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Cannibalism and year-class strength in Atlantic cod (*Gadus morhua* L.) in Arcto-boreal ecosystems (Barents Sea, Iceland, and eastern Newfoundland)

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Stomach content data collected from cod caught during offshore resource assessment surveys in three Arcto-boreal ecosystems (the Barents Sea and the shelves off Iceland and eastern Newfoundland) were examined to determine the prevalence of cannibalism, and to identify possible factors associated with variability in prevalence. Cannibalism provides a minor source of food, except for the largest predators. Cannibalism increases with predator length. Most prey are less than 40 cm in length and less than 3 years old. In each region, cannibalism occurs over most of the area surveyed, but is most prevalent where the smallest cod have been found in bottom trawl surveys. The frequency of occurrence of cannibalism recorded in recent years (late 1970s to the present) has usually been low (<1%) in all regions. Much higher values were reported from the Barents Sea in 1949–1960. In the Barents Sea, the frequency of occurrence of cannibalism increased with the abundance of juvenile cod. There was little support for the hypothesis that the frequency of cannibalism increased when the abundance of capelin, the major prey of cod, was low. It can be demonstrated that cod eat large numbers of their young, especially those of ages 0–2, but the mortality rate imposed cannot be calculated without independent estimates of the abundance of young cod. Mortality imposed by cannibalism and competition is estimated without stomach content data for Icelandic cod. This is done by modelling the change in abundance from the pelagic 0-group stage, as measured by pelagic trawl surveys, to age 3, as estimated by VPA.

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Introduction

Cannibalism is a common phenomenon in animals (Fox, 1975; Polis, 1981), and has been found in at least 36 families of teleost fish (Smith and Reay, 1991). Among the Gadidae, it has been reported in cod (*Gadus morhua*) from the Gulf of St Lawrence (Waiwood and Majkowski, 1984), the Flemish Cap (Lilly, 1987), northeastern Newfoundland (Lilly, 1991), Greenland (Hansen, 1949), Iceland (Pálsson, 1983), the Barents Sea (Mehl, 1989, 1991), the North Sea (Daan, 1973), and the Baltic Sea (Arntz, 1978). Predation on conspecifics is generally a minor source of food for cod, a notable exception being the cod of landlocked Ogac Lake on Baffin Island. For this stock, the lack of alternate prey of suitable size makes cannibalism a vital source of energy and a major determinant of population size structure (Patriquin, 1967).

In other stocks, the major interest for stock dynamics is the importance of cannibalism in influencing recruitment to the fishery. This is part of the broader question of whether mortality at the juvenile stage is sufficiently high and variable to affect recruitment (Sissenwine, 1984; Lilly, 1987). The number of juvenile cod eaten by conspecifics may be influenced by several factors, including the following:

1. The number consumed may increase with the number alive at a specified size (or age) because the frequency of encounters with potential predators will increase (Ponomarenko, 1968).
2. As the abundance of larger fish increases, the probability that each juvenile will encounter a potential cannibal increases. This has been cited as a potential mechanism for a decline in recruitment at high stock levels (Ricker, 1954, 1975), although Ricker (1954, p. 613) was of the opinion that cannibalism will probably not prove to be important in regulating more than a minority of populations.
3. The number of juveniles consumed may vary in accordance with several factors which may be grouped under the term intra-cohort density dependence. As the abundance of juveniles increases, (a) the fish may spread into areas where they are more vulnerable to predation (Ricker, 1954), (b) the duration of the vulnerable phase may increase because of a decrease in growth rate attending competition for resources (Ricker, 1954), (c) the ability of the fish to escape potential predators may be reduced if nutritional condition is low because of competition (Ponomarenko, 1965), and (d) predators may be attracted to the higher prey densities (aggregative numerical response).
4. A shortage of resources (e.g. food, space, cover), due to factors other than intra-specific competition, could result in slower growth, poorer condition or movement into areas of higher vulnerability, with the consequences mentioned above.
5. Shortage of food for older cod may result in increased cannibalism. This has been hypothesized to have occurred in the Barents Sea in 1985–1987 as a result of a decline in the biomass of capelin, the major prey of cod in that area in recent years (Mehl, 1989, 1991).
6. Changes in the physical environment, especially temperature, may cause changes in the distributions of juveniles or older cod, thereby affecting the degree of spatial overlap and the frequency of encounter.

In order to understand the potential impact of cannibalism on year-class strength, it is necessary to distinguish among the above processes and to determine the importance of each. Our first objective is to review and document the extent of cannibalism in the cod inhabiting the Arcto-boreal shelves off southern Labrador and northeastern Newfoundland, around Iceland, and in the Barents Sea and Svalbard area. Analyses will be limited to stomachs collected during resource assessment surveys in offshore waters. Our second objective is to use these data, especially those from the Barents Sea, to test hypotheses 1 and 5 above. We then use data from the Barents Sea to illustrate a method for estimating the quantity and number of cod consumed by cod. Finally, we use abundance estimates from pelagic trawl surveys and virtual population analysis (Icelandic cod) to illustrate a method, independent of stomach content data, for estimating the mortality imposed by cannibalism.

Materials and methods

Sampling

The survey design, stomach sampling protocol, and method of stomach content analysis varied within and among areas (ICES, 1992a). The number of stomachs sampled in the three areas, by year and length group, is given in Tables 1a–c.

In the Newfoundland area, cod were caught during random depth-stratified bottom trawl surveys during November–December 1978 and 1980–1992 on the southern Labrador Shelf and Northeast Newfoundland Shelf (Northwest Atlantic Fisheries Organization Divisions 2J+3K) (Lilly, 1991; Lilly and Davis, 1993). The intent, not always attained, was to collect stomachs from a length-stratified sample of cod from every station. The number and weight of cod and other prey occurring in the stomachs was recorded separately for each predator. The fork length (FL) of each predator and prey was recorded to the nearest centimetre.

In the Iceland area, cod were caught mainly in the north and east during fixed station surveys prior to 1985, and during semi-stratified random surveys starting in 1985 (Pálsson *et al.*, 1989). Stomachs were collected during surveys in March 1979–1992 and September–November 1980–1992. Stomach sampling was stratified with respect to subareas and predator length (Pálsson, 1983; Magnússon and Pálsson, 1989). All stomachs from a specific sample (station and length group) were bulked, and the number and weight of cod and other prey were recorded for each sample, together with the number of stomachs contributing to the sample. The total length (cm) of the predators is provided here as the mid-point of the length group. Lengths are available for individual prey.

In the Barents Sea and Svalbard area, cod were caught at various times of the year during surveys conducted by Norway since 1984 and Russia since 1986 (Mehl, 1989; Mehl and Yaragina, 1992). Stations were fixed, stratified-random, or selected on the basis of acoustic information. Stomachs were collected from a length-stratified sample of cod from each survey stratum. The number and weight of cod and other prey occurring in each individual stomach was recorded for each length group of prey. Lengths (FL, cm) are available for each individual predator, but prey lengths are recorded by mid-point of length group. Stomach content data collected by Russia from 1949 to 1982 and by Norway in 1981 and 1982 have been added to the common Norway (IMR)–Russia (PINRO) database.

Table 1a. NEWFOUNDLAND COD. Number of stomachs analysed by predator length group and year in 1978 and 1980–1992.

	Predator length group (cm)												
	10–14	15–19	20–24	25–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100–119	Total
1978	0	0	0	13	143	240	267	212	124	30	4	2	1035
1980	0	2	11	35	142	227	495	489	267	98	25	4	1795
1981	0	0	1	67	173	218	297	324	207	88	23	5	1403
1982	0	41	42	168	416	489	551	608	483	185	68	24	3075
1983	2	32	79	249	317	529	446	590	358	120	31	7	2760
1984	1	19	90	151	425	479	522	510	359	121	39	17	2733
1985	0	5	18	75	474	488	621	433	265	47	7	2	2435
1986	0	14	26	91	327	552	526	368	165	48	4	0	2121
1987	0	14	41	41	256	578	661	360	161	38	10	2	2162
1988	3	87	55	92	301	303	517	342	113	19	0	0	1832
1989	0	75	121	262	451	360	422	312	54	16	0	0	2073
1990	0	28	72	151	391	275	204	134	21	2	0	0	1278
1991	0	3	20	152	448	534	233	140	53	6	0	1	1590
1992	0	2	8	40	327	318	70	12	0	0	0	0	777
Total	6	322	584	1587	4591	5590	5832	4834	2630	818	211	64	27069

Table 1b. ICELANDIC COD. Number of stomachs analysed by predator length group and year in 1979–1992.

	Predator length group (cm)													
	7–9	10–14	15–19	20–24	25–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100–119	Total
1979	114	140	154	179	173	149	134	92	45	18	6	1	1	1206
1980	117	101	124	207	244	299	312	333	352	221	194	132	45	2681
1981	93	122	167	233	245	614	605	671	885	635	592	364	116	5342
1982	18	99	149	224	234	385	580	769	890	885	646	273	122	5274
1983	29	76	84	177	229	353	508	575	635	621	385	133	45	3850
1984	22	147	56	85	118	159	256	307	318	303	197	62	23	2053
1985	34	117	111	194	205	320	321	402	399	358	237	133	62	2893
1986	10	143	113	129	157	168	227	251	261	258	203	72	45	2037
1987	7	59	78	122	126	161	242	300	308	308	291	162	116	2280
1988	19	58	61	108	136	258	345	410	449	415	266	149	84	2758
1989	31	59	82	157	155	219	277	325	324	301	195	144	89	2358
1990	34	109	77	160	229	355	420	484	515	406	297	139	99	3324
1991	17	88	62	164	236	345	390	456	451	374	277	116	61	3037
1992	4	78	127	335	425	485	439	497	539	427	338	172	69	3935
Total	549	1396	1445	2474	2912	4270	5056	5872	6371	5530	4124	2052	977	43028

ICELANDIC COD. Number of samples analysed by predator length group and year in 1979–1992.

	Predator length group (cm)													
	7–9	10–14	15–19	20–24	25–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100–119	Total
1979	22	23	24	23	25	25	29	31	22	11	5	1	1	242
1980	26	37	51	57	64	53	51	56	69	65	65	59	21	674
1981	21	33	53	71	63	109	92	92	115	108	118	110	56	1041
1982	6	31	47	61	61	70	106	134	159	173	174	94	57	1173
1983	14	25	33	42	53	56	66	82	95	105	98	54	20	743
1984	9	35	20	30	38	39	41	53	56	71	66	27	13	498
1985	11	19	32	36	47	62	64	73	68	71	81	67	31	662
1986	5	31	32	22	35	41	50	61	65	71	64	42	31	550
1987	3	13	14	19	20	25	37	55	57	56	63	52	39	453
1988	5	16	19	36	45	60	74	75	83	93	92	75	48	721
1989	11	22	31	44	55	63	69	80	79	81	74	63	50	722
1990	16	31	37	50	74	99	109	131	143	125	11	82	63	1075
1991	7	31	29	50	72	92	101	122	119	116	11	60	37	955
1992	4	38	50	82	108	119	116	130	137	121	126	76	42	1149
Total	160	385	472	623	760	913	1005	1175	1267	1267	1260	862	509	10658

Table 1c. BARENTS SEA COD. Number of stomachs analysed by predator length group and year in 1949–1960, 1973, 1975, 1980–1982, and 1984–1992.

	Predator length group (cm)													
	7–9	10–14	15–19	20–24	25–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100–119	Total
1949	0	0	0	0	0	1	19	62	59	32	11	3	2	189
1950	0	0	0	0	0	1	10	73	72	24	9	3	1	193
1951	0	0	0	0	0	0	0	2	3	12	7	0	1	25
1952	0	0	4	0	1	8	74	242	126	92	55	12	2	616
1953	0	0	0	0	2	150	457	334	115	42	18	6	0	1124
1954	0	0	0	0	0	3	44	75	30	22	7	2	0	183
1955	0	0	0	0	0	0	4	65	77	25	14	3	0	188
1956	0	0	0	2	2	9	67	284	364	175	66	32	4	1005
1957	0	0	2	45	33	56	80	89	75	62	38	30	12	522
1958	0	0	1	7	6	30	29	101	122	85	57	10	5	453
1959	0	0	0	0	2	50	162	411	270	96	37	11	3	1042
1960	0	0	0	0	0	0	4	60	44	37	21	2	3	171
1973	0	0	0	0	0	10	63	51	39	6	3	2	0	174
1975	0	0	0	0	0	74	125	0	0	0	0	0	0	199
1980	11	0	0	0	0	0	106	354	116	15	1	1	4	608
1981	6	8	2	0	1	8	31	87	181	73	4	0	6	407
1982	0	0	0	11	32	194	193	174	143	70	14	1	1	833
1984	3	157	334	335	275	640	747	508	372	245	67	12	32	3727
1985	23	79	251	380	421	664	831	762	433	175	87	28	18	4152
1986	37	213	204	284	333	1111	1210	1344	1040	201	38	15	13	6043
1987	4	44	161	308	329	1005	1590	1165	908	349	60	17	4	5944
1988	3	11	33	145	214	810	1750	1695	607	234	66	19	9	5596
1989	11	109	40	100	207	918	1731	2228	1771	517	115	29	16	7792
1990	9	176	164	213	213	747	1011	1581	2031	1364	437	65	38	8049
1991	2	202	231	199	338	852	829	908	909	922	470	119	15	5996
1992	10	125	152	154	141	294	370	403	367	337	287	183	62	2885
Total	119	1124	1579	2183	2550	7635	11537	13058	10274	5212	1989	605	251	58116

Stomach data analysis

The degree and relative importance of cannibalism was expressed using two indices: (1) percent frequency of occurrence (the number of stomachs containing cod expressed as a percentage of the total number of stomachs in a sample) and (2) percent weight (the weight of cod expressed as a percentage of the total weight of the contents of all stomachs in a sample). Because the stomachs from Iceland were bulked, it was necessary to apply the following correction procedure to estimate the frequency of occurrence on an individual stomach basis. Let p denote the probability of observing cod in an individual stomach. Thus, the probability of a stomach being empty is $1-p$ and the probability is $(1-p)^n$ that a bulk of n stomachs is empty (or does not contain the prey in question). It follows that the probability, H, of occurrence within a bulk is given by $H = 1-(1-p)^n$. This equation can now be inverted to yield $p = 1-(1-H)^{1/n}$, which describes the probability of occurrence in individual stomachs based on observations of occurrence in bulked samples. The input value for H is given in Table 3b. As an input value for n the average number of stomachs in bulked samples has been used, as shown in the following text table:

Year	1979	1980	1981	1982	1983	1984	1985
n	4.9	3.9	5.1	4.5	5.2	4.1	4.4
Year	1986	1987	1988	1989	1990	1991	1992
n	3.7	5.0	3.8	3.3	3.1	3.2	3.4

To determine whether cannibalism was positively associated with the availability of juvenile cod and negatively associated with the availability of major prey, the frequency of occurrence of cannibalism in Barents Sea cod was compared with (i) the year-class strength of cod as measured during pelagic 0-group surveys and (ii) the availability of capelin, as approximated by the capelin biomass estimated during acoustic surveys in autumn and the quantity of capelin in cod stomachs. The latter was expressed as a mean partial fullness index (Fahrig *et al.*, 1993) calculated as:

$$PFI_c = \frac{1}{n}\sum_{j=1}^{n}\frac{W_{cj}}{L_j^3} \times 10^4$$

where W_{cj} is the weight of capelin in fish j, L_j is the length of fish j, and n is the number of fish in the sample.

Estimating consumption of cod by cod

The number of cod-at-age consumed each year by the cod in the Barents Sea was estimated using the method of Mehl (1989, 1991) and Bogstad and Mehl (1992). The consumption (tonnes) by size group j in season 1 (C_{jl}) is given by

$$C_{jl} = \sum_{k,n} R_{jkln} \times XN_{nl} \times XP_{kln} \times (10^6 \times 24 \times 182.5)$$

where R_{jkln} is the ration ($g \times h^{-1}$) of prey size group j for predator age group n in area k and season l (half-year), XN_{nl} is the number of individuals of predator age group n in season l and XP_{kln} is the proportion of individuals of predator age group n in area k and season 1. Ration was estimated from the stomach content data and a model for estimating evacuation rate provided by dos Santos and Jobling (1992), as modified by Bogstad and Mehl (1992). The number of cod-at-age was taken from the Arctic Fisheries Working Group Report (ICES, 1993b). It was assumed that the spawning component is outside the Barents Sea for three months during the first half of the year (Godø, 1989). The quantity (in tonnes) of cod consumed by size group was converted to numbers consumed by age group using the method of Mehl (1989). Mean weight of each prey size group was mainly calculated using $W = c \times l^3$, where c was calculated using survey data in each half year and l was the median length in the size group. For the 0-group, prey weights were in some cases taken directly from stomach content data.

Results

Variability in cannibalism

The relationships between the lengths of cod consumed and the lengths of their predators were similar in the three areas (Figs. 1–3). Predator lengths ranged upward from about 30 cm, and prey lengths ranged upward from about 5 cm, with very few instances of prey larger than 40 cm. The maximum prey size was about 50% of the predator length, and the range of prey size increased with predator size. 0-group cod (<10 cm) were preyed upon in relatively large numbers by a wide size range of predators in Iceland waters and the Barents Sea, but were not common prey off Newfoundland (Fig. 4).

The contribution of cod to the total stomach content weight generally increased with predator size in all three areas (Fig. 5, Tables 2a–c). On average, the contribution was nil or small (≤1%) in cod less than 50 cm and increased to 5.1%, 8.2%, and 8.5% in 100–119 cm cod in the waters of Newfoundland and Iceland, and in the Barents Sea, respectively. Cannibalism in small cod (7–14 cm) was found only occasionally off Iceland.

Occurrences of cannibalism were broadly distributed in each of the areas. In the Newfoundland region, cannibalism was most intensive toward the coast off southern Labrador and northeastern Newfoundland, but was also recorded on some of the offshore banks (Fig. 6). In Icelandic waters, cannibalism occurred most frequently off the northwestern and northern coasts. It was less intense off the eastern coast and recorded only occasionally off the southern coast. The frequency of cannibalism was generally higher close to the coast than in offshore areas, but was not recorded within fjords,

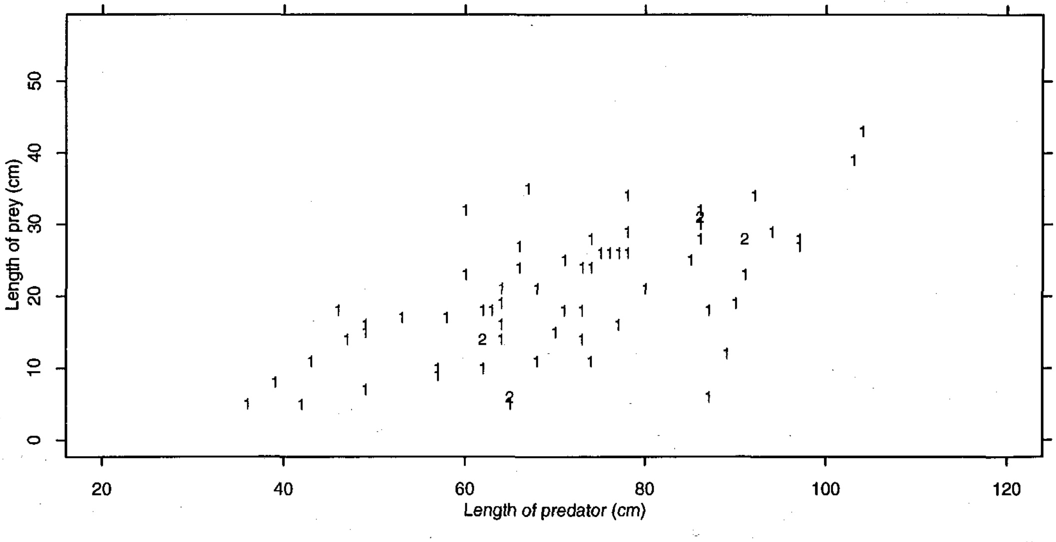


Figure 1. Plot of prey size versus predator size for Newfoundland cod. Number of prey behind each sample are indicated.

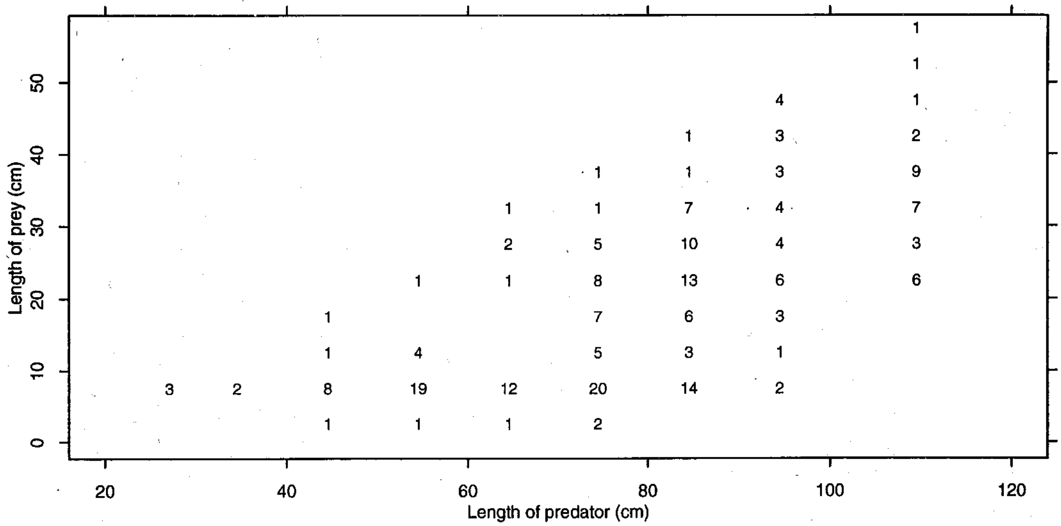


Figure 2. Plot of prey size versus predator size for Icelandic cod. Number of prey behind each sample are indicated.

such as those of the northwestern and northern coasts (Fig. 7). In the Barents Sea area, cannibalism occurred most frequently in the east and in the Svalbard area, mainly within the 200 m isobath (Fig. 8). During the period 1984–1992 cannibalism was recorded in the Barents Sea every year, whereas in the Svalbard area it was observed mainly in years of extensive cannibalism. More than half of the occurrences in the Svalbard area were recorded during 1949–1960.

The frequency of occurrence of cannibalism varied among years in each of the areas (Fig. 9, Tables 3a–c). In the waters off Newfoundland, occurrence was highest in 1983–1984 and 1989–1990. There was a positive correlation between the frequency of occurrence of cannibalism and an index of abundance of juvenile cod ($r = 0.82$; $p < 0.001$; $n = 14$), where the index in year t was calculated as the mean catch (number) per tow of cod aged 1 and 2 in autumn research surveys in NAFO Divisions 2J, 3K, and 3L combined (Bishop *et al.*, 1993). In Icelandic waters, the frequency of occurrence tended to be somewhat higher during 1979–1985 than in more recent years. In the Barents Sea, cannibalism was very

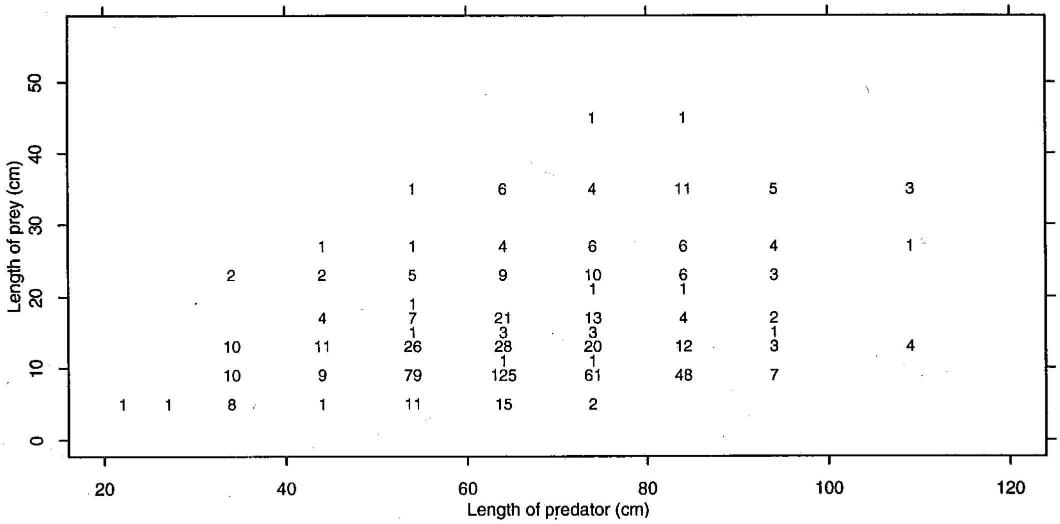
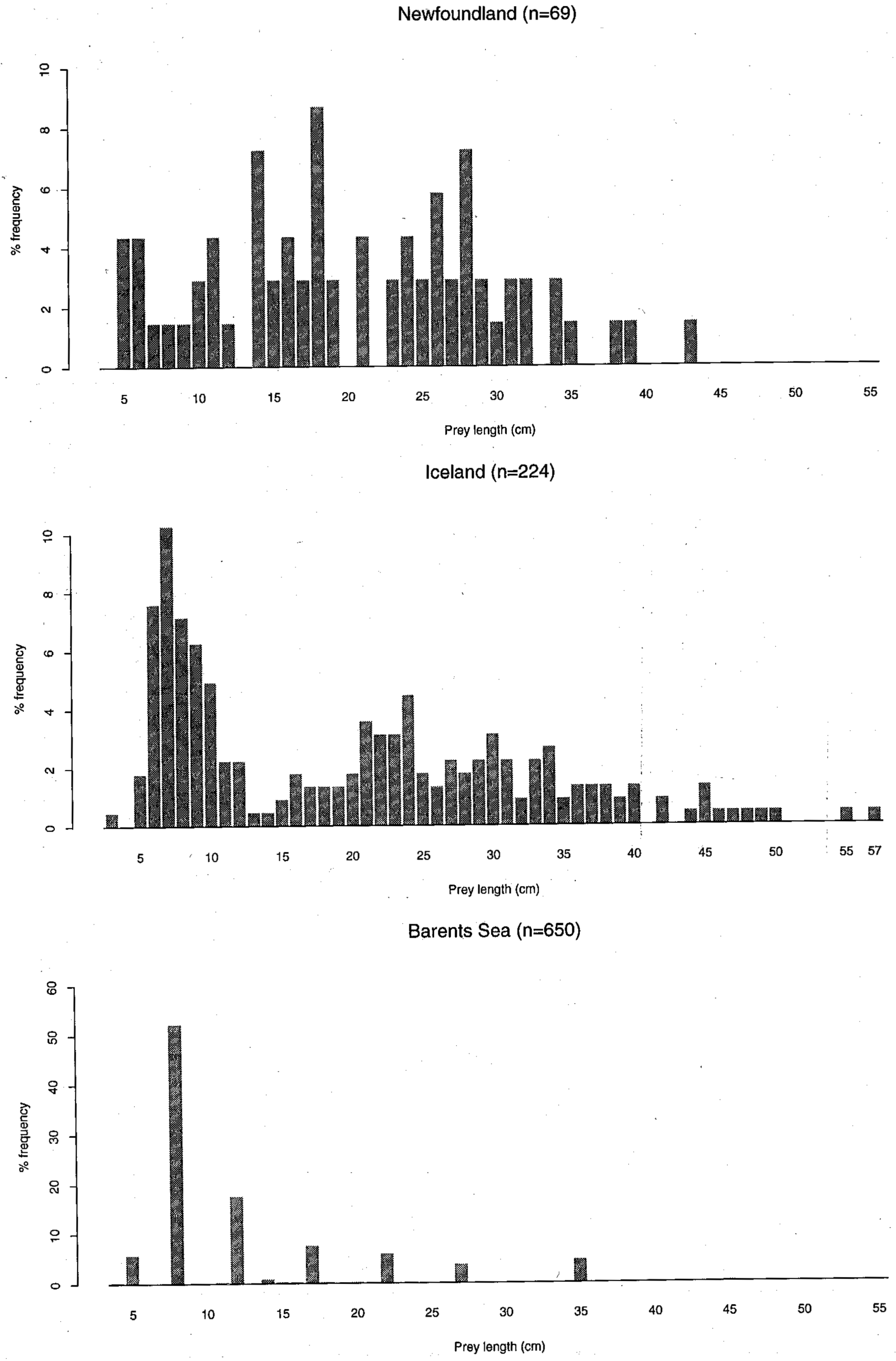


Figure 3. Plot of prey size versus predator size for Barents Sea cod. Number of prey behind each sample are indicated.


Newfoundland (n=69)

Iceland (n=224)

Barents Sea (n=650)

Figure 4. Numerical distribution (%) of cod as prey of cod with respect to prey length.

high in many years during 1949–1960. In more recent years (1984–1992), the frequency of occurrence was relatively low, and at a level similar to that observed off Newfoundland and Iceland. Peaks occurred in 1985–1986 and 1991–1992.

Seasonal variability in cannibalism was investigated in Icelandic waters and in the Barents Sea (Fig. 10). In both areas cannibalism is generally higher and more variable in the autumn than in the winter or spring. This is probably related to the higher abundance and availability of prey shortly after the settlement of the 0-group.

Annual variability in factors which might influence the frequency of occurrence of cannibalism in the Barents Sea is illustrated in Figure 11. During the period 1984–1992 the frequency of occurrence of cannibalism was positively correlated with an index of juvenile abundance, but not negatively correlated with either the biomass of capelin or the quantity of capelin in cod stomachs (Fig. 11, Table 4).

Table 2a. NEWFOUNDLAND COD. Weight percentages of cod in stomach content of cod in 1978 and 1980–1992.

	Predator length group (cm)											
	10–14	15–19	20–24	25–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100–119
1978	–	–	–	0.0	0.0	0.0	0.0	0.0	5.2	1.2	0.0	0.0
1980	–	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0
1981	–	–	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
1982	–	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.6	0.5	3.1	5.3
1983	0.0	0.0	0.0	0.0	0.2	2.0	1.5	0.1	3.3	2.9	0.0	0.0
1984	0.0	0.0	0.0	0.0	0.0	+	0.0	2.2	1.9	0.1	8.5	8.1
1985	–	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	0.0	22.2	0.0
1986	–	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.3	54.0	–
1987	–	0.0	0.0	0.0	0.0	0.0	0.0	1.1	2.0	7.2	11.2	0.0
1988	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.3	0.0	–	–
1989	–	0.0	0.0	0.0	0.0	0.0	2.3	2.2	1.1	14.9	–	–
1990	–	0.0	0.0	0.0	0.0	0.0	0.4	1.8	16.7	94.1	–	–
1991	–	0.0	0.0	0.0	0.0	0.0	0.0	12.0	15.4	0.0	–	0.0
1992	–	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–	–	–	–
Pooled mean	0.0	0.0	0.0	0.0	0.01	0.2	0.3	1.1	2.0	2.3	4.8	5.1

Table 2b. ICELANDIC COD. Weight percentages of cod in stomach content of cod in 1979–1992.

	Predator length group (cm)												
	7–9	10–14	15–19	20–24	25–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100–119
1979	0.0	0.0	0.0	0.0	0.0	0.5	5.6	16.6	39.2	16.8	89.6	0.0	0.0
1980	0.0	0.0	0.0	0.0	3.2	0.0	0.0	1.3	23.2	27.1	0.4	7.1	21.2
1981	0.0	0.0	0.0	0.0	0.0	0.0	1.6	5.7	1.4	31.3	6.8	2.0	30.4
1982	0.0	0.0	0.0	0.0	0.0	1.4	0.0	0.0	1.4	5.4	16.0	8.0	24.5
1983	0.0	0.0	0.0	0.0	0.0	2.1	0.0	1.2	0.7	4.1	30.1	54.5	20.6
1984	0.0	0.0	0.0	0.0	0.0	0.0	1.6	0.6	0.0	14.2	19.0	7.3	40.1
1985	0.0	0.0	0.0	0.0	22.7	0.0	5.3	8.0	7.6	9.3	6.1	4.7	13.2
1986	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.6	2.6	7.0	0.0
1987	0.0	0.0	0.0	0.0	0.0	5.7	0.0	1.8	8.4	3.9	19.3	0.0	0.0
1988	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.6	0.2	6.8	15.0	41.1	0.1
1989	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	3.7	2.3	3.5	14.0	12.5
1990	80.1	35.8	0.0	0.0	0.0	3.0	0.0	4.6	0.0	7.6	19.0	9.6	22.7
1991	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.8	8.6	10.1	17.0	11.0
1992	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.9	0.0	0.4	5.4	3.9	10.6
Pooled mean	1.0	1.0	0	0	0.4	0.1	0.3	0.6	1.0	2.2	4.7	6.6	8.2

Table 2c. BARENTS SEA COD. Weight percentages of cod in stomach content of cod in 1949–1960, 1973, 1975, 1980–1982, and 1984–1992.

	Predator length group (cm)												
	7–9	10–14	15–19	20–24	25–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100–119
1949	–	–	–	–	–	100.0	1.0	5.0	1.9	8.3	0.2	0.0	80.0
1950	–	–	–	–	–	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0
1951	–	–	–	–	–	–	–	0.0	10.0	9.7	3.1	–	0.0
1952	–	–	0.0	–	0.0	17.1	9.2	24.1	10.0	6.5	4.9	2.6	0.0
1953	–	–	–	–	0.0	0.0	0.3	1.0	0.1	8.1	9.0	1.0	–
1954	–	–	–	–	–	0.0	28.7	27.1	0.0	39.6	46.1	0.0	–
1955	–	–	–	–	–	–	0.0	9.1	2.2	10.1	0.0	0.0	–
1956	–	–	–	0.0	0.0	31.4	6.0	7.0	12.9	45.1	15.1	20.1	0.0
1957	–	–	0.0	0.0	5.0	3.9	1.5	2.6	12.4	11.3	6.0	6.8	33.5
1958	–	–	0.0	0.0	0.0	4.3	3.4	33.1	26.7	32.9	30.3	12.8	3.4
1959	–	–	–	–	0.0	3.1	5.9	9.5	22.6	25.1	31.3	84.1	36.1
1960	–	–	–	–	–	–	0.0	8.4	0.0	1.7	2.7	0.0	0.0
1973	–	–	–	–	–	0.0	0.0	0.0	0.0	98.8	99.8	100.0	–
1975	–	–	–	–	–	0.0	0.0	–	–	–	–	–	–
1980	0.0	–	–	–	–	–	0.0	0.0	0.0	42.0	0.0	0.0	0.0
1981	0.0	0.0	0.0	–	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–	0.0
1982	–	–	–	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
1984	0.0	0.0	0.0	0.0	0.0	0.6	0.2	0.2	0.8	7.2	0.0	0.0	3.5
1985	0.0	0.0	0.0	0.1	2.9	0.4	1.6	0.7	0.5	2.9	4.0	14.1	31.4
1986	0.0	0.0	0.0	0.0	0.0	3.5	0.5	2.1	1.7	8.1	26.0	36.2	0.0
1987	0.0	0.0	0.0	0.0	0.0	0.7	0.2	1.1	2.9	2.7	14.0	25.4	0.0
1988	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.7	0.4	2.2	0.0	0.0	0.5
1989	0.0	0.0	0.0	0.0	0.0	0.9	0.2	0.1	0.8	0.1	0.0	0.0	0.5
1990	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.4	0.5	0.1	0.7	0.0	0.0
1991	0.0	0.0	0.0	0.0	0.0	+	0.0	0.2	0.4	+	1.5	3.1	13.3
1992	0.0	0.0	0.0	0.0	1.1	0.7	0.5	0.0	4.3	0.5	0.4	5.8	0.0
Pooled mean	0.0	0.0	0.0	+	0.2	1.1	0.5	1.5	1.8	3.2	4.6	7.3	8.5

Table 3a. NEWFOUNDLANDIC COD. Frequency of occurrence (%) of cannibalism in cod stomachs, based on individual stomachs, in 1978 and 1980–1992.

	Predator length group (cm)												Pooled mean (≥30 cm)
	10–14	15–19	20–24	25–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100–119	
1978	–	–	–	0.0	0.0	0.0	0.0	0.0	1.6	3.3	0.0	0.0	0.3
1980	–	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.1
1981	–	–	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.1
1982	–	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.2	0.5	2.9	4.2	0.2
1983	0.0	0.0	0.0	0.0	0.6	0.8	0.5	0.3	1.4	1.7	0.0	0.0	0.7
1984	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.6	0.8	1.7	7.7	5.9	0.6
1985	–	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	14.3	0.0	0.2
1986	–	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.1	25.0	–	0.1
1987	–	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.6	2.6	10.0	0.0	0.2
1988	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	1.8	0.0	–	–	0.4
1989	–	0.0	0.0	0.0	0.0	0.0	1.2	1.6	1.9	6.3	–	–	0.7
1990	–	0.0	0.0	0.0	0.0	0.0	0.5	1.5	4.8	50.0	–	–	0.5
1991	–	0.0	0.0	0.0	0.0	0.0	0.0	2.1	3.8	0.0	–	0.0	0.4
1992	–	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–	–	–	–	0.0

Table 3b. ICELANDIC COD. Frequency of occurrence (%) of cannibalism in cod stomachs, based on bulked samples, in 1979–1992.

	Predator length group (cm)													Pooled mean	Pooled mean
	7–9	10–14	15–19	20–24	25–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100–119	(≥30 cm)	corrected
1979	0.0	0.0	0.0	0.0	0.0	8.0	6.9	6.5	13.6	9.1	60.0	0.0	0.0	10.4	2.2
1980	0.0	0.0	0.0	0.0	1.6	0.0	0.0	5.4	4.3	6.2	1.5	6.8	14.3	4.6	1.2
1981	0.0	0.0	0.0	0.0	0.0	0.0	2.2	2.2	1.7	6.5	5.9	3.6	12.5	3.9	0.8
1982	0.0	0.0	0.0	0.0	0.0	1.4	0.0	0.0	0.6	2.3	5.2	5.0	7.0	2.5	0.6
1983	0.0	0.0	0.0	0.0	0.0	1.8	0.0	4.9	4.2	3.8	10.2	20.4	15.0	6.4	1.3
1984	0.0	0.0	0.0	0.0	0.0	0.0	4.9	1.9	0.0	5.6	6.1	3.7	15.4	3.8	0.9
1985	0.0	0.0	0.0	0.0	2.1	0.0	6.2	4.1	5.9	9.9	6.2	4.5	12.9	5.8	1.3
1986	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	1.6	2.4	0.0	0.7	0.2
1987	0.0	0.0	0.0	0.0	0.0	4.0	0.0	1.8	1.8	1.8	6.3	0.0	0.0	2.1	0.4
1988	0.0	0.0	0.0	0.0	0.0	0.0	4.1	1.3	1.2	4.3	5.4	12.0	2.1	4.0	1.1
1989	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	1.3	2.5	1.4	4.8	4.0	1.8	0.5
1990	6.2	3.2	0.0	0.0	0.0	1.0	0.0	0.8	0.0	0.8	3.5	2.4	7.9	1.6	0.5
1991	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7	2.6	8.4	10.0	5.4	3.0	0.9
1992	0.0	0.0	0.0	0.0	0.0	0.0	0.9	1.5	0.0	0.8	3.2	2.6	9.5	1.6	0.5

Table 3c. BARENTS SEA COD. Frequency of occurrence (%) of cannibalism in cod stomachs, based on individual stomachs, in 1949–1960, 1973, 1975, 1980–1982, and 1984–1992.

	Predator length group (cm)													Pooled mean
	7–9	10–14	15–19	20–24	25–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100–119	(≥30 cm)
1949	–	–	–	–	–	100.0	5.3	6.5	11.9	12.5	9.1	0.0	50.0	10.1
1950	–	–	–	–	–	0.0	0.0	0.0	1.4	0.0	0.0	0.0	0.0	0.5
1951	–	–	–	–	–	–	–	0.0	33.3	8.3	28.6	–	0.0	16.0
1952	–	–	0.0	–	0.0	12.5	5.4	12.8	11.9	12.0	9.1	25.0	0.0	11.5
1953	–	–	–	–	0.0	0.0	0.2	1.5	0.9	7.1	11.1	33.3	–	1.2
1954	–	–	–	–	–	0.0	6.8	6.7	0.0	9.1	28.6	0.0	–	6.6
1955	–	–	–	–	–	–	0.0	4.6	5.2	8.0	0.0	0.0	–	4.8
1956	–	–	–	0.0	0.0	11.1	11.9	11.6	12.6	28.0	27.3	18.8	0.0	16.1
1957	–	–	0.0	0.0	3.0	7.1	5.0	4.5	6.7	11.3	2.6	3.3	16.7	6.3
1958	–	–	0.0	0.0	0.0	3.3	13.8	26.7	27.9	20.0	24.6	10.5	40.0	23.9
1959	–	–	–	–	0.0	4.0	4.3	9.7	15.6	14.6	13.5	2.7	33.3	11.2
1960	–	–	–	–	–	–	0.0	18.3	0.0	2.7	9.5	0.0	0.0	8.2
1973	–	–	–	–	–	0.0	0.0	0.0	0.0	16.7	33.3	50.0	–	1.7
1975	–	–	–	–	–	0.0	0.0	–	–	–	–	–	–	0.0
1980	0.0	–	–	–	–	–	0.0	0.0	0.0	6.7	0.0	0.0	0.0	0.2
1981	0.0	0.0	0.0	–	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–	0.0	0.0
1982	–	–	–	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
1984	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.2	0.3	1.6	0.0	0.0	3.1	0.3
1985	0.0	0.0	0.0	0.3	0.5	0.7	0.8	0.7	0.5	2.3	2.3	7.1	5.6	0.9
1986	0.0	0.0	0.0	0.0	0.0	0.5	0.6	1.1	1.7	4.0	17.9	26.7	0.0	1.3
1987	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.2	0.7	2.0	11.7	11.8	0.0	0.5
1988	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.4	0.7	0.9	0.0	0.0	11.1	0.3
1989	0.0	0.0	0.0	0.0	0.0	0.4	0.1	0.3	0.3	0.6	0.0	0.0	6.3	0.3
1990	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.3	0.4	0.1	0.7	0.0	0.0	0.3
1991	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.2	0.6	1.3	1.3	0.3	13.3	0.6
1992	0.0	0.0	0.0	0.0	0.7	0.7	0.8	0.0	1.6	0.6	0.3	2.2	0.0	0.8

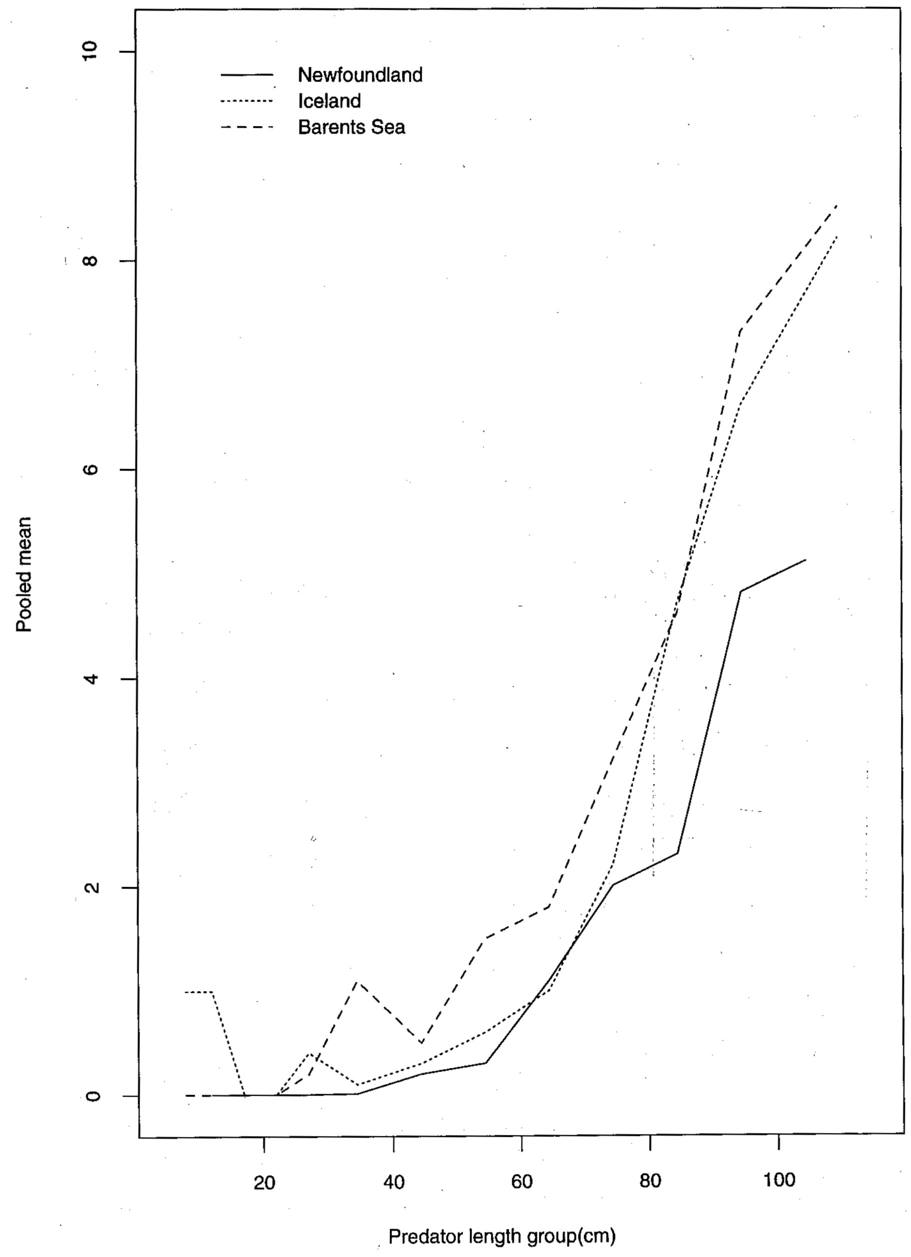


Figure 5. Variation in cannibalism with predator length measured as percentage weight of stomach content (pooled mean).

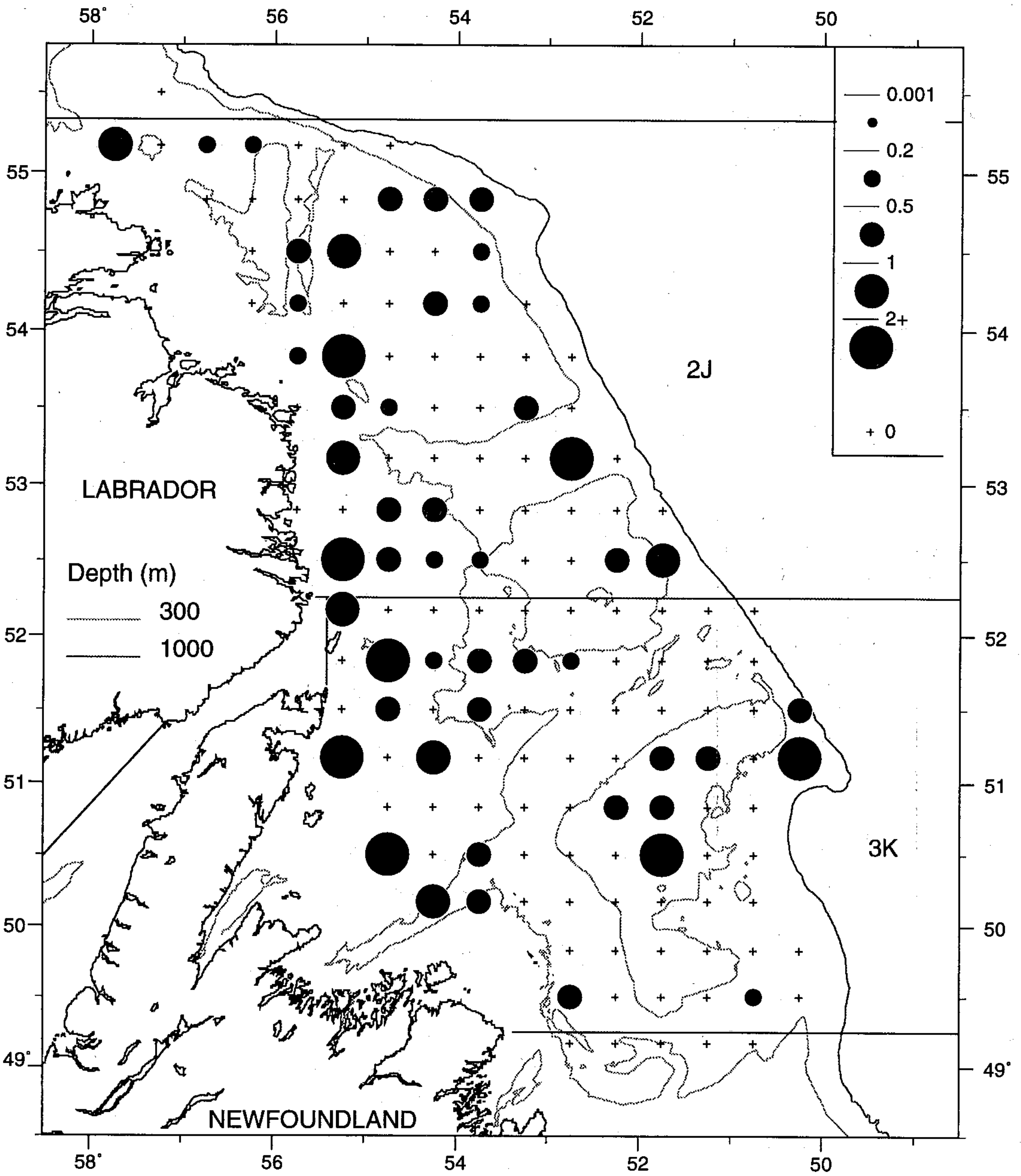


Figure 6. Spatial variation in frequency of occurrence of cannibalism in Newfoundland waters in the autumns of 1978 and 1980–1992. All stomachs collected from cod larger than 29 cm within squares of 20′ latitude and 30′ longitude were pooled. Squares with less than 20 stomachs were excluded. + indicates no occurrence.

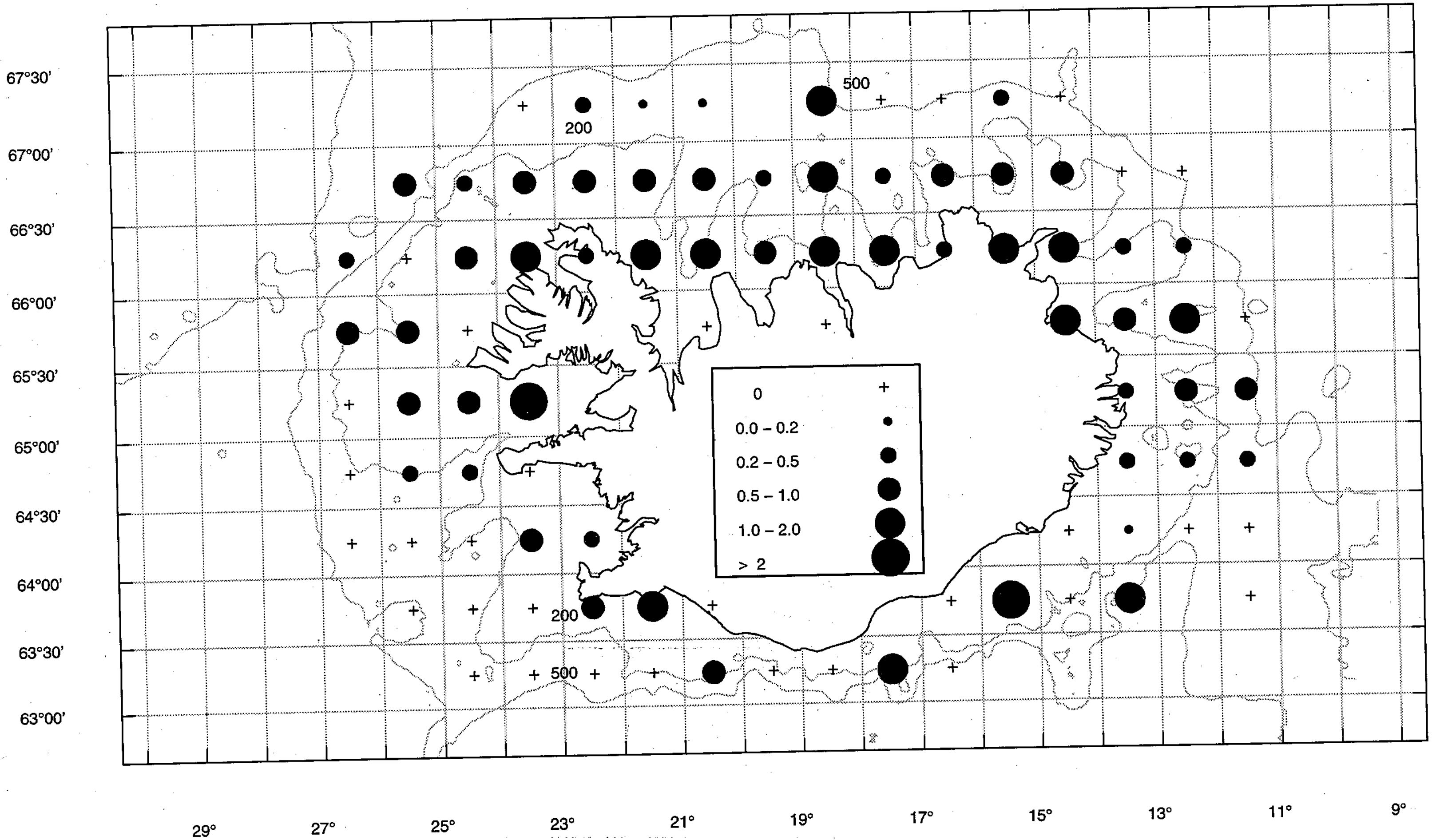


Figure 7. Spatial variation in frequency of occurrence of cannibalism in Icelandic waters 1979–1993. All stomachs collected from cod larger than 29 cm within squares of 30′ latitude and 60′ longitude were pooled. Squares with less than 20 stomachs were excluded. + indicates no occurrence.

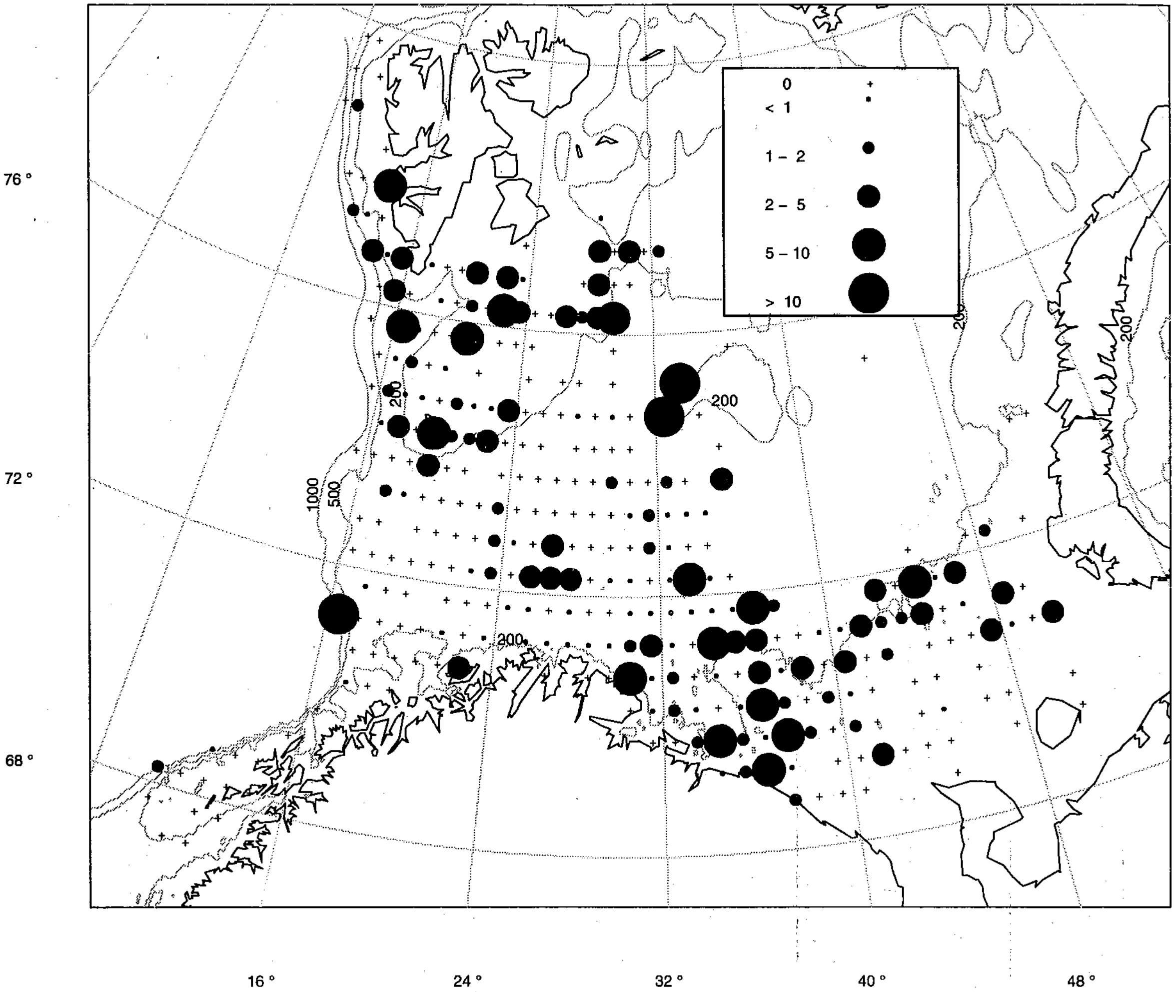


Figure 8. Spatial variation in frequency of occurrence of cannibalism in the Barents Sea 1949–1992. All stomachs collected from cod larger than 29 cm within squares of 30′ latitude and 60′ longitude were pooled. Squares with less than 20 stomachs were excluded. + indicates no occurrence.

Table 4. Correlations between the frequency of occurrence (FO) of cannibalism in cod in the Barents Sea, by half year, and juvenile abundance, capelin biomass, and the mean quantity of capelin in cod stomachs, expressed as a partial fullness index (PFI_c). See Fig. 11. For each pair, the number in parentheses is the probability that the correlation coefficient is zero. n = 9 in all cases.

	Juvenile abundance	Capelin biomass	PFI_c
FO (first half)	0.732 (0.025)	0.041 (0.917)	−0.021 (0.958)
FO (second half)	0.731 (0.025)	0.212 (0.583)	0.334 (0.380)

Consumption of cod by cod in the Barents Sea

Estimation of the contribution of cannibalism to the mortality of juvenile cod requires knowledge of the number of juveniles consumed at age. We used data from the Barents Sea in 1984–1991 to illustrate the magnitude and variability of the total consumption (tonnes) and the consumption (in numbers) of individual age groups (Table 5). The consumption in tonnes increased by a factor of almost 4 from 1984 to 1986 and then decreased to low levels in 1988 and 1989 before increasing again. The estimated consumption in numbers varied greatly among years, especially for the 0-group. Figures for the 1-group seemed to be more stable

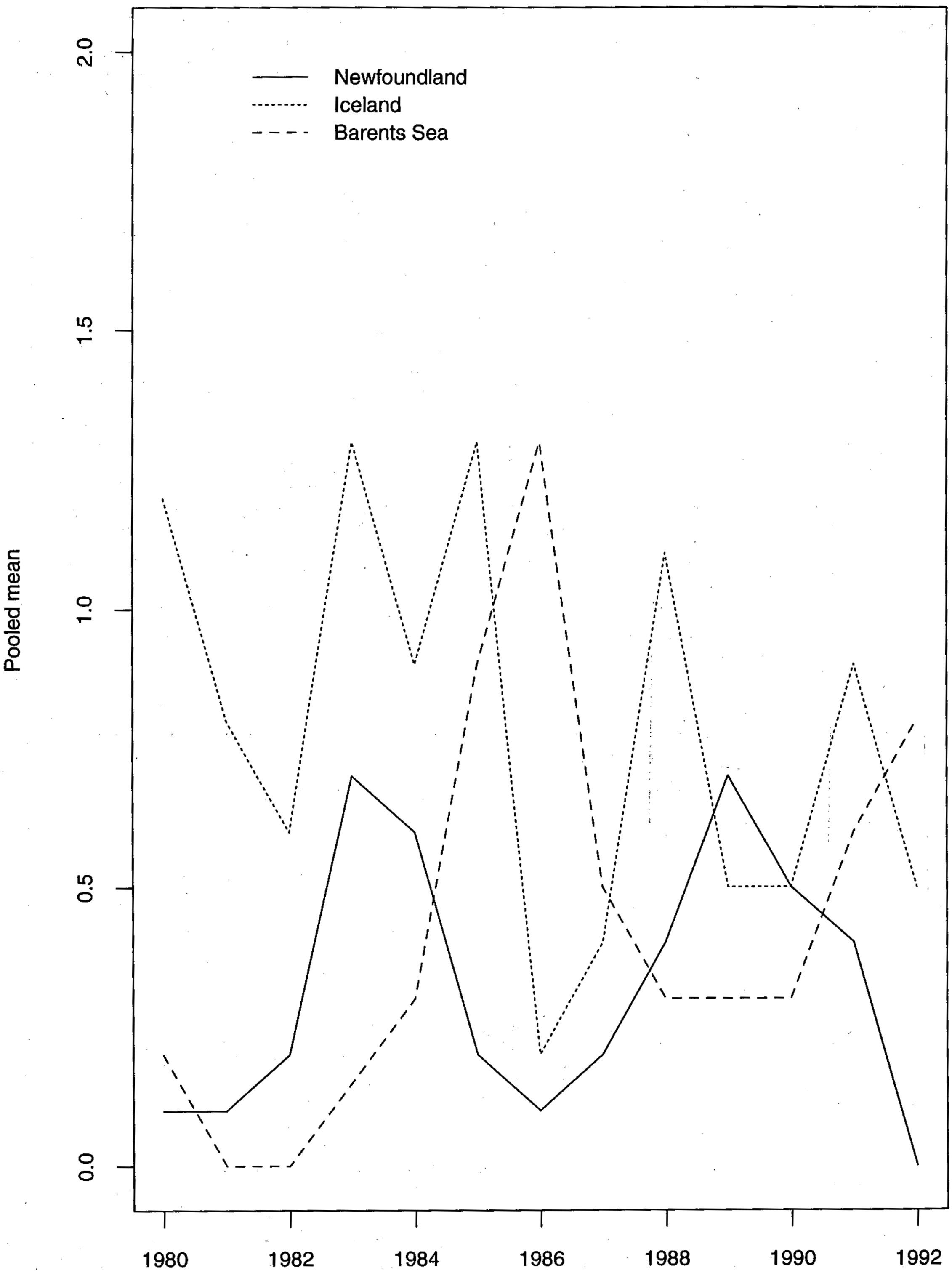
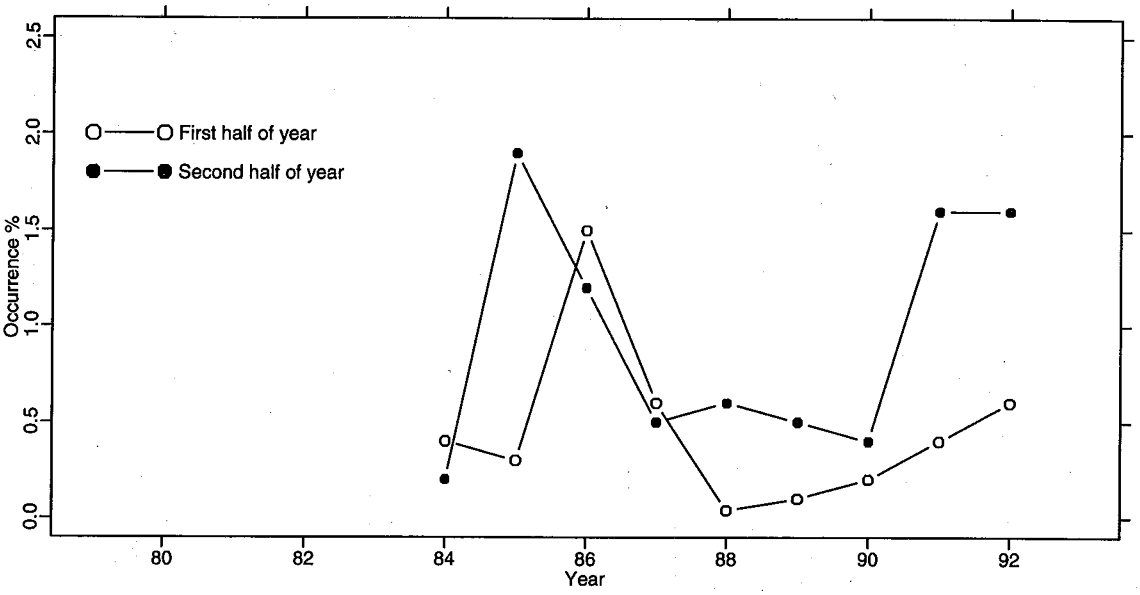


Figure 9. Year-to-year variability of cannibalism measured as percentage occurrence in predator length range 30–119 cm (pooled mean).



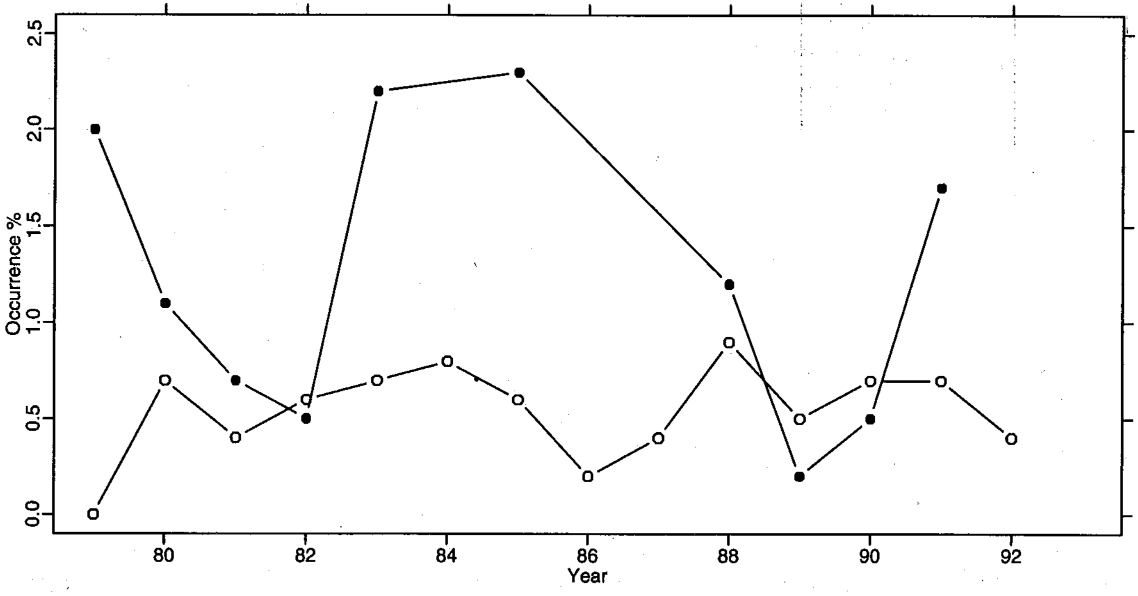


Figure 10. Year-to-year variability of cannibalism with respect to seasons measured as percentage occurrence in predator length range 30–119 cm (pooled mean), by half years in the Barents Sea and in March and autumn (September–December) in Icelandic waters.

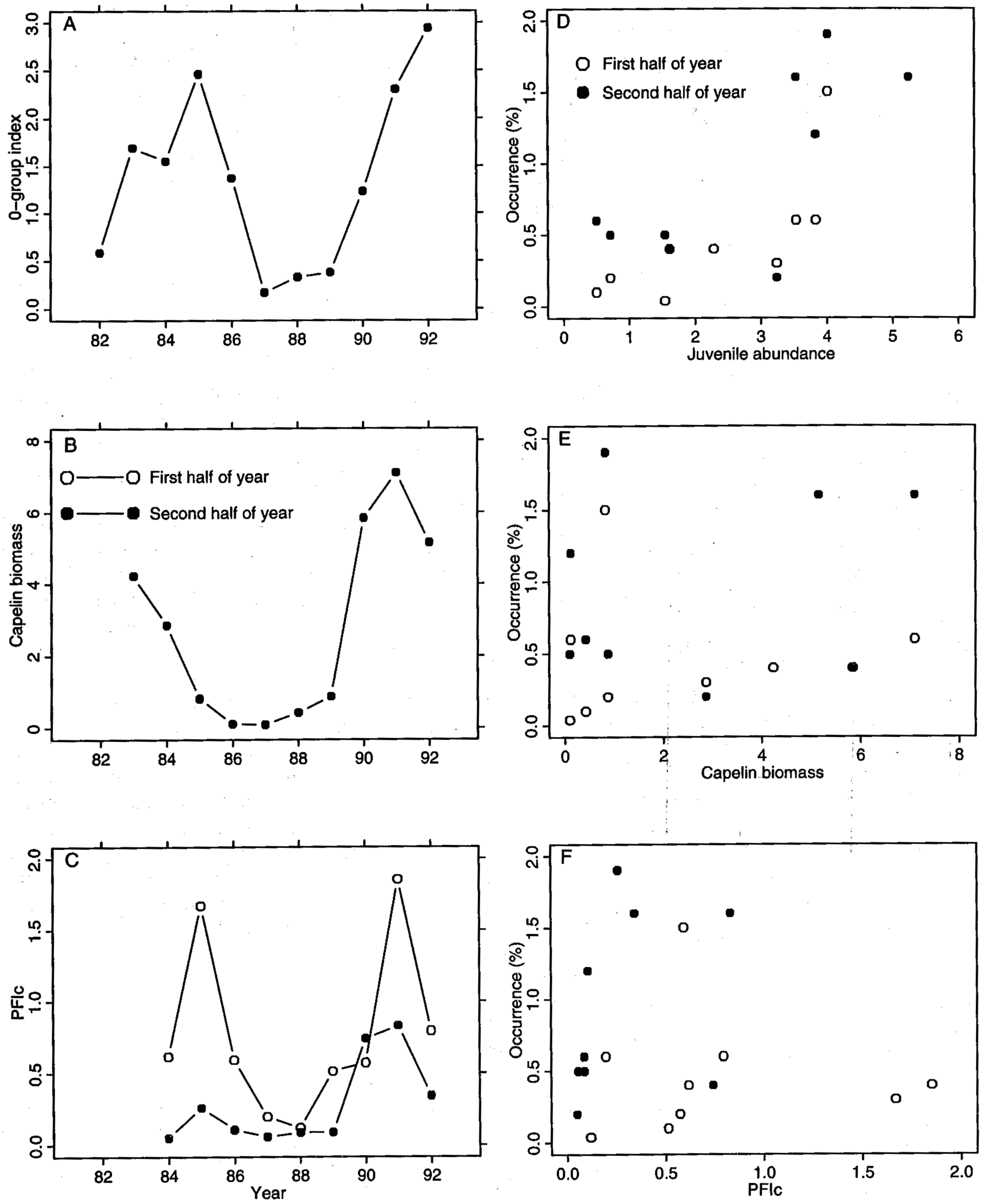


Figure 11. Annual variability in factors which might influence the frequency of occurrence of cannibalism in the Barents Sea. A. Abundance of juvenile cod as determined during pelagic 0-group surveys in late summer (ICES, 1992b). B. Biomass of capelin 1 year and older, as determined during acoustic surveys in the autumn (ICES, 1994). C. Average quantity of capelin in cod stomachs (PFIc), by half year. D. Frequency of occurrence of cannibalism by half year vs. juvenile cod abundance, where an index of juvenile abundance in the first half of year t was calculated as the sum of the indices from pelagic 0-group surveys in years t−1 and t−2, and an index for the second half of the year was calculated as the sum of the indices in years t and t−1. E. Frequency of occurrence by half year vs. capelin biomass, where capelin biomass for the first half of the year was that estimated in the autumn of year t−1 and the biomass for the second half was the estimate from year t. F. Frequency of occurrence versus PFIc, by half year.

Table 5. Consumption of cod by cod (numbers in millions) in the Barents Sea by prey age.

	Prey age group				Total consumption	
	0	I	II	III	(numbers)	(1000 t)
1984	–	504.0	70.0	0.6	574.6	33.2
1985	909.8	294.3	205.1	9.3	1418.5	52.6
1986	61.3	587.2	432.0	372.1	1352.6	125.0
1987	826.7	210.3	350.5	3.6	1391.1	32.8
1988	38.2	566.8	28.3	+	633.3	11.6
1989	1361.4	218.1	0.4	–	1579.9	11.4
1990	–	226.7	50.4	–	277.1	34.5
1991	95.3	246.7	111.9	71.8	543.7	53.6

(200–600 million). In absolute numbers consumed, the 1985 year class seems to have been the most affected (1850 million consumed).

A simple model of predation applied to Icelandic cod

Different models can be used in an attempt to estimate the effect of cannibalism. The following approach is a slight extension of that used by Pope and Woolner (1981) and provides a means of estimating the effect of cannibalism, independent of any evidence from stomach sampling. As will be seen, the actual effects estimated from the model may be due to either cannibalism or competition, since the two effects cannot be distinguished based on the data sets used.

Nilssen *et al.* (1994) constructed a stock and recruitment model for Northeast Arctic cod. They found that the recruitment increases with temperature and with higher spawning stock biomass but declines with increasing juvenile biomass. The form of the spawning stock–recruitment relationship indicates that recruitment increases roughly as the square root of spawning-stock abundance.

The recruitment process in Icelandic waters may be separated into several stages. The first stage can be taken from the time of spawning, mainly in April, to the time of settlement, roughly in September. During this period the eggs and larvae drift from the major spawning areas off the south and west coast clockwise around Iceland to the main nursery areas off the north and east coast. The first measurements of year-class strength are made near the end of the first period, during the 0-group survey in August–September. Later, in March, a groundfish survey is conducted. This survey provides indices of abundance which are used in tuning the VPA estimates.

Cannibalism of eggs and larvae in the southern and western areas has not so far been observed and will not be considered in the analysis. It is, however, well established that cannibalism occurs in the northern and eastern areas and therefore it is reasonable to start a model of cannibalism at the time of the 0-group survey. This separates the pre-recruit (juvenile) period into two parts: the period from spawning to the 0-group survey, and from the time of the 0-group survey until the time of recruitment at age 3 to the fishery.

The original model by Pope and Woolner (1981) connected the VPA estimates of recruitment with other factors, such as spawning stock size, abundance of immature fish and abundance of other species in order to separate out the effects of spawning, cannibalism, and predation.

To investigate further the processes involved, a composite model can be used. Pope and Woolner's approach allows the inclusion of various terms in such a fashion as to first estimate the stock–recruitment function and then add onto that function the effects of different factors, entered basically like M-values. The spatial distribution of adults and juvenile cod in Icelandic waters is such that mature fish would be expected to contribute to the abundance through the usual stock–recruitment curve, whereas there is spatial overlap after 0-group settlement with the older immature fish. A composite model of the two stages can therefore be written as follows:

$$\mathrm{I}_0 = \alpha \mathrm{S}^{\beta}$$

$$\mathrm{R}_3 = \xi \mathrm{I}_0^{\eta}\, \mathrm{e}^{\zeta \mathrm{J}},$$

The first equation describes the period from spawning to settlement (Fig. 12, top) and the second the period from settlement to the 3-group stage (Figure 12, middle). In these equations, I_0 denotes the 0-group index and R_3 the VPA recruitment at age 3. S is the spawning-stock biomass and J an index of the abundance of immature fish (juveniles) which may prey on the year class in question. The various constants need to be estimated by the use of regression.

This provides a means to test separately the processes involved before and after the settlement stage. The first model basically is a Cushing curve (Cushing, 1973). This

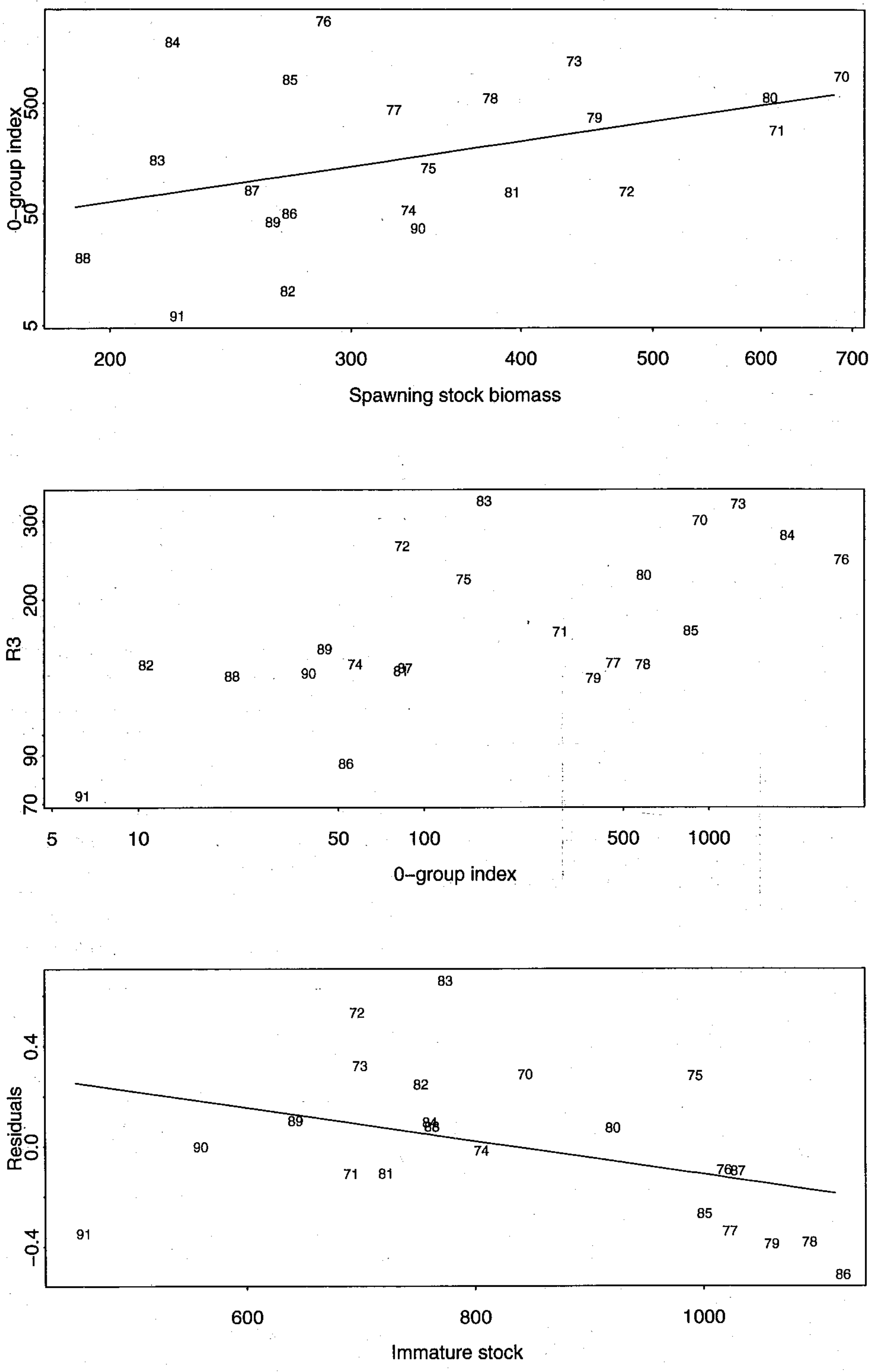


Figure 12. Basis for simple models of predation by Icelandic cod (Table 6). Top: 0-group index versus spawning-stock biomass. Middle: 0-group index versus VPA 3-group. Bottom: Residuals from regression of R_3 on 0-group (I_0) versus immature stock (J).

model can easily be fitted and tested on a log-scale and it is found that the model is marginally significant ($p = 0.07$) which in itself is a very interesting result. It should be noted (as in Pope and Woolner, 1991) that cannibalism by adults during the pre-settlement stage is already in this equation. This particular cannibalism will be incorporated in the regression and it appears in reduced values of the 0-group index with increasing spawning stock size in Figure 12.

The second equation is much more interesting, however. This formulation allows ζJ to appear like an M-value affecting the 0–2 group cod: the second equation first describes how a given 0-group survives to become 3-group in an "average" year, if there were no older year classes (Fig. 12, middle). The $e^{\zeta J}$-term then acts to diminish this in accordance with the size of the older, but immature, year classes (Fig. 12 bottom). In this equation, J is based on VPA values for the abundance of immature cod age 3 and older, but shifted by one year so as to provide an index of the abundance of immature 2+ cod in the year of spawning. Units of measurements are given with the data in Table 6. It should be noted that spurious correlation is not introduced between the variables in the second equation through tuning, since only groundfish survey but not 0-group survey indices are used to tune the VPA.

Other factors can be used in both equations, for example J can be added to the first one and S to the second. Basic regression analysis indicates that no such additions are significant. This gives support to the hypothesis that the effect of the SSB is completely described during the pre-settlement stage and that the effect of cannibalism/competition is mostly a function of the amount of older immature fish on the nursing grounds.

Table 6. Input data for a model of the mortality induced by cannibalism in Icelandic cod (SSB = spawning-stock biomass, '000 t, J = juvenile stock, '000 t, R_3 = recruitment at age 3, millions and I_0 = 0-group index).

	SSB	J	R_3	I_0
1970	678.742	837.545	300.418	873
1971	608.973	684.324	169.263	283
1972	472.207	690.300	263.221	79
1973	431.856	692.639	326.284	1191
1974	326.652	799.028	143.285	54
1975	337.628	986.362	221.651	130
1976	282.578	1011.59	245.472	2743
1977	318.643	1016.62	143.982	435
1978	374.998	1086.02	143.163	552
1979	447.179	1053.00	133.346	370
1980	601.718	914.336	226.258	558
1981	389.082	715.310	138.628	78
1982	266.122	746.255	143.084	10
1983	213.546	767.857	331.452	153
1984	219.014	753.965	277.658	1772
1985	267.120	994.235	170.280	812
1986	266.754	1115.12	86.206	50
1987	250.569	1023.62	140.657	81
1988	188.486	755.740	135.000	20
1989	259.479	636.227	155.000	42
1990	331.919	553.647	137.000	37
1991	220.958	451.556	73.000	6

The second equation was linearized by taking logarithms on both sides and fitted to data from the period 1970–1991 (Table 6, ICES, 1993a). The R^2-value from the regression is 0.54 and the parameters in the equation were significantly different from zero:

Parameter	Coefficient of	Value	Std. Error	t value
$\ln(\xi)$		4.8429	0.2972	16.2975
η	ln(I0)	0.2011	0.0424	4.7386
ζ	J	−0.8554	0.3869	−2.2109

Now, the term ζJ, which appears as an M-value, reflects an overall M over the period from the beginning of September in year 0 through December of year 2, i.e., 2.33 years. Since the average of J is 0.831, the point estimate, −0.855, of ζ indicates that M inflicted on 0–2 group cod may be in the order of 0.71 due to cannibalism, as an average value over the years 1970–1991.

It can be deduced that the confidence interval for the ζ-value is roughly from −1.6 to −0.08, corresponding to an average 2.33-year M-value in the range 0.067 to 1.35.

Several important questions immediately come up, one of which is whether the significance of these results is simply due to a few outliers. Regression diagnostics do indeed indicate that there are several highly influential points and outliers. Stepwise deletion of such points is a useful way to consider the sensitivity of the result. The following table summarizes the effects of outlier deletion and also of changes in model assumptions.

Model $\ln(R_3) = \ln(\xi) +$ $\eta \ln(I_0) + \zeta J$	Years	Coefficients Intercept $\ln(\xi)$	 ln (I_0) η	 J ζ
Linear regression	1970–1991	4.843	0.201	−0.855
	Omit 91	5.254	0.174	−1.143
	Omit 90,91	5.478	0.167	−1.342
	Omit 83,90,91	5.352	0.167	−1.229
Least median squares regression	1970–1991	5.954	0.152	−1.796
Robust (M-estimation) regression		4.893	0.197	−0.900
L1 (median absolute residual) regression		4.868	0.180	−0.784
Least trimmed squares regression		4.944	0.233	−1.304
GLM with gamma error and log link		4.954	0.194	−0.904

It is seen that the coefficient of J varies from −1.8 to −0.9, depending on the model assumptions made, corresponding to a 2.33-year average M-value in the range 0.75–1.50. The range may seem somewhat wide, but it should be noted that in all cases the coefficient does have the expected (negative) sign.

The natural mortality due to cannibalism would be expected to be decreasing with respect to age and this decrease may even be expected to be exponential. A simpler approach may be taken, assuming that the 2.33-year value of 0.71 represents the sum of monthly M-values which decrease linearly from the last September as 0-group to zero in January as 3-year-olds. This yields estimates average M due to cannibalism (or competition) as 0.19 during September–December of the 0-group stage, 0.39 as 1-group, and 0.14 as 2-group.

Discussion

In offshore waters of northeastern Newfoundland, Iceland, and the Barents Sea, cannibalism is rare in cod less than 30 cm in length, but becomes more frequent as the cod grow. A comparison between lengths recorded in this study and aging data published elsewhere indicates that many prey are 0-group, especially off Iceland and in the Barents Sea, and that most prey are younger than 3 years. Almost all the cannibals were at least twice the length of their prey and most were more than three times longer. Therefore, most of the cannibalism documented in this study involves intercohort predation. This appears to be the norm among cannibalistic fish (Smith and Reay, 1991). Intracohort cannibalism was recorded only in 0-group cod off Iceland in autumn 1990.

The contribution of cannibalism to the diet of cod, expressed on a percentage weight basis, increased with cod length in all three areas. It was highest in the Barents Sea, lowest off Newfoundland, and intermediate off Iceland, but did not exceed 9% on average even in the largest cod. Cannibalism has been found to account for a larger part of the diet in other gadid species, such as walleye pollock, *Theragra chalcogramma* (Dwyer *et al.*, 1987) and several hakes, *Merluccius* spp. (Lleonart *et al.*, 1985; Clay *et al.*, 1984).

The distribution of cannibalism in three areas is in general agreement with the distribution of small fish as determined by trawl surveys. In the Newfoundland area, cannibalism was high on the coastal shelf off southern Labrador and northeastern Newfoundland, where small cod have been caught most consistently during autumn bottom-trawl surveys (Anderson, 1993). Observations on the outer banks correspond to areas where older (age 2 and 3) cod are common. In the Iceland area, cannibalism was most commonly recorded in the north, which is consistent with Pálsson's (1980) finding that the most important nursery grounds were located off the north and northern northwest coasts. In the Barents Sea, cannibalism occurred most frequently in the east and in the Svalbard area, where overlap between large and small cod is most common. An examination of the distribution of cannibalism by age group of the prey is beyond the scope of this article, but may provide information on ontogenetic shifts in distribution and susceptibility to cannibalism.

The frequency of occurrence of cannibalism increases with the abundance of juvenile cod. In the Newfoundland area, the frequency of occurrence of cannibalism was positively correlated with the catch of young cod in bottom trawl surveys. In the Iceland area, the frequency of occurrence was somewhat higher in 1979–1985 than in more recent years, which is consistent with better recruitment during the earlier period. In the Barents Sea, the frequency of occurrence of cannibalism during the period 1984–1992 was positively correlated with indices of abundance of pelagic 0-group cod. The frequency of occurrence in all three areas was much lower than had been reported from stomach collections in the Barents Sea during the period 1949–1960. This may be related to higher levels of recruitment in the earlier period, but it is also possible that higher values in the earlier period were caused in part by smaller sample sizes from more restricted areas and time periods. Additional research is required before it can be concluded that cannibalism in cod in the Barents Sea was much more common in the 1950s than in more recent years.

The hypothesis that cannibalism in Barents Sea cod increases in years of low abundance of major prey was not supported. A negative correlation was not found between the frequency of occurrence of cannibalism and either the biomass of capelin or the average quantity of capelin found in cod stomachs. This conclusion must be treated with caution because of uncertainties in the calculation of each variable and the shortness of the time-series.

The estimates of the number of cod consumed by cod in the Barents Sea are of the same order of magnitude as the strength of an average year class at age 3 (600 million), as estimated by virtual population analysis (ICES, 1993b). The accuracy and precision of such estimates of consumption are difficult to judge. As noted by many investigators (e.g. Dwyer *et al.*, 1987; Magnússon and Pálsson, 1989; Mehl, 1989; Bowering and Lilly, 1992), there is considerable uncertainty in many of the values entering such calculations, including the stock abundance estimates, the stomach content data, and the parameters of the gastric evacuation model. Of particular concern is the potential variability in the timing of resource assessment surveys relative to the timing of settlement of the 0-group juveniles. Even when the numbers of young cod consumed by older cod can be reliably estimated, it will be difficult to evaluate the contribution of cannibalism to total natural mortality without measures of absolute abundance over time. In instances where cannibalism is thought to be a major contributor to total natural mortality, it may be included in a virtual population analysis, but some value for the remaining natural mortality must still be assumed (Lleonart *et al.*, 1985).

The data reported in this study are confined to offshore waters covered by bottom trawl surveys. The extent of cannibalism landward of the survey areas is unknown, but might be important. For example, 0-group and 1-group cod are abundant in shallow coastal waters of eastern Newfoundland (Methven and Bajdik, 1994) and older juveniles (ages 2 and 3) are commonly caught and observed (Stevenson *et al.*, 1984; Clark and Green, 1990). Cannibalism has been found in cod near the coast, especially at times other than the few weeks in early summer when capelin are aggregated at the coast to spawn (Templeman, 1965; G. R. Lilly, unpubl. data).

The frequent occurrence of cannibalism on 0-group off Iceland and in the Barents Sea contrasts with the low occurrence found off Newfoundland. This may be related to the degree of overlap between demersal 0-group and larger conspecifics. The high abundance of juvenile cod in shallow coastal waters of eastern Newfoundland, and the lack of evidence for large numbers in adjacent offshore waters, has led to the hypothesis that the nursery area for this stock is inshore (Templeman, 1981). Juvenile cod have been reported in coastal waters elsewhere, such as in Norway (Godø *et al.*, 1989; Olsen and Soldal, 1989; Tveite, 1984) and the British Isles (Hawkins *et al.*, 1985; Riley and Parnell, 1984). In such habitats, the juveniles may be physically separated from larger cod, at least for much of the year, and may be less susceptible to predation. However, there are also observations of abundant juveniles in shelf habitats, such as Georges Bank (Lough *et al.*, 1989), the southern Grand Bank of Newfoundland (S. J. Walsh, Dept. of Fisheries and Oceans, St John's, Newfoundland, Canada, pers. comm.), Flemish Cap (Lilly, 1987), Iceland shelf (Pálsson, 1980), and the Barents Sea (Ponomarenko, 1984). In such areas there may be greater opportunity for cannibalism. Studies of ontogenetic changes in distribution in each stock are vital to understanding the intensity of cannibalism and its potential for influencing recruitment.

Models for the relationship between the abundance of 0-group and the number of recruits as 3-group indicate that there is a positive relationship. Further, the abundance of older, immature fish has a negative effect on the survival. However, the abundance of mature fish does not show a significant effect. This may seem in contrast with the results obtained elsewhere concerning the diet of cod in different length groups, but it is clear that the abundance of the mature fish is much less than of the immatures, and hence relative stomach contents do not reflect the relative mortalities inflicted by the different stock components.

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