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The Northeast Arctic cod stock's consumption of commercially exploited prey species in 1984–1986

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In order to evaluate the growing influence of Northeast Arctic cod (*Gadus morhua*) on some commercially exploited prey species, the annual consumption of these species by the cod stock has been estimated for 1984–1986. The estimates are based on stomach content weights and composition data from more than 11 000 cod sampled throughout the area of distribution at different times of the year, temperature-correlated digestion times from the North Sea, the number of cod in each age group during the years in question, and the geographical distribution of each group.

The main prey species during the period was capelin (*Mallotus villosus*), and in 1985 the consumption approached two million tonnes, while in 1986 it was less than half of this. The next most important prey was deep-sea shrimp (*Pandalus borealis*), the consumption of which dropped from about 0.6 million tonnes in 1984 to below 0.3 million tonnes in 1986. Measured in numbers consumed, there was also a considerable consumption of young redfish (*Sebastes* spp.) and herring (*Clupea harengus*), and in the last years also of young cod and haddock (*Melanogrammus aeglefinus*). The results show that the growing cod stock has had a great impact on some of the commercially exploited prey species in 1984–1986, and some year classes may have been seriously reduced by this predation.

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Introduction

The stock size of Northeast Arctic cod (*Gadus morhua*) has been increasing during recent years (Anon., 1987c), while the stock sizes of some of its most important prey species have decreased drastically. Barents Sea capelin (*Mallotus villosus*) is seriously depleted (Anon., 1987b), the stock size of deep-sea shrimp (*Pandalus borealis*) is more than halved (Hylen and Øynes, 1986), and young age groups of Norwegian spring-spawning herring (*Clupea harengus*) are almost absent from the Barents Sea at the moment (Anon., 1987b). In order to evaluate the influence of the growing cod stock on some commercially exploited prey species, its annual consumption of deep-sea shrimp, capelin, herring, redfish (*Sebastes* spp.), and young cod and haddock (*Melanogrammus aeglefinus*) has been estimated for 1984–1986.

The cod's consumption of Barents Sea capelin was earlier estimated by Ponomarenko and Ponomarenko (1975) and Ponomarenko *et al.* (1978), but they do not present any data for other prey species. Estimates of the cod's food consumption were also made in other areas, e.g., the North Sea (Daan, 1973, 1975, 1983), the North Sea and the Faroe plateau (Jones, 1978), off Eastern Newfoundland and in the Gulf of St. Lawrence (Minet and Perodou, 1978), the Baltic and the Kattegat (Bagge, 1981), Georges Bank (Cohen and Grosslein, 1981), the southwestern Gulf of St. Lawrence (Waiwood and Majkowski, 1984), and Icelandic waters (Magnússon and Pálsson, 1989).

Materials and methods

The cod stock's food consumption has been estimated using mainly the same method of calculation as in Mehl and Westgård (1983). The consumption in tonnes of prey species i, prey size group j in season l ($C_{i,j,l}$) is given by:

$$C_{i,j,l} = \Sigma_{k,n} F_n \times \overline{W}_{k,l,n} \times R_{i,j,k,l,n} \times XN_{l,n} \times XP_{k,l,n} \times \times \text{const},$$

F_n = proportion of mean stomach content digested per day for predator age group n,

$\overline{W}_{k,l,n}$ = mean stomach content in grams in area k and season l for predator age group n,

$\overline{R}_{i,j,k,l,n}$ = proportion of the weight of the stomach content that was prey species i, size group j, in area k and season l for predator age group n,

$XN_{l,n}$ = number of individuals of predator age group n in season l,

$XP_{k,l,n}$ = proportion of individuals of predator age group n in area k and season l,

const = scaling factor to get the consumption in tonnes per season.

The proportion of mean stomach content digested per day is found by combining data on digestion times for different sizes of cod from the North Sea (Daan, 1973) with length-at-age data for the Barents Sea cod (unpubl. data), applying the same temperature correlation for the digestion coefficient as used by the *ad hoc* Multispecies Assessment Working Group in the North Sea (Anon., 1987a):

$$\delta = \delta_0 \times e^{0.096(T_0 - T)}$$

where δ_0 is the experimentally obtained digestion coefficient at temperature T_0. The digestion experiments of Daan (1973) were carried out at 12 °C, while the mean temperature for the Barents Sea is set at 3 °C (unpubl. data).

The digestion data used for the different cod age groups, F_n, were the following:

	Age group						
	1	2	3	4	5	6	7+
Mean length at age (cm)	12.7	22.5	34.4	50.4	60.0	70.2	85.0
Proportion digested per day	1.124	0.634	0.416	0.284	0.238	0.204	0.168

For comparative purposes, additional consumption estimates have been made using an exponential model and preliminary data on gastric evacuation rates for cod from an experiment now in progress in Balsfjord in nothern Norway (J. Santos, pers. comm.). The water temperatures here are very much the same as in the Barents Sea and vary between 0 °C and 5 °C. Santos has found that evacuation rates vary with temperature, prey species, prey size, and meal (ration) size, whereas predator size does not seem to be an important factor. An average of the data he has obtained so far for the prey species deep-sea shrimp, capelin, and herring is used. For redfish, haddock, and cod (as prey) the same data are used as for herring, and the prey group "others" uses an average of the data from all the prey species used in the experiments. The values used are given in the text table below:

	Prey species						
	Shrimp	Capelin	Herring	Cod	Haddock	Redfish	"Others"
Gastric evacuation rate (1/h)	0.028	0.033	0.022	0.022	0.022	0.022	0.030

The exponential model used for estimating the consumption was the following:

$$C_{i,j,l} = \Sigma_{k,n} F_i \times \overline{W}_{k,l,n} \times R_{i,j,k,l,n} \times XN_{l,n} \times XP_{k,l,n} \times \times \text{const},$$

where

F_i = rate of gastric evacuation (1/h) of prey species i,

and the other components are the same as above (the constant is multiplied by 24).

The stomach content data used in the calculations were collected during a stomach sampling programme in connection with the construction of a multispecies model for the Barents Sea (Mehl, 1986a). The methods used for sampling, analysis, and data recording and processing were mainly the same as those used for the North Sea "Stomach sampling project" (Anon., 1980, 1981; Westgård, 1982; Mehl, 1986b). Samples were collected on board Norwegian research vessels during rou-

tine surveys in the Barents Sea and in the Spitsbergen area. The Barents Sea was covered mainly from the end of January until the beginning of March, from the end of April until the beginning of June, and from the beginning of September until the beginning of November, while the Spitsbergen area was covered only from the end of July until the end of September. The gears used were bottom (shrimp) trawl and pelagic trawl. The trawl stations were randomly spread within each stratum of the investigated area, and sampling continued over 24 hours per day. For each station with biological sampling (otoliths, etc.) the aim was to collect up to ten stomachs per 10-cm predator size group. Stomachs of fish which had regurgitated were not included in the samples. Each stomach was frozen separately, and data on each predator's length, age, weight, sex, and maturity stage and the number caught per hour fishing per trawl station were recorded together with station data for the total sample.

Figure 1 shows the geographical distribution by model area for the total number of stomachs collected, and the following text table summarizes the number sampled by predator size group, season (winter/spring = W–S and summer/autumn = S–A), and year.

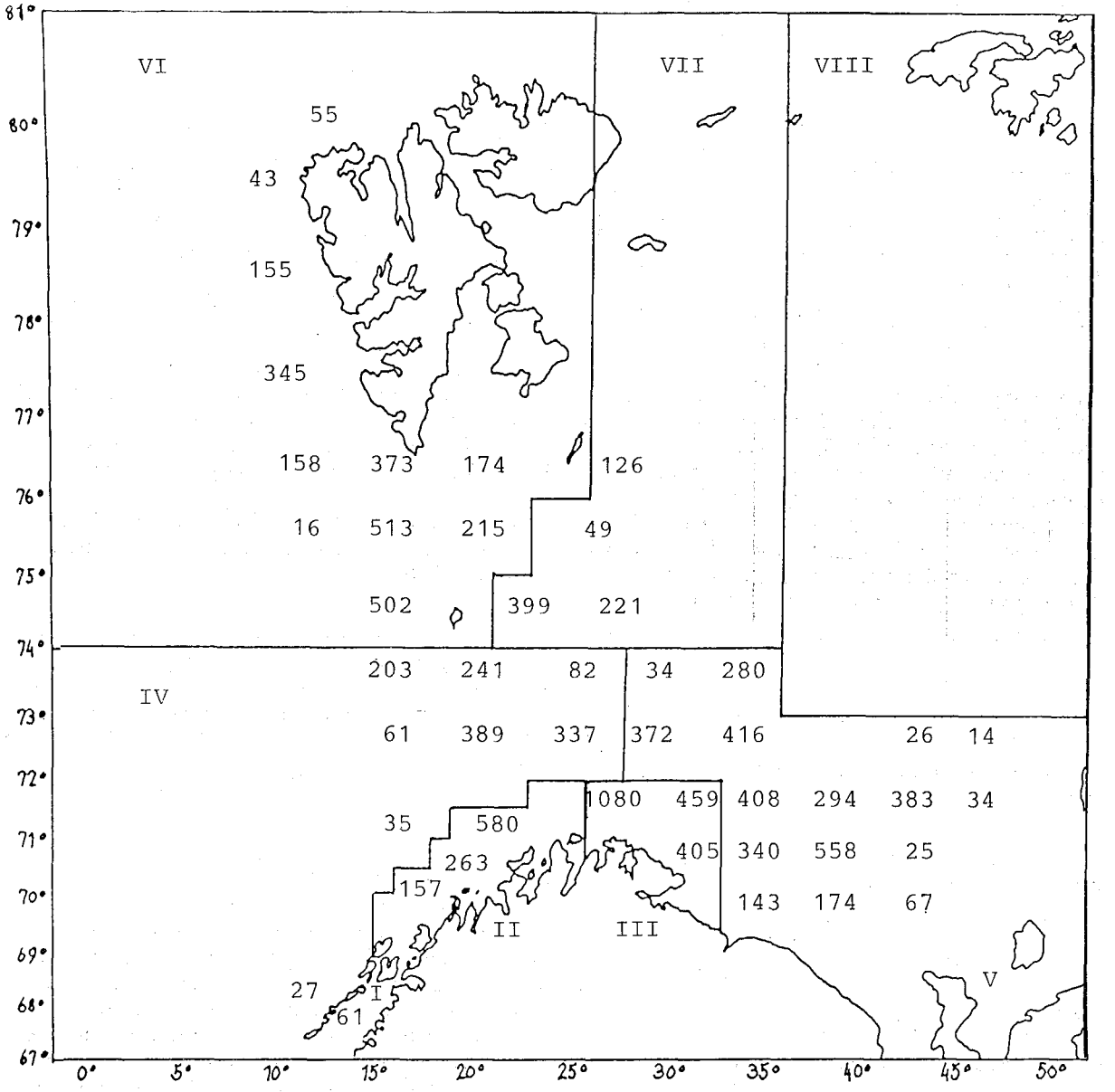

Figure 1. Geographical distribution by model areas I–VIII for 11 292 cod stomachs sampled in the Barents Sea in 1984–1986.

Season	Predator size group (cm)							
	< 20	20–29	30–39	40–49	50–59	60–69	> 70	Sum
				1984				
W–S	293	212	317	193	210	128	80	1 433
S–A	220	398	323	554	298	244	261	2 298
				1985				
W–S	149	480	389	560	393	247	176	2 394
S–A	210	323	272	212	235	118	115	1 485
				1986				
W–S	204	216	337	305	244	168	97	1 571
S–A	185	325	400	373	332	362	134	2 111
Sum	1 261	1 954	2 038	2 197	1 712	1 267	863	11 292

In the laboratory the plastic bags containing the stomachs were put in cold water and the stomachs were opened as soon as practicable. Fish prey and shrimps were identified to species level when possible; other prey were identified to species level when practical. Each recognizable prey species, genus, or family was split into size groups and damp dried on bibulos paper. Number and total wet weight, measured to the nearest milligram, were recorded for each size group of each prey category separately.

The results were aggregated by predator age group, model area (II+IV, III+V, and VI+VII), and season. The weight of each prey size group was adjusted by distributing the unidentified component of the diet proportionally among the various identified components, taking into account the level of identification (as in Anon., 1984a). The actual data on stomach content composition and weights used for the different predator age groups, areas, seasons, and years are presented in the Appendix. Because area VI+VII is sampled only once a year, the data collected during the second half of one year are also used for the first half of the next year. The data collected in 1984 were also used for the first part of 1984. During the second half of 1985 the sampling in the southern part of the Barents Sea (areas II+IV and III+V) was rather poor. Because of the large seasonal changes in the diet in these areas (Mehl, 1986a), the data collected for the second part of 1984 in the same areas were used. But the content of deep-sea shrimp was reduced to the same level (by percentage) as in area VI+VII during the second part of 1985, because of the all-over reduction of the shrimp stock from 1984 to 1985 (Tveranger and Øynes, 1985).

The number in each age group in the Northeast Arctic cod stock by season and year is based on Anon. (1986a). For the different seasons, the number in the middle of the season is used. This is found by reducing the number at the beginning of the year, using one fourth of the yearly natural and fishing mortality for each quarter. For age groups 1 and 2, the number at the beginning of the year is found by back-calculating the estimates used in the prognosis (Anon., 1986a), using natural mortality (M) = 0.2. Number by age group, season, and year is given in Table 1.

The allocation of individuals of each age group over area and season in the different years is based on acoustic survey data (Hylen *et al.*, 1986; Godø *et al.*, 1987) and data given by Raknes and Nakken (1984).

The ratio between areas II+IV and III+V is assumed to be the same as in 1986 for all three years. Table 2 presents the data used.

The consumption of different prey size groups was then estimated. For capelin, herring, cod, and haddock the amount consumed of each size group per season was converted to the amount consumed of each age group, using data on mean weight and age composition within each fish prey size group in the season in question

Table 1. Millions of individuals of each age group by season and year for the Northeast Arctic cod stock in 1984–1986 (from Anon., 1986a). W–S = winter/spring; S–A = summer/autumn.

Season	Age group						
	1	2	3	4	5	6	7+
				1984			
W–S	2 127	785	285	123	71	51	40
S–A	1 925	710	254	105	56	37	23
				1985			
W–S	1 134	1 742	639	218	84	40	37
S–A	1 026	1 576	569	178	63	26	25
				1986			
W–S	1 560	929	1 416	486	139	45	32
S–A	1 412	840	1 262	398	105	30	22

Table 2. Proportion of individuals by age group, area, season, and year for the Northeast Arctic cod stock in 1984–1986.

Area	Season	Age group						
		1	2	3	4	5	6	7+
					1984			
II+IV	W–S	0.000	0.000	0.062	0.358	0.662	0.906	0.962
	S–A	0.000	0.000	0.062	0.358	0.623	0.883	0.924
III+V	W–S	0.979	0.922	0.907	0.592	0.299	0.071	0.000
	S–A	0.979	0.922	0.907	0.592	0.299	0.071	0.000
VI+VII	W–S	0.021	0.078	0.031	0.050	0.039	0.023	0.038
	S–A	0.021	0.078	0.031	0.050	0.078	0.046	0.076
					1985			
II+IV	W–S	0.000	0.000	0.057	0.288	0.664	0.840	0.923
	S–A	0.000	0.000	0.057	0.288	0.631	0.737	0.847
III+V	W–S	0.654	0.917	0.854	0.479	0.302	0.050	0.000
	S–A	0.654	0.917	0.854	0.479	0.302	0.050	0.000
VI+VII	W–S	0.346	0.082	0.087	0.233	0.033	0.102	0.077
	S–A	0.346	0.082	0.087	0.233	0.066	0.204	0.153
					1986			
II+IV	W–S	0.000	0.000	0.057	0.332	0.660	0.883	0.848
	S–A	0.000	0.000	0.057	0.332	0.615	0.833	0.600
III+V	W–S	0.991	0.868	0.846	0.550	0.295	0.033	0.000
	S–A	0.991	0.868	0.846	0.550	0.295	0.033	0.000
VI+VII	W–S	0.009	0.132	0.096	0.119	0.045	0.050	0.152
	S–A	0.009	0.132	0.096	0.119	0.090	0.100	0.400

(Anon., 1985, 1986b, 1987b, and unpubl. data). The numbers consumed of each age group were also calculated, and the results have been compared with the different prey stock sizes.

When the feeding model based on Santos' data is used, only the total yearly consumption of the different prey species is estimated.

Results

1. Total consumption

Table 3 summarizes the cod stock's consumption of the main prey species for the different years. Capelin and deep-sea shrimp were the most important prey species during the period. Redfish was the second most important fish prey, followed by herring. Young cod (cannibalism) and haddock contributed less than 5% (by weight) to the total consumption in all three years.

The group "others" increased its importance through the period, and in 1986 made up almost 50% of the total consumption. The most important species in this group were Norway pout (*Trisopterus esmarkii*), polar cod (*Boreogadus saida*), blue whiting (*Micromesistius poutassou*), young long rough dab (*Hippoglossoides platessoides*), amphipods (Hyperiidae), and krill (*Euphausiacea*).

The cod stock's total consumption was highest in 1985, both in tonnes and relative to the biomass of the

Table 3. The Northeast Arctic cod stock's consumption in 1000 tonnes of commercially exploited prey species in 1984–1986.

Prey species	1984		1985		1986	
	Consump.	%	Consump.	%	Consump.	%
Deep-sea shrimp	676	30	320	8	269	7
Capelin	573	25	1 814	44	856	22
Herring	113	5	345	8	215	6
Redfish	299	13	209	5	339	9
Cod	13	1	38	1	112	3
Haddock	68	3	75	2	163	4
"Others"	533	23	1 320	32	1 860	49
Total	2 275	100	4 121	100	3 814	100
Consumption/ cod biomass, 1 Jan.	2.2		2.7		1.9	

Table 4. The Northeast Arctic cod stock's consumption in 1000 tonnes of commercially exploited prey species in 1984–1986, using an alternative feeding model.

Prey species	1984		1985		1986	
	Consump.	%	Consump.	%	Consump.	%
Deep-sea shrimp	939	25	475	7	514	6
Capelin	1 392	38	4 149	56	2 042	25
Herring	113	3	352	5	305	4
Redfish	448	12	293	4	584	7
Cod	33	1	97	1	294	4
Haddock	61	2	71	1	295	4
"Others"	723	19	1 936	26	4 116	50
Total	3 709	100	7 373	100	8 150	100
Consumption/ cod biomass, 1 Jan.	3.6		4.7		4.0	

cod stock at the beginning of the year. In 1986 the relative consumption was about 30 % lower than in the previous year, and only 1.9 times the biomass of the cod stock.

For comparative purposes, estimates of the yearly consumption of the different species based on a feeding model using Santos' data have been made. The results are presented in Table 4. This model gives a total yearly consumption 1.6–2.1 times higher than the other model. The species differences are greatest for capelin

Table 5. The Northeast Arctic cod stock's consumption in 1000 tonnes of different size groups of commercially exploited prey species in 1984–1986.

Prey species	Prey size group (cm)					Sum
	0–4	5–9	10–14	15–19	20–30	
			1984			
Deep-sea shrimp	82	502	93	–	–	677
Capelin	2	109	416	46	–	573
Herring	–	43	68	2	–	113
Redfish	20	222	31	10	16	299
Cod	–	–	+	3	10	13
Haddock	–	–	61	6	1	68
Sum	104	876	669	67	27	1 743
%	6	50	38	4	2	100
			1985			
Deep-sea shrimp	15	263	42	–	–	320
Capelin	–	97	1 038	679	–	1 814
Herring	–	104	222	19	–	345
Redfish	19	105	67	4	14	209
Cod	1	3	1	2	31	38
Haddock	–	–	67	82	+	75
Sum	35	572	1 437	712	45	2 801
%	1	21	51	25	2	100
			1986			
Deep-sea shrimp	18	193	58	–	–	269
Capelin	–	9	715	132	–	856
Herring	–	6	96	87	26	215
Redfish	36	125	86	92	–	339
Cod	–	4	6	3	99	112
Haddock	–	–	15	10	138	163
Sum	54	337	976	324	263	1 954
%	3	17	50	17	13	100

and young cod, and the consumption of these species has increased 2–3 times.

2. Prey size preference

Table 5 shows the cod stock's consumption of different size groups of the six prey species. In all three years, more than 80 % (by weight) of the amount consumed of the six species was in the size range 5–19 cm. The dominating size group of deep-sea shrimp was 5–9 cm (total body length, excluding claws), of capelin 10–14 cm, of herring 10–14 cm, of redfish 5–9 cm, and of young cod 20–29 cm. For haddock, the dominating size group was 10–14 cm in 1984–1985 and 20–29 cm in 1986.

3. Consumption of commercially exploited prey species

3.1. Capelin

The cod stock's consumption of different age groups of capelin is presented in Table 6. Most of this consumption takes place during the first half of the year, on average about 90 % measured both in biomass and numbers consumed. During the three-year period the consumption was highest in 1985, when it exceeded 1.8 million tonnes and made up almost 70 % of the cod's total consumption for the first half of the year and 44 % on average for the year. In 1986 capelin contributed only 22 % (by weight) to the cod stock's consumption. Age groups 2–4 were dominant, and measured in tonnes, age group 3 was most heavily preyed on in all three years. Measured in numbers consumed, age group 2 dominated in 1984, while age group 3 dominated in 1985–1986.

3.2. Herring

Table 7 shows the cod's consumption of different age groups of herring in the period. Herring began to make up an increasing part of the cod stock's consumption during the second part of 1984. The consumption was highest in 1985, with almost 350 000 tonnes and 8 % of the total consumption. During the second part of 1986 the consumption of herring was reduced to only 3 % of

Table 6. The Northeast Arctic cod stock's consumption of different age groups of capelin in tonnes × 10^{-3} and numbers × 10^{-9} by season in 1984–1986, compared with the biomass and numbers at age of capelin.

Age group	Biomass consumed				% of biomass[a]	Numbers consumed				% of stock[b]
	W–S	S–A	Sum	%		W–S	S–A	Sum	%	
					1984					
Eggs	2	–	2	+	–	–	–	–	–	–
1	2	34	36	6	–	2	11	13	13	–
2	110	36	146	26	9	47	5	53	52	14
3	203	8	211	37	11	20	1	21	21	14
4	177	+	177	31	25	14	+	14	14	61
5	1	–	1	+	15	+	–	+	+	–
Sum	495	78	573	100		83	18	101	100	
%	86	14	100			82	18	100		
% of total cons.	45	7	25							
					1985					
1	8	77	78	4	–	1	21	22	8	–
2	294	80	374	21	70	88	11	99	37	38
3	923	37	960	53	68	116	3	119	45	86
4	401	1	402	22	45	27	+	27	10	84
Sum	1 619	195	1 814	100		232	35	268	100	
%	89	11	100			87	13	100		
% of total cons.	69	11	44							
					1986					
1	5	24	29	3	–	5	5	10	9	–
2	145	23	168	20	98	33	2	35	32	91
3	364	15	379	44	95	42	1	43	39	91
4	262	+	262	31	87	21	+	21	19	101
5	18	–	18	2	123	1	–	1	1	117
Sum	794	62	856	100		102	8	110	100	
%	93	7	100			92	8	100		
% of total cons.	48	3	22							

[a] Biomass of the stock measured in September of the previous year (Anon., 1984b; Anon., 1985; Anon., 1986b).
[b] Numbers in the stock estimated 1 January (Anon., 1987b).

Table 7. The Northeast Arctic cod stock's consumption of different age groups of herring in tonnes × 10^{-3} and numbers × 10^{-9} by season in 1984–1986, compared with the numbers at age of herring.

Age group	Biomass consumed				Numbers consumed				% of stock
	W–S	S–A	Sum	%	W–S	S–A	Sum	%	
				1984					
0	–	46	46	41	–	12	12	63	192[a]
1	11	55	66	58	3	4	7	36	16[b]
2	1	–	1	1	+	–	+	+	3[c]
Sum	12	101	113	100	3	16	19	99	
%	11	89	100		16	84	100		
% of total cons.	1	9	5						
				1985					
0	–	207	207	60	–	35	35	70	85[d]
1	50	+	50	14	10	+	10	20	154[e]
2	88	+	88	26	5	+	5	10	13[f]
Sum	138	207	345	100	15	35	50	100	
%	40	60	100		30	70	100		
% of total cons.	6	12	8						
				1986					
1	60	57	117	55	7	3	10	77	–
2	12	4	16	7	1	+	1	8	–
3	82	–	82	38	2	–	2	15	12[g]
Sum	154	61	215	100	10	3	13	100	
%	72	28	100		77	23	100		
% of total cons.	9	3	6						

[a] Estimated November 1984 (Anon., 1986b).
[b] Estimated June 1984 (Anon., 1986b).
[c] VPA 1986 (Anon., 1987b).
[d] Estimated September 1985 (Anon., 1986b).
[e] Estimated November 1984 (Anon., 1986b).
[f] Estimated May 1985 (Anon., 1986b).
[g] Estimated January 1986 (Anon., 1987b).

the total consumption. The predation was on age groups 0–3. Measured in biomass (tonnes) consumed, age groups 0 and 1 were the most important in 1984, age group 0 (and 2) in 1985, and age groups 1 and 3 in 1986. Measured in numbers consumed, age group 0 dominated in 1984–1985 and age group 1 in 1986.

3.3. Young cod

In Table 8 the cod's consumption of cod (cannibalism) is summarized. As a percentage of the total consumption, young cod was not very important during the period, contributing only 3 % at the highest in 1986. The predation was on age groups 0–3, and measured in tonnes consumed, age group 1 dominated in 1984, age group 2 in 1985, and age groups 2–3 in 1986. Measured in numbers consumed, the 1-group dominated in 1984, the 0-group in 1985, and the 1- (and 2-) groups in 1986.

3.4. Haddock

The next table (9) shows the consumption of young haddock. The amount consumed was higher than that of young cod in all three years, and highest in 1986, when haddock made up 7 % of the total consumption during the second part of the year. In all years the consumption was highest during the second half of the year. Age groups 0–3 were preyed on, and measured in biomass consumed, age group 0 dominated in 1984, age groups 0 and 1 in 1985, and age group 2 in 1986. Measured in numbers consumed, the 0-group was most important in 1984, the 0- and 1-groups in 1985, and the 1- and 2-groups in 1986.

3.5. Redfish

Table 10 presents the cod stock's consumption of different size groups of redfish in the period. Owing to lack of data, it has not been possible to convert the consumption data on redfish into age groups and numbers consumed. Measured in biomass consumed, the consumption was highest in 1986. The relative consumption was highest in 1984, when redfish made up 17 % of the total consumption during the first part of the year. Redfish of 0–24 cm were preyed on. In all three years size group 5–9 cm was dominant during the first part of the year and was also the most important for the total year.

Table 8. The Northeast Arctic cod stock's consumption of different age groups of young cod in tonnes × 10^{-3} and numbers × 10^{-6} by season in 1984–1986, compared with the numbers at age of young cod.

Age group	Biomass consumed				Numbers consumed				% of stock	
	W–S	S–A	Sum	%	W–S	S–A	Sum	%	VPA[a]	Aco.[b]
				1984						
1	1	10	11	85	42	108	150	88	7	6
2	1	1	2	15	6	13	19	11	2	4
3	+	+	+	+	+	+	+	+	+	+
Sum	2	11	13	100	48	121	169	99		
%	15	85	100		28	72	100			
% of total cons.	+	1	<1							
				1985						
0	–	3	3	8	–	2 506	2 506	83	–	–
1	1	5	6	16	205	125	330	11	28	64
2	15	11	26	68	117	41	158	5	9	11
3	3	–	3	8	8	–	8	+	1	1
Sum	19	19	38	100	330	2 672	3 002	99		
%	50	50	100		11	89	100			
% of total cons.	1	1	1							
				1986						
0	–	0.2	0.2	+	–	85	85	6	–	–
1	5	7	12	11	289	344	623	47	38	84
2	25	23	48	43	229	158	387	29	40	58
3	16	36	52	46	99	137	236	18	16	16
Sum	46	66	112	100	617	714	1 331	100		
%	41	59	100		46	54	100			
% of total cons.	3	3	3							

[a] VPA 1986 and back-calculation of the prognosis estimates (Anon., 1986a).
[b] Estimates of year-class abundance from acoustic surveys (Hylen *et al.*, 1986).

During the second part of the year, size group 0–4 cm and size groups > 10 cm became more important; in 1985 size group 10–14 cm dominated, and in 1986 size group 15–19 cm.

3.6. Deep-sea shrimp

The last table (11) gives the consumption data for deep-sea shrimp. The consumption of shrimp was highest in 1984. About 675 000 tonnes were consumed, and during the second part of the year shrimp contributed 36 % to the total consumption and 30 % on average for the year. In 1985 this percentage dropped below 10, and in 1986 the consumption of shrimp was less than 270 000 tonnes and only 7 % of the total consumption. In all three years size group 5–9 cm was the most important (72–82 %), during both the first and second parts of the year.

Discussion

The annual food consumption of the Northeast Arctic cod stock during the period 1984–1986 varied in species composition, average prey size, and amount consumed, and it had a great impact on some commercially exploited prey species.

In 1984 deep-sea shrimp was the most important prey species. The amount consumed was 143 % of the biomass estimated during the shrimp surveys in 1984, but it should be noted that not all of the Barents Sea is covered during those surveys and that the estimates are only based on what was caught by bottom trawl. There is also evidence for shrimp being evacuated at a slower rate than, e.g., capelin (J. Santos, pers. comm.). This would at least alter the rations of consumed shrimp and capelin, and possibly lower the total consumption of shrimp. Capelin was the second most important prey, and in numbers cod consumed most of age group 2 and in tonnes most of age group 3, which reflects the stock composition during the acoustic cruise the previous autumn (Anon., 1984b). During the first part of the year there was also a high consumption of young redfish, and the recruitment indices for redfish were among the highest observed during the period 1979–1986 (Anon., 1987c). During the second part of 1984 there was an

increase of herring in the amount consumed. By weight most of this was of the relatively strong 1983 year class, but in numbers the 0-group dominated, and the total consumption was 192 % of the number estimated in the acoustic survey in November. The 1984 year class came out with a fairly high index in the 0-group survey (Anon., 1986b), and the same report assumes that the later disappearance of this year class was caused by predation, which the present results support. Young haddock contributed only 3 % to the total consumption, but a relatively high number of 0- and 1-groups were consumed compared with the stock estimates. However, it should be noted that the numbers-at-age estimates for young cod and haddock are uncertain and normally too low. Also, the use of prey-weight percentages in the model for estimating the consumption overemphasizes the importance of large single prey eaten by few individuals, distributing their weight over the whole predator population, e.g., haddock, herring, and young cod.

From 1984 to 1985 the consumption of shrimp was reduced by more than 50 %, and so were the biomass estimates (Tveranger and Øynes, 1985). However, the consumption of capelin was more than three times higher in 1985 than in 1984. One reason for this is that a much higher proportion of the cod stock was large enough to eat capelin. There may also have been a greater overlap between the two stocks at the time of sampling during the first part of the year, resulting in a higher stomach content of capelin. In the present model the consumption is proportional to the average stomach content. J. Santos (pers. comm.) has found that large meals are evacuated at a slower rate than small meals, and Bromley (1987, 1988) found that gastric evacuation is constant and independent of the level of stomach content. Both these findings would reduce the difference between the consumption of capelin in 1984 and 1985. Age group 3 of capelin was the most important, both in tonnes and numbers consumed, as in the stock-abundance estimates of the previous autumn (Anon., 1985). In 1985 the cod's consumption influenced the capelin stock more drastically, and about 85 % of the estimated number of 3- and 4-groups was consumed during the year. The consumption of herring also in-

Table 9. The Northeast Arctic cod stock's consumption of different age groups of haddock in tonnes $\times 10^{-3}$ and numbers $\times 10^{-6}$ by season in 1984–1986, compared with the numbers at age of haddock.

Age group	Biomass consumed				Numbers consumed				% of stock	
	W–S	S–A	Sum	%	W–S	S–A	Sum	%	VPA[a]	Aco.[b]
				1984						
0	–	45	45	66	–	3 245	3 245	74	–	–
1	11	11	22	32	587	516	1 103	25	105	51
2	1	+	1	1	11	+	11	+	2	1
3	–	+	+	+	–	+	+	+	+	+
Sum	12	56	68	99	598	3 761	4 358	99		
%	18	82	100		14	86	100			
% of total cons.	1	5	3							
				1985						
0	–	41	41	54	–	2 936	2 936	60	–	–
1	21	13	34	45	1 350	614	1 964	40	659	190
2	0.4	+	0.4	1	10	+	10	+	1	1
Sum	21	54	75	100	1 360	3 550	4 910	100		
%	28	72	100		28	72	100			
% of total cons.	1	3	2							
				1986						
0	–	2	2	1	–	125	125	6	–	–
1	20	2	22	14	968	968	1 007	53	676	278
2	2	96	98	60	44	584	628	33	257	111
3	0.1	41	41	25	3	143	146	8	21	7
Sum	22	141	163	100	1 015	891	1 906	100		
%	13	87	100		53	47	100			
% of total cons.	1	7	4							

[a] VPA 1986 and back-calculation of the prognosis estimates (Anon., 1986b).
[b] Estimates of year-class abundance from acoustic surveys (Hylen *et al.*, 1986).

Table 10. The Northeast Arctic cod stock's consumption of different size groups of redfish in tonnes × 10^{-3} by season in 1984–1986.

Prey size	Winter/ spring	Summer/ autumn	Sum	%
		1984		
0– 4 cm ...	13	7	20	7
5– 9 cm ...	171	52	223	75
10–14 cm ...	4	27	31	10
15–19 cm ...	4	5	9	3
20–24 cm ...	–	16	16	5
Sum	193	106	299	100
%	65	35	100	
% of total cons.....	17	9	13	
		1985		
0– 4 cm ...	1	18	19	9
5– 9 cm ...	31	74	105	50
10–14 cm ...	6	61	67	32
15–19 cm ...	1	3	4	2
20–24 cm ...	–	14	14	7
Sum	39	170	209	100
%	19	81	100	
% of total cons.	2	9	5	
		1986		
0– 4 cm ...	11	24	35	11
5– 9 cm ...	108	18	126	37
10–14 cm ...	51	35	86	25
15–19 cm ...	27	65	92	27
Sum	197	142	339	100
%	58	42	100	
% of total cons.	12	7	9	

Table 11. The Northeast Arctic cod stock's consumption of different size groups of deep-sea shrimp in tonnes × 10^{-3} by season in 1984–1986, compared with the estimated biomass of shrimps.

Prey size	Winter/ spring	Summer/ autumn	Sum	%	% of biom.[a]
		1984			
0– 4 cm .	42	40	82	12	
5– 9 cm .	161	340	501	74	
10–14 cm .	53	40	93	14	
Sum	256	420	676	100	143
%	38	62	100		
% of total cons.	23	36	30		
		1985			
0– 4 cm .	14	2	16	5	
5– 9 cm .	196	67	263	82	
10–14 cm .	27	14	41	13	
Sum	237	83	320	100	127
%	74	26	100		
% of total cons.	10	5	8		
		1986			
0– 4 cm .	4	15	19	7	
5– 9 cm .	70	122	192	71	
10–14 cm .	32	26	58	22	
Sum	106	163	269	100	148
%	39	61	100		
% of total cons.	6	8	7		

[a] Biomass estimated by bottom trawl in the main shrimp area (Hylen *et al.*, 1984; Tveranger and Øynes, 1985; Hylen and Øynes, 1986).

creased by three times from 1984 to 1985, and again the 1984 year class of herring was most seriously affected, with 154 % of the estimate from the previous autumn being consumed. But both in tonnes and numbers most of the consumption was of the the 0-group: 85 % of the estimated number in the acoustic 0-group survey. Results from the international survey in the autumn of 1986 indicated a severe reduction of the 1985 year class of herring (Anon., 1987b). As in 1984, the consumption of 1-group haddock was extremely high compared with the estimated numbers in the stock. The consumption of young cod showed an increasing tendency.

In 1986 there was a further decrease in the consumption of shrimp, and the estimated shrimp biomass decreased by more than 30 % (Hylen and Øynes, 1986). The consumption of capelin was more than halved, but cod still consumed an increasing part of the remaining capelin stock (almost 100 % of what was estimated to be left of age groups 2, 3, 4, and 5, measured both in biomass during the previous autumn and in numbers at the beginning of the year). However, when consumption is compared with the biomass of the capelin stock, it should be noted that the biomass is estimated at a given moment only. The capelin stock's production during the year is also available for consumption. Again age group 3 was dominant, as in the stock (Anon., 1986b). At the end of 1986 the capelin stock was seriously depleted (Anon., 1987b). The consumption of herring was about 60 % of that in 1985, and age group 1 was dominant. During the first part of the year the 1983 year class contributed most by weight, but during the second part of 1986 there was no predation on this herring year class because it had migrated out of the Barents Sea (Røttingen, 1987). The consumption of young cod was almost three times higher in 1986 than in 1985, and compared with the numbers at age, the predation pressure on the 1- and 2-groups was considerable. The consumption of young haddock was more than doubled, and the numbers consumed of, especially, the 1-group, but also the 2-group, were extremely high compared with the estimated numbers in the stock. The consumption of redfish was about 50 % higher than in 1985, and most of this increase came from a higher contribution from size groups 10–14 and 15–19 cm.

In 1984 and 1985 the cod stock's total consumption was 2.2–2.7 times the biomass of the cod stock at the beginning of the year and consisted mainly of capelin, deep-sea shrimp, herring, and redfish. By the end of 1986 the stock size of capelin in the Barents Sea was seriously depleted because of fishing and predation; the stock size of deep-sea shrimp was severely reduced because of predation, fishing, and poor recruitment; and herring was almost absent because of predation and migration. Therefore the cod stock's total consumption dropped below two times the stock biomass in 1986. This occurred in spite of the fact that cod consumed an increasing amount of redfish, young cod, and haddock and a broader variety of other prey species. The lack of enough suitable prey species has changed migratory patterns and reduced growth in the Northeast Arctic cod stock during recent years (Godø *et al.*, 1987).

The estimated annual consumption of capelin in 1984–1986, about 0.4 to 1.2 times the biomass of the cod stock, is somewhat lower than that estimated by Ponomarenko and Ponomarenko (1975) and Ponomarenko *et al.* (1978). The latter found that the cod stock consumed 2.4–2.7 times its own biomass of capelin. Both studies applied another feeding model (the diurnal coefficient found by Novikova (1962)), which gives a higher consumption. Besides that, in the middle of the 1970s the capelin stock was several times higher than in 1984–1986 (Anon., 1986b). Lilly (1984) found that in times of low capelin abundance the total quantity of food consumed is lower. Ponomarenko and Yaragina (1978) found a considerable similarity between the curves of the calculated capelin biomass and its frequency in cod, and Magnússon and Pálsson (1989) suggest low predation rates at low capelin stock levels. Lilly (1987) reviews studies where it is estimated that the consumption of capelin per unit biomass of cod ranged from 0.8 to 2.4 annually. The results of the present investigation are at the lower end of this range.

The estimated total annual consumption of about 2.5 times the biomass of the cod stock is, however, lower than that found in the studies mentioned in the Introduction, and not high enough to explain the growth of the cod stock in 1984–1985. When the alternative feeding model based on Santos' data is used, the total annual consumption is about four times the biomass of the cod stock, or on average 1.1 % of an individual cod's bodyweight per day. This is in better accordance with the growth estimates as well as with the results of the studies cited. Laevastu and Larkins (1981) report annual food consumption of three to four times the mean biomass per year for different fish stocks. When the first model is run without any temperature correlation for the digestion coefficient, the consumption estimates are at the same level as when the alternative model is used. It is therefore probably not valid to transfer a temperature relationship from the North Sea to the Barents Sea. Compared with the model using data from the North Sea, the alternative gives a relatively higher consumption of prey species that are evacuated quickly and of prey species that are consumed by older cod. This is because the other model uses the same evacuation rate for different prey species and a slower rate for the older predators, while the alternative model has different evacuation rates for different prey species but the same rates for different predator age groups. This results in a relatively higher consumption of capelin and young cod in all three years and a relatively higher total consumption during the last year because of an older age structure in the cod stock. Still, there is a decrease in total yearly consumption relative to the biomass of the cod stock from 1985 to 1986.

Assuming that the number of cod in each age group is correct, some of the prey-species year classes would have been even more overconsumed, using the alternative feeding model. But subsequent results show that some year classes of cod have probably been overestimated lately (Godø *et al.*, 1987). Because of sampling error, the number- (and biomass-) at-age estimates of both predator and prey species, as well as the estimate of quantity consumed, should be regarded more as indices than as absolute data. The consumption estimates are perhaps the least reliable because they involve a number of uncertain factors. Unfortunately, no error estimate has yet been made in connection with the consumption estimates. But there is no doubt that the Northeast Arctic cod stock has had a great impact on some of the commercially exploited prey species in 1984–1986, and some year classes may have been severely reduced by this consumption, apart from the remaining cod stock having its resources seriously reduced. These problems will probably be better understood when a multispecies model taking all essential factors into account is in operation.

References

Anon. 1980. Report of the *ad hoc* Working Group on Multispecies Assessment Model Testing. ICES CM 1980/G: 2.

Anon. 1981. Draft manual for the Stomach Sampling Project. Netherlands Institute for Fishery Investigations, IJmuiden. 43 pp.

Anon. 1984a. Report of the meeting of the coordinators of the Stomach Sampling Project 1981. ICES CM 1984/G: 37.

Anon. 1984b. Atlanto-Scandian Herring and Capelin Working Group Report. ICES CM 1984/Assess: 4.

Anon. 1985. Report of the Atlanto-Scandian Herring and Capelin Working Group. ICES CM 1985/Assess: 4.

Anon. 1986a. ACFM 1986 working document. North-East Arctic cod and haddock fishing mortalities–VPA and projection of catch and biomass. Unpubl.

Anon. 1986b. Report of the Atlanto-Scandian Herring and Capelin Working Group. ICES CM 1986/Assess: 7.

Anon. 1987a. Report of the *ad hoc* Multispecies Assessment Working Group. ICES CM 1987/Assess: 9.

Anon. 1987b. Report of the Working Group on Atlanto-Scandian Herring and Capelin. ICES CM 1987/Assess: 8.

Anon. 1987c. Report of the Arctic Fisheries Working Group. ICES CM 1987/Assess: 5.

Bagge, O. 1981. The yearly consumption of cod in the Baltic and Kattegat as estimated from stomach content. ICES CM 1981/J: 27.

Bromley, P. J. 1987. The effects of food type, meal size and body weight on digestion and gastric evacuation in turbot, *Scophthalmus maximus* L. J. Fish. Biol., 30: 501–512.
Bromley, P. J. 1988. Gastric digestion and evacuation in whiting (*Merlangius merlangus*). J. Fish. Biol. (In press).
Cohen, E., and Grosslein, M. 1981. Food consumption in five species of fish on Georges Bank. ICES CM 1981/G: 68.
Daan, N. 1973. A quantitative analysis of the food intake of North Sea cod, *Gadus morhua*. Neth. J. Sea Res., 6(4): 479–517.
Daan, N. 1975. Consumption and production in North Sea cod, *Gadus morhua*: an assessment of the ecological status of the stock. Neth. J. Sea Res., 9 (1): 24–55.
Daan, N. 1983. Analysis of the cod samples collected during the 1981 Stomach Sampling Project. ICES CM 1983/G: 61.
Godø, O. R., Hylen, A., Jacobsen, J. A., Jakobsen, T., Mehl, S., Nedreås, K., and Sunnanå, K. 1987. Estimates of stock size of northeast Arctic cod and haddock from survey data 1986/1987. ICES CM 1987/G: 37.
Hylen, A., Jakobsen, T., Nakken, O., Nedreås, K., and Sunnanå, K. 1986. Preliminary report of the Norwegian investigations on young cod and haddock in the Barents Sea. ICES CM 1986/G: 76.
Hylen, A., Tveranger, B., and Øynes, P. 1984. Norwegian investigations on the deep sea shrimp (*Pandalus borealis*) in the Barents Sea in April–May 1984 and in the Spitsbergen area in July–August 1984. ICES CM 1984/K: 21.
Hylen, A., and Øynes, P. 1986. Results of stratified trawl surveys for shrimps (*Pandalus borealis*) in the Barents Sea and the Svalbard region in 1986. ICES CM 1986/K: 34.
Jones, R. 1978. Estimates of the food consumption of haddock (*Melanogrammus aeglefinus*) and cod (*Gadus morhua*). J. Cons. int. Explor. Mer, 38: 18–27.
Laevastu, T., and Larkins, H. A. 1981. Marine fisheries ecosystem. Its quantitative evaluation and management. Fishing News Books Ltd., Farnham. 161 pp.
Lilly, G. R. 1984. Predation by Atlantic cod on shrimp and crabs off northeastern Newfoundland in autumn of 1977–1982. ICES CM 1984/G: 53.
Lilly, G. R. 1987. Interaction between Atlantic cod (*Gadus morhua*) and capelin (*Mallotus villosus*) off Labrador and eastern Newfoundland: a review. Can. Tech. Rep. Fish. aquat. Sci., No. 1567. 37 pp.
Magnússon, K. G., and Pálsson, Ó. K. 1988. Trophic ecological relationships of Icelandic cod. This volume, pp. 206–224.
Mehl, S. 1986a. Stomach contents of North-East Arctic cod and possible changes in the diet the last years. ICES CM 1986/G: 29.
Mehl, S. 1986b. Revised and modified programs for storing, analysis and presentation of taxonomic and quantitative stomach contents data. Internal report no. BN 8601, Institute of Marine Research, Bergen. 62 pp.
Mehl, S., and Westgård, T. 1983. The diet and consumption of mackerel in the North Sea. (A preliminary report). ICES CM 1983/H: 34.
Minet, J. P., and Perodou, J. B. 1978. Predation of cod, *Gadus morhua,* on capelin, *Mallotus villosus,* off eastern Newfoundland and in the Gulf of St. Lawrence. ICNAF Res. Bull., No. 13: 11–20.
Novikova, N. S. 1962. Some data on the food rations of cod and haddock from the Barents Sea. Doklady Akademii Nauk SSSR, 146 (4): 960–962.
Ponomarenko, I. Y., and Yaragina, N. A. 1978. Year-to-year and seasonal fluctuations in the feeding of the Barents Sea cod on capelin in 1947–1976. ICES CM 1978/G: 24.
Ponomarenko, V. P., and Ponomarenko, I. Y. 1975. Consumption of the Barents Sea capelin by cod and haddock. ICES CM 1975/F: 10.
Ponomarenko, V. P., Ponomarenko, I. Y., and Yaragina, N. A. 1978. Consumption of the Barents Sea capelin by cod and haddock in 1974–1976. ICES CM 1978/G: 23.
Raknes, A., and Nakken, O. 1984. Geographical distribution (in percentage of numbers) throughout the year for each age group of cod in the Barents Sea. Unpubl.
Røttingen, I. 1987. Data on the 1983 year class of Norwegian spring spawning herring from the period June 1985 – August 1986. ICES CM 1987/H: 19.
Tveranger, B., and Øynes, P. 1985. Results of stratified trawl surveys for shrimps (*Pandalus borealis*) in the Barents Sea in May and in the Svalbard region in July–August 1985. ICES CM 1985/K: 50.
Waiwood, K., and Majkowski, J. 1984. Food consumption and diet composition of cod, *Gadus morhua,* inhabiting the southwestern Gulf of St. Lawrence. Env. Biol. Fish., 11: 63–78.
Westgård, T. 1982. Programs for handling and analyses of stomach contents data. ICES CM 1982/H: 21.

Appendix

Stomach content composition of commercially exploited prey species in weight percentage by predator age group, area, season, and year for Northeast Arctic cod in 1984–1986. W–S = winter/spring; S–A = summer/autumn.

Area: II+IV Season: W–S 1984

Prey species	Size group (cm)	Predator age group						
		1	2	3	4	5	6	7+
Deep-sea shrimp	0– 4	–	–	0.1	0.1	0.0	0.1	0.0
	5– 9	–	–	5.2	4.9	3.5	8.2	4.3
	10–14	–	–	0.0	0.4	1.4	1.4	1.8
Capelin	5– 9	–	–	2.8	5.4	9.8	7.3	5.1
	10–14	–	–	56.0	60.0	60.8	57.6	61.9
	15–19	–	–	17.8	8.0	7.4	16.2	6.1
Cod	10–14	–	–	1.7	0.0	0.0	0.0	0.0
Redfish	0– 4	–	–	0.0	0.0	0.2	0.5	0.2
	5– 9	–	–	13.5	20.7	13.7	8.1	20.5
	10–14	–	–	0.8	0.0	1.3	0.0	0.0
"Others"		–	–	1.9	0.0	1.8	0.4	0.2
Weight per stomach (g)		–	–	16.4	26.5	39.5	49.5	81.3
Number of stomachs analysed		–	–	55	67	64	53	14

Area: II+IV Season: S–A 1984

Prey species	Size group (cm)	Predator age group						
		1	2	3	4	5	6	7+
Deep-sea shrimp	0– 4	–	–	0.0	0.0	0.8	0.1	0.0
	5– 9	–	–	27.4	17.6	42.9	22.4	7.4
	10–14	–	–	1.7	6.3	5.9	8.7	5.0
Capelin	10–14	–	–	12.6	0.0	0.3	0.0	0.0
	15–19	–	–	0.0	0.0	2.3	0.0	0.0
Cod	20–30	–	–	0.0	0.0	10.4	0.0	11.1
Haddock	10–14	–	–	0.0	5.2	3.3	0.0	0.0
	15–19	–	–	0.0	0.0	0.0	5.6	0.0
Redfish	0– 4	–	–	1.6	0.0	0.0	0.0	0.0
	5– 9	–	–	5.3	1.7	12.0	1.3	0.0
	10–14	–	–	21.8	0.0	8.0	12.0	0.0
	15–19	–	–	0.0	0.0	0.0	14.3	0.0
	20–30	–	–	0.0	0.0	0.0	11.0	25.0
"Others"		–	–	29.6	69.1	14.1	25.2	51.1
Weight per stomach (g)		–	–	8.0	8.7	22.9	27.7	71.4
Number of stomachs analysed		–	–	83	60	77	47	16

Area: III+V Season: W–S 1984

Prey species	Size group (cm)	Predator age group						
		1	2	3	4	5	6	7+
Deep-sea shrimp	0– 4	17.7	1.8	5.3	1.5	1.4	0.2	–
	5– 9	0.0	20.2	30.4	25.7	25.3	22.9	–
	10–14	0.0	9.0	7.3	12.3	5.8	11.2	–
Capelin	0– 5	0.0	0.8	0.0	0.0	0.0	0.0	–
	5– 9	34.2	1.3	0.6	0.0	0.0	0.0	–
	10–14	0.0	37.4	18.7	19.3	11.7	3.5	–
	15–19	0.0	2.0	1.2	4.4	2.1	0.0	–
Herring	5– 9	4.9	0.0	0.0	0.0	0.0	0.0	–
Cod	10–14	0.0	0.0	0.0	0.0	0.4	0.0	–
	15–19	0.0	0.0	0.0	0.0	0.0	15.1	–
Haddock	10–14	0.0	0.0	1.6	5.3	1.6	4.5	–
	15–19	0.0	0.0	0.0	1.5	6.0	0.0	–
	20–30	0.0	0.0	0.0	0.0	5.4	0.0	–
Redfish	0– 4	2.9	1.3	1.4	1.7	1.1	6.8	–
	5– 9	2.4	16.0	24.8	23.4	34.1	27.7	–
	10–14	0.0	0.0	1.0	0.5	1.2	0.0	–
	15–19	0.0	0.0	2.1	0.0	0.0	0.0	–
"Others"		37.6	9.7	5.4	4.6	3.2	7.9	–
Weight per stomach (g)		0.3	3.3	8.6	16.9	22.7	26.7	–
Number of stomachs analysed		290	304	184	150	95	55	–

Area: III+V Season: S–A 1984

Prey species	Size group (cm)	Predator age group						
		1	2	3	4	5	6	7+
Deep-sea shrimp	0– 4	7.6	1.9	2.2	1.9	0.0	1.4	–
	5– 9	24.5	43.6	18.3	52.8	26.3	24.0	–
	10–14	0.0	5.7	3.5	1.4	9.0	7.5	–
Capelin	5– 9	0.0	4.6	3.2	1.7	0.0	0.0	–
	10–14	0.0	11.1	0.0	0.0	0.0	0.0	–
Herring	5– 9	0.0	7.8	4.4	0.0	0.0	0.0	–
	10–14	0.0	6.5	21.9	0.0	0.0	0.0	–
	15–19	0.0	0.0	0.0	2.6	0.0	0.0	–
Cod	15–19	0.0	0.0	0.0	0.0	14.2	0.0	–
	20–30	0.0	0.0	0.0	0.0	0.0	3.8	–
Haddock	10–14	9.5	4.1	0.0	0.0	0.0	0.0	–
	15–19	0.0	0.0	0.0	0.0	15.3	0.0	–
	20–30	0.0	0.0	0.0	0.0	0.0	3.6	–
Redfish	0– 4	0.0	1.4	0.4	5.3	0.0	0.0	–
	5– 9	3.4	6.1	1.3	10.5	1.1	0.7	–
	10–14	0.0	0.0	10.0	0.0	4.2	1.0	–
	20–30	0.0	0.0	0.0	0.0	0.0	11.3	–
"Others"		55.4	6.9	34.8	24.0	29.9	46.6	–
Weight per stomach (g)		0.9	4.8	9.4	8.7	20.1	38.9	–
Number of stomachs analysed		160	193	177	132	65	73	–

Area: VI+VII Season: W–S 1984

Prey species	Size group (cm)	Predator age group						
		1	2	3	4	5	6	7+
Deep-sea shrimp	0– 4	4.9	1.2	0.8	0.9	2.2	0.0	0.0
	5– 9	11.6	12.9	19.7	19.8	25.6	18.9	5.0
	10–14	0.0	1.2	4.4	3.1	10.5	13.4	0.7
Capelin	5– 9	15.0	5.4	0.0	2.3	2.0	0.3	0.6
	10–14	0.0	14.0	6.8	6.5	3.6	3.0	8.9
	15–19	0.0	0.0	0.0	3.5	0.0	1.6	0.0
Herring	10–14	0.0	4.6	4.1	7.2	16.7	12.8	0.0
	15–19	0.0	0.0	0.0	2.9	7.7	0.0	0.0
Cod	20–30	0.0	0.0	0.0	0.0	0.0	0.0	6.7
Haddock	10–14	0.0	1.4	8.8	1.4	0.0	0.0	0.0
Redfish	0– 4	0.6	0.0	0.0	0.0	0.0	0.0	0.0
	5– 9	0.0	4.4	11.5	22.8	9.3	24.1	0.3
	10–14	0.0	0.0	3.7	3.4	1.6	0.0	0.0
	15–19	0.0	0.0	0.0	0.0	5.7	0.0	2.4
"Others"		68.1	54.6	39.3	29.0	13.7	26.0	74.8
Weight per stomach (g)		1.2	7.1	10.8	22.0	39.0	60.7	164.6
Number of stomachs analysed		233	342	97	113	114	32	16

Area: VI+VII Season: S–A 1984

Prey species	Size group (cm)	Predator age group						
		1	2	3	4	5	6	7+
Deep-sea shrimp	0– 4	4.9	1.2	0.8	0.9	2.2	0.0	0.0
	5– 9	11.6	12.9	19.7	19.8	25.6	18.9	5.0
	10–14	0.0	1.2	4.4	3.1	10.5	13.4	0.7
Capelin	5– 9	15.0	5.4	0.0	2.3	2.0	0.3	0.6
	10–14	0.0	14.0	6.8	6.5	3.6	3.0	8.9
	15–19	0.0	0.0	0.0	3.5	0.0	1.6	0.0
Herring	10–14	0.0	4.6	4.1	7.2	16.7	12.8	0.0
	15–19	0.0	0.0	0.0	2.9	7.7	0.0	0.0
Cod	20–30	0.0	0.0	0.0	0.0	0.0	0.0	6.7
Haddock	10–14	0.0	1.4	8.8	1.4	0.0	0.0	0.0
Redfish	0– 4	0.6	0.0	0.0	0.0	0.0	0.0	0.0
	5– 9	0.0	4.4	11.5	22.8	9.3	24.1	0.3
	10–14	0.0	0.0	3.7	3.4	1.6	0.0	0.0
	15–19	0.0	0.0	0.0	0.0	5.7	0.0	2.4
"Others"		68.1	54.6	39.3	29.0	13.7	26.0	74.8
Weight per stomach (g)		1.2	7.1	10.8	22.0	39.0	60.7	164.6
Number of stomachs analysed		233	242	97	113	114	32	16

Area: II+IV Season: W–S 1985

Prey species	Size group (cm)	Predator age group						
		1	2	3	4	5	6	7+
Deep-sea shrimp	5– 9	–	–	2.2	0.1	9.1	0.2	0.1
	10–14	–	–	0.0	0.3	0.0	0.3	0.0
Capelin	5– 9	–	–	6.4	4.2	1.5	1.2	0.0
	10–14	–	–	32.9	54.1	36.6	70.8	50.4
	15–19	–	–	56.9	39.5	54.9	26.4	37.7
Herring	10–14	–	–	0.0	0.3	0.0	0.6	0.0
	15–19	–	–	0.0	0.7	0.0	0.0	0.6
Cod	20–30	–	–	0.0	0.0	0.0	0.0	10.8
Haddock	10–14	–	–	0.0	0.0	0.5	0.0	0.0
"Others"		–	–	1.5	0.7	1.3	0.5	0.3
Weight per stomach (g)		–	–	22.1	47.9	46.1	79.2	140.4
Number of stomachs analysed		–	–	163	164	97	70	58

Area: II+IV Season: S–A 1985

Prey species	Size group (cm)	Predator age group						
		1	2	3	4	5	6	7+
Deep-sea shrimp	0– 4	–	–	0.0	0.0	0.0	0.2	0.0
	5– 9	–	–	2.7	2.7	0.3	3.5	0.0
	10–14	–	–	2.3	2.2	2.3	0.0	1.5
Capelin	10–14	–	–	12.6	0.0	0.3	0.0	0.0
	15–19	–	–	0.0	0.0	2.3	0.0	0.0
Cod	20–30	–	–	0.0	0.0	10.4	0.0	11.1
Haddock	10–14	–	–	0.0	5.2	3.3	0.0	0.0
	15–19	–	–	0.0	0.0	0.0	5.6	0.0
Redfish	0– 4	–	–	1.6	0.0	0.0	0.0	0.0
	5– 9	–	–	5.3	1.7	12.0	1.3	0.0
	10–14	–	–	21.8	0.0	8.0	12.0	0.0
	15–19	–	–	0.0	0.0	0.0	14.3	0.0
	20–30	–	–	0.0	0.0	0.0	11.0	25.6
"Others"		–	–	53.7	88.4	61.6	52.7	62.0
Weight per stomach (g)		–	–	8.0	8.7	22.9	27.7	71.4
Number of stomachs analysed		–	–	83	60	77	47	16

Area: III+V Season: W–S 1985

Prey species	Size group (cm)	Predator age group						
		1	2	3	4	5	6	7+
Deep-sea shrimp	0– 4	0.0	1.2	0.0	0.0	0.0	0.0	–
	5– 9	0.0	14.8	5.9	6.7	11.9	4.0	–
	10–14	0.0	0.8	1.6	1.4	5.3	2.4	–
Capelin	5– 9	0.0	1.1	0.0	1.3	2.6	0.0	–
	10–14	0.0	45.0	39.9	41.6	34.5	0.0	–
	15–19	0.0	12.5	44.0	38.9	34.2	79.2	–
Herring	5– 9	0.0	4.6	0.2	0.0	0.0	0.0	–
	10–14	0.0	10.3	2.7	2.9	5.1	0.0	–
	15–19	0.0	0.0	1.7	1.8	0.0	4.7	–
Cod	5– 9	0.0	0.0	0.1	0.0	0.0	0.0	–
	20–30	0.0	0.0	0.0	0.6	0.0	0.0	–
Haddock	10–14	0.0	2.0	0.0	0.2	0.4	0.0	–
	15–19	0.0	0.0	0.3	0.0	1.0	2.3	–
Redfish	5 –9	0.0	0.4	0.1	1.1	0.6	0.4	–
	10–14	0.0	0.0	0.0	1.3	1.6	0.0	–
"Others"		100.0	7.1	3.1	1.8	2.7	7.1	–
Weight per stomach (g)		0.3	2.9	15.7	30.2	38.9	74.6	–
Number of stomachs analysed		42	525	396	341	136	48	–

Area: III+V Season: S–A 1985

Prey species	Size group (cm)	Predator age group						
		1	2	3	4	5	6	7+
Deep-sea shrimp	0– 4	0.0	0.2	0.0	0.0	0.0	0.0	–
	5– 9	0.0	5.9	2.7	2.7	0.3	3.5	–
	10–14	0.0	0.0	2.3	2.2	2.3	0.0	–
Capelin	5– 9	0.0	4.6	3.2	1.7	0.0	0.0	–
	10–14	0.0	11.1	0.0	0.0	0.0	0.0	–
Herring	5– 9	0.0	7.8	4.4	0.0	0.0	0.0	–
	10–14	0.0	6.5	21.9	0.0	0.0	0.0	–
	15–19	0.0	0.0	0.0	2.6	0.0	0.0	–
Cod	15–19	0.0	0.0	0.0	0.0	14.2	0.0	–
	20–30	0.0	0.0	0.0	0.0	0.0	3.8	–
Haddock	10–14	9.5	4.1	0.0	0.0	0.0	0.0	–
	15–19	0.0	0.0	0.0	0.0	15.3	0.0	–
	20–30	0.0	0.0	0.0	0.0	0.0	3.6	–
Redfish	0– 4	0.0	1.4	0.4	5.3	0.0	0.0	–
	5– 9	3.4	6.1	1.3	10.5	1.1	0.7	–
	10–14	0.0	0.0	10.0	0.0	4.2	1.0	–
	20–30	0.0	0.0	0.0	0.0	0.0	11.3	–
"Others"		87.6	52.9	53.8	75.2	62.6	75.8	–
Weight per stomach (g)		0.9	4.8	9.4	8.7	20.1	38.9	–
Number of stomachs analysed		160	193	177	132	65	73	–

Area: VI+VIII Season: W–S 1985

Prey species	Size group (cm)	Predator age group						
		1	2	3	4	5	6	7+
Deep-sea shrimp	0– 4	4.9	1.2	0.8	0.9	2.2	0.0	0.0
	5– 9	11.6	12.9	19.7	19.8	25.6	18.9	5.0
	10–14	0.0	1.2	4.4	3.1	10.5	13.4	0.7
Capelin	5– 9	15.0	5.4	0.0	2.3	2.0	0.3	0.6
	10–14	0.0	14.0	6.8	6.5	3.6	3.0	8.9
	15–19	0.0	0.0	0.0	3.5	0.0	1.6	0.0
Herring	10–14	0.0	4.6	4.1	7.2	16.7	12.8	0.0
	15–19	0.0	0.0	0.0	2.9	7.7	0.0	0.0
Cod	20–30	0.0	0.0	0.0	0.0	0.0	0.0	6.7
Haddock	10–14	0.0	1.4	8.8	1.4	0.0	0.0	0.0
Redfish	0– 4	0.6	0.0	0.0	0.0	0.0	0.0	0.0
	5– 9	0.0	4.4	11.5	22.8	9.3	24.1	0.3
	10–14	0.0	0.0	3.7	3.4	1.6	0.0	0.0
	15–19	0.0	0.0	0.0	0.0	5.7	0.0	2.4
"Others"		68.1	54.6	39.3	29.0	13.7	26.0	74.8
Weight per stomach (g)		1.2	7.1	10.8	22.0	39.0	60.7	164.6
Number of stomachs analysed		233	342	97	113	114	32	16

Area: VI+VIII Season: S–A 1985

Prey species	Size group (cm)	Predator age group						
		1	2	3	4	5	6	7+
Deep-sea shrimp	0– 4	0.0	0.2	0.0	0.0	0.0	0.2	0.0
	5– 9	0.0	5.9	2.7	2.7	0.3	3.5	0.0
	10–14	0.0	0.0	2.3	2.2	2.3	0.0	1.5
Capelin	5– 9	0.0	1.4	3.2	0.0	9.6	0.0	0.0
	10–14	18.2	22.6	15.4	24.1	19.1	0.0	5.8
Cod	0– 5	1.1	0.0	0.0	0.0	0.0	0.0	0.0
	5– 9	0.0	2.5	1.5	0.7	0.0	0.0	0.0
	10–14	0.0	0.0	1.1	0.0	1.4	0.0	0.0
	20–30	0.0	0.0	0.0	0.0	4.6	8.5	18.2
Haddock	10–14	0.0	0.0	0.0	2.3	0.0	0.0	0.0
	15–19	0.0	0.0	2.9	0.0	3.3	0.0	0.0
Redfish	0– 4	3.0	0.5	0.0	0.9	0.0	0.0	0.0
	5– 9	0.0	1.5	2.4	5.4	1.8	1.5	0.0
	10–14	0.0	1.8	2.7	9.5	9.0	43.5	15.0
	15–19	0.0	0.0	0.0	0.0	8.8	0.0	0.0
"Others"		77.7	60.3	63.5	52.4	39.5	42.8	59.2
Weight per stomach (g)		1.0	3.8	14.5	23.8	37.7	57.1	120.7
Number of stomachs analysed		161	373	215	106	60	33	8

Area: II+IV Season: W–S 1986

Prey species	Size group (cm)	Predator age group						
		1	2	3	4	5	6	7+
Deep-sea shrimp	5– 9	–	–	11.9	10.6	1.1	1.2	0.9
	10–14	–	–	2.1	3.1	0.4	3.4	0.4
Capelin	5– 9	–	–	0.0	0.0	1.9	0.0	0.0
	10–14	–	–	32.5	54.2	34.6	19.7	50.5
	15–19	–	–	33.2	0.0	4.1	10.3	0.0
Herring	20–30	–	–	0.0	0.0	11.5	0.0	0.0
Cod	20–30	–	–	0.0	0.0	0.0	10.3	25.0
Haddock	15–19	–	–	0.0	2.5	0.0	0.0	0.0
Redfish	0– 4	–	–	9.5	0.0	0.0	0.0	0.0
	5– 9	–	–	4.7	0.7	3.1	1.4	5.1
	10–14	–	–	0.0	2.5	0.0	0.0	6.2
	15–19	–	–	0.0	5.0	11.6	21.1	2.9
"Others"		–	–	6.3	20.7	31.7	32.7	8.9
Weight per stomach (g)		–	–	7.2	13.0	17.3	29.2	137.4
Number of stomachs analysed		–	–	57	87	89	45	15

Area: II+IV Season: S–A 1986

Prey species	Size group (cm)	Predator age group						
		1	2	3	4	5	6	7+
Deep-sea shrimp	0– 4	–	–	0.0	2.5	0.0	0.0	0.0
	5– 9	–	–	10.7	3.9	3.4	0.0	0.0
	10–14	–	–	1.5	1.8	0.2	0.0	0.0
Capelin	5– 9	–	–	0.0	0.0	0.2	0.0	0.0
	10–14	–	–	8.1	1.2	0.5	0.0	0.0
Herring	10–14	–	–	5.6	0.0	0.0	0.0	0.0
	15–19	–	–	0.0	1.7	7.1	0.0	0.0
Cod	10–14	–	–	0.0	0.0	1.3	0.0	0.0
	15–19	–	–	0.0	0.0	1.1	0.0	0.0
	20–30	–	–	0.0	0.0	0.0	32.3	32.3
Haddock	10–14	–	–	0.0	1.1	0.0	0.0	0.0
	20–30	–	–	0.0	19.7	0.0	11.6	11.6
Redfish	0– 4	–	–	0.3	0.0	0.0	0.0	0.0
	5– 9	–	–	1.9	0.0	0.5	0.0	0.0
	10–14	–	–	0.0	2.0	9.0	5.6	5.6
	15–19	–	–	0.0	3.3	12.1	17.4	17.4
"Others"		–	–	71.6	62.8	65.0	33.1	33.1
Weight per stomach (g)		–	–	7.2	30.5	62.9	110.8	122.6
Number of stomachs analysed		–	–	166	103	81	15	18

Area: III+V Season: W–S 1986

Prey species	Size group (cm)	Predator age group						
		1	2	3	4	5	6	7+
Deep-sea shrimp	0– 4	1.4	0.9	0.2	0.3	0.4	0.0	–
	5– 9	0.0	6.7	4.1	5.0	1.6	0.7	–
	10–14	0.0	0.0	1.2	6.3	4.5	0.8	–
Capelin	10–14	0.0	64.8	50.1	9.1	54.3	28.0	–
	15–19	0.0	0.0	4.0	41.5	23.3	36.8	–
Herring	5– 9	0.0	0.0	1.0	0.0	0.0	0.0	–
	10–14	0.0	0.0	9.5	3.9	0.0	0.0	–
	15–19	0.0	0.0	10.7	0.0	2.5	0.0	–
	20–30	0.0	0.0	0.0	11.1	0.0	0.0	–
Cod	20–30	0.0	0.0	0.0	0.0	3.2	6.0	–
Haddock	10–14	0.0	6.4	0.0	1.0	0.0	0.0	–
	15–19	0.0	0.0	0.0	0.0	0.0	19.0	–
Redfish	0– 4	0.0	0.1	0.7	1.3	0.0	0.0	–
	5– 9	0.0	7.1	10.1	10.6	4.8	0.1	–
	10–14	0.0	0.0	3.7	1.8	0.0	0.0	–
"Others"		98.6	14.0	4.9	8.1	5.1	6.7	–
Weight per stomach (g)		0.03	1.6	6.2	11.6	40.0	113.8	–
Number of stomachs analysed		92	107	340	153	89	25	–

Area: III+V Season: S–A 1986

Prey species	Size group (cm)	Predator age group						
		1	2	3	4	5	6	7+
Deep-sea shrimp	0– 4	0.0	0.6	0.0	2.7	0.0	0.0	–
	5– 9	0.0	15.0	9.2	4.4	4.0	0.0	–
	10–14	0.0	0.0	1.6	2.1	0.3	0.0	–
Capelin	5– 9	0.0	0.0	0.0	0.0	0.2	0.0	–
	10–14	0.0	0.0	8.4	0.0	0.7	0.0	–
Herring	10–14	0.0	0.0	5.8	0.0	0.0	0.0	–
	15–19	0.0	0.0	0.0	0.0	9.2	0.0	–
Cod	10–14	0.0	0.0	0.0	0.0	1.7	0.0	–
	15–19	0.0	0.0	0.0	0.0	1.4	0.0	–
	20–30	0.0	0.0	0.0	0.0	0.0	46.0	–
Haddock	20–30	0.0	0.0	0.0	23.1	0.0	16.7	–
Redfish	0– 4	19.0	0.0	0.3	0.0	0.0	0.0	–
	5– 9	0.0	0.0	2.0	0.2	0.7	0.0	–
	10–14	0.0	0.0	0.0	0.0	1.2	0.0	–
	15–19	0.0	0.0	0.0	0.0	5.0	25.3	–
"Others"		81.0	83.0	72.6	67.6	75.6	11.2	–
Weight per stomach (g)		0.4	1.4	7.3	29.7	70.5	112.8	–
Number of stomachs analysed		30	78	155	92	61	7	–

Area: VI+VII Season: W–S 1986

Prey species	Size group (cm)	Predator age group						
		1	2	3	4	5	6	7+
Deep-sea shrimp	0– 4	0.0	0.2	0.0	0.0	0.0	0.2	0.0
	5– 9	0.0	5.9	2.7	2.7	0.3	3.5	0.0
	10–14	0.0	0.0	2.3	2.2	2.3	0.0	1.5
Capelin	5– 9	0.0	1.4	3.2	0.0	9.6	0.0	0.0
	10–14	18.2	22.6	15.4	24.1	19.1	0.0	5.8
Cod	0– 5	1.1	0.0	0.0	0.0	0.0	0.0	0.0
	5– 9	0.0	2.5	1.5	0.7	0.0	0.0	0.0
	10–14	0.0	0.0	1.1	0.0	1.4	0.0	0.0
	20–30	0.0	0.0	0.0	0.0	4.6	8.5	18.2
Haddock	10–14	0.0	0.0	0.0	2.3	0.0	0.0	0.0
	15–19	0.0	0.0	2.9	0.0	3.3	0.0	0.0
Redfish	0– 4	3.0	0.5	0.0	0.9	0.0	0.0	0.0
	5– 9	0.0	1.5	2.4	5.4	1.8	1.5	0.0
	10–14	0.0	1.8	2.7	9.5	9.0	43.5	15.0
	15–19	0.0	0.0	0.0	0.0	8.8	0.0	0.0
"Others"		77.7	60.3	65.5	52.4	39.5	42.8	59.2
Weight per stomach (g)		1.0	3.8	14.5	23.8	37.7	57.1	120.7
Number of stomachs analysed		161	373	215	106	60	33	8

Area: VI+VII Season: S–A 1986

Prey species	Size group (cm)	Predator age group						
		1	2	3	4	5	6	7+
Deep-sea shrimp	5– 9	4.1	5.1	5.7	5.5	4.4	3.1	0.2
	10–14	0.0	0.0	4.0	1.0	0.5	0.9	0.1
Capelin	5– 9	0.0	0.0	0.0	0.1	3.2	0.8	0.0
	10–14	0.0	0.0	3.2	1.7	2.7	0.0	0.0
Cod	5– 9	0.0	0.0	0.3	0.0	0.1	0.0	0.0
	10–14	0.0	0.0	0.0	0.1	0.0	0.8	0.0
	20–30	0.0	0.0	0.0	0.0	1.3	13.9	4.5
Redfish	5– 9	0.0	2.2	2.0	0.4	0.6	0.0	0.0
	10–14	0.0	0.0	0.6	3.6	6.7	0.0	0.0
	15–19	0.0	0.0	0.0	1.4	0.0	0.0	2.7
"Others"		95.9	92.6	84.3	86.5	78.9	80.6	91.8
Weight per stomach (g)		1.0	2.2	9.0	36.4	54.7	82.6	322.9
Number of stomachs analysed		16	142	339	282	160	32	17