Seasonal and interannual variability in grey seal diets on Sable Island, eastern Scotian Shelf

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ABSTRACT

We studied seasonal and interannual variability in the diet of grey seals (*Halichoerus grypus*) using faecal samples collected from Sable Island, Nova Scotia between 1991 and 1998. More than 28,000 prey from at least 28 taxa were identified from 1,245 faecal samples collect mainly in spring, fall and winter. Sand lance (*Ammodytes dubius*) dominated the diet in all season and years, but the importance of this and other species varied over time. There was also evidence of seasonal and interannual variation in the size of prey consumed both within and among species. We compared diet composition with estimates of prey numbers and biomass from annual research trawl surveys conducted in March and July. Species-specific numerical corrections were applied to otolith counts to account for the complete digestion of otoliths, and fish catchability correction factors applied to trawl survey catches to account for trawl selectivity. Based on an odds ratio index of prey selectivity, grey seals positively selected sand lance in both seasons. Other species were either relatively avoided or eaten roughly in proportion to their estimated abundance.

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INTRODUCTION

Both intrinsic and environmental factors such as sex, age, season, geographic location, and prey abundance and distribution are known to affect the diets of pinnipeds (reviewed in Bowen and Siniff 1999, Bowen *et al.* 2002). Seasonal and geographic variability in pinniped diets are thought to be driven mainly by changes in the relative abundance and distribution of prey (Sinclair *et al.* 1994, Thompson *et al.* 1996, Bowen and Harrison 1993, 1996), but demographic factors such as sex and age can underlie differences in diets in addition to the effects of prey characteristics (e.g., Lawson *et al.* 1995, Beck *et al.* 2005). Interannual variability in prey abundance and distribution can affect the composition of pinniped diets over longer time scales (Sinclair *et al.* 1994, Bowen and Harrison 1996, Lawson *et al.* 1997). Nevertheless, there are still relatively few examples of how diet changes over time and how those changes might relate to prey availability (Bailey and Ainley 1982, Nilssen *et al.* 1994, Thompson *et al.* 1996, Lawson *et al.* 1997, Mori and Boyd 2004) in large marine carnivores.

In the northwest Atlantic, grey seals (*Halichoerus grypus*) (Fig. 1) inhabit both coastal and offshore waters of the continental shelves from the Gulf of Maine to southern Labrador (Mansfield and Beck 1977, Stobo *et al.* 1990). During the breeding season, adults concentrate mainly near Sable Island and in the southern Gulf of St. Lawrence, where about 90% of pups are born (Stobo and Zwanenburg 1990). Based on flipper-tag recoveries outside the breeding season, grey seals are known to range widely throughout eastern Canadian waters (Stobo *et al.* 1990). Recent data from satellite-tagged adults indicates extensive foraging on offshore banks on the Scotian Shelf, particularly Sable/Western Bank (Bowen *et al.* 2005), reflecting the importance of this offshore area.

Fig. 1. *Grey seals off Sable Island, Canada. (Photo: W. D. Bowen)*

In a previous study, we described the diet of grey seals near Sable Island based on faecal samples collected between 1991 and early 1993 (Bowen and Harrison 1994). A preliminary comparison between the species in the grey seal diet with those caught in bottom-trawl, research surveys suggested that both prey abundance and distribution were important determinants of diet. However, the small number of comparisons over several years limited the inferences that could be drawn from that study. The present study investigates the extent to which the diet of grey seals may have changed during an 8 year period, the extent to which inter-annual changes in diets near Sable Island can be understood in terms of changes in the abundance and distribution of major prey species and evidence of prey selection by grey seals. Sampling in a consistent way from a single site has the advantage of removing sources of variability that might otherwise mask underlying changes in diet.

METHODS

Grey seal faecal samples were collected at haul-out sites on Sable Island, Canada (43° 55' N, 60° 00' W) seasonally between July 1991 and January 1998 (Table 1). On any given day, grey seals hauled out at dozens of sites along the more than 80 km of shoreline. Typically, only 5 - 10 reasonably fresh samples were collected on 1 day and no more than 2 samples were taken from a single haul-out site to minimize the effects of cluster sampling. Each sample was placed in a plastic bag and stored at -20° C. Otoliths and other prey hard parts were recovered from faecal samples following laboratory techniques described in Bowen and Harrison (1994). Prey identification was based primarily on the identification of sagittal otoliths and squid beaks. Feathers, shell fragments and other hard parts were used to indicate the presence of invertebrates and bird remains found in the samples, accounting for about 3% of prey occurrences. Otoliths were identified, using an 8 or 16 power binocular dissecting microscope, with the aid of a reference collection of otoliths collected from prey species on the Scotian Shelf. Squid beaks were identified with the aid of published descriptions (Clarke 1986).

To estimate the number of prey in each sample, we matched right and left otoliths (and upper and lower squid beaks) from individual prey species. When right and left otoliths could not be distinguished, the number of prey was estimated by dividing the total number of otoliths by 2. Unmatched otoliths and squid beaks were counted as a single prey. Following Bowen and Harrison

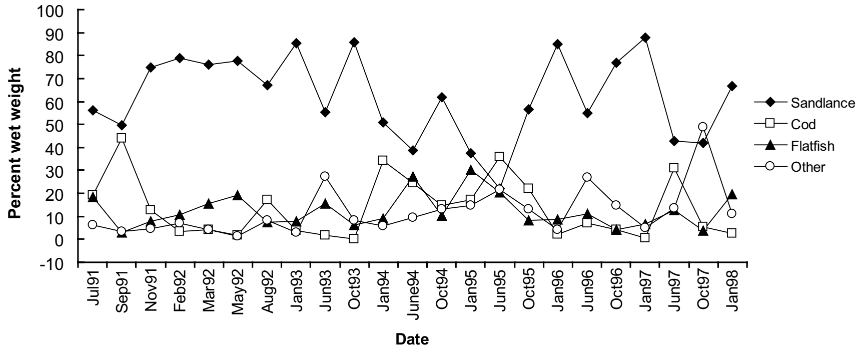

Fig. 2 *Interannual variation in the major prey taxa eaten by grey seals at Sable Island, 1991-1998. (Scientific names in Appendix)*

(1994) only otoliths judged to have undergone minimal or no erosion were measured and used to estimate the length and mass of prey. We estimated the degree of erosion by comparing the surface features of recovered otoliths with specimens from our reference collection. To derive estimates of total prey weight consumed, individual prey identified from unmeasured otoliths were assigned a mean length based on the average of measured otoliths of the same species within years and seasons, provided that at least 5 of these otoliths were measured; otherwise, an overall average from all 8 years of the study period was used. Length was measured along the midline of the otolith from the anterior edge to the posterior edge. Rostral length of lower beaks was used to estimate squid size following Clarke (1986). Percentage of otoliths measured varied among species, but typically ranged from 45% to 100% with the following exceptions: unspecified gadoid 25.8%, sand lance 9.3%, silver hake (*Merluccius bilinearis*) 20.1%, and unspecified flounder 13.5%. The low percentage for sand lance was primarily due to the need to sub-sample from the large number of otoliths recovered. Due to severe erosion or breakage, approximately 6.0% of recovered otoliths were classified as unknown fish. These otoliths were excluded in deriving estimates of prey size and prey mass consumed. Approximately 47% of the gadoid and flatfish otoliths recovered could not be identified to species level and were placed in unknown categories (Table 2). We felt that excluding these prey from further analysis would underestimate their contribution to the diet. Therefore, we prorated the unknown gadoid and flatfish to species level based upon the proportion of identified species within each group. To preserve any interannual or seasonal variation in the data, we prorated fish within seasons and also within years provided that at least 20 fish were positively identified to species level. If not, we used the overall proportion of identified species derived from all years of data within each season.

To derive estimates of prey size from otolith length (OL) and squid beak length, we used the same regression equations as Bowen

Table 1. Grey seal faecal samples containing prey hard parts collected at Sable Island, 1991-1998.

		Year								
		1991[1]	1992[1]	1993[1]	1994	1995	1996	1997	1998	Total
Spring	May/June		43	30	59	77	102	99		410
Summer	July/Aug	50	59	27						136
	Sept/Oct	52		14	22	71	87	59		305
Winter	Nov/Dec	49		45						94
	Jan/Feb		41		45	33	48	70	32	269
	Mar/Apr		54							54
Year	Total	151	197	116	126	181	237	228	32	1,268

[1]from Bowen and Harrison (1996)

Table 2. Combined diet[1] of grey seals between May, 1993 and January, 1998. (Scientific names in Appendix)

Species	No. of occurrences	% sample occurrence	Number prey estimated	% total number	Prey wt (kg) estimated	% of total prey wt
Sand lance	644	75.4	24,385	85.00	433.9	61.7
Atlantic cod	209	24.5	522	1.80	93.2	13.3
Silver hake	134	15.7	368	1.30	53.1	7.6
Yellowtail flounder	180	21.1	517	1.80	30.7	4.4
American plaice	158	18.5	461	1.60	29.9	4.3
Capelin	84	9.8	808	2.80	13.8	2.0
Longhorn sculpin	55	6.4	128	0.40	20.6	2.9
Redfish	36	4.2	152	0.50	7.0	1.0
Pollock	13	1.5	15	0.10	5.1	0.7
Haddock	25	2.9	50	0.20	5.3	0.8
Atlantic herring	13	1.5	26	0.10	3.5	0.5
Hake	56	6.6	89	0.30	2.8	0.4
Ocean pout	10	1.2	17	0.10	1.2	0.2
Witch flounder	28	3.3	56	0.20	1.3	0.2
Winter flounder	8	0.9	5	0.02	1.1	0.2
Squid (beaks)	9	1.1	9	0.03	0.5	0.1
Fourbeard rockling	6	0.7	13	0.10	0.2	0.0
Unknown flounder	198	23.2	578	2.00		
Unknown gadoid	139	16.3	331	1.20		
Unknown fish	68	8.0	77	0.30		
Crab spp.	17	2.0	21	0.10		
Skates	20	2.3	20	0.10		
Bivalve	12	1.4	17	0.10		
Gastropod	12	1.4	14	0.10		
Mailed sculpin 9	1.1	9	0.03			
Unknown bird	4	0.5	4	0.01		
Sea Urchin	4	0.5	4	0.01		
Mackerel	3	0.4	3	0.01		
Atlantic sea raven 1	0.1	1	0.00			
Windowpane Flounder 1	0.1	1	0.00			
Atlantic halibut	1	0.1	1	0.00		
No prey found	80	9.4				
Totals	2,237		28,702	100.00	703.2	100.0

[1]1991 to 1992 data given in Bowen and Harrison (1994)

and Harrison (1994), with the exception of four-beard rockling, *Enchelyopus cimbrius*:

W = 0.1752(OL)3.482

where W is fish wt (g) (Härkönen1986) and Atlantic cod (*Gadus morhua*), for which 2 regression equations were used. Atlantic cod was given special treatment due to recent evidence that both the size at age of cod and their physical condition (*i.e.* mass at a given length) have declined markedly from the mid-1980's to 1992, at which time no further decrease was observed (Fanning *et al.* 1996). To determine if the relationship between otolith length and fish size had also changed, we measured 125 cod collected in the vicinity of Sable Island during the July, 1996 groundfish research vessel survey. The resulting equations:

FL = 1.03671(OL)1.3999 and
W (g) = 0.00585(OL)4.4127

where FL is fish length (cm), predict significantly smaller fish than the regression published by Hunt (1992) for Scotian Shelf cod sampled from 1984 to 1987 and used in our earlier study of grey seal diets (Bowen and Harrison 1994). We applied these new regression equations in estimating the size of cod from faecal samples collected after January 1993, while samples collected prior to this time were treated using the regression given by Hunt (1992).

To relate the diet of grey seals to the availability of potential prey, we extracted data from the annual research vessel (RV) survey database maintained by Department of Fisheries and Oceans, Canada. Conducted in the months of March and July since 1970, these stratified-random surveys use a Westren2A bottom trawl equipped with a 19 mm mesh liner to capture small fish normally not retained in commercial trawls. Given the estimated swimming speeds of seals and rate of food passage through the gut, we estimated that faeces collected on Sable Island would generally have come from a distance of ~ 80 km from the island (see Bowen and Harrison 1994). Therefore, we selected only those fishing stations that were within approximately 80 km of any point on Sable Island and summarized those data at the level of strata that roughly approximated offshore banks (see Bowen and Harrison 1994). These banks are known to be frequently used foraging areas for grey seals, based on satellite locations (Bowen *et al.* 2005).

The RV surveys use bottom trawls that are highly selective in terms of the kinds of fish caught. Bottom-dwelling fish such as cod, haddock (*Melanogrammus aeglefinus*), and flounders have a higher probability of encountering the trawl than do pelagic species such as herring (*Clupea harengus harengus*) and capelin (*Mallotus villosus*) that spend most of their time higher in the water column. Also under-represented in the RV surveys is sand lance, the most abundant species in the diets of grey seals

Table 3. Seasonal and interannual variation in estimated percent wet weight of main species consumed by grey seals near Sable Island, from 1991 to 1998. (Scientific names in Appendix.)

		Year							
Season	**Species**	**1991**	**1992**	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**
Winter	Sandlance	75.1	78.7	85.3	61.2	39.7	86.3	88.0	66.8
	Flatfish*	7.8	10.7	7.9	4.2	31.2	8.2	6.5	19.6
	Atlantic cod	12.7	3.5	3.7	28.1	13.1	1.2	0.8	2.5
	Longhorn Sculpin	0.0	0.0	0.0	1.7	9.3	2.2	1.9	7.8
	Silver hake	1.5	0.4	0.0	1.5	2.4	0.4	1.4	1.5
	Capelin	0.1	3.8	0.3	0.0	0.0	0.1	0.2	0.0
Spring	Sandlance	56.0	78.7	74.1	52.1	24.1	54.8	42.7	
	Flatfish	18.5	19.4	4.4	12.2	22.7	11.3	12.7	
	Atlantic cod	19.2	1.6	2.1	23.2	28.7	6.9	31.1	
	Longhorn Sculpin	0.0	0.0	0.0	2.8	4.3	5.9	8.5	
	Silver hake	5	0.1	0.0	3.6	7.1	3.9	0.7	
	Capelin	0.0	0.0	0.0	0.7	6.1	15.0	0.4	
Fall	Sandlance	49.7	67.2	89.2	70.2	60.3	76.8	42.1	
	Flatfish	2.9	7.5	2.1	3.3	8.6	4.1	3.6	
	Atlantic cod	44.1	17.2	0.0	12.7	16.8	4.2	5.6	
	Longhorn Sculpin	0.0	0.0	0.0	0.0	0.0	0.0	0.4	
	Silver hake	3.1	5.6	5.5	10.0	10.4	8.8	46.6	
	Capelin	0.0	0.0	0.0	0.0	0.0	0.0	0.0	

Table 4. Seasonal variation in measured prey lengths for 4 species in the grey seal diet, all years combined. (Scientific names in Appendix.)

Species	Season	n	Mean (cm)	Kruskal Wallis P-value
Sand lance	spring	736	16.2	
	summer	224	14.8	
	fall	908	16.2	
	winter	929	16.8	<0.001
Atlantic cod	spring	117	26.7	
	summer	37	23.2	
	fall	100	26.0	
	winter	54	22.0	0.005
American	spring	88	22.5	
plaice	summer	9	24.8	
	fall	34	20.2	
	winter	86	21.0	0.033
Yellowtail	spring	131	21.4	
flounder	summer	18	23.6	
	fall	53	17.8	
	winter	77	21.0	<0.001

near Sable Island (Bowen and Harrison 1994). Survey catches of this species are extremely variable and are not considered useful annual indices of sand lance abundance (Frank 1996).

Catches from bottom trawl surveys were corrected for differences in catchability - the probability that an individual species will be captured by the gear. Catchability coefficients were derived empirically by comparing survey catch rates with abundance estimates from commercial fisheries (Sparholt 1990), or subjectively through a general knowledge of fishing gear, fish behaviour, and ecological factors such as seasonal availability (Edwards 1968, Scott 1971). In this study, we attempted to compensate for differences in catchability among fish caught in the Scotian Shelf RV surveys using correction factors published by Scott (1971) for Scotian Shelf groundfish and Sparholt (1990) for pelagic species (Appendix). In deriving a total catchability factor to apply to the results of a single summer survey, Scott chose to distinguish among availability, vulnerability (to the gear), and seasonal factors. However, since we currently have RV survey results from both the winter and summer time periods, we chose to exclude the seasonal component of Scott's catchability factors. Where there was no correction factor available for species encountered in our surveys, we applied the coefficient published for a related species (e.g., Vahl's eelpout (*Lycodes gracilis*) and ocean pout (*Gymnelus viridis*)) or an average (mean) coefficient from species within the same general class of fish.

Attempts to reconstruct the diets of pinnipeds are confounded by several sources of error, including the erosion or complete digestion of otoliths and other prey hard parts prior to recovery in seal faeces or stomachs (reviewed in Bowen and Siniff 1999). For example, robust otoliths typically found in gadoid species such as cod and pollock (*Pollachius virens*) tend to be less susceptible to erosion during passage through the seals' digestive system than the less robust otoliths found in herring and capelin (Bowen 2000). Although several authors have attempted to correct for variable rates of otolith erosion in their studies (Harvey 1989, Hammond and Prime 1990), we chose not to use correction factors for otolith erosion in an earlier investigation of grey seal diets (Bowen and Harrison 1994) because few correction factors were available for the prey species we encountered. Recently, a number of new correction factors have been derived based on captive feeding studies using seals (reviewed in Bowen 2000), thus we attempted to correct for complete digestion of otoliths (Appendix).

We used the odds ratio (Fleiss 1981) as an index of prey selectivity. This is given by:

$$O = (p_1 \bullet q_2)/(p_2 \bullet q_1)$$

where p_1 is the proportion of prey in the diet, p_2 is the proportion of that prey in the environment, q_1 is the proportion of the contributed by all other prey, and q_2 is the relative abundance of all other prey in the environment. Taking logs of this ratio results in an index whereby positive values indicate positive selection for a particular prey species whereas negative values indicate prey that where consumed less than might be expected based on their relative abundance. An index value of 2 indicates that a prey species occurred in the diet about 100 times more than would be expected based on its relative abundance. As the composition of the diet and prey abundance are measured with error and bias, we considered values greater than 2 and -2 as indicating selection and relative avoidance of prey, respectively.

Differences in diet were tested by Analysis of Variance (ANOVA) conducted using the General Linear Model (GLM) framework in SPSS version 11.5.

RESULTS

Of 1,295 grey seal faecal samples collected from May 1991 to January 1998, 1,245 (96.1%) contained hard parts that could be used to identify prey (Table 1). Only collections in Jan/Feb 1994 and 1995 had a high proportion of samples which contained no hard parts. About 69% of the samples were collected from the May to October period.

Overall, 28 species or higher taxa were consumed by grey seals between May 1993 and January 1998 (Table 2). During this period, diet was dominated by sand lance, followed by Atlantic cod, silver hake, and several species of flounders, which combined accounted for an estimated 91.3% of biomass eaten. Numerically, sand lance was also the most frequently consumed prey.

There was considerable variation in the composition of the diet both seasonally and among years (Table 3). However, only in Atlantic cod and sand lance was there evidence for significant variation. Atlantic cod was significantly less abundant in the diets in 1992 and 1993 compared to the mid 1990s (GLM, ANOVA *P* = 0.025, Table 3). Although cod tended to be consumed more in the spring and summer than in the fall and winter, this difference was not significant (GLM, ANOVA *P* = 0.095). The importance of sand lance in the diet varied significantly both seasonally (GLM, ANOVA *P* = 0.027), and among years (GLM, ANOVA *P* = 0.028). Among years, grey seal were estimated to have consumed less sand lance in 1995 than

Table 5. Interanual variation in measured prey lengths for 4 species in the grey seal diet, all years combined. (Scientific names in Appendix.)

Species	Year	n	Mean (cm)	Kruskal Wallis P-value
Sand lance	91	330	15.4	
	92	450	14.5	
	93	238	16.4	
	94	235	17.5	
	95	349	15.7	
	96	602	16.2	
	97	505	18.0	
	98	88	17.7	<0.001
Atlantic	91	39	28.5	
cod	92	38	20.6	
	93	8	15.2	
	94	33	30.0	
	95	81	26.2	
	96	62	21.3	
	97	47	27.9	<0.001
American	91	2	22.8	
plaice	92	18	25.1	
	93	12	22.4	
	94	12	23.8	
	95	84	21.3	
	96	50	20.5	
	97	31	21.1	
	98	8	21.0	0.09
Yellowtail	91	13	23.0	
flounder	92	14	21.3	
	93	8	22.8	
	94	18	23.0	
	95	79	21.7	
	96	66	19.1	
	97	59	20.6	
	98	22	18.8	0.005

in 1992, although in general there was greater variability and a tendency to consume less sand lance in the later half of the study (Fig. 2).

For those species with sufficient data, there was evidence of both seasonal and interannual changes in the size of prey consumed (Tables 4, 5). Sand lance eaten in the summer was smaller than in other seasons, whereas, the flounders were larger. Atlantic cod eaten by seals were larger in the spring and fall than at other times of the year.

Indices of prey selectivity were computed for 13 species consumed by grey seals for which we had reasonable estimates of prey abundance (Table 6). Of these, grey seals exhibited positive selection for sand lance in both summer and winter and ocean pout in summer. There was some evidence that grey seals exhibited negative selection for Atlantic cod, particularly during the winter. Similarly, haddock, pollock, silver hake, redfish (*Sebastes marinus*) and longhorn sculpin (*Myoxocephalus octodecemspinosus*) were apparently relatively underused by grey seals. American plaice (*Hippoglossoides platessoides*), witch (*Glyptocephalus cynoglossus*) and yellowtail flounder (*Limanda ferruginea*) were consumed roughly in proportion to their abundance, particularly during summer.

DISCUSSION

Our 8-yr study confirms previous results from this Northwest Atlantic population (*e.g.* Bowen *et al.* 1993) that grey seals are generalist predators, consuming more than 2 dozen species or prey taxa. However, despite the diversity of taxa consumed by grey seals only a few prey species accounted for most the diet in any season or year. This observation is consistent with the pattern seen in other populations of this species (*e.g.* Hammond *et al.* 1994), and in other pinnipeds (Bowen and Siniff 1999).

Estimating the diet of pinnipeds from prey structures recovered from faeces presents a number of difficulties (Jobling and Breiby 1986). The sources of error and bias are well documented in the general literature (e.g., Pierce and Boyle 1991, Bowen and Siniff 1999) and are the same as those discussed in an earlier paper dealing with the first several years of this study (Bowen and Harrison 1994). With respect to the interpretation of our results, it is important to remember that some otoliths will have been eroded while others completed digested and that prey species differ in the extent to which they are subject to these effects. This can distort the relative importance of prey in the diet and the size of prey eaten. We attempted to minimize these effects by only measuring otoliths which we judged to have been minimally eroded. Further in our log-odds analysis of prey selection, we corrected for the fraction of otoliths that would have been completely lost during digestion by applying, admittedly rough, available number correction factors. We did not apply these number correction factors in estimating the seasonal or interannual diet so that our new estimates could easily be compared to previous data.

Seasonal and interannual changes in the diet of grey seals (Hammond *et al.* 1994, Bowen *et al.* 1993) and other pinniped species (Lake *et al.* 2003, Tollit *et al.* 1997, Lawson and Stenson 1995) are now well documented. Our results provide further evidence of seasonal and interannual changes in grey seal diet and underscore the need to consider this variation in attempting to understand the impact of grey seal predation on prey populations. Although seasonal variability is evident, we note that there was some variation in the months sampled within each season. This variation might have contributed to the observed pattern, but is unlikely to have generated the pattern given the distribution of samples over time.

Sand lance was the dominant prey consumed by grey seals in all but 2 of the 23 samples collected between 1991 and 1998 (Fig. 2). However, the amplitude of the variability appears to have increased in the latter part of the period. It is difficult to interpret these interannual changes as the bottom trawl research surveys do not sample sand lance well. For example, no sand lance were caught in the surveys conducted in 1992-1994, yet this species accounted for over 60% of the estimated diet in those years. Similarly, over the period of our study Atlantic cod biomass declined (Fu *et al.* 2001), but there is only weak evidence of declining trend in the importance of cod in the diet of grey seals. By contrast, consumption of longhorn sculpin, silver hake, and capelin all increased in 1 or

Table 6. Log-odds ratios of selected prey in the diet of grey seals, based on numbers and wet weight, during summer and winter, 1991-1997 data combined.

	Summer		Winter	
Species	**Numbers**	**Wet mass (kg)**	**Numbers**	**Wet mass (kg)**
Sand lance	2.1	3.0	4.4	8.1
Atlantic cod	-1.0	-1.0	-4.4	-3.9
Haddock	-4.3	-4.6	-3.7	-5.0
Pollock	-2.6	-2.6	-4.5	-5.3
Silver hake	-3.3	-2.4	-4.4	-1.9
White hake	0.8	-0.6	-0.7	0.6
Redfish	-2.9	-2.4	-4.2	-2.5
American plaice	0.0	0.8	-1.6	-0.1
Yellowtail flounder	-0.3	0.3	-1.4	0.5
Winter flounder	-4.1	-2.9	0.0	1.8
Witch	-0.1	0.3	-1.5	0.2
Longhorn sculpin	-1.8	-0.6	-3.0	-0.9
Ocean pout	2.1	2.3	1.7	--

more seasons during the later half of the study. However, those trends did not correspond well with estimated biomass changes in the survey.

There is some evidence that pinniped predation rate varies with changes in prey abundance. For example, Bailey and Ainley (1982) showed that predation by California sea lions (*Zalophus californianus*) on Pacific hake (*Mercluccius productus*) declined as the abundance of 2- to 4-year-old hake, the ages most commonly eaten, declined. Similarly, Sinclair *et al.* (1994) found that interannual variation in the importance of walleye Pollock (*Theragra chalcogramma*) in the diet of northern fur seals (*Callorhinus ursinus*) was positively related to pollock year-class strength. Bowen and Harrison (1994) found that generally the more abundant and widespread species comprised a larger fraction of the diet in grey seals.

However, there is growing evidence for prey selection; that is the representation of prey species in the diet that is disproportionate to their abundance. Lawson *et al.* (1998) found evidence of positive selection for both capelin and Arctic cod (*Boreogadus saida*) by harp seals (*Phoca groenlandica*) off northwestern Newfoundland based on a comparison of diets with trawl estimates of prey biomass. By comparing interannual estimates of prey biomass with changes in harbour seal (*Phoca vitulina*) diets, Tollit *et al.* (1997) found strong evidence of selection which appeared to depend somewhat on the relative abundance of other prey species. Our data add to the weight of evidence for selective predation in pinnipeds. We found evidence for positive selection of sand lance in both summer and winter, negative selection among several gadoid species, and roughly proportional selection in several of the species of flounder. Although we acknowledge that the conclusions from odds ratios must be considered tentative, given the difficulties in estimating both the diet and the abundance of prey species from trawl surveys, these results do suggest that predation in grey seals is influenced by factors other than relative prey abundance. Prey quality (i.e., energy density, e.g. Budge *et al.* 2002) and profitability are known to vary (Bowen *et al.* 2002) among the species eaten by grey seals and thus presumably influence prey choice.

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