cape Breton and by American plaice in Cabot Strait, but also included

Table 4. Contribution (% mass) of sandlance, herring, cod, flatfish, and hake to the diet of grey seals by location, year, sex, and number of samples (*N*) reconstructed from stomach contents.

Location	Year	Sex	*N*	Sandlance	Herring	Cod	Flatfish	Hake
CB	1999	F	4	0.4	0.0	12.8	26.0	53.6
CB	2000	F	3	0.6	62.0	10.9	3.7	11.1
CB	2002	F	6	7.1	0.0	0.0	7.7	81.9
CB	2003	F	14	31.4	6.6	4.8	10.2	33.5
CB	2004	F	0					
CB	2008	F	6	2.9	0.0	2.1	37.6	4.4
CB	2010	F	2	0.0	0.0	67.8	0.8	28.5
CB	1999	M	11	0.4	1.4	25.2	6.7	61.3
CB	2000	M	13	0.6	62.0	10.9	3.7	11.1
CB	2002	M	8	17.4	0.0	6.0	1.8	72.5
CB	2003	M	6	66.5	0.4	0.0	14.7	15.3
CB	2004	M	4	53.8	0.0	2.0	31.5	4.6
CB	2008	M	2	0.0	0.0	2.3	63.8	19.8
CB	2010	M	3	95.6	0.0	0.0	0.0	0.0
CS	2008	F	29	4.0	60.8	0.0	28.8	3.4
CS	2008	M	41	0.5	10.5	65.8	8.2	10.1
CS	2010	F	1	0.0	0.0	14.2	29.3	22.5
CS	2010	M	29	0.5	0.1	79.8	3.8	14.8
CS	2011	F	6	34.7	4.2	34.1	19.3	0.0
CS	2011	M	23	5.8	0.2	56.7	27.9	4.6
CSO	2011	F	7	18.8	7.5	55.9	8.6	0.0
CSO	2011	M	8	4.4	0.3	59.4	25.8	5.2
CSA	2011	M	7	0.1	0.0	9.5	34.2	19.8

Locations are Cape Breton (CB), Cabot Strait (CS, November to December), Cabot Strait October (CSO), and Cabot Strait April (CBA).

yellow-tailed flounder, and windowpane. Seals consumed fish 5 to 51 cm long in this group. Significant differences were observed between samples in mean length (ANOVA $F = 16.4$, d.f. = 3,249, $p < 0.0001$; Figure 2, Table 7), with seals consuming significantly longer flatfish in Cabot Strait in 2011 ($p < 0.05$).

Discussion

Our results show that cod and white hake are a major component of the grey seal diet in the Cabot Strait area, during the late fall and winter, particularly among males. The contribution of cod (average 68.4% in stomachs, 46.5% in intestines of males: Table 3) to the grey seal diet in this area is much greater than that has been reported previously, where cod has comprised up to 25% of stomach contents of grey seals in Iceland, 21.6% reported from scat samples in the United Kingdom (summarized in Table 2, in O'Boyle and Sinclair, 2012), 10% in the Baltic Sea (Lundström *et al*. 2010) and 19–25% for the Scotian shelf off the east coast of Canada (Bowen *et al*., 1993; Bowen and Harrison, 1994). The length of cod consumed (mean = 33–45 cm, range 10–77 cm, Table 7) in samples from Cabot Strait is also much larger than the mean length of 26–28 cm, that has generally been reported for Northwest Atlantic grey seal diets in the sGSL and on the Scotian Shelf (Bowen *et al*., 1993; Hammill *et al*., 2007a,b), but similar in size to cod consumed by grey seals in the United Kingdom (average 38–44 cm, range 10–80 cm) (summarized in Table 3, in O'Boyle and Sinclair, 2012).

Hake was more important than cod in the diet of seals collected off the western coast of Cape Breton between September and January. In summer and early autumn, sGSL hake are concentrated in this area, particularly since the early 1990s, with densities highest in the shallow waters of St Georges Bay and the deeper waters of the

Table 5. Contribution (% mass) of sandlance, herring, cod, flatfish, and hake to the diet of grey seals by location, year, sex, and number of samples (N) reconstructed from intestine contents.

Location	Year	Sex	N	Sandlance	Herring	Cod	Flatfish	Hake
CB	1996	F	3	0.0	0.0	0.0	100.0	0.0
CB	1996	M	2	44.5	0.0	0.0	55.4	0.0
CB	1999	F	6	28.3	10.2	13.9	9.0	34.1
CB	1999	M	21	8.0	5.6	17.8	11.7	35.7
CB	2000	F	6	20.4	33.9	2.7	26.5	13.2
CB	2000	M	17	22.6	40.9	9.3	12.2	11.2
CB	2002	F	10	82.2	6.0	3.9	2.6	4.0
CB	2002	M	12	87.2	1.6	3.9	2.2	2.5
CB	2003	F	15	0.5	3.0	4.3	44.3	9.8
CB	2003	M	14	43.9	0.6	10.8	22.6	5.9
CB	2004	F	4	0.0	0.0	1.8	82.5	0.0
CB	2004	M	5	14.3	8.4	1.9	8.7	5.0
CB	2008	F	17	5.9	1.4	1.8	67.5	10.3
CB	2008	M	7	2.2	0.0	5.7	70.2	4.9
CB	2010	F	4	0.0	1.8	26.5	42.1	18.4
CB	2010	M	3	36.0	0.0	4.5	0.0	21.8
CB	2011	F	4	0.0	0.0	17.0	7.3	0.0
CB	2011	M	4	1.9	0.0	40.8	0.0	7.9
CS	2008	F	20	59.5	7.3	7.3	20.3	0.4
CS	2008	M	54	6.1	16.4	31.2	35.9	6.9
CS	2010	F	7	0.8	0.0	54.4	28.1	2.4
CS	2010	M	67	0.9	0.1	63.6	21.6	5.2
CS	2011	F	8	20.9	0.0	3.3	73.4	0.6
CS	2011	M	45	4.0	0.2	39.8	49.1	3.4
CSO	2011	F	10	4.9	23.9	25.7	31.0	3.2
CSO	2011	M	17	3.1	3.1	9.6	83.1	2.0
CSA	2011	M	9	0.0	1.9	14.2	62.1	3.2

Locations are Cape Breton (CB), Cabot Strait (CS, November to December), Cabot Strait October (CSO), and Cabot Strait April (CBA).

Table 6. Reconstructed diet composition and 95% confidence limits in parentheses, average reconstructed mass and standard deviation (SD), and number of tracts examined (*N*) from stomach and intestine contents of grey seals collected from Cabot Strait on 30 April and between 12 and 24 October 2011.

	Stomach			Intestines		
		October			October	
Prey	April Males	Males	Females	April Male	Male	Female
Atlantic Cod	9.5 (0 – 13.8)	59.4 (52.6 – 67.0)	55.8.0 (28.5 – 68.1)	14.2 (2.8 – 20.6)	9.6 (4.8 – 17.8)	25.7 (7.2 – 49.2)
Atlantic Herring		0.3 (0.1 – 0.4)	7.5 (3.0 – 11.0)	2.0 (0 – 3.8)	3.1 (0 – 2.1)	23.9 (4.1 – 41.9)
Atlantic Mackerel		2.4 (0.8 – 3.2)	3.6 (1.1 – 6.5)		0.5 (0 – 1.2)	3.8 (0 – 7.1)
Capelin	20.1.0 (6.6 – 50.1)	0.1 (0 – 0.2)	<0.1	18.0 (5.8 – 36.0)		
Eelpouts	1.1 (0 – 1.6)			0.4 (0 – 0.8)	<0.1	
Flatfish	16.2 (0 – 39.2)	25.5 (17.6 – 30.6)	7.9 (0 – 14.7)	52.3 (31.2 – 62.0)	78.8 (61.2 – 87.3)	31.0 (0 – 0 – 47.5)
Winter Flounder			0.6 (0 – 1.3)			
Sandlance	0.1 (0 – 0.3)	4.4 (2.3 – 5.9)	18.8 (4.8 – 34.0)		3.1 (0.6 – 6.9)	4.9 (0.3 – 9.0)
Sculpin		<0.1	0.3 (0 – 0.6)		<0.1	3.0 (0 – 6.4)
Redfish		<0.1			0.1 (0 – 0.2)	0.2 (0 – 0.4)
White Hake	19.8 (0 – 28.8)	5.5 (3.9 – 6.7)		3.2 (1.5 – 5.0)	2.0 (1.1 – 3.4)	3.2 (0 – 5.6)
Four beard rockling						
Cunner			0.6 (0 – 1.1)			
American plaice	18.1 (0 – 26.2)	0.2 (0.1 – 0.3)		9.9 (1.0 – 17.9)	4.3 (0 – 9.8)	
Wolfish	15.1 (0 – 37.6)	0.4 (0 – 0.6)			0.3 (0 – 0.6)	
Silver hake		0.7 (0.2 – 1.0)	1.5 (0 – 2.9)			
Unidentified Fish		0.6 (0.2 – 0.8)	3.2 (0 – 6.2)		0.2 (0 – 0.5)	4.2 (0 – 9.1)
Average mass (SD)	1519 (2430)	39657 (45107)	11688 (12145)	15799 (11717)	28293 (36731)	3592 (1936)
N	7	8	7	9	17	10

Intestine samples have been adjusted by applying numerical correction factors.

Cape Breton Trough (Swain *et al.*, 2012b). These areas are less important for cod in September, though the Cape Breton Trough was historically an important migration route for cod in November (Swain *et al.*, 2012a).

Sex differences in the timing and magnitude of energy expenditure for reproduction may result in sex-specific seasonal patterns of energy storage and utilization, particularly among capital-breeding species such as the grey seal (Beck *et al.*, 2003). Differences in seasonal energy storage patterns may also affect spatial distribution patterns as each sex attempts to maximize energy accumulation and reduce intersexual competition during key foraging periods (Breed *et al.*, 2006). During summer months, both male and female grey seals overlap more broadly than at other times of the year (Breed *et al.*, 2006; Harvey *et al.*, 2008). In November, grey seals in the GSL leave their summering area and migrate towards the sGSL or the Scotian Shelf, off the east coast of Nova Scotia (Figure 1) (Harvey *et al.*, 2008). Harvey *et al.* (2012) noted that males foraged in Cabot Strait, while females foraged further south on the Scotian Shelf. Indeed, one of our samplers commented that few females were seen in Cabot Strait during late fall (R. Courtney pers. comm.). As outlined earlier, most fish exit the sGSL in November to overwinter in Cabot Strait. Therefore, predators moving into Cabot Strait at this time would have access to a very rich prey field. Male zones of potential foraging activity within this area were associated with high densities of large herring, small size-classes of plaice, hake and redfish, and all sizes of cod, but of these species, cod were the most abundant (Harvey *et al.*, 2012) which could account for why cod were the most abundant prey in male diets. At this time of year, demersal species such as cod would also have reached their highest energy density (Dutil *et al.*, 2003). The heavier reconstructed diets from animals collected in Cabot Strait, compared with Cape Breton Island suggest that animals were feeding more intensively in this area, which coincides with a period of rapid increase in stored energy among both female and particularly male grey seals, during the last 3 months before breeding (Beck *et al.*, 2003).

In 2011, sampling started earlier than previous years, so we separated out the October 2011 samples, from the November to early January samples, if cod had not yet started migrating into the Cabot Strait area (Comeau *et al.*, 2002). Cod were still present in the April 2011 diet, but they comprised a lower proportion of the diet than was observed in winter samples, This is likely due to a decline in cod abundance in Cabot Strait as cod migrated back into the sGSL (Sinclair and Currie, 1994; Comeau *et al.*, 2002), though a change in diet preferences might also be at play. By April, the condition of cod has declined (Dutil *et al.*, 2003) and seals may be searching for more energy-rich prey as they attempt to rebuild energy stores after breeding (Beck *et al.*, 2003).

Over the last few decades, our general understanding of diet in marine mammals has improved immensely. Several approaches have been developed including analyses of digestive tract and faecal contents (Murie and Lavigne, 1986; Tollit *et al.*, 1997, 2003; Grellier and Hammond, 2006; Hammill *et al.*, 2007a,b), as well as fatty acid and stable isotope analyses (Iverson *et al.*, 2004; Hammill *et al.*, 2005). However, all of these approaches have different biases associated with them, complicating attempts to understand true diet composition (e.g. Rosen and Tollit, 2012; Bowen and Iverson, 2013). This is problematic because in the absence of an accurate diet for seals, trophic modelling approaches aimed at understanding the predator's influence on fish populations, such as mass balance models, extended single-species assessment models, or minimum realistic models, could provide misleading results (Benoît *et al.*, 2011).

Major limitations to the use of hard parts to reconstruct ingested prey to quantify diet composition include underestimating hard part size due to erosion and the failure to find hard parts in the

Table 7. Species, location, number of samples (N), mean length (cm), standard deviation (SD), and Tukey significance differences in lengths of fish consumed by grey seals.

Location/sample	*N*	Mean	SD	Minimum	Maximum	Tukey significance
Atlantic cod						
C Breton	37	26	8.5	10	43	C
Cabot Strait 2008	114	33	11.4	11	66	B
Cabot Strait 2010	161	42	11.2	19	77	A
Cabot Strait 2011	146	45	10.1	17	62	A
White Hake						
C Breton	225	26	6.8	11	51	B
Cabot Strait 2008	108	27	8.1	10	53	B
Cabot Strait 2010	21	24	16.9	5	63	B
Cabot Strait 2011	25	36	11.3	21	64	A
Atlantic herring						
C Breton	76	29	3.1	11	35	A
Cabot Strait 2008	121	24	2.9	10	29	B
Cabot Strait 2011	27	28	2.1	25	31	A
Flatfish						
C Breton	112	25	6.4	5	37	A
Cabot Strait 2008	54	26	7.1	7	41	A
Cabot Strait 2010	33	25	7.3	11	39	A
Cabot Strait 2011	54	32	7.1	10	51	B

sample because of complete digestion (Tollit *et al.*, 1997, 2003; Grellier and Hammond, 2006). In controlled feeding experiments conducted using grey seals, large otoliths had greater digestion coefficients than small otoliths. Therefore, the size of prey with large otoliths (i.e. larger prey) would be most underestimated if digestion coefficients were not applied (Grellier and Hammond, 2006). In this study, we did not correct for otolith erosion since grade-specific digestion coefficients for cod are not available, but this bias may be small. Based on a small sample of recovered otoliths ($N = 13$), Grellier and Hammond (2006) reported a digestive coefficient for pristine and moderately digested otoliths of only 3% for all large gadoids.

The application of NCF to prey items recovered from the intestines mitigates some of the problems associated with loss, or different evacuation rates, of fragile otoliths (Tollit *et al.*, 1997, 2003; Bowen, 2000; Grellier and Hammond, 2006), but NCF have not been developed for all species and have not been developed

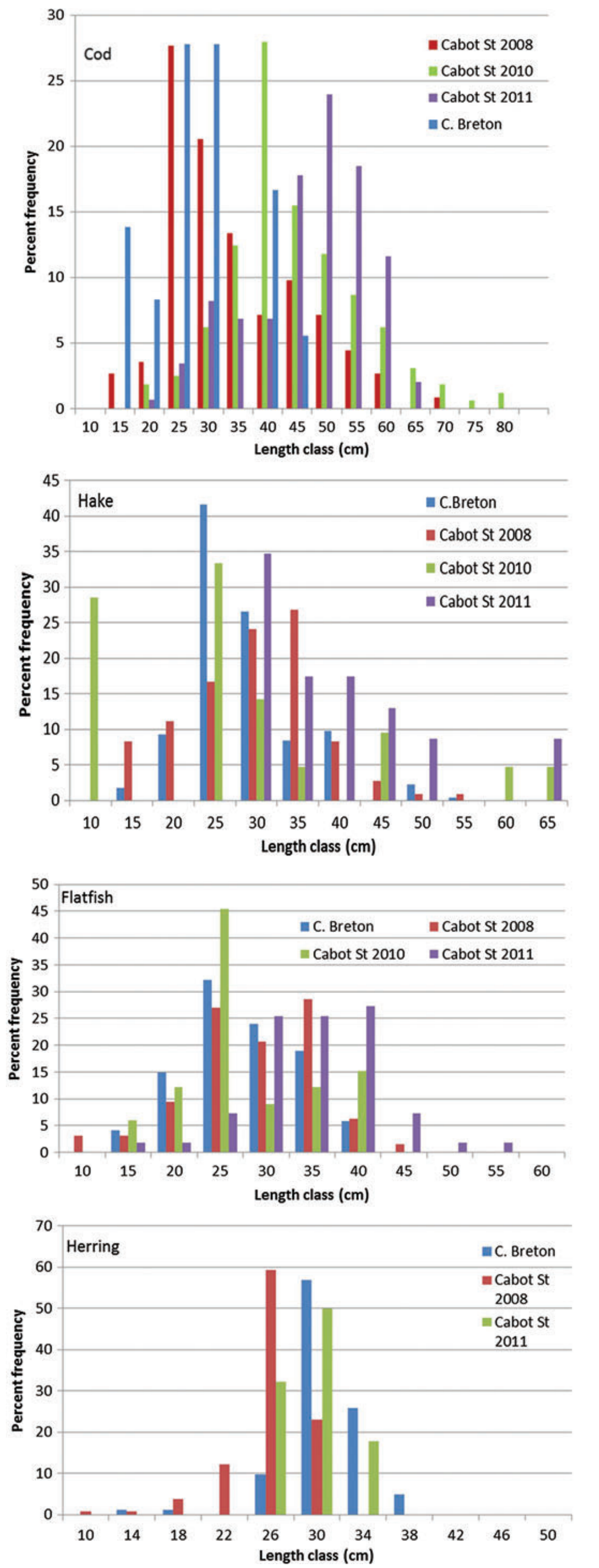

Figure 2. Per cent length frequency distribution of fish consumed by seals from Cape Breton Island, and Cabot Strait.

experimentally for material recovered from stomachs. Thus stomach contents may overestimate the contribution to the diet of species with large, rugged otoliths.

The presence of otoliths within digestive tracts depends on time since ingestion. In three species of phocids, fragile herring otoliths began to disappear from stomach contents within 3 h of ingestion and none were detected 13 h after ingestion, whereas within the intestine, hard parts may reflect feeding over the last 3–4 d (Murie and Lavigne, 1986; Grellier and Hammond, 2006). For samples collected immediately after feeding, stomach contents provide information on recent local feeding, but beyond a few hours stomachs are often empty because passage rates are so rapid. Intestines are more likely to contain food remains, but these may represent several meals, and if animals have been moving, then they may represent feeding over a larger area than assumed.

The lack of recovery of sGSL cod and white hake is due to very high natural mortality among large, mature fish (Chouinard *et al.*, 2005; Swain and Chouinard, 2008; Swain *et al.*, 2012b). Predation by grey seals has been hypothesized to be a potential source of this mortality (Benoît and Swain, 2008; Benoît *et al.*, 2011; Chouinard *et al.*, 2005). To fully evaluate the role of seal predation on fish recovery, information on mortality due to seal predation must be examined within the context of its contribution to overall fish mortality. Quantifying the relative importance of seal predation mortality requires information on consumption by seals, which in turn depends on spatial and temporal overlap between predators and their prey, population energy requirements, and diet composition (Harwood and Croxall, 1988; Harwood, 1992; Matthiopoulos *et al.*, 2008; Benoît *et al.*, 2011).

A challenge to understanding diet composition is obtaining samples throughout the animal's range and throughout the year. Grey seals are large and difficult to handle, adding to the logistical challenges of sampling in more offshore areas, particularly during the more inclement autumn–winter period. Overall, the species compositions of male and female diets are similar, but the contribution of demersal species is more important among males, while pelagic species are generally more important for females (Beck *et al.*, 2007). This study has shown that in areas where Atlantic cod and hake are aggregated, they can comprise a very significant component of the grey seal diet.

Acknowledgements

We thank R. Courtney, G. Organ, and W. Murphy, for the collection of samples in the field; P. Carter, J. Guerin, D. Mackinnon, S, J. Flight, P. Rivard, and S. Turgeon, for sorting samples and species identification and P. Carter and D. McKinnon for assistance in building up the database. W.D. Bowen (Bedford Institute) assembled the NCF table. A. Mosnier developed the bootstrap routine. Financial support was provided by the Department of Fisheries and Oceans under the CDEENA, Atlantic Seal Research and Laroque Programs.

References

Agresti, A. 2007. An introduction to categorical data analysis. John Wiley & Sons, Inc., Hoboken, NJ, USA.

Beck, C. A., Bowen, W. D., and Iverson, S. J. 2003. Sex differences in the seasonal patterns of energy storage and expenditure in a phocid seal. Journal of Animal Ecology, 72: 280–291.

Beck, C. A., Iverson, S. J., Bowen, W. D., and Blanchard, W. 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.

Benoît, D., and Bowen, W. D. 1990. Summer diet of grey seals (*Halichoerus grypus*) at Anticosti Island, Gulf of St Lawrence, Canada. Canadian Bulletin of Fisheries Aquatic Science, 222: 227–242.

Benoît, H. P., and Swain, D. P. 2008. Impacts of environmental change and direct and indirect harvesting effects on the dynamics of a marine fish community. Canadian Journal of Fisheries and Aquatic Science, 65: 2088–2104.

Benoît, H. P., Swain, D. P., Bowen, W. D., Breed, G. A., Hammill, M. O., and Harvey, V. 2011. Can predation by grey seals explain elevated natural mortality in three fish species in the southern Gulf of St. Lawrence? Marine Ecology Progress Series, 442: 149–167.

Bowen, W. D. 2000. Reconstruction of pinniped diets: accounting for complete digestion of otoliths and cephalopod beaks. Canadian Journal of Fisheries and Aquatic Science, 57: 898–905.

Bowen, W. D., and Harrison, G. D. 1994. Offshore diet of grey seals *Halichoerus grypus* near Sable Island, Canada. Marine Ecology Progress Series, 112: 1–11.

Bowen, W. D., and Iverson, S. J. 2013. Methods of estimating marine mammal diets: A review of validation experiments and sources of bias and uncertainty. Marine Mammal Science, 29: 719–754.

Bowen, W. D., Lawson, J. W., and Beck, B. 1993. Seasonal and geographic variation in the species composition and size of prey consumed by grey seals (*Halichoerus grypus*) on the Scotian Shelf. Canadian Journal of Fisheries and Aquatic Science, 50: 1768–1778.

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

Bundy, A., Heymans, J. J., Morissette, L., and Savenkoff, C. 2009. Seals, cod and forage fish: a comparative exploration of variations in the theme of stock collapse and ecosystem change in four Northwest Atlantic ecosystems. Progress in Oceanography. 81: 188–206.

Campana, S. E. 2004. Photographic Atlas of Fish Otoliths of the Northwest Atlantic Ocean. NRC Press, Ottawa, ON.

Chouinard, G. A., Swain, D. P., Hammill, M. O., and Poirier, G. A. 2005. Correspondence between changes in grey seal population abundance and variation in natural mortality of southern Gulf of St. Lawrence cod. Canadian Journal of Fisheries and Aquatic Science, 62: 1991–2000.

Clarke, M. R. (ed.) 1986. A handbook for the identification of cephalopod beaks. Clarendon Press, Oxford. 273 pp.

Clay, D. 1991. Seasonal distribution of demersal fish (Osteichthyes) and skates (Chondrichthyes) in the southeastern Gulf of St. Lawrence. Canadian Special Publication of Fisheries and Aquatic Sciences, 113: 241–259.

Comeau, L. A., Campana, S. E., and Chouinard, G. A. 2002. Timing of Atlantic cod (*Gadus morhua* L.) seasonal migrations in the southern Gulf of St Lawrence: interannual variability and proximate control. ICES Journal of Marine Science, 59: 333–351.

Darbyson, E., and Benoît, H. P. 2003. An atlas of the seasonal distribution of marine fish and invertebrates in the southern Gulf of St. Lawrence. Canadian Data Report Fisheries and Aquatic Science, 1113: 294 pp.

Dutil, J-D., Lambert, Y., and Chabot, D. 2003. Winter and spring changes in condition factor and energy reserves of wild cod compared with changes observed during food-deprivation in the laboratory. ICES Journal of Marine Science, 60: 780–786.

Grellier, K., and Hammond, P. S. 2006. Robust digestion and passage rate estimates for hard parts of grey seal (*Halichoerus grypus*) prey. Canadian Journal of Fisheries and Aquatic Science, 63: 1982–1998.

Hammill, M. O., Lesage, V., and Carter, P. 2005. Problems associated with determining diet composition in harp seals by reconstruction of stomach contents or faecal samples. Canadian Journal of Zoology, 83:1365–1372.

Hammill, M. O., Gosselin, J. F., and Stenson, G. B. 2007a. Abundance of Northwest Atlantic grey seals in Canadian waters. NAMMCO Scientific Publication, 6: 99–115.

Hammill, M. O., Stenson, G. B., Proust, F., Carter, P., and McKinnon, D. 2007b. Feeding by grey seals in the Gulf of St. Lawrence and around Newfoundland. *In* Grey seals in the North Atlantic and the Baltic, pp. 135–152. Ed. by T. Haug, M. Hammill, and D. Olafsdottir. NAMMCO Scientific Publication 6. 227 pp.

Härkönen, T. 1986. Guide to the otoliths of the bony fishes of the northeast Atlantic. Danbiu Aps, Sweden. 256 pp.

Harvey, V., Côté, S. D., and Hammill, M. O. 2008. The ecology of 3-D space use in a sexually dimorphic mammal. Ecography, 31: 371–380.

Harvey, V., Hammill, M. O., Swain, D. P., Breed, G. A., Lydersen, C., and Kovacs, K. M. 2012. Winter foraging by a top predator, the grey seal *Halichoerus grypus*, in relation to the distribution of prey. Marine Ecology Progress Series, 462: 273–286.

Harwood, J. 1992. Assessing the competitive effects of marine mammal predation on commercial fisheries. South Africa Journal of Marine Science, 12: 689–693.

Harwood, J., and Croxall, J. P. 1988. The assessment of competition between seals and commercial fisheries in the North Sea and Antarctic. Marine Mammal Science, 4: 13–33.

Iverson, S. J., Field, C., Bowen, W. D., and Blanchard, W. 2004. Quantitative fatty acid signature analysis: a new method of estimating predator diets. Ecological Monographs, 74: 211–235.

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

Lundström, K., Hjerne, O., Alexandersson, K., and Karlsson, O. 2007. Estimation of grey seal (*Halichoerus grypus*) diet composition in the Baltic Sea. *In* Grey seals in the North Atlantic and the Baltic, pp. 177–196. Ed. by T. Haug, M. Hammill, and D. Olafsdottir. NAMMCO Scientific Publication 6. 227 pp.

Lundström, K., Hjerne, O., Lunneryd, S-G., and Karlsson, O. 2010. Understanding the diet composition of marine mammals: grey seals (*Halichoerus grypus*) in the Baltic Sea. ICES Journal of Marine Science, 67: 1230–1239.

Matthiopoulos, J., Smout, S., Winship, A. J., Thompson, D., Boyd, I. L., and Harwood, J. 2008. Getting beneath the surface of marine mammal–fisheries competition. Mammalian Reviews 2008, 38: 167–188.

Murie, D. J., and Lavigne, D. M. 1986. Interpretation of otoliths in stomach content analysis of phocid seals: quantifying fish consumption. Canadian Journal of Zoology, 64: 1152–1157.

Myers, R. A., Hutchings, J. A., and Barrowman, N. J. 1997. Why do fish stocks collapse? The example of cod in Atlantic Canada. Ecological Applications, 7: 91–106.

O'Boyle, R., and Sinclair, M. 2012. Seal-cod interactions on the eastern Scotian shelf: Reconsideration of modeling assumptions. Fisheries Research, 115–116: 1–13.

Rosen, D. A. S., and Tollit, D. J. 2012. Effects of phylogeny and prey type on fatty acid calibration coefficients in three pinniped species: implications for the QFASA dietary quantification technique. Marine Ecology Progress Series, 467: 263–276.

Shelton, P. A., Sinclair, A. F. G., Chouinard, G. A., Mohn, R., and Duplisea, D. 2006. Fishing under low productivity conditions is further delaying recovery of Northwest Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Science, 63: 235–238.

Sinclair, A., and Currie, L. 1994. Timing of cod migrations into and out of the Gulf of St. Lawrence based on commercial fisheries, 1986–93. Department of Fisheries and Oceans Atlantic Fisheries. Research. Document 94/47.

Sinclair, A. F., and Murawski, S. A. 1997. Why have groundfish stocks declined? In Northwest Atlantic groundfish: perspectives on a fishery collapse, pp. 71–93. Ed. by J. Boreman, B. S. Nakashima, J. A. Wilson, and R. L. Kendall. American Fisheries Society, Bethesda, MD.

Swain, D. P., and Chouinard, G. A. 2008. Predicted extirpation of the dominant demersal fish in a large marine ecosystem: Atlantic cod (*Gadus morhua)* in the southern Gulf of St. Lawrence. Canadian Journal of Fisheries and Aquatic Science, 65: 2315–2319.

Swain, D. P., Chouinard, G. A., Morin, R., and Drinkwater, K. F. 1998. Seasonal variation in the habitat associations of Atlantic cod (*Gadus morhua*) and American plaice (*Hippoglossoides platessoides*) from the southern Gulf of St. Lawrence. Canadian Journal of Fisheries and Aquatic Science, 55: 2548–2561.

Swain, D. P., Frank, K. T., and Maillet, G. 2001. Delineating stocks of Atlantic cod (*Gadus morhua*) in the Gulf of St. Lawrence and Cabot Strait areas using vertebral number. ICES Journal of Marine Science, 58: 253–269.

Swain, D. P., Hurlbut, T. R., and Benoît, H. P. 2012b. Pre-COSEWIC review of variation in the abundance, distribution and productivity of white hake (*Urophycis tenuis*) in the southern Gulf of St. Lawrence, 1971–2010.)). Canadian Science Advisory Secretariat Research Document 2012/066. 77 pp. Available at: http://www.dfo-mpo.gc.ca/csas-sccs/index-eng.htm.

Swain, D. P., Savoie, L., and Aubry, E. 2012a. Recovery potential assessment for the Laurentian south designatable unit of Atlantic cod (*Gadus morhua*): the southern Gulf of St Lawrence cod stock (NAFO Div. 4T-4Vn (Nov-Apr)). Canadian Science Advisory Secretariat Research Document. 2012/052. 54 pp. Available at: http://www.dfo-mpo.gc.ca/csas-sccs/index-eng.htm.

Tollit, D. J., Heaslip, S. G., Barrick, R. L., and Trites, A. W. 2007. Impact of diet-index selection and the digestion of prey hard remains on determining the diet of the Steller sea lion (*Eumetopias jubatus*). Canadian Journal of Zoology, 85: 1–15.

Tollit, D. J., Steward, M. J., Thompson, P. M., Pierce, G. J., Santos, M. B., and Hughes, S. 1997. Species and size differences in the digestion of otoliths and beaks: implications for estimates of pinniped diet composition. Canadian Journal of Fisheries and Aquatic Science, 54: 105–119.

Tollit, D. J., Wong, M., Winship, A. J., Rosen, D. A. S., and Trites, A. W. 2003. Quantifying errors associated with using prey skeletal structures from fecal samples to determine the diet of Steller's sea lion (*Eumetopias jubatus*). Marine Mammal Science, 19: 724–744.

Handling editor: Simon Northridge