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Estimated Prey Consumption by Harp seals (*Phoca groenlandica*), Hooded seals (*Cystophora cristata*), Grey seals (*Halichoerus grypus*) and Harbour seals (*Phoca vitulina*) in Atlantic Canada

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Abstract

Consumption of prey by harp (*Phoca groenlandica*), hooded (*Cystophora cristata*), grey (*Halichoerus grypus*), and harbour (*Phoca vitulina*) seals in Atlantic Canada was estimated for the period 1990–96 by synthesizing and integrating information on individual energy requirements, population size, distribution and diet composition. Total annual consumption by these four species increased from 3.1 million to 4.0 million tons over the seven-year period. Seventy-seven percent (by weight) of the total prey consumption consisted of fish, of which capelin and sand lance were the dominant species accounting for 49% (by weight) of the total fish consumed. The majority (74%) of total prey consumption occurred off southern Labrador and Newfoundland (Div. 2J and 3KL), followed by the northern Gulf of St Lawrence (Div. 4RS) (18%), and the eastern Scotian Shelf (Div. 4VsW) (4%). Harp seals were the most important predator, accounting for 82% of total consumption, followed by hooded seals (10% of total prey consumption), grey seals (7.8%), and harbour seals (0.2%). Regional differences existed in predation impacts of the four pinnipeds; harp seals were most important in Div. 2J and 3KL and in Div. 4RS, hooded seals were most important in Div. 2J and 3KL and Div. 3M (Flemish Cap), while grey seal predation predominated in the southern Gulf of St. Lawrence (Div. 4T) and on the Scotian Shelf (Div. 4VsW). Of the 3.1 million tons of fish consumed by the four species of seals in 1996, only about 20% accounted for commercial species such as Greenland halibut (7%), Atlantic cod (6%), redfish (4%), and Atlantic herring (3%). Most of the consumption of these commercial species consisted of juveniles.

Key words: feeding/food, grey seals, harbour seals, harp seals, hooded seals, Northwest Atlantic Ocean

Introduction

The failure in the Canadian east coast groundfish fishery has been attributed to a combination of excess harvesting, uncertain biological assessments and ineffective fisheries management (FRCC, 1999). Although fishery closures were enacted in the early-1990s, few groundfish stocks have shown signs of significant recovery (FRCC, 1999).

Like elsewhere in the world, fish stocks in Canada have traditionally been managed on a single species basis, although it has long been recognized that a multispecies approach would be more appropriate (Mercer, 1982). Multispecies models offer an improvement over the single species approach because they tend to explicitly account for predator-prey relationships among species (Sparre, 1991). Unfortunately, these models are extremely data intensive (Walters *et al*., 1997), and often ignore lower trophic levels, giving a very incomplete picture of overall energy flows (Christensen and Pauly, 1993; Christensen, 1995).

Over the last two decades, seal populations in Atlantic Canada have increased markedly (Mohn and Bowen, 1996; Hammill *et al*., 1997; Stenson *et al.*, 1997a). Marine mammals, because of their large size and abundance, are thought to have an important influence on the structure and function of many marine ecosystems (Bowen, 1997). However, little empirical evidence exists on the ecosystem impact of marine mammals. One obvious impact is that large quantities of prey are consumed by marine mammals. Evaluating the magnitude of this consumption requires information on population size, energetic requirements, diet composition, size-classes and energy density of the prey, as well as the distribution of marine mammal feeding effort (Harwood and Croxall, 1988; Harwood, 1992).

Four species of seals are common in the waters of Atlantic Canada. Grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) are abundant year-round along the coast from the northeastern United States to Hamilton Inlet and in the Gulf of St Lawrence (Mansfield, 1967), while harp seals (*Phoca groenlandica*) and hooded seals (*Cystophora cristata*) are seasonal residents (Sergeant, 1976). In 1994, harp seals were estimated to have consumed 88 000 tons (95% CI: 46 000–140 000 tons) of Atlantic cod off the Labrador and east coast of Newfoundland, and 54 000 tons of cod (95% CI: 14 000–102 000 tons) in the Gulf of St Lawrence (Stenson *et al*., 1997a). In 1993, grey seals were estimated to have consumed 39 000 tons of cod off the Atlantic coast of Nova Scotia and in the Gulf of St Lawrence (Hammill and Mohn, MS 1994). Hammill *et al*. (1997) estimated that during 1991–95 hooded seals annually consumed between 63 and 100 tons of Atlantic cod in the Gulf of St Lawrence.

The principal objective of this study was to estimate prey consumption by seals in Atlantic Canada. In this study, estimates of total prey consumption are derived for harp, hooded, grey and harbour seals in Northwest Atlantic waters off southern Labrador and Newfoundland (NAFO Div. 2J and 3KL), in the northern Gulf of St. Lawrence (Div. 4RS), the southern Gulf of St. Lawrence (Div. 4T), the eastern Scotian Shelf (Div. 4VsW), the Flemish Cap (Div. 3M), and in 'Other' waters of Atlantic Canada (Bay of Fundy: Div. 4X; southern coast of Newfoundland: Subdiv. 3Ps). The relative importance of predation by each species in each area is identified and evaluated.

Materials and Methods

Estimates of prey consumption were developed by modeling changes in population size, energy requirements, diet composition and seasonal changes in distribution for each of the four pinniped species (Appendix 1).

Population Dynamics

Age-specific estimates of harp seal abundance were obtained using the approach of Shelton *et al.* (1996), projected forward to 1996 taking into account available harvest data. Shelton *et al.* (1996) modeled the dynamics of harp seals using two formulations: one in which pup mortality was assumed equal to adult mortality, and another in which pup mortality was equal to three times the adult mortality rate. Mammals typically have a 'U'-shaped mortality curve with high mortality rates at birth that decline as maturity is attained but which increase in old age (Caughley, 1977). Therefore, the second formulation of the model was used. The model was also updated by incorporating revised catch statistics from the Greenland harvest (Stenson *et al.*, MS 1999).

For grey, hooded and harbour seals, the dynamics of these populations were reconstructed by modifying estimates of survivorship and age-specific reproductive rates to produce a transition matrix (Leslie, 1945) which generated the observed population changes. To determine the stable age composition, the models were initiated with a starting population of 500 pups and the populations 'grown' until there were no changes in the proportional age composition. For hooded and grey seals, total population abundance estimates are lacking; only data on pup production are available. Hence, total population sizes were derived by dividing the pup production in each species by the fraction of pups expected in a population having the modeled stable age structure. The number of animals in each age-class was then determined by multiplying the total population by the proportion of animals in each age-class from the population model. A similar approach was used for harbour seals by allowing a population of 500 pups to grow until no further changes occurred in the proportional age composition. Total population size was then multiplied by the proportion age composition in the 'stable' population to derive the population age distribution.

In all cases, first-year pup mortality was assumed to be greater than mortality in older (age 1+)

seals. The mortality rate of older seals was assumed to be constant across years and cohorts. Mortality rates of males and females were assumed to be identical, and the sex ratio at birth was assumed to be 1:1.

Energy Requirements

Energy requirements were assumed to be constant throughout the year. Age-specific energy requirements were calculated using:

$$GEI_i = GP_i * (AF*293 *BM_i^{0.75})/ME$$

where GEI_i is daily gross energy intake (kjoules/day) at age i, and GP is the additional energy required by young seals (< age 6). GP_i was set at 1.8, 1.6, 1.4, 1.3, 1.1, 1.1, and 1.0 for animals aged 0, 1, 2, 3, 4, 5, and ≥6 yrs respectively (Olesiuk, 1993). The activity factor (AF) was assumed to be 2 (Worthy, 1990) to approximate the average daily energy requirements as a multiple of the basal metabolic rate ($293*BM_i^{0.75}$; Kleiber 1975) where BM_i is body mass-at-age in kg. The metabolizable energy (ME) was set at 0.83 (Ronald *et al.*, 1984) based on the assumption that seals primarily consume fish. Growth in body mass-at-age i (BM_i) was modeled using a re-parameterized form of the Gompertz growth curve (Hammill *et al.*, 1995):

$$BM_i = W_\infty \left(\frac{W_0}{W_\infty}\right)^{\exp\left[\frac{k_0 \cdot i}{W_0 \ln\left(W_0/W_\infty\right)}\right]}$$

where body mass (BM_i), asymptotic weight W_∞, and weight at birth (W_0) are in kg, i is age (in years) and k_0 is the rate of growth at birth (Table 1). Parameters of the growth curves for each species were determined using Proc NLIN (SAS Institute, 1987).

Seasonal Distribution

The study region off eastern Canada was divided into six areas based upon NAFO scientific and statistical Divisions and Subdivisions. These areas included: eastern Newfoundland and southern Labrador (Div. 2J and 3KL); the northern Gulf of St Lawrence (Div. 4RS); the southern Gulf of St Lawrence (Div. 4T); the eastern Scotian Shelf (Div. 4VsW); the Flemish Cap (Div. 3M) and 'Other' used primarily for grey and harbour seals in the Bay of Fundy (Div. 4X) and along the southern coast Newfoundland (Subdiv. 3Ps) (Fig. 1). The seasonal distribution of each species in each of these areas was estimated from field observations, tag returns, aerial survey observations, historical catch data, anecdotal reports and satellite telemetry.

Diet Composition

The proportion of each prey species in the diet was determined by reconstructing the wet weight of prey ingested from stomach and/or faeces samples. Where possible, diet composition was analyzed by season and location. No correction was made for unidentified fish. In deriving annual consumption estimates, diet compositions were assumed to remain constant throughout the 1990–96

TABLE 1. Parameters used in the Gompertz growth curves to estimate body size in harp, hooded, grey and harbour seals. N = Number of individuals measured.

Species/sex	N	Asymtotic weight ($W\infty$) (kg)	Weight at t_o (W_0) (kg)	Growth rate (k_0)(kg/y)	Source
Harp seal-male	967	102.60	34.20	11.27	Chabot *et al.* (1996)
Harp seal-female	800	98.60	30.80	12.30	Chabot *et al.* (1996)
Hooded seal-male	289	256.66	36.79	30.71	Stenson (unpubl.)
Hooded seal-female	744	187.07	38.22	19.54	Stenson (unpubl.)
Grey seal-male	95	250.44	48.58	19.50	Hammill (unpubl.)
Grey seal-female	166	188.21	53.92	12.54	Hammill (unpubl.)
Harbour seal-male	70	93.13	22.62	10.51	Lesage (unpubl.)[1]
Harbour seal-female	53	74.91	19.52	10.35	Lesage (unpubl.)[1]

[1] V. Lesage, Maurice-Lamontagne Institute, Mont-Joli, Quebec, Canada.

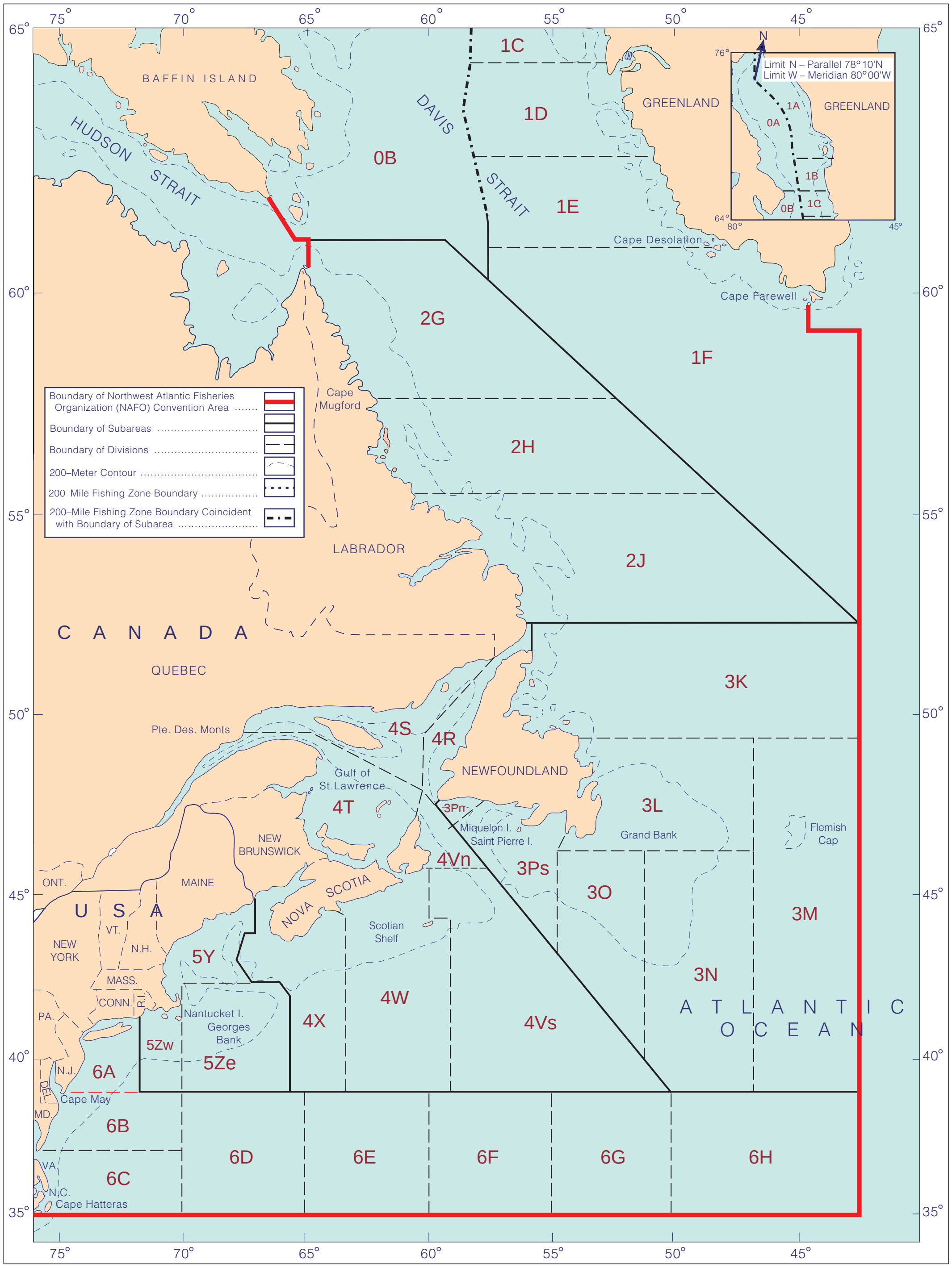

Fig. 1. Northwest Atlantic Fisheries Organization (NAFO) Scientific and Statistical Divisions and Subdivisions. Area designations used in the seal study include: eastern Newfoundland and southern Labrador (Div. 2J3KL); northern Gulf of St. Lawrence (Div. 4RS); southern Gulf of St. Lawrence (Div. 4T); eastern Nova Scotian Shelf (Div. 4VsW); Flemish Cap (Div. 3M); and 'Other' [Bay of Fundy: Div. 4X; southern coast of Newfoundland: Subdiv. 3Ps].

period. The mean energy density of prey items in each area/season was estimated using a weighted average of published energy values for individual prey species (Croxall and Prince, 1982; Griffiths, 1977; Hislop *et al.*, 1991; Hodder *et al.*, 1973; Tyler, 1973; Percy and Fife, 1981; Montevecchi and Piatt, 1984; Steimle and Terranova, 1984; Proust, 1996; Martensson *et al.*, 1996; Lawson *et al.*, 1995b, 1998b; Chabot, Institute Maurice Lamontagne, Department of Fisheries and Oceans, Quebec, unpubl. data).

Prey Size

The size composition of Atlantic cod (*Gadus morhua*), Atlantic herring (*Clupea harengus*), redfish (*Sebastes* spp.) and Greenland halibut (*Reinhardtius Hippoglossoides*) consumed by seals was estimated using size frequency data from seal dietary studies (harp seals: Lawson and Stenson, 1997; hooded seals: Ross, MS 1993; grey seals: Benoit and Bowen, 1990; Proust, 1996; harbour seals: Bowen and Harrison, 1996).

Results

Changes in population size have been routinely monitored in harp, hooded and grey seals (Bowen *et al.*, 1987; Stobo and Zwanenberg, 1990; Zwanenberg and Bowen, 1990; Shelton *et al.*, 1997; Stenson *et al.*, 1997b; Hammill *et al.*, 1998; Stenson *et al.*, MS 1999). The abundance of harbour seals, however, has never been adequately censused in Atlantic Canada. Harp seals are the most abundant pinnipeds, with a total population size in eastern Canada estimated to be 4.2 million in 1990, increasing to 5.2 million animals in 1996 (Stenson *et al.*, MS 1999). Hooded seals increased from 470 000 animals in 1990 to about 627 000 in 1996, while grey seals increased from approximately 97 000 animals in 1990 to 173 000 animals in 1996. Harbour seal abundance increased from about 23 000 animals in 1990 to 32 000 in 1996 (Table 2).

Total estimated prey consumption for the four seal species combined increased from 3.1 million tons in 1990 to 4.0 million tons in 1996 (Table 3). Most of this consumption (74%) occurred off eastern Newfoundland and southern Labrador (Div. 2J and 3KL), followed by the northern Gulf of St Lawrence (Div. 4RS) (18%), the eastern Scotian Shelf (Div. 4VsW) (4%), the southern Gulf of St Lawrence (Div. 4T) (1%), and the Flemish Cap (Div. 3M) (0.9%) (Table 4). Consumption of fish accounted for 77% by weight of the total prey consumed by seals (Table 5). Fish accounted for 72% of the total prey consumed by seals in Div. 2J and 3KL, and for between 87% and 97% in the other areas (Table 5). Three prey items accounted for over half (51%) of the total consumption (Table 5): capelin (*Mallotus villosus*) (26%), shrimp (*Pandalus* spp.) (13%) and sand lance (*Ammodytes* spp.) (12%). However, the relative importance of forage species differed among areas. In Div. 2J and 3KL, capelin, shrimp and sand lance accounted for 24%, 17% and 12%, respectively, of the total prey consumed by seals. In the northern Gulf of St Lawrence (Div. 4RS), the most important prey items were capelin (45%), redfish (*Sebastes* spp.) (13%) and pleuronectid flounders (10%). On the Flemish Cap (Div. 3M), Greenland halibut (*Reinhardtius hippoglossoides*) (32%), witch flounder (*Glyptocephalus cynoglossus*) (16%), squid (13%) and Atlantic cod (*Gadus morhua*) (10%) were the principal prey items, while in the eastern Scotian Shelf (Div. 4VsW) and in the southern Gulf of St. Lawrence (Div. 4T), sand lance and Atlantic cod were the major forage species.

TABLE 2. Estimated population abundance (number of animals) of harp, hooded, grey and harbour seals in Atlantic Canada between 1990–96, and annual net rates of population increase.

Year	Harp seal (3.87%/yr)	Hooded seal (4.8 %/yr)	Grey seal (9.7 %/yr)	Harbour seal (5.6%/yr)
1990	4 193 200	469 900	96 900	22 800
1991	4 355 000	493 000	106 600	24 100
1992	4 556 200	517 200	117 400	25 500
1993	4 694 200	542 700	129 000	27 000
1994	4 915 800	569 400	142 400	28 500
1995	5 075 600	597 300	156 100	30 100
1996	5 236 800	626 700	173 500	31 900

During the 1990–96 period, seal consumption of Greenland halibut increased from 159 000 tons to 207 000 tons; Atlantic cod from 132 000 tons to 184 000 tons; redfish from 105 000 tons to 134 500 tons; and Atlantic herring from 60 000 tons to 84 000 tons (Table 3). However, together these commercial species accounted for only about 20% of the total fish consumption by seals and only 15% of the aggregate prey consumption.

Harp seals were the most important pinniped predator (Tables 6 and 7) accounting for 78% of the total consumption of fish by seals and 82% of the overall prey consumption, followed by hooded

TABLE 3. Estimated prey consumption (tons) by harp, hooded, grey and harbour seals in Atlantic Canada, 1990–96.

	Year						
Prey Species	1990	1991	1992	1993	1994	1995	1996
Capelin (*Mallotus villosus*)	825 560	866 841	894 200	924 671	968 402	1 001 626	1 037 741
Sand lance (*Ammodytes* sp.)	352 640	371 153	392 630	411 984	437 481	459 436	484 764
Pleuronectidae	211 743	222 973	231 051	240 167	252 380	262 489	273 548
Greenland halibut (*Reinhardtius hippglossoides*)	158 737	165 878	173 812	181 266	190 037	198 197	206 895
Atlantic cod (*Gadus morhua*)	132 426	140 858	147 349	155 258	164 753	173 731	183 740
Arctic cod (*Boreogadus saida*)	146 104	151 665	158 514	163 630	171 306	177 115	183 049
Redfish (*Sebastes* sp.)	105 279	112 491	114 041	118 552	124 266	129 175	134 489
Atlantic herring (*Clupea harengus*)	60 320	64 108	67 147	70 704	75 093	79 177	83 688
Witch flounder (*Glyptocephalus cynoglossus*)	42 540	44 632	46 826	49 129	51 545	54 079	56 738
Grenadier (Macrouridae)	19 557	20 732	21 980	23 330	24 781	26 325	28 005
American Plaice (*Hippoglossoides platessoides*)	13 260	13 798	14 451	14 967	15 710	16 290	16 905
Sculpin (*Myxocephalus* sp.)	12 931	13 597	14 016	14 506	15 200	15 742	16 321
Blue hake (*Antimora rostrata*)	11 524	12 090	12 684	13 308	13 962	14 648	15 368
Mackerel (*Scomber scombrus*)	8 842	9 607	10 410	11 340	12 369	13 445	14 706
Silver hake (*Merluccius bilinearis*)	8 076	8 889	9 580	10 462	11 468	12 543	13 761
Windowpane (*Scopthalmus aquosus*)	10 654	11 029	11 480	11 915	12 478	12 949	13 458
Gadus sp.	5 902	6 204	6 349	6 554	6 843	7 094	7 356
Lumpfish (*Cyclopterus lumpus*)	3 812	4 111	4 417	4 775	5 168	5 568	6 044
Lancetfish (*Alepisaurus* sp.)	4 390	4 606	4 832	5 070	5 319	5 580	5 855
Wolffish (*Anarhichas* sp.)	3 754	4 029	4 306	4 632	4 988	5 343	5 770
White hake (*Urophycis tenuis*)	4 363	4 549	4 742	4 905	5 141	5 317	5 512
Pollock (*Pollachius virens*)	2 313	2 538	2 785	3 062	3 371	3 709	4 091
Haddock (*Melanogrammus aeglefinus*)	2 766	2 979	3 009	3 140	3 304	3 446	3 605
Atlantic salmon (*Salmo salar*)	2 467	2 652	2 688	2 807	2 955	3 084	3 229
Ocean pout (*Macrozoarces americanus*)	1 649	1 770	1 891	2 033	2 189	2 345	2 531
Eelpout (*Lycodes* sp.)	1 139	1 196	1 256	1 319	1 385	1 454	1 528
Yellowtail flounder (*Pleuronectes ferrugineus*)	956	1 027	1 098	1 182	1 274	1 365	1 475
Alewife (*Alosa pseudoharengus*)	687	735	779	832	891	948	1 019
Skates (*Raja* sp.)	554	595	637	686	739	793	857
Rainbow smelt (*Osmerus mordax*)	189	200	204	212	222	230	238
Winter flounder (*Pleuronectes americanus*)	110	117	125	133	142	151	162
Cunner (*Tautogolabrus adspersus*)	52	56	59	64	68	73	78
Other Fish	225 327	234 624	244 421	252 558	264 405	273 650	283 132
Total Fish	2 380 623	2 502 329	2 603 769	2 709 153	2 849 635	2 967 117	3 095 658
Shrimp	421 680	437 879	457 158	471 688	493 761	510 215	527 202
Squid	56 823	59 963	62 937	66 186	69 842	73 510	77 442
Euphausiid	4 761	4 943	5 166	5 331	5 582	5 768	5 957
Other Invertebrates	239 262	249 449	259 317	267 755	280 324	289 602	299 585
Total Invertebrates	722 526	752 234	784 578	810 960	849 509	879 095	910 186
Total Prey	3 103 149	3 254 563	3 388 347	3 520 113	3 699 144	3 846 212	4 005 844

TABLE 4. Estimated total prey consumption (tons) by harp, hooded, grey and harbour seals in Atlantic Canada in 1996, by NAFO area and prey species (see species list in Table 3).

	NAFO Area						
Prey Species	2J3KL	4RS	3M	4VsW	4T	Other	Total
Capelin	711 736	323 539	332	179	826	1 129	1 037 741
Sand lance	345 429	6 182	0	88 892	18 662	25 599	484 764
Pleuronectidae	179 224	72 706	3 067	12 626	2 498	3 427	273 548
Greenland halibut	191 270	3 913	11 677	0	15	20	206 895
Atlantic cod	82 494	56 099	3 732	24 260	7 235	9 920	183 740
Arctic cod	180 763	2 286	0	0	0	0	183 049
Redfish	34 505	97 002	1 219	1 164	252	347	134 489
Atlantic herring	35 845	27 816	0	12 953	2 989	4 085	83 688
Witch flounder	50 989	0	5 727	0	9	13	56 738
Grenadier	18 751	0	2 106	4 241	1 225	1 682	28 005
American plaice	15 141	1 214	0	0	232	318	16 905
Sculpin	10 431	5 723	0	7	68	92	16 321
Blue hake	13 816	0	1 552	0	0	0	15 368
Mackerel	7	5 396	0	5 038	1 799	2 466	14 706
Silver hake	3	3 047	0	7 678	1 279	1 754	13 761
Windowpane	0	13 458	0	0	0	0	13 458
Gadus sp.	3 902	3 155	0	224	33	42	7 356
Lumpfish	0	2 646	0	0	1 433	1 965	6 044
Lancetfish	5 263	0	591	0	0	1	5 855
Wolffish	0	3 934	0	0	774	1 062	5 770
White hake	4 713	624	0	94	35	46	5 512
Pollock	60	222	0	2 767	443	599	4 091
Haddock	0	3 421	0	3	76	105	3 605
Atlantic salmon	103	2 993	0	0	56	77	3 229
Ocean pout	4	1 688	0	26	343	470	2 531
Eelpout	1 316	42	148	0	9	13	1 528
Yellowtail flounder	0	967	0	0	214	294	1 475
Alewife	9	771	0	55	79	105	1 019
Skates	0	539	0	0	134	184	857
Smelt	102	135	0	0	1	0	238
Winter flounder	6	69	0	42	19	26	162
Cunner	1	45	0	10	9	13	78
Other Fish	258 267	22 326	2 143	297	44	55	283 132
Total Fish	2 144 150	661 958	32 294	160 556	40 791	55 909	3 095 658
Shrimp	513 456	13 541	0	154	23	28	527 202
Squid	55 270	7 367	4 656	7 034	1 317	1 798	77 442
Euphausiids	5 891	66	0	0	0	0	5 957
Other Invertebrates	262 009	37 548	0	21	3	4	299 585
Total Invertebrates	836 626	58 522	4 656	7 209	1 343	1 830	910 186
Total Prey	2 980 776	720 480	36 950	167 765	42 134	57 739	4 005 844
% of Annual Total	74.4%	18.0%	0.9%	4.2%	1.1%	1.4%	

seals (12% fish; 10% total) and grey seals (10% fish; 8% total). Harbour seals accounted for an insignificant percentage (0.2%) of the total prey consumption.

The predation impacts of each of the four seal species differed by area (Tables 8 and 9). Off eastern Newfoundland and Labrador (Div. 2J and 3KL) where both harp and hooded seals are abundant,

TABLE 5. Estimated total prey consumption (% by weight) by harp, hooded, grey and harbour seals in Atlantic Canada in 1996, by NAFO area and prey species (see species list in Table 3).

	NAFO Area						
Prey Species	2J3KL	4RS	3M	4VsW	4T	Other	All Areas
Capelin	23.9	44.9	0.9	0.1	2.0	2.0	25.9
Sand lance	11.6	0.9	0.0	53.0	44.3	44.3	12.1
Pleuronectidae	6.0	10.1	8.3	7.5	5.9	5.9	6.8
Greenland halibut	6.4	0.5	31.6	0.0	0.0	0.0	5.2
Atlantic cod	2.8	7.8	10.1	14.5	17.2	17.2	4.6
Arctic cod	6.1	0.3	0.0	0.0	0.0	0.0	4.6
Redfish	1.2	13.5	3.3	0.7	0.6	0.6	3.4
Atlantic herring	1.2	3.9	0.0	7.7	7.1	7.1	2.1
Witch flounder	1.7	0.0	15.5	0.0	0.0	0.0	1.4
Grenadier	0.6	0.0	5.7	2.5	2.9	2.9	0.7
American plaice	0.5	0.2	0.0	0.0	0.6	0.6	0.4
Sculpin	0.3	0.8	0.0	0.0	0.2	0.2	0.4
Blue hake	0.5	0.0	4.2	0.0	0.0	0.0	0.4
Mackerel	0.0	0.7	0.0	3.0	4.3	4.3	0.4
Silver hake	0.0	0.4	0.0	4.6	3.0	3.0	0.3
Windowpane	0.0	1.9	0.0	0.0	0.0	0.0	0.3
Gadus sp.	0.1	0.4	0.0	0.1	0.1	0.1	0.2
Lumpfish	0.0	0.4	0.0	0.0	3.4	3.4	0.2
Lancetfish	0.2	0.0	1.6	0.0	0.0	0.0	0.1
Wolffish	0.0	0.5	0.0	0.0	1.8	1.8	0.1
White hake	0.2	0.1	0.0	0.1	0.1	0.1	0.1
Pollock	0.0	0.0	0.0	1.6	1.1	1.0	0.1
Haddock	0.0	0.5	0.0	0.0	0.2	0.2	0.1
Atlantic salmon	0.0	0.4	0.0	0.0	0.1	0.1	0.1
Ocean pout	0.0	0.2	0.0	0.0	0.8	0.8	0.1
Eelpout	0.0	0.0	0.4	0.0	0.0	0.0	0.0
Yellowtail flounder	0.0	0.1	0.0	0.0	0.5	0.5	0.0
Alewife	0.0	0.1	0.0	0.0	0.2	0.2	0.0
Skates	0.0	0.1	0.0	0.0	0.3	0.3	0.0
Smelt	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Winter flounder	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cunner	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other Fish	8.7	3.1	5.8	0.2	0.1	0.1	7.1
Total Fish	71.9	91.9	87.4	95.7	96.8	96.8	77.3
Shrimp	17.2	1.9	0.0	0.1	0.1	0.0	13.2
Squid	1.9	1.0	12.6	4.2	3.1	3.1	1.9
Euphausiids	0.2	0.0	0.0	0.0	0.0	0.0	0.1
Other Invertebrates	8.8	5.2	0.0	0.0	0.0	0.0	7.5
Total Invertebrates	28.1	8.1	12.6	4.3	3.2	3.2	22.7
Total Prey	100.0	100.0	100.0	100.0	100.0	100.0	100.0

harp seals were the most important pinniped predator accounting for 88% of the total prey consumed by seals in this area, 59% of the Atlantic cod consumed, 86% of the capelin consumed, and more than 97% of the pinniped consumption of Arctic cod (*Boreogadus saida*) and capelin (Table 9). Hooded seals were responsible for most of the pinniped consumption of redfish (52%) and Greenland halibut

TABLE 6. Estimated prey consumption (tons) in Atlantic Canada in 1996, by NAFO area and major prey type, for four species of seals.

		NAFO Area						
Seal Species		2J3KL	4RS	3M	4VsW	4T	Other	All Areas
Harp Seal	Fish Prey	1 824 791	602 173	0	0	0	0	2 426 964
	Invertebrate Prey	792 638	57 526	0	0	0	0	850 164
	Total Prey	2 617 429	659 699	0	0	0	0	3 277 128
Hooded Seal	Fish Prey	319 008	8 297	32 294	0	0	0	359 599
	Invertebrate Prey	43 894	643	4 656	0	0	0	49 193
	Total Prey	362 902	8 940	36 950	0	0	0	408 792
Grey Seal	Fish Prey	0	50 185	0	158 135	40 430	55 460	304 210
	Invertebrate Prey	0	0	0	6 553	1 245	1 709	9 507
	Total Prey	0	50 185	0	164 688	41 675	57 169	313 717
Harbour Seal	Fish Prey	351	1 303	0	2 421	361	449	4 885
	Invertebrate Prey	94	353	0	656	98	121	1 322
	Total Prey	445	1 656	0	3 077	459	570	6 207
Totals	Fish Prey	2 144 150	661 958	32 294	160 556	40 791	55 909	3 095 658
	Invertebrate Prey	836 626	58 522	4 656	7 209	1 343	1 830	910 186
	Total Prey	2 980 776	720 480	36 950	167 765	42 134	57 739	4 005 844

TABLE 7. Percentage distribution, within each NAFO area, of major prey type consumption (tons) in Atlantic Canada in 1996, for four species of seals.

		NAFO Area						
Seal Species		2J3KL	4RS	3M	4VsW	4T	Other	All Areas
Harp Seal	Fish Prey	61.2	83.6	0.0	0.0	0.0	0.0	60.6
	Invertebrate Prey	26.6	8.0	0.0	0.0	0.0	0.0	21.2
	Total Prey	87.8	91.6	0.0	0.0	0.0	0.0	81.8
Hooded Seal	Fish Prey	10.7	1.2	87.4	0.0	0.0	0.0	9.0
	Invertebrate Prey	1.5	0.1	12.6	0.0	0.0	0.0	1.2
	Total Prey	12.2	1.2	100.0	0.0	0.0	0.0	10.2
Grey Seal	Fish Prey	0.0	7.0	0.0	94.3	96.0	96.1	7.6
	Invertebrate Prey	0.0	0.0	0.0	3.9	3.0	3.0	0.2
	Total Prey	0.0	7.0	0.0	98.2	98.9	99.0	7.8
Harbour Seal	Fish Prey	0.0	0.2	0.0	1.4	0.9	0.8	0.1
	Invertebrate Prey	0.0	0.0	0.0	0.4	0.2	0.2	0.0
	Total Prey	0.0	0.2	0.0	1.8	1.1	1.0	0.2
Totals	Fish Prey	71.9	91.9	87.4	95.7	96.8	96.8	77.3
	Invertebrate Prey	28.1	8.1	12.6	4.3	3.2	3.2	22.7
	Total Prey	100.0	100.0	100.0	100.0	100.0	100.0	100.0

(62%) in the region (Table 9). On the Flemish Cap (Div. 3M), hooded seals accounted for all of the seal predation. In the northern Gulf (Div. 4RS), the four seal species are present at different times of the year; harp seals are the most abundant, followed by grey, hooded and harbour seals. In this region, harp seals were the most important pinniped predator of redfish (98%), capelin (97%), sand lance (95%), Atlantic cod (75%) and Atlantic herring (*Clupea harengus*) (64%) (Table 9). Grey seals in Div. 4RS were an important predator of Atlantic herring (29%) and Atlantic cod (25%), while hooded

TABLE 8. Estimated consumption (tons), by NAFO area, of some important prey items consumed by four species of seals in 1996.

Seal Species	Prey Species	NAFO Area 2J3KL	4RS	3M	4VsW	4T	Other	All Areas
Harp Seal	Capelin	708 648	314 412					1 023 060
	Arctic cod	175 843	990					176 833
	Sand lance	345 429	5 871					351 300
	G. halibut	72 996						72 996
	Atl. Cod	48 835	42 089					90 924
	Atl. Herring	30 980	17 878					48 858
	Redfish	16 657	95 128					111 785
	All Species	1 399 388	476 368					1 875 756
Hooded Seal	Capelin	3 063	27	333				3 423
	Arctic cod	4 921	1 296					6 217
	Sand lance							
	G. halibut	118 273	3 773	11 677				133 723
	Atl. Cod	33 633	107	3 732				37 472
	Atl. Herring	4 751	1 252					6 003
	Redfish	17 847	1 842	1 219				20 908
	All Species	182 488	8 297	16 961				207 746
Grey Seal	Capelin		9 004			799	1 097	10 900
	Arctic cod							
	Sand lance		310		88 892	18 662	25 600	133 464
	G. halibut		140			15	21	176
	Atl. Cod		13 803		24 074	7 207	9 887	54 971
	Atl. Herring		8 260		12 160	2 870	3 938	27 228
	Redfish		24		1 151	250	343	1 768
	All Species		31 541		126 277	29 803	40 886	228 507
Harbour Seal	Capelin	26	96		179	27	33	361
	Arctic cod							
	Sand lance							
	G. halibut							
	Atl. Cod	27	100		185	28	34	374
	Atl. Herring	115	427		793	118	146	1 599
	Redfish	2	7		13	2	2	26
	All Species	170	630		1 170	175	215	2 360
Totals	Capelin	711 737	323 539	333	179	826	1 130	1 037 744
	Arctic cod	180 764	2 286	0	0	0	0	183 050
	Sand lance	345 429	6 181	0	88 892	18 662	25 600	484 764
	G. halibut	191 269	3 913	11 677	0	15	21	206 895
	Atl. Cod	82 495	56 099	3 732	24 259	7 235	9 921	183 741
	Atl. Herring	35 846	27 817	0	12 953	2 988	4 084	83 688
	Redfish	34 506	97 001	1 219	1 164	252	345	134 487
	All Species	1 582 046	516 836	16 961	127 447	29 978	41 101	2 314 369

seals accounted for nearly all (96%) of the consumption of Greenland halibut by seals in this region. On the eastern Scotian Shelf (Div. 4VsW) and in the southern Gulf (Div. 4T), grey seals were the dominant pinniped predator accounting for virtually all (99%) of the prey consumption by seals in these two areas.

Most of the consumption of Atlantic cod, Atlantic herring and redfish by seals was comprised of small, juvenile fish (Table 10). In 1996, 95% of the Atlantic cod consumed by seals were less than 40 cm in length, 90% of the herring consumed were less than 30 cm, and 89% of the redfish consumed were less than 25 cm in length.

TABLE 9. Estimated percentage consumption of principal prey species, within each NAFO area, by four species of seals.

Seal Species	Prey Species	NAFO Area 2J3KL	4RS	3M	4VsW	4T	Other	All Areas
Harp Seal	Capelin	99.57	97.18					98.59
	Arctic Cod	97.28	43.31					96.60
	Sand lance	100.00	94.98					72.47
	G. halibut	38.16	0.00					35.28
	Atl. Cod	59.20	75.03					49.48
	Atl. Herring	86.43	64.27					58.38
	Redfish	48.27	98.07					83.12
	All Species	88.45	92.17					81.05
Hooded Seal	Capelin	0.43	0.01	100.00				0.33
	Arctic Cod	2.72	56.69					3.40
	Sand lance	0.00	0.00					
	G. halibut	61.84	96.42	100.00				64.63
	Atl. Cod	40.77	0.19	100.00				20.39
	Atl. Herring	13.25	4.50					7.17
	Redfish	51.72	1.90	100.00				15.55
	All Species	11.53	1.61	100.00				8.98
Grey Seal	Capelin		2.78			96.73	97.08	1.05
	Arctic Cod							
	Sand lance		5.02		100.00	100.00	100.00	27.53
	G. halibut		3.58			100.00	100.00	0.09
	Atl. Cod		24.60		99.24	99.61	99.66	29.92
	Atl. Herring		29.69		93.88	96.05	96.43	32.54
	Redfish		0.02		98.88	99.21	99.42	1.31
	All Species		6.10		99.08	99.42	99.48	9.87
Harbour Seal	Capelin		0.03		100.00	3.27	2.92	0.03
	Arctic Cod							
	Sand lance							
	G. halibut							
	Atl. Cod	0.03	0.18		0.76	0.39	0.34	0.20
	Atl. Herring	0.32	1.54		6.12	3.95	3.57	1.91
	Redfish	0.01	0.01		1.12	0.79	0.58	0.02
	All Species	0.01	0.12		0.92	0.58	0.52	0.10

Discussion

During model development, several assumptions were made, which may or may not have been realistic. We did not assess the sensitivity of our consumption estimates to the model parameters used in deriving these values – since we used the same model structure as in previous seal feeding and consumption studies (Hammill and Mohn, MS 1994; Mohn and Bowen, 1996; Stenson *et al.*, 1997a). These earlier studies found that pinniped population size was the most important factor affecting fish consumption estimates (Hammill and Mohn, MS 1994; Stenson *et al.*, 1997a). Typically, the annual net rate of increase of seal populations is relatively low (3–10% per year) and reliable estimates of population size are available for most of the pinniped species in eastern Canada.

We assumed that average daily age specific energy requirements of seals could be described by a simple equation, where energy intake is a function of body mass$^{0.75}$ multiplied by constants to account for energy requirements due to activity and growth. We did not vary these constants with season, age- or sex-class or diet composition. Although changes in activity and growth do occur, these are poorly documented. Nevertheless, such changes can have a major impact on consumption estimates (Mohn and Bowen, 1996). Age-body mass relationships in our study were based on samples collected after reproduction (when body mass is near the

TABLE 10. Consumption (tons) of Atlantic cod, Atlantic herring and redfish by seals in 1996 in the northern Gulf of St. Lawrence (NAFO Divs. 4RS), by size group of prey.

	Atlantic cod					
	<40 cm		>40 cm		Total	
Seal Species	tons	% of Total	tons	% of Total	tons	% of Total
Harp Seal	41 542	98.7	547	1.3	42 089	75.2
Hooded Seal						
Grey Seal	11 733	85.0	2 070	15.0	13 803	24.7
Harbour Seal	99	99.0	1	1.0	100	0.2
Total	53 374	95.3	2 618	4.7	55 992	100.0

	Atlantic herring					
	<30 cm		>30 cm		Total	
Seal Species	tons	% of Total	tons	% of Total	tons	% of Total
Harp Seal	16 984	95.0	894	5.0	17 878	64.3
Hooded Seal	901	72.0	351	28.0	1 252	4.5
Grey Seal	6 938	84.0	1 322	16.0	8 260	29.7
Harbour Seal	268	62.9	158	37.1	426	1.5
Total	25 091	90.2	2 725	9.8	27 816	100.0

	Redfish					
	<25 cm		>25 cm		Total	
Seal Species	tons	% of Total	tons	% of Total	tons	% of Total
Harp Seal	85 616	90.0	9 512	10.0	95 128	98.1
Hooded Seal	1 105	60.0	737	40.0	1 842	1.9
Grey Seal	14	58.3	10	41.7	24	< 0.1
Harbour Seal	Redfish size frequency data not available					
Total	86 735	89.4	10 259	10.6	96 994	100.0

annual minimum) and thus underestimate total annual energy requirements. Our approach did not take into account seasonal changes in energy requirements associated with reproduction and moult. However, these energetic costs are unlikely to have a major impact on the annual estimates of energy requirements as Olesiuk (1993) estimated that the additional energy costs associated with reproduction only add about 5% to the total energy requirements of a population. Also, much of the costs associated with reproduction are offset by a reduction in energy requirements during moulting (Ryg and Øritsland, 1991). However, our assumption that consumption rates do not change during lactation, breeding and moulting periods (when most adults reduce caloric intake and rely on fat reserves to meet their energetic needs) could lead to overestimating consumption if more limited geographical areas or particular seasons were being considered. There is also some evidence of different seasonal distributions between males and females, as well as sex-specific changes in body condition. For example, after breeding, female harp seals leave the whelping area and feed intensively (Sergeant, 1991; Stenson and Hammill, Northwest Atlantic Fisheries Centre, St. John's, Canada, unpubl. data) to replace a portion of the energy reserves expended during lactation (Beck *et al*., 1993a, b; Chabot *et al*., 1996). Males remain near the whelping patch (Sergeant, 1991; Stenson and Hammill, Northwest Atlantic Fisheries Centre, St. John's, Canada, unpubl. data), and continue to lose mass until early April when the moult begins (Chabot *et al*., 1996).

Consumption estimates of individual fish species are strongly affected by the seasonal distribution patterns of the various seal species, and spatial/ temporal variations in pinniped diet composition.

Quantitative information on the spatial distribution of seals throughout the year is limited, and large changes in diet composition can occur across years, seasons and geographical areas (Mohn and Bowen, 1996; Shelton *et al*., 1997). Unfortunately, apart from the harp seals off eastern Newfoundland, temporal and spatial changes in diet composition are not well documented. Stenson *et al.* (1997a) compared annual estimates of harp seal consumption of Arctic cod, capelin and Atlantic cod off eastern Newfoundland between 1981 and 1994, using both annual and pooled diet composition data. Large annual changes (e.g. 50%–200%) in the consumption of major prey species (such as Arctic cod and capelin) were not tracked very well using a pooled average diet, suggesting that important trends in consumption were being masked. Shelton *et al*. (1997) also examined the effects of uncertainty in the values of population size, energy requirements, residency time, diet composition and prey energy density used by Stenson *et al*. (1997a) and found that uncertainty associated with the population estimates had the least effect on the overall uncertainty of consumption estimates, while diet composition had the greatest effect.

Invertebrates comprised an important component (12%–26%, by weight) of the diet of harp, hooded and harbour seals (Table 6). For hooded and harbour seals, the main invertebrate prey is squid (Appendix Tables 4 and 8). Squid beaks tend to remain lodged in the stomach rugae of seals, which may lead to an overestimation of their dietary importance (Bigg and Fawcett, 1985). With either fish or squid, diet composition can be reconstructed using otolith or beak size, respectively (corrected for digestive state *versus* body size relationships). However, for most other invertebrates, diet enumeration depends on counting whole prey items and/or recognizable body parts such as eyes or carapaces. Owing to the lower metabolizable energy of invertebrates – and the difficulty in reconstructing the invertebrate component of the diet – we have probably underestimated the role of invertebrates in seal diets, particularly for harp seals. Hence, total prey consumption has likely been underestimated, while fish consumption has probably been overestimated.

The pinniped species for which the greatest amount of information exists (and for which we have the greatest confidence in consumption estimates) is the harp seal. Good data exist on abundance (Shelton *et al*., 1996; Stenson *et al*., 1997a; Stenson *et al*., MS 1999) and body size (Chabot *et al*., 1996). Extensive data are also available on geographical and seasonal variations in the diet of harp seals off Newfoundland (Lawson *et al*., 1995; Lawson and Stenson, 1995, 1997), although less information exists for harp seals in the Gulf of St Lawrence. The available data indicate that the importance of Atlantic cod in the diet of harp seals did not change during 1990 to 1996, despite the extremely low abundance of the Atlantic cod stock in the Newfoundland region (Div. 2J and 3KL) during this time period (Lilly *et al*., MS 1999).

The population dynamics and diet of grey seals is also quite well known. Estimates of abundance are available for both the Sable Island and northern Gulf of St. Lawrence grey seal population components (Zwanenberg and Bowen, 1990; Hammill and Mohn, MS 1994; Mohn and Bowen, 1996) and diet composition and consumption estimates exist for both components (Benoit and Bowen, 1990; Murie and Lavigne, 1992; Bowen *et al*., 1993; Bowen and Harrison, 1994; Proust, 1996). However, dietary data for grey seals in the southern Gulf and 'Other' areas is poor. Even less is known about hooded seals; the available data are limited to a few studies on abundance (Bowen *et al.*, 1987; Stenson *et al*., 1997b) and feeding in nearshore (Ross, 1993) and offshore (Lawson and Stenson, Northwest Atlantic Fisheries Centre, St. John's, Newfoundland, Canada, unpubl. data) areas of Newfoundland. No information exists on the diet of hooded seals in the Gulf of St. Lawrence. In this latter area, prey composition was assumed to be identical to that of hooded seals in inshore Newfoundland. If this assumption is incorrect, the 'true' estimate of consumption by hooded seals in the Gulf could be significantly different from that calculated.

The species for which the least is known is the harbour seal. Our estimates of abundance and distribution are based on work conducted in the 1970s (Boulva and McLaren, 1979) and only a single diet study exists (Bowen and Harrison, 1996). However, the harbour seal population is so small relative to the other three seal species that changes in assumptions concerning the diet of harbour seals would have little effect on the estimates of total and regional pinniped prey consumption.

Estimates of consumption by grey and harp seals presented in this paper differ from earlier estimates (Hammill and Mohn MS 1994; Stenson *et al*., 1997a). Our estimates of grey seal consumption: (a) lack a correction factor for unidentified dietary components; (b) do not include a specific cost for the heat increment of feeding; (c) use a lower non-Sable Island population size than Hammill and Mohn (MS 1994); and (d) include a higher proportion of cod in the diet of the northern Gulf of St. Lawrence grey seal component (Proust, 1996). Also, we used the average diet composition of grey seals in the northern Gulf and Scotian Shelf areas to characterize the diets of grey seals in the southern Gulf of St. Lawrence (Div. 4T) and 'Other' regions.

The present estimates of harp seal consumption differ from those provided by Stenson *et al*. (1997a) in several ways: (1) we used slightly lower estimates for the incremental costs of growth (GP); (2) we limited consumption to the southern part of the harp seal range (Div. 2J and 3KL and Div. 4RS); and (3) we used population size estimates that assumed pup mortality was greater than adult mortality and which also accounted for a substantially higher harvest of harp seals in Greenland (Stenson *et al.*, MS 1999). Our estimates of consumption also reflect a major change in the spatial distribution of harp seals within Div. 2J and 3KL. Satellite telemetry results indicate that only 11–14% of harp seals occur in nearshore regions (<50 km). Thus, diet composition data for the nearshore area was applied to a smaller fraction of the population than in Stenson *et al.* (1997a).

Little is known about the factors affecting prey selection by seals. A comparison of harp seal stomach content data collected off Newfoundland with prey abundance data collected from research trawl surveys suggests that harp seals preferentially select capelin (and possibly Arctic cod), but are neutrally selective towards Atlantic cod, American plaice and Greenland halibut (Lawson *et al.*, 1998a). Different species of seals also seem to forage on different size groups of prey. For example, in the northern Gulf of St. Lawrence (Div. 4RS), harp seals appear to consume Atlantic cod that are primarily 10–20 cm long (Lawson and Stenson, 1995a), grey seals seem to prefer cod around 15–30 cm (Benoit and Bowen, 1990; Bowen *et al.*, 1993), while hooded seals prefer cod 25–35 cm in length (Ross, MS 1993).

The size range of prey consumed by seals can also shift over time. In the northern Gulf, Benoit and Bowen (1990) reported that 85% of the Atlantic cod consumed by grey seals were <40 cm in length. In 1992, Proust (1996) found that 51% of the Atlantic cod consumed by grey seals were >40 cm in length. Shifts in the size range of prey consumed have also been noted in other areas. Hammond *et al*. (1994) reported on seasonal changes in the length-frequency distributions of cod, whiting, saithe, sandeels and American plaice consumed by grey seals off northeastern Scotland, while Tollit *et al*. (1997) noted inter-annual changes in the size distributions of herring and sprat consumed by harbour seals. Bowen *et al*. (1993) documented differences in the size distributions of cod consumed by grey seals between inshore and offshore areas on the Scotian Shelf, while Stansbury *et al*. (MS 1998) and Lilly *et al*. (MS 1999) observed annual differences in the size range of cod consumed by harp seals in waters off Newfoundland.

Predation is an omnipresent, but ephemeral feature of marine ecosystems. Population removals by predation can exceed fisheries harvests, yet it is often assumed that fishing mortality alone is responsible for variations in fish survival (Bax, 1998). Our estimates of consumption indicate that seals in Atlantic Canada consume large quantities of fish – but seal predation is only one of several sources of mortality to fish stocks. Realistically, it will not be possible to assess the relative impact of seal predation on fish stock abundance until other sources of natural mortality are quantified. Multispecies predation models indicate that consumption by fish of other fish can exceed that of marine mammals (Overholtz *et al.*, 1991; Trites *et al.*, 1997). Conceptually, multispecies approaches offer the greatest potential to fully evaluate the mortality impacts of predators, but the data requirements of these approaches are too demanding to be of likely use in the near future. Less data intensive, mass-balance types of models (Trites *et al.*, 1997; Walters *et al.*, 1997) are apt to provide more timely insights into ecosystem structure and the relative importance of various species. These insights, in turn, may stimulate more dynamic and predictive modeling efforts that focus on key species. Such efforts would help place predation by seals within the context of overall natural mortality, and facilitate an accurate and synoptic assessment of the impacts of seals on fish stocks.

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Appendix 1. Description of Biology and Model Parameters Used to Estimate Prey Consumption of Harp, Hooded, Grey, and Harbour Seals

a) Harp Seals

Population Dynamics. Harp seals in the Northwest Atlantic whelp on the pack ice off the Newfoundland east coast (the Front) and in the Gulf of St. Lawrence (Sergeant, 1991). Total pup production increased from 578 000 animals in 1990 to 702 900 animals in 1994 (Stenson *et al*., 1993, 1996). Changes in population size were based on the model used by Stenson *et al*. (MS 1999). The population model – derived from that of Shelton *et al*. (1996) – was updated by incorporating revised estimates of harp seal catches in Greenland and additional data on: (a) recent harvests; (b) age composition of the catches; and (c) current reproductive rates. Pup mortality was assumed to be three times the mortality rate of older seals. Unreported catches were assumed to be 5% for young-of-the-year animals taken off Canada, and 50% for all other age groups.

Seasonal Distribution. Harp seals are highly migratory; our knowledge of their seasonal distribution (Appendix Table 1) is primarily based on historical catch data, tag returns and, more recently, satellite telemetry. The Gulf and Newfoundland components of the population intermingle during the non-breeding period, summering in the Canadian Arctic and/or West Greenland. During the autumn and early winter, seals from both components move southward along the Labrador coast. Whelping occurs in the Gulf of St. Lawrence or southern Labrador. After whelping, the animals moult before returning north. Annual changes in ice conditions or food availability (Sergeant, 1991) affect the seasonal movements of the population.

Assumptions concerning the seasonal distribution of harp seals in Div. 2J and 3KL were revised from those of Stenson *et al*. (1997a). Based on the work of Kapel and Rosing-Asvid (1996) and Sergeant (1991), 20% of all age groups were assumed to remain in the Arctic throughout the year. The residency period in Div. 2J and 3KL was considered to be 21 November to 6 July based on satellite telemetry tracking data (Stenson and Sjare, MS 1997). One-third of the adult population and 20% of juveniles (ages 1–4) were assumed to enter the Gulf of St. Lawrence on 1 December and remain there until 30 May. A small proportion (5%) of the seals that migrated southward were assumed to remain in the study area for the entire year, with the proportion in each area that same as for the winter period.

The proportion of energy obtained by harp seals in the offshore and nearshore areas in Div. 2J and 3KL was also modified from that in Stenson *et al*. (1997a). We assumed that 89% and 86% of the energy required in summer and winter periods, respectively, was obtained in offshore areas (as opposed to 55% in Stenson *et al*. 1997a). Our estimates were derived by plotting the locations of seals in Div. 2J and 3KL [obtained from the satellite tracking study described in Stenson and Sjare (MS 1997)] and determining the proportion of sites within 30 km of the coast (Stenson, Northwest Atlantic Fisheries Centre, St. John's, Nfld., Canada, unpubl. data) where the nearshore diet samples were obtained. Increasing the width of the nearshore band to 50 km did not significantly increase the proportion of seals in the inshore region (Stenson, Northwest Atlantic Fisheries Centre, St. John's, Nfld., Canada, unpubl. data).

Diet. Diet composition of harp seals in the Gulf (Appendix Table 2) was derived by taking the mean proportions of each prey item in the diet samples collected by Murie and Lavigne (1991), Beck et al. (1993b) and Lawson *et al*. (1995). The dietary data from Lawson *et al*. (1995) were supplemented by additional samples collected from the west coast of Newfoundland (Stenson and Lawson, Northwest Atlantic Fisheries Centre, St. John's, Nfld., Canada, unpubl. data).

The diet composition of harp seals off Newfoundland was based on material from Lawson and Stenson (1995, 1997), Lawson *et al*. (1995) and Stenson and McKinnon (Northwest Atlantic Fisheries Centre, St. John's, Nfld., Canada, unpubl. data). Samples were divided geographically (nearshore/offshore) and by season (summer/ winter) (Appendix Table 2). Seasonal diets in the nearshore area were estimated by averaging the proportion of each prey species in the available seasonal samples (from 1982, 1986, 1990–93; see Stenson *et al.*, 1997a; Lilly *et al.*, MS 1999; and Stenson and McKinnon, Northwest Atlantic Fisheries Centre, St. John's, Nfld., Canada, unpubl. data).

APPENDIX TABLE 1. Percentage of annual energy requirements obtained by harp seals in different areas of the Northwest Atlantic.

NAFO Area	Pups/Juveniles Winter (Oct–Mar)	Pups/Juveniles Summer (Apr–Sep)	Adults Winter (Oct–Mar)	Adults Summer (Apr–Sep)
Div. 2J3KL (inshore)	3.32	2.14	2.82	1.91
Div. 2J3KL (offshore)	20.41	17.31	17.35	15.58
Div. 4RS (Northern Gulf)	5.47	2.99	9.03	4.95
SA 0+1 (Arctic)	20.66	27.70	20.66	27.70
All Areas	49.86	50.14	49.86	50.14

APPENDIX TABLE 2. Harp seal diet composition data (% wet weight) used to estimate prey consumption.

Species	Newfoundland Nearshore Summer	Newfoundland Nearshore Winter	Newfoundland Offshore Summer	Newfoundland Offshore Winter	Gulf All
Arctic cod	23.0	50.8	0.8	2.2	0.1
Atlantic cod	5.1	3.0	2.1	1.0	6.4
Capelin	21.1	11.2	34.7	30.9	47.7
Atlantic herring	12.6	7.3	0.0	0.0	2.7
Sand lance	0.5	0.2	30.5	0.0	0.9
Redfish	0.3	<0.1	1.1	0.3	14.4
Greenland halibut	1.5	1.0	4.8	2.0	0.0
American plaice	1.1	0.2	0.1	1.1	0.0
Pleuronectidae	2.1	0.6	7.4	5.7	11.0
Windowpane	0.0	0.0	0.0	0.0	2.0
Atlantic salmon	0.1	0.0	0.0	0.0	0.4
Sculpin	0.6	1.8	0.2	0.3	0.8
Silver hake	0.0	0.0	0.0	0.0	0.5
White hake	0.0	0.3	0.4	0.1	0.1
Smelt	0.0	0.1	0.0	0.0	<0.1
Alewife	0.0	0.0	0.0	0.0	<0.1
Haddock	0.0	0.0	0.0	0.0	0.4
Gadus sp.	0.7	1.4	<0.1	<0.1	0.5
Other Fish	11.7	9.9	0.5	14.7	3.4
Total Fish	80.4	87.8	82.6	58.3	91.3
Shrimp	5.5	1.3	6.8	31.2	2.0
Squid	0.9	0.7	0.2	0.6	1.0
Euphausiid	3.8	0.6	<0.1	0.0	<0.1
Other Invertebrates	9.4	9.6	10.4	9.9	5.7
Total Invertebrates	19.6	12.2	17.4	41.7	8.7
Total Prey	100.0	100.0	100.0	100.0	100.0
Mean Energy Content (Kjoules/gram)	6.2	5.6	6.0	6.0	6.3

b) **Hooded Seals**

Population Dynamics. Hooded seals whelp during March on the pack ice off the Newfoundland east coast (the Front), in the Gulf of St. Lawrence, and in the Davis Strait (Sergeant, 1976). Little is known about stock affinities between the three population groups. In 1984, pup production was estimated to be 62 400 animals at the Front and 19 000 animals in Davis Strait (Bowen *et al.*, 1987). Pup production was not determined in the Gulf. In 1990, pup production was estimated to be 83 100 at the Front (Stenson *et al.*, 1997b) and 2 006 in the Gulf (Hammill *et al.*, 1992). Current estimates of abundance are not available for any of the three whelping patches. An annual population rate of increase of 4.8% in Newfoundland waters was calculated from the 1984 and 1990 estimates of pup production at the Front, and applied to the Gulf population. Reproductive rates were set at 0.028, 0.262, 0.504, 0.654, 0.734, 0.802, 0.850, 0.908, and 0.970 for ages 3 to 11+ years (Stenson, Northwest Atlantic Fisheries Centre, St. John's, Nfld., Canada, unpubl. data). Adult mortality was set at 9% per year, intermediate to values of 0.07 and 0.13 used in other studies (Myers and Stenson, 1996; Hammill *et al.*, 1997). Juvenile mortality was initially set at 3 times the adult mortality rate ($3 \times 9\% = 27\%$) and then increased to 40%, generating a total net annual population increase of 4.8%.

Seasonal Distribution. Seasonal distributions (Appendix Table 3) were based on: (1) satellite telemetry data obtained after whelping had occurred at the Front and in the Gulf (Stenson and Hammill, Northwest Atlantic Fisheries Centre, St. John's, Nfld., Canada, unpubl. data); (2) observations by fishermen and hunters; and (3) historical accounts (Comeau, 1945). We assumed that all pups and one-year-old seals remained in Arctic waters (Subareas 0+1). As well, we assumed that only 20% of juveniles aged 2+ and 3+ returned each year to the Front (Div. 2J and 3KL) or to the northern Gulf (Div. 4RS). All adults were assumed to annually return to one or the other of these areas.

Diet. Dietary data (Appendix Table 4) were divided into inshore (Ross, MS 1993) and offshore components (Lawson and Stenson, Northwest Atlantic Fisheries Centre, St. John's, Nfld., Canada, unpubl. data). Inshore data from the Front was used to estimate hooded seal consumption in the Gulf.

c) **Grey Seals**

Population Dynamics. Most grey seals whelp on either Sable Island or on the Gulf of St Lawrence pack ice. Although the two groups form a single stock (Boskovic *et al.*, 1996), it is convenient to consider seals in the two areas as separate groups. Pup production estimates from the 1980s are available from both groups (Stobo and Zwanenburg, 1990; Hammill *et al.*, 1998). The population was reconstructed and projected forwards from 1990 to 1996, using age-specific reproductive rates of 0.176, 0.860, and 0.876 for animals aged 4, 5 and 6 years, respectively (Hammill and Gosselin, 1995). Adult survival rates were set at 0.96. To achieve the reported rate of increase in the Sable Island herd (12.6%; Zwanenburg and Bowen, 1990), juvenile survivorship was set at 0.787. The Sable Island component thus increased from 62 920 animals in 1990 to 128 500 animals in 1996. The dynamics of the non-Sable Island group were different owing to: (1) culling on the whelping patch from 1980 to 1984; (2) a bounty hunt which was discontinued in 1990; and (3) the likelihood of higher pup mortality due to the instability of the pack ice habitat

APPENDIX TABLE 3. Quarterly distribution (% of total population in each area) of Gulf of St. Lawrence (Gulf Herd) and eastern Newfoundland (Front Herd) hooded seals [see text "Seasonal Distribution" for explanation of the proportions of the herds remaining in the Arctic.]

	Gulf Herd				Front Herd			
NAFO Area	Q1	Q2	Q3	Q4	Q1	Q2	Q3	Q4
Div. 4RS (Northern Gulf)	100	100	0	17	0	0	0	0
Div. 2J3KL (Inshore)	0	0	0	1	10	3	0	3
Div. 2J3KL (Offshore)	0	0	0	15	90	31	0	30
Div. 3M (Flemish Cap)	0	0	0	0	0	17	0	0
Arctic (SA 0 + 1)	0	0	100	67	0	49	100	67
All Areas	100	100	100	100	100	100	100	100

APPENDIX TABLE 4. Hooded seal diet composition data (% wet weight) used to estimate prey consumption.

Species	NAFO Area: Gulf (Div. 4RS) & Div. 2J3KL (Inshore)	NAFO Area: Div. 2J3KL (Offshore)
Arctic cod	14.5	0.0
Atlantic cod	1.2	10.1
Capelin	0.3	0.9
Atlantic herring	14.0	0.0
Witch flounder	0.0	15.5
Redfish	20.6	3.3
Greenland halibut	42.2	31.6
Pleuronectidae	0.0	8.3
Grenadier	0.0	5.7
Blue hake	0.0	4.2
Lancetfish	0.0	1.6
Eelpout	0.0	0.4
Other Fish	0.0	5.8
Total Fish	92.8	87.4
Squid	7.2	12.6
Total Prey	100.0	100.0
Mean Energy Content Kjoules/gram)	5.4	5.2

(Zwanenburg and Bowen, 1990; Hammill *et al.*, 1998). Mark-recapture studies indicate that pup production of the non-Sable Island component was increasing at 7.4%, although a 1997 aerial suggested that the increase was only about 3.4% (Hammill, MS 1999). Assuming no differences in adult survival rates between the Gulf and Sable Island components of the population, we set pup survival at 0.329 to achieve an increase in pup production of ≈3.4% between 1984 and 1996. Using all of the parameters above, the total grey seal population increased from 96 900 animals in 1990 to 173 500 animals in 1996 (Table 2).

Seasonal Distribution. The seasonal distribution of grey seals (Appendix Table 5) followed that reported in Hammill and Mohn (MS 1994).

Diet. Dietary information on grey seals in the northern Gulf Div. 4RS) and on the eastern Scotian Shelf (Div. 4VsW) is available from several studies (Bowen *et al.*, 1993; Bowen and Harrison, 1994, 1996) (Appendix Table 6). Knowledge of grey seal diets in the southern Gulf and 'Other' areas, however, is based on very limited sampling. For the northern Gulf, all available sampling data (Benoit and Bowen, 1990; Murie and Lavigne, 1992; Proust, 1996) were combined and the average contribution of each prey species was calculated. Dietary data for the Scotian Shelf were divided into summer (April–September) and winter (October–March) components (Bowen *et al.*, 1993; Bowen and Harrison, 1994). Diet composition for the southern Gulf and 'Other' regions was based on an average diet using samples from all areas.

d) **Harbour seals**

Population Dynamics. The harbour seal is widely distributed throughout Atlantic Canada; however, there are no reliable estimates of population abundance or trends in stock size. In 1973, the population was estimated at 12 700 animals (Boulva and McLaren, 1979) and thought to be declining at 4% per year due to high bounty takes. In 1976, the bounty program was eliminated. To reconstruct the dynamics of the Atlantic harbour seal population, we assumed that 12 700 animals existed in 1973, and that the population declined at

APPENDIX TABLE 5. Quarterly distribution (% of total population in each area) of Gulf of St. Lawrence (Gulf Herd) and Sable Island (Sable Herd) grey seals.

	Gulf Herd				Sable Herd			
NAFO Area	Q1	Q2	Q3	Q4	Q1	Q2	Q3	Q4
Div. 4RS (Northern Gulf)	10.0	35.0	60.0	50.0	0.0	12.5	7.5	5.0
Div. 4T (Southern Gulf)	70.0	35.0	10.0	30.0	0.0	12.5	7.5	0.0
Div. 4VsW (Eastern Scotian Shelf)	10.0	20.0	20.0	10.0	90.0	50.0	50.0	80.0
Other (Div. 4X; Subdiv. 3Ps)	10.0	10.0	10.0	10.0	10.0	25.0	35.0	15.0
All Areas	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

APPENDIX TABLE 6. Grey seal diet composition data (% wet weight) used to estimate prey consumption.

	Eastern Scotian Shelf (Div. 4VsW)			Southern Gulf (Div. 4T)&
Species	Summer	Winter	Northern Gulf (Div. 4RS)	Other (4X; 3Ps)
Capelin	0.0	0.0	6.0	1.2
Sand lance	47.2	65.1	0.9	45.1
Pleuronectidae	8.1	7.0	0.0	6.0
Greenland halibut	0.0	0.0	0.2	<0.1
Atlantic cod	17.6	9.7	41.2	19.1
Redfish	0.6	0.9	0.1	0.6
Atlantic herring	11.0	1.5	12.5	7.5
Witch flounder	0.0	0.0	0.1	0.0
American plaice	0.0	0.0	3.7	0.7
Sculpin	0.0	0.0	1.1	0.2
Mackerel	0.1	7.9	5.7	4.3
Silver hake	7.1	0.6	0.0	3.1
Lumpfish	0.0	0.0	7.4	1.5
Wolffish	0.0	0.0	6.0	1.2
White hake	0.0	0.0	0.3	0.1
Pollock	2.3	0.0	0.0	0.9
Haddock	0.0	0.0	1.2	0.2
Atlantic salmon	0.0	0.0	0.9	0.2
Ocean pout	0.0	0.0	5.5	1.1
Eelpout	0.0	0.0	0.1	<0.1
Yellowtail flounder	0.0	0.0	3.4	0.7
Alewife	0.0	0.0	1.1	0.2
Skates	0.0	0.0	2.2	0.4
Winter flounder	0.0	0.0	0.2	0.0
Cunner	0.0	0.0	0.1	<0.1
Other Fish	1.4	4.5	0.0	2.4
Total Fish	95.4	97.2	99.9	97.0
Squid	4.6	2.8	0.1	3.0
Total Prey	100.0	100.0	100.0	100.0
Mean Energy Content (Kjoules/gram)	5.9	6.3	5.9	6.1

APPENDIX TABLE 7. Quarterly distribution (% of total population in each area) of harbour seals, by area, in Atlantic Canada.

NAFO Area	Q1	Q2	Q3	Q4
Div. 4RS (Northern Gulf)	26.4	26.4	26.4	26.4
Div. 4T (Southern Gulf)	8.0	8.0	8.0	8.0
Div. 2J3KL (Newfoundland)	7.9	7.9	7.9	7.9
Div. 4VsW (Eastern Scotian Shelf)	48.0	48.0	48.0	48.0
Other (Div. 4X; Subdiv. 3Ps)	9.7	9.7	9.7	9.7
All Areas	100.0	100.0	100.0	100.0

4% per year until 1976 when the bounty program ceased. As harbour seals appear to be increasing in the Bay of Fundy, around the Nova Scotian coast, and in the St. Lawrence Estuary (Stobo and Fowler, 1994; V. Lesage, Institute Maurice Lamontagne, Mont Joli, Quebec, Canada, unpubl. data), we assumed that the total harbour seal population in eastern Canada has been increasing since 1976. Adult survivorship was therefore set at 0.9 and juvenile mortality rates were assumed to be 3 times the adult mortality rate (i.e., 3×0.1), resulting in a juvenile survival rate of 0.7. Age specific reproductive rates were set at 0.27, 0.55, 0.79 and 0.94 for animals aged 4+, 5+, 6+ and >6+, respectively (Boulva and McLaren, 1979). These parameters resulted in a net rate of increase of 5.6% per year, and generated an increase in population size from 22 800 animals in 1990 to 31 900 animals in 1996 (Table 2).

Seasonal Distribution. The geographical distribution of the population was based on the findings of Boulva and McLaren (1979). As satellite telemetry data indicate that harbour seals are relatively sedentary (Lesage and Hammill, Institute Maurice Lamontagne, Mont Joli, Quebec, Canada, unpubl. data), we assumed that there were no seasonal changes in the areal distribution of the population during the year (Appendix Table 7).

Diet. Quantitative diet information for harbour seals is quite limited. Bowen and Harrison (1996) examined the diet composition of harbour seal in the Bay of Fundy and on the Nova Scotia eastern shore. Their dietary findings for harbour seals were applied in all areas for all seasons (Appendix Table 8).

APPENDIX TABLE 8. Harbour seal diet composition data (% wet weight) used to estimate prey consumption.

Species	% Wet Weight
Atlantic herring	24.4
Pollock	12.7
Atlantic cod	5.7
Capelin	5.5
White hake	2.9
Alewife	1.7
Mackerel	1.4
Winter flounder	1.3
Ocean pout	0.8
Silver hake	0.7
Redfish	0.4
Cunner	0.3
Sculpin	0.2
Haddock	0.1
Blueback herring	0.1
Butterfish	1.1
Fourspot flounder	0.1
Other Fish	19.1
Total Fish	78.5
Squid	14.8
Crab	0.4
Other Invertebrates	6.3
Total Invertebrates	21.5
Total Prey	100.0
Mean Energy Content (Kjoules/gram)	5.3