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Northwest Atlantic



Fisheries Organization

Serial No. N735

NAFO SCR Doc. 83/IX/70

FIFTH ANNUAL MEETING - SEPTEMBER 1983

The Feeding Habits of Demersal Fish Species in Icelandic Waters¹

by

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¹ This is published in Rit Fiskideildar, 7(1), 1983 (Journal of the Marine Research Institute Reykjavik).

TABLE 1
Summary of investigations on food and feeding of marine fish species in Icelandic waters.

Author	Year of publ.	Species investigated		Age or length of predator	Grouping of predator by age or length	Methods of prey evaluation
		Number	Names (Number of stomachs)			
Ólafsson	1772	2	Haddock, catfish			Qualitative description
Faber	1829	33				Qualitative description
Sæmundsson	1926	92				Qualitative description
Thompson	1929	1	Haddock (110)		None	Displacement volume
Jespersen	1932	1	Herring (3455)	Adult	None	"Volume after settlement"
Meschkat	1936	1	Cod (1245)	Adult	None	Numbers; frequency of occurrence
Fríðriksson	1944	1	Herring (15836)	Adult	None	Displ. volume
Óskarsson	1944	1	Haddock	Juvenile	None	Qualitative description
Brown and Cheng	1946	2	Cod (231), haddock (40)	Adult	None	Numbers
Fríðriksson and Timmermann	1950	1	Haddock (1890)	Adult	None	Qualitative description
Rae	1963	1	Megrim (420)	11-60 cm	5 length groups	Freq. of occurrence; Displ. volume
Einarsson	1960	1	Redfish (120)	Larvae <45 mm	4 length groups	Qualitative description
Jónsson	1966	1	Dab (485)	2-11 years	16-25, 26-30, >30 cm	Qualitative description
Bainbridge and McKay	1968	2	Cod (190), redfish (870)	Larvae <30 mm	1 mm length groups	Numbers; weight
Rae	1968	1	Cod (2943)	21-135 cm	21-50, 51-135 cm	Freq. of occurrence; "degree of fullness"
—	1969	1	Witch (105)	11-50 cm	4 length groups	Freq. of occurrence; Displ. volume
Pálsson	1973	6	Redfish (565), capelin (449), snake blenny (120), cod (363), haddock (159), blue whiting (85)	0-group 31-128 mm	0-5 length groups	Numbers; dry weight
Ingimarsson	1974	1	Haddock (200)	13-80 cm	None	Numbers
Steinarsson	1979	3	Lemon sole (119), megrim (205), witch (153)	21-60 cm	4 length groups (10 cm each)	Numbers; displ. volume
Pálsson	1980a	3	Cod (1433), haddock (1476), whiting (637)	Juvenile	0, I, II group by quarters	Displ. volume
—	1980b ¹⁾	5	Cod (1211), redfish (251), haddock (507), catfish (440), long rough dab (417)	Juv.-adult	5-10 length groups (10 cm each)	Wet weight
—	1981 ²⁾	5				

¹⁾ Presentation of material sampled in 1979. Cod and haddock included in the present paper.

²⁾ Preliminary presentation of material sampled mainly in 1980. Included in the present paper.

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ABSTRACT

On the basis of material sampled in 1976-81 the feeding habits of seven demersal fish species in Icelandic waters are described.

The feeding of cod is characterized by the preference for fish prey, particularly pelagic species such as *M. villosus* and *M. poussou*. Pronounced seasonal, regional and year to year variations are observed. With increasing length of cod the food composition changes clearly from planktonic and benthic prey (Euphausiacea) over to small pelagic fish (*M. villosus*), and finally to large pelagic (*M. poussou*) or demersal fish (*Sebastes*, *G. morhua*) in the largest predator length groups. On an annual basis *M. villosus* is by far the most important prey and is estimated to yield 30% of the food of cod. The preference of cod for a particular prey is found to depend on the size of the predator in relation to that of the prey. However, this relationship may differ with respect to a particular prey as well as on a seasonal basis.

With respect to prey preference redfish may be classified as a zooplanktonic feeder, preying mainly on Euphausiacea and Calanoida. Saithe may be described as a transitional predator of zooplanktonic (Euphausiacea) and nektonic (*M. villosus*) animals. Haddock, plaice, long rough dab and catfish, on the other hand, are preferably benthic feeders, which mainly prey on Ophiuroidea and Polychaeta, although occasionally they are fish consumers.

The average quantity of the stomach content is related to predator length by a power function, with different regression coefficients for each predator. In this respect variations for a particular predator are also observed on a seasonal or a year to year basis.

From the point of view of general trophic relationships the predatory impact of cod is of greatest interest, particularly in the context of quantifying relevant predator-prey interactions of commercially exploited fish stocks.

INTRODUCTION

The otolith has sometimes been referred to as the "passport" of the fish. Although somewhat exaggerated this reflects quite well the emphasis of fisheries science in the last decades. However, it is well known that a passport contains more information than age. One is the occupation of the bearer. The content of the fish stomach gives information on the "occupation" of the fish, i. e. its trophic status in the ecosystem. Therefore, the stomach must be considered as an essential part of the "passport" of the fish

and should be studied with no less effort than the otolith.

The food of fish in Icelandic waters was described in a scientific publication, presumably for the first time, as early as 1772, when Eggert Ólafsson made brief remarks on the food of haddock and catfish. More than half a century later Friedrich Faber (1829) published his account of the natural history of fishes around Iceland which includes qualitative descriptions of the food of 33 marine fish species. In the beginning of this century Bjarni Sæmundsson (1926) gave a similar, although more accurate, descrip-

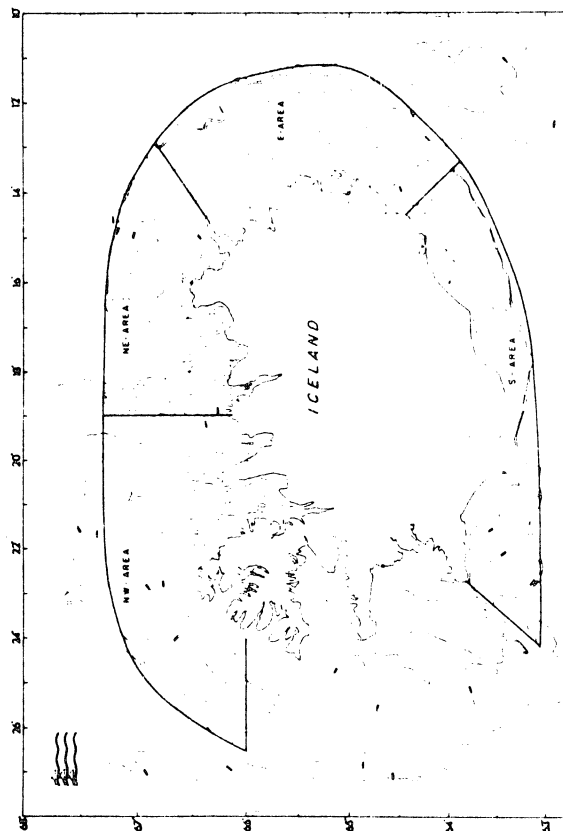


Fig. 1. The division of Icelandic waters into areas for the investigation of the food of demersal fish species.

tion of virtually all fish species known in Icelandic waters at that time.

During the last 50 years these qualitative descriptions were followed by several publications, in which qualitative methods gradually gave way to quantitative ones (Table 1). Furthermore, grouping of the predator has been increasingly adopted in the last two decades. These publications cover 14 fish species (Table 2). The cod have been most thoroughly investigated, taking into account the coverage of different life stages and the methods applied, followed by haddock and redfish. In the thirties the feeding of the adult herring stock was intensively studied. In other cases the material has been rather limited with respect to the number of stomachs analysed for food. Nevertheless, the available results give a good description of

the general feeding ecology of the most important demersal fish stocks in Icelandic waters.

In recent years the attention of marine scientists has been increasingly directed to species interaction. This interest is not only of purely scientific origin, but may also be related to the obvious need of modern fisheries management to quantify the predator-prey relationships which affect commercially important fish stocks. Thus, efforts to investigate the food of commercial fish stocks have been initiated in several countries of the North Atlantic in the last years (Anon., 1980), in order to establish the biological basis for species interaction models of fish stocks. This paper describes investigations on the food of demersal fish species carried out in Icelandic waters since 1976.

TABLE 2
Number of fish stomachs analysed for food in Icelandic waters by species and life stages according to publications during 1929-80.

Species	Life stage				Total
	Larvae	Pre-Group	Juvenile	Juv.-adult	
Herring	—	—	—	19,291	19,291
Capelin	—	449	—	—	449
Cod	190	363	1,433	4,154	7,616
Haddock	—	159	1,476	617	4,382
Blue whiting	—	85	—	—	85
Whiting	—	—	637	—	637
Catfish	—	—	—	440	440
Snake blenny	—	120	—	—	120
Redfish	990	565	—	251	1,806
Megrim	—	—	—	625	625
Witch	—	—	—	258	258
Long rough dab	—	—	—	417	417
Dab	—	—	—	385	385
Lemon sole	—	—	—	119	119

MATERIAL

The material includes seven demersal fish species in Icelandic waters. Their average share in the Icelandic demersal catch of 550,000 tons during 1976-1981 is shown in the following (Anon., 1982):

Common name	Scientific name (Jonsson, 1970)	Percentage of demersal catch
Cod	Gadus morhua morhua (L.)	66.9
Haddock	Melanogrammus aeglefinus (L.)	8.3
Saithe	Pollachius virens (L.)	9.6
Carfish	Anarhichas lupus L.	1.8
Redfish	Sebastes marinus marinus (L.)	9.8
Long rough dab	Hippoglossoides platessoides (Bloch)	0.0
Plaice	Pleuronectes platessa L.	0.8
Total		97.2

The species dealt with thus represent the major exploited demersal fish stocks in Icelandic waters. The long rough dab is not commercially exploited, although it is probably the most common flatfish on Icelandic fishing grounds.

Systematic sampling of fish stomachs was

carried out from May 1976 in the continental shelf waters around Iceland. Most of the material was sampled in the northern and eastern waters (NW-, NE-, and E-areas, Fig. 1). Limited material was sampled in the southern area, but none at all off the west

coast (Table 3). From the beginning the main object of this project was to investigate the feeding of cod. Haddock was sporadically sampled in the first three years. In 1979 catfish, redfish and long rough dab were included. The main results obtained from the material sampled in 1979 were described by

TABLE 4
Number of cod stomachs analysed for food by predator length groups and sampling periods.

Length group (cm)	Sampling period (year and month)																
	1976			1977			1978			1979		1980			1981		
	5	8-9	11	3	7	11-12	2-3	6-7	12	3	11-12	3	7	10-11	3-4	9	11
5-9	0	0	12	0	0	7	0	0	0	25	39	—	—	—	—	—	—
7-9	—	—	—	—	—	—	—	—	—	—	—	28	0	98	45	37	1
10-14	—	—	—	—	—	—	—	—	—	—	—	49	13	43	97	26	6
10-19	44	21	25	101	34	167	46	57	22	55	60	—	—	—	—	—	—
15-19	—	—	—	—	—	—	—	—	—	—	—	56	39	29	29	71	57
20-24	—	—	—	—	—	—	—	—	—	—	—	79	55	73	86	60	91
20-29	145	20	45	110	54	211	81	140	273	73	68	—	—	—	—	—	—
25-29	—	—	—	—	—	—	—	—	—	—	—	80	80	91	95	74	75
30-39	146	49	51	82	77	222	106	154	453	79	70	90	97	112	330	125	126
40-49	114	60	133	158	136	208	95	168	392	89	69	97	101	115	113	145	166
50-59	83	63	185	184	199	249	125	174	347	83	73	—	103	116	120	151	189
50-69	—	—	—	—	—	—	—	—	—	—	—	116	—	—	—	—	—
60-69	69	64	135	168	181	269	128	185	338	60	72	—	103	112	326	154	195
70-79	45	48	76	88	131	164	73	124	260	59	65	—	90	110	106	161	177
70-99	—	—	—	—	—	—	—	—	—	—	—	162	—	—	—	—	—
80-89	10	18	21	47	71	93	22	57	111	24	64	—	94	100	98	142	136
90-99	8	6	11	5	23	35	18	20	42	3	52	—	69	63	62	92	118
100-109	0	6	0	1	8	7	3	6	11	1	19	—	34	11	11	—	—
100-129	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	36	57
100-149	—	—	—	—	—	—	—	—	—	—	—	27	—	—	—	—	—
110-119	0	1	1	0	6	2	4	5	1	1	7	—	17	2	1	—	—
120-129	0	0	0	0	0	0	0	3	0	0	1	—	11	1	1	—	—
130-139	0	2	0	0	1	2	1	0	1	1	0	—	2	1	0	—	—
Total	664	238	695	944	921	1,636	702	1,093	2,251	553	659	784	908	1,077	1,520	1,274	1,394

TABLE 3
Number of fish stomachs analysed for food in 1976-81 by predator species, area and sampling periods. 10 indicates that sampling was planned, but no stomachs were found. — No sampling planned in the area or predator length group in question. Applies to Tables 1-6)

Sampling period (year and month)																		
Predator	Area	1976			1977			1978			1979			1980			Total	
		5	8-9	11	1	7	11-12	1	7	11-12	1	7	11-12	1	7	11-12		
Cod	NW	330	208	106	250	416	693	161	515	726	239	204	319	471	481	487	6,175	
	NE	32	119	349	408	244	564	315	999	885	233	254	510	346	477	5,183		
	E	302	31	180	206	261	359	226	179	640	111	201	302	539	438	4,330		
	S	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Total	664	358	695	944	921	1,636	702	1,093	2,251	553	659	784	908	1,077	1,520	17,433	
Haddock	NW	—	34	56	95	—	—	131	274	64	102	96	123	211	125	—	1,311	
	NE	—	39	10	50	—	—	—	212	75	79	94	105	109	138	—	801	
	E	—	—	108	132	—	—	92	422	90	97	263	59	191	60	—	1,514	
	S	435	—	—	—	—	—	—	—	—	—	—	—	192	191	126	—	944
	Total	435	73	174	277	—	—	223	908	229	276	645	476	617	313	—	—	4,670
Saithe	NW	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	65	
	NE	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	49	
	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	87	
	S	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	12	
	Total	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	213
Calfish	NW	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	106	
	NE	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	499	
	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	833	
	S	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	19	
	Total	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2,157
Redfish	NW	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	683	
	NE	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	429	
	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	505	
	S	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	57	
	Total	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1,674
Lung rough lab	Total	—	—	—	—	—	—	—	—	109	142	322	307	451	263	—	—	575
	NW	—	—	—	—	—	—	—	—	72	61	96	126	115	105	—	—	664
	NE	—	—	—	—	—	—	—	—	102	51	98	137	106	100	—	—	657
	E	—	—	—	—	—	—	—	—	61	70	141	153	92	98	—	—	197
	S	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Plaice	Total	—	—	—	—	—	—	—	—	335	182	335	481	497	393	—	—	2,123
	NW	—	—	—	—	—	—	—	—	—	—	—	—	72	23	42	—	137
	NE	—	—	—	—	—	—	—	—	—	—	—	—	41	30	54	—	125
	E	—	—	—	—	—	—	—	—	—	—	—	—	34	65	56	—	155
	S	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total	Total	—	—	—	—	—	—	—	—	—	—	—	—	147	118	152	—	417

In order to cover size specific changes in the feeding habits of the predators, their length range has been divided into length groups (Tables 4-6). The smallest length groups have not always been adequately sampled since the juvenile fish are not accessible to the bottom trawl used for sampling, or these fish are not available in the survey area. The largest length groups are often poorly sampled because of the scarcity of the oldest fish. The medium length groups, on the other hand, have been adequately sampled, and will not be dealt with any further as far as catfish, redfish and long rough dab are concerned, because of its limitations compared to the material sampled later. Saithe and plaice were sampled in limited numbers in 1980 and 1981. The most effective sampling was carried out in 1980 and in March 1981. In general the sampling has covered the relevant distribution areas of the predator species except for plaice and adult redfish, which are also found off the southwest and the west coast.

TABLE 5
Number of haddock and suite stomachs analysed for food by predator length groups and sampling periods.

Length group (cm)	Sampling period (year and month)											
	Haddock						Suite					
	1976	1977	1978	1979	1980	1981	1980	1981	1981	1981	1981	1981
5-9	0	0	0	0	0	0	0	0	0	0	0	0
7-9	—	—	—	—	—	—	—	—	—	—	—	—
10-14	—	—	—	—	—	—	—	—	—	—	—	—
15-19	42	0	50	103	18	105	35	44	0	101	42	0
20-24	—	—	—	—	—	—	—	—	—	—	—	—
25-29	—	—	—	—	—	—	—	—	—	—	—	—
30-34	56	10	20	41	32	96	31	42	—	—	—	—
35-39	—	—	—	—	—	—	—	—	—	—	—	—
40-44	90	19	27	60	50	241	50	40	141	86	94	55
45-49	95	20	29	50	53	193	54	47	142	90	115	62
50-54	84	14	26	23	52	151	42	41	66	101	60	11
55-59	—	—	—	—	—	—	—	—	—	—	—	—
60-64	—	—	—	—	—	—	—	—	—	—	—	—
65-69	46	10	8	0	16	87	16	41	53	78	13	12
70-74	22	0	10	0	2	35	1	17	38	40	2	13
75-79	—	—	—	—	—	—	—	—	—	—	—	—
80-84	0	0	4	0	0	0	0	3	3	3	0	6
85-89	0	0	0	0	0	0	0	0	0	0	0	1
90-94	0	0	0	0	0	0	0	0	0	0	0	1
95-99	0	0	0	0	0	0	0	0	0	0	0	1
Total	435	73	174	277	223	908	229	278	645	478	637	313

quately sampled. In general the sampling covers the life span of the predators in the areas sampled, from demersal 0-group to the oldest age groups.

METHODS

The methods of sampling and stomach content analysis have been developing gradually since 1976.

The division of the predators into length groups has not been the same throughout the study period. In 1976-79 they were divided into 10 cm groups. In 1980 new length groups were introduced according to a recommendation of the "Ad hoc Working Group of Multi Species Assessment Model Testing" of the International Council for the Exploration of the Sea (ICES) (Anon. 1980). The recommended length groups

were used in the survey of March 1980 (see Tables in Appendix). Later, however, when the results of the material sampled in 1979 had been analysed (Pålsson 1980b), it seemed possible that in the large length classes (above 50 cm) the division used might not reveal sufficiently some major changes in the food composition of the cod in that length range. Therefore, in later surveys 10 cm length groups were also applied for lengths over 50 cm. Since September 1981 fish of the length range 100-129 cm have been treated as one length group.

It has been attempted to sample in each haul or a defined area 10 stomachs of each predator length group. If this was not achieved in one haul the lacking stomachs were not, in the period 1976-79, sampled in additional hauls. In 1980, on the other hand, the main areas (Fig. 1) were split up into 3

TABLE 6

Number of eel, redfish, long rough dab and plaice stomachs analysed for food by predator length groups and sampling periods.

Length group (cm)	Sampling period (year and month)											
	Eel				Redfish				Long rough dab			
	1980	1981	1981	1981	1980	1981	1981	1981	1980	1981	1981	1981
5-6	0	0	0	0	1	1	0	17	0	12	0	2
7-9	5	4	15	22	23	7	27	45	6	19	36	20
10-14	25	17	48	30	55	57	54	35	35	73	90	59
15-19	46	42	52	35	45	53	64	47	60	87	96	65
20-24	49	41	56	42	56	78	67	32	66	88	68	67
25-29	46	49	51	35	55	58	75	33	70	65	78	18
30-34	63	50	67	56	73	84	95	42	72	82	72	70
35-39	58	54	62	83	14	46	55	12	26	55	37	40
40-44	71	64	49	83	0	3	14	0	0	0	0	0
45-49	—	54	25	63	—	0	0	0	—	0	0	0
50-54	—	29	16	14	0	0	0	0	0	0	0	0
55-59	—	14	2	3	—	0	0	0	—	0	0	0
60-64	—	0	4	1	—	0	0	0	—	0	0	0
65-69	—	—	—	—	—	—	—	—	—	—	—	—
70-74	—	—	—	—	—	—	—	—	—	—	—	—
75-79	—	—	—	—	—	—	—	—	—	—	—	—
80-84	—	—	—	—	—	—	—	—	—	—	—	—
85-89	—	—	—	—	—	—	—	—	—	—	—	—
90-94	—	—	—	—	—	—	—	—	—	—	—	—
Total	385	418	447	467	322	387	451	263	335	481	497	393

¹⁾ Length group 50-69 cm

²⁾ Length group 70-99 cm

approximately equal sub-areas with respect to the sampling of cod stomachs, whereas 2 sub-areas were considered sufficient for the other predator species. Finally, in 1981, the number of sub-areas was increased to four with respect to cod and three for the other predators. In each sub-area 10 stomachs were sampled for each length group, occasionally in one haul, but more often in several hauls. In the smallest and the largest length groups, however, the sampling of 10 stomachs could at times not even be achieved from 5-15 hauls in a particular sub-area. The length of a standard haul was 2.0 nautical miles.

The number of stomachs without food have been recorded for each year except 1979.

Throughout the study period the level of prey identification has changed considerably. In 1976-78 the stomach content was

analysed at sea. Therefore, the prey identification had to be carried out on a short-cut basis, and was limited to a grouping into 4 "ecological groups" (eco-groups): 1) Nektonic animals, mainly various fish species as well as cephalopods, 2) planktonic animals such as euphausiids, pelagic amphipods, Medusae and chaetognaths, 3) shrimps of various species, and 4) benthic animals such as polychaetes, crabs, benthic amphipods and echinoderms. In 1979 and subsequent years the sampling was extended to include five fish species, and the samples preserved in a 4% formalin-seawater solution for a later, more accurate analysis. Subsequently fish prey was usually identified to species, whereas other prey was identified to groups of similar living condition and body shape. Euphausiacea, Hyperidae, Polychaeta and Ophiuroidea are examples of such prey groups. In a few cases, however, other prey

THE FOOD OF COD

1) The food composition

a) *Seasonal and year to year variations.* The seasonal and year to year variation in the food composition of cod during the period May 1976 through March 1981 is shown in Fig. 2 in terms of displacement volume or weight percentage of the eco-groups previously defined.

Nekton was by far the predominant food in all seasons and years except in May 1976 and June-July 1978 when benthic and planktonic prey provided the bulk of the food. In general the proportion of nekton increased with increasing predator length, whereas the smallest predators preyed almost exclusively on other eco-groups. The proportion of nekton usually exceeded 50% for predators somewhat smaller than 50 cm in length. Exceptions to this were mainly recorded during the summer of 1978 and 1980 and also in May 1976 and December 1978.

Plankton provided virtually always the principal food of the smallest fish, usually decreasing in importance with increasing predator length. On the whole planktonic prey was the second most common food, and it was usually more dominant in the diet during summer than in other seasons.

The role of shrimps and benthic food varied with both seasons and years. Occasionally these prey groups provided a considerable part of the food, e. g. in May 1976 and November 1977. Generally the importance of these eco-groups decreased with increasing predator length.

The seasonal variations of the food of cod in 1980 and 1981 are shown in more details in Fig. 3. Except for shrimps as a whole and fish eggs, prey species or groups will in the text, tables and figures be referred to with Latin names, whereas common names will be used for the predators.

A marked seasonal variation exists in the feeding (Fig. 3). In late winter (March) *Mallotus villosus* were by and large the predo-

than fish were identified to species or genus, e. g. *Calanus finmarchicus*, *Nephrops norvegicus* or *Parachanna*. In spite of these changes in the level of prey identification the results from the different periods can be compared since the division into eco-groups has been retained.

The method of quantifying the prey was changed slightly in 1979. Prior to 1979 the quantity of the various eco-groups was recorded as a displacement volume, and number of prey animals. Since 1979, however, weighing has been made of the wet biomass of each prey species or prey group. Furthermore, since 1980, the length of fish prey has been recorded when possible.

Since 1980 the results of the analyses have been weighted according to the number of predators on which each sample is based. Consequently, the number of predators in a unit haul have been recorded for each length group of the predators. The average weight per stomach of prey *j* in predator length group *i* is given by:

$$\bar{W}_{ij} = \frac{\sum_{k=1}^m N_{ik} \bar{W}_{ijk}}{\sum_{k=1}^m N_{ik}}$$

where *k* denotes a given sample, *W* = prey weight in sample, *N* = number of predators in a unit haul, *n* = number of stomachs in sample, *m* = number of samples.

RESULTS

Detailed information is given in the Appendix on the food composition of cod (Tables I-VI) and haddock (Tables VII-X), and the composition and quantity of the food of catfish (Tables XI-XIV), redfish (Tables XV-XVIII) and long rough dab (Tables XIX-XXII).

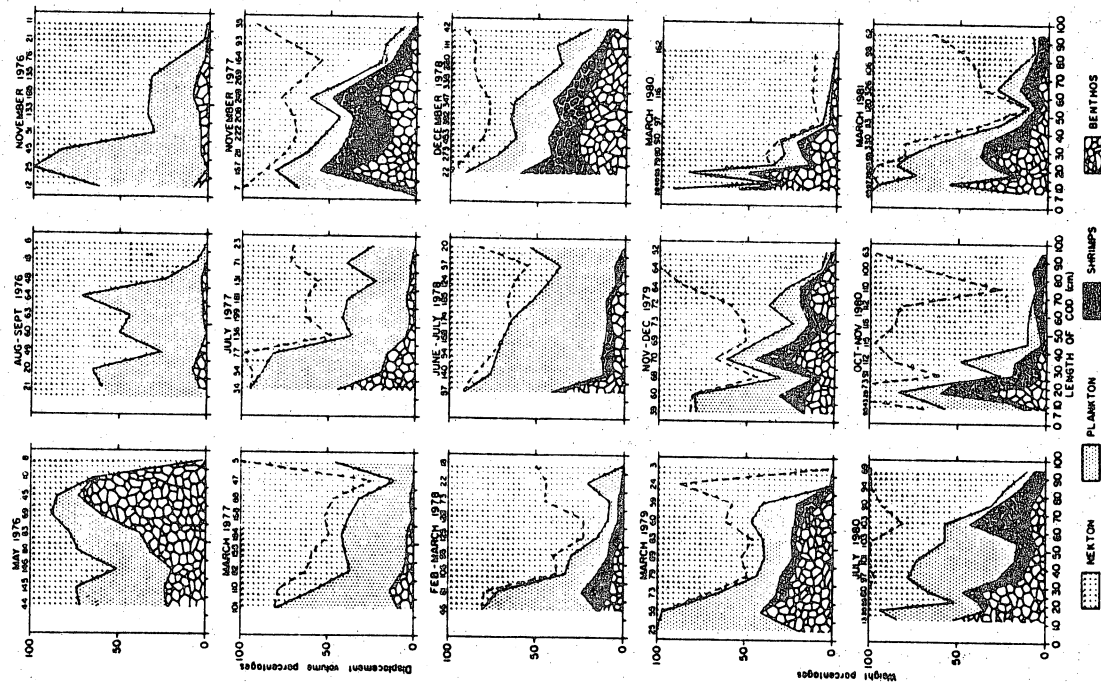


Fig. 2. The composition of the food of cod (weight or volume percentages) in relation to predator length (cm) at different times during 1976-81, on the basis of ecological grouping of the prey. The broken line divides the nekton into *M. villosus* (upper part) and other nektonic prey (lower part). Shrimps were recorded as benthos prior to November 1977. The number of stomachs analysed in each predator length group is given at the top of each illustration.

curred, however, quite rapidly, especially in winter, when predators larger than 30 cm had mostly become fish consumers. In summer, on the other hand, this shift was more gradual so that the bulk of the food of cod smaller than 70 cm consisted of prey other than fish, mainly Euphausiacea, shrimps and Polychaeta.

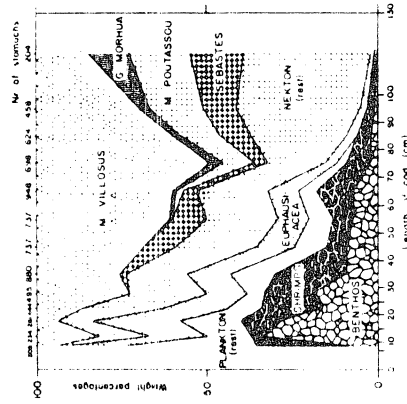


Fig. 4. The average composition of the food of cod in 1980-81 is shown in Fig. 4. The most outstanding features are the predominant role of *M. villosus* in the food, as well as the continuous shift in the food composition as the length of the cod increases, from pelagic and benthic invertebrates over to *M. villosus* and other fish. The area covered by *M. villosus* in Fig. 4 can be regarded as an approximate measure of the importance of this prey as food for the cod stock as a whole. By this measure *M. villosus* yield 30% of the food on an annual basis, and exceed by large any other prey group in importance as food for cod.

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minant prey, especially in 1980. In summer (July 1980) *Micromesistius poutassou*, shrimps and Euphausiacea were the most important prey of the larger, intermediate and smaller predators respectively. In late summer (September 1981) *M. poutassou* were still of considerable importance, followed by *Pandalus*, *M. villosus* and *Gadus morhua*. During the summer season (July, September) prey other than fish, mainly Euphausiacea, shrimps and benthic animals, were clearly more prominent in the food than during winter. In early winter (October-November) *M. villosus* and *Sebastes* were the dominating prey.

In addition to the seasonal variation a considerable variation between years is apparent. Thus in March 1980 *M. villosus* was the predominant prey of virtually all size groups. One year later, however, Euphausiacea and other planktonic as well as benthic prey were more abundant in the food of the smallest predators, whereas *Sebastes* and Gadidae substituted *M. villosus* in the larger predator length groups. Furthermore, in early winter 1980, *Sebastes* were mainly selected by predators in the length range 40-69 cm. One year later, however, this prey was mainly consumed by predators larger than 90 cm. This variation may be related to differences in the prey size and probably also abundance of *Sebastes* in the two years in question.

Shrimps, mainly *Pandalus borealis*, were in September 1981 particularly predominant in the food of the smaller predators. They yielded also a considerable part of the diet in July and October-November 1980, although the predators were of different length range. Apparently, this prey was less important in late winter as food for cod.

Euphausiacea and other planktonic prey as well as Gammaridea, Polychaeta and other benthic prey were in general of great importance as food for the smallest predators in all seasons in 1980 and 1981. The change from these animals to fish prey oc-

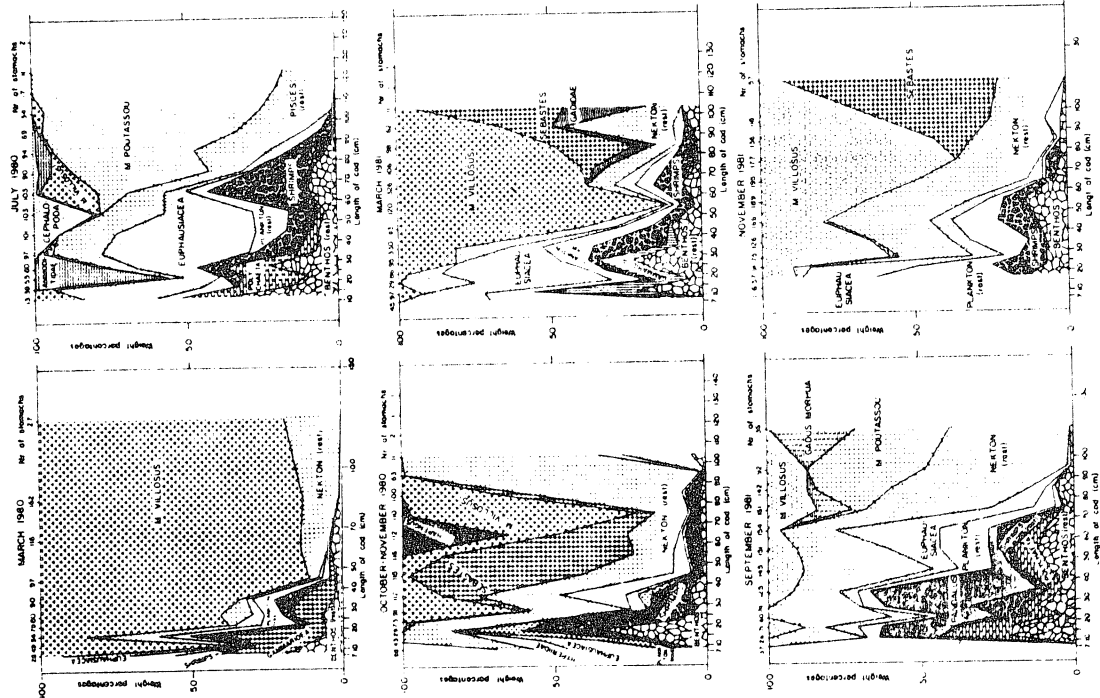


Fig. 3. The composition of the food of cod (weight percentages) in relation to predator length (cm) in March, July, October-November 1980 and March, September, November 1981. (For details see Appendix Tables I-VI).

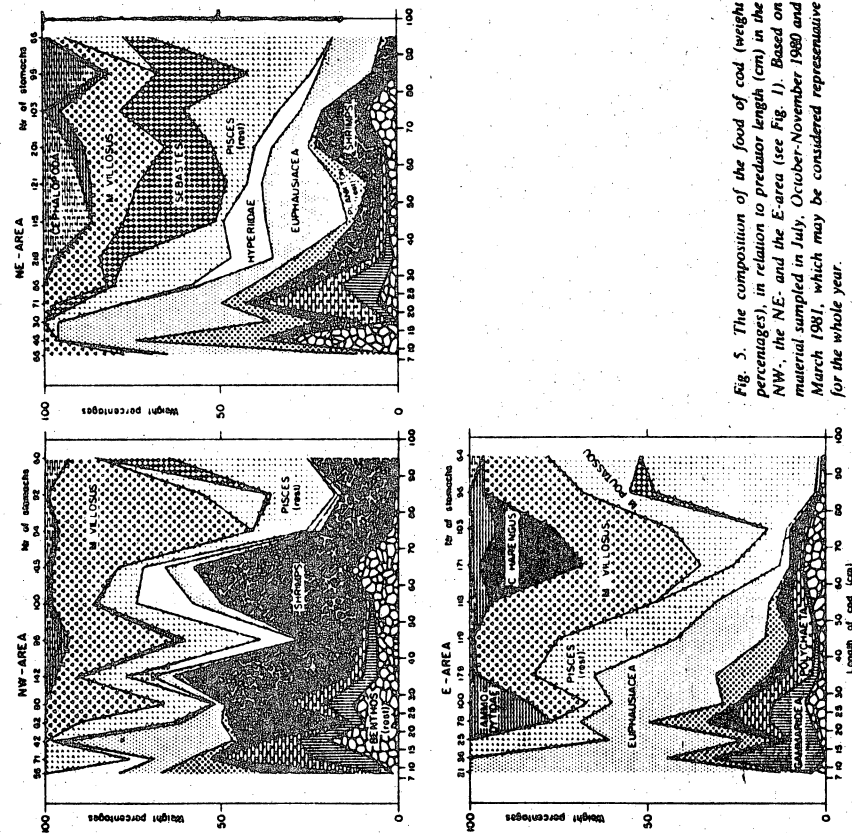


Fig. 5. The composition of the food of cod (weight percentages), in relation to predator length (cm) in the NW-, the NE- and the E-area (see Fig. 1). Based on material sampled in July, October-November 1980 and March 1981, which may be considered representative for the whole year.

b) *Regional variations.* Considerable regional variations were generally observed for the most important prey (Fig. 5). *M. villosus* were particularly predominant in the food in the NW- and E-areas, but less important in the NE-area, where *Sebastes* and Cephalopoda increased in importance as prey. In the E-area *M. poutassou* together with *M. villosus*, were a significant part of the diet

NW-area, contributed significantly to the food in the NE-area, especially for the smaller predators. In the E-area this prey provided the bulk of the food for predators of the smaller length range. The shrimps, on the other hand, showed a different regional variation. In the NW-area they were clearly the most predominant prey of all but the smallest predator length groups. The consumption of this particular prey, however, was relatively limited in the NE-area and negligible in the E-area.

This regional variation in shrimp consumption by cod is indeed, in general agreement with the regional distribution of the commercial catch of *Pandalus*, which is mainly taken in the NW-area (95% of the total landings in 1980 and 1981). The catch in the NE-area is only limited (5%), and negligible in the E-area (Anon., 1982).

2) Stomach content quantity

One of the crucial questions in fish species interaction regards the quantity of food consumed by a specific predator. Quantification of the stomach content is considered to be the first step in an empirical approach to this problem.

The quantity of the stomach content (empty stomachs included) has been described as a power function of the length of the predator (Daan, 1973):

$$\bar{W} = a \cdot L^b$$

where $\bar{W}$ = average quantity of stomach content (grams), L = length of predator (cm) and a and b are regression of coefficients.

The coefficients of this relationship can be assumed to be functions of the food consumption.

In this paper the material of each predator species has been divided into different length groups. When correlating the quantity of the stomach content to length, the

modal lengths of the different predator length groups have been used.

a) *Seasonal and year to year variations.* The quantity of the stomach content in different seasons and years during the period 1976-81 is given in Table 7 and illustrated in Figs. 6 and 7. The regression coefficients are given in Table 8. The coefficients (a and b) vary over a rather wide range, and they are inversely related to each other, irrespective of seasons or years.

Apparently, the seasonal variation in stomach content does not follow the same pat-

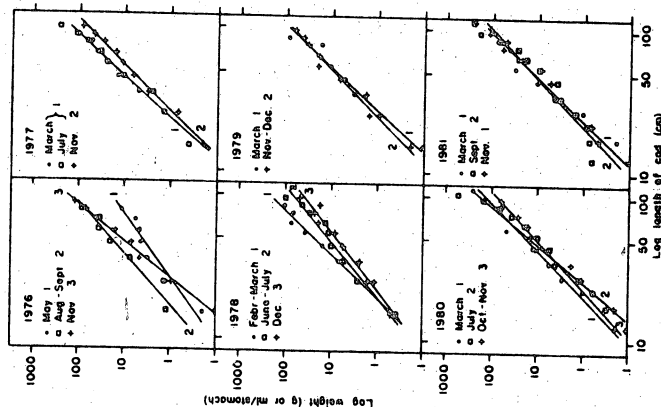


Fig. 6. Seasonal variations of the average quantity of the stomach content of cod (ml (1976-1978) or grams (1979-1981) per stomach) in relation to predator length (cm) in 1976-81 (Tables 7 and 8).

TABLE 7
The quantity of the stomach contents of cod (ml per stomach in 1976-78; grams per stomach in 1979-81) with respect to predator length groups, and seasons. Length groups where less than 20 stomachs were analysed are omitted (see Table 4).

Season (Month and year)	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	100-109	110-119	120-129	
May 1976	—	0.2	—	—	1.2	—	3.1	4.4	4.6	5.5	11.8	—	—	—	
Aug. - Sept. 1976	—	1.2	—	—	1.3	—	7.0	20.3	35.0	33.3	82.9	—	—	—	
November 1976	—	0.1	—	—	0.9	—	4.6	6.8	15.1	37.8	69.9	117.2	—	—	
March 1977	—	0.2	—	—	1.4	—	5.1	13.9	24.0	42.0	52.5	97.1	—	—	
July 1977	—	0.4	—	—	1.4	—	2.4	11.4	24.4	34.9	67.5	117.4	272.8	—	
November 1977	—	0.2	—	—	0.7	—	3.0	6.2	11.1	15.8	28.3	46.3	84.6	—	
Febr. - March 1978	—	0.5	—	—	1.5	—	6.9	16.4	37.1	73.4	86.3	146.3	—	—	
June - July 1978	—	0.4	—	—	2.7	—	5.4	9.9	13.8	13.4	30.0	42.5	99.6	—	
December 1978	—	0.5	—	—	1.1	—	2.4	3.7	8.2	19.4	17.5	31.6	48.9	—	
March 1979	—	0.1	—	—	1.1	—	3.4	5.7	8.2	19.4	17.5	31.6	48.9	—	
Nov. - Dec. 1979	—	0.2	—	—	1.5	—	1.9	6.9	21.6	19.6	35.4	41.5	65.4	—	
March 1980	—	—	—	—	—	—	5.4	12.8	26.5	—	75.8	—	268 (U)	—	
July 1980	0.2	—	0.3	1.0	—	—	2.9	5.2	10.0	19.3	34.4	68.8	152.4	537.8	
Oct. - Nov. 1980	—	0.3	0.6	—	1.2	—	4.2	5.2	10.0	16.1	26.6	65.5	61.8	—	
March 1981	0.1	—	0.2	0.6	—	—	1.4	1.8	11.2	33.1	30.0	43.2	82.9	88.7	
September 1981	0.1	0.3	—	0.7	—	—	1.1	3.3	13.2	33.1	18.9	29.3	76.7	202.8	
November 1981	0.7	—	0.8	0.9	—	—	1.5	4.6	4.0	9.7	24.8	62.4	52.6	126.7	
November 1981	—	—	0.5	0.7	—	—	1.6	3.6	5.8	8.7	24.8	62.4	52.6	262.6	

U) Length group 50-69 cm

1) 70-99 cm

2) 100-149 cm

term in different years. In all cases, however, the stomach content was largest in late winter (February-March) or in summer (June-September) (Fig. 6). Combining all years the stomach content was virtually identical in these two seasons, whereas it was somewhat smaller in the months October-December (Fig. 7d).

In 1976 seasonal variability in stomach content was unusually pronounced, mainly due to significantly reduced level of stomach content in May. This might be related to reduced feeding intensity during the spawning or postspawning period as suggested by Rae (1968) on the basis of the proportion of empty stomachs.

As illustrated in Fig. 7 there is a considerable variation between years in the level of stomach content found for the different seasons. This variation is least pronounced in late winter and nearly constant throughout the predator length range. In the other seasons, however, the variation is quite different with respect to predator length.

Apparently, the main year to year variation

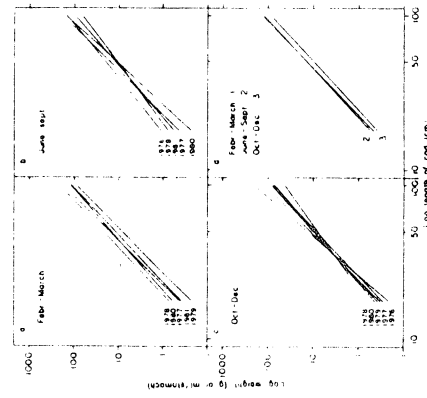


Fig. 7. The relation between the average quantity of the stomach content of cod (ml (1976-1978) or grams (1979-1981) per stomach) and predator length (cm) with respect to year to year variations in February-March (a), June-September (b) and October-December (c), and average seasonal variation over the period 1976-81 (d) (Tables 7 and 8).

tions occurred in the years 1976-79. This might be connected with the less advanced methods of sampling and data treatment applied in these years. However, the coefficient of determination (Table 8) does not indicate a reduced quality of the results in this respect.

TABLE 8

Power function regression coefficients (a and b) and coefficient of determination (r^2), describing the average volume (1976-78) or weight (1979-81) of the stomach content of cod (ml or grams per stomach, empty stomachs included) in relation to predator length (cm) by seasons.

Season (Month and year)	a	b	r^2
May	$6.29 \cdot 10^{-4}$	2.27	0.94
Aug. - Sept.	$3.46 \cdot 10^{-4}$	2.82	0.93
November	$2.31 \cdot 10^{-4}$	3.98	0.99
March	$1.70 \cdot 10^{-3}$	3.52	0.99
July	$1.78 \cdot 10^{-3}$	3.52	0.97
November	$2.75 \cdot 10^{-3}$	3.23	0.99
Febr. - March	$5.56 \cdot 10^{-3}$	3.30	0.98
June - July	$4.21 \cdot 10^{-4}$	2.61	0.96
December	$4.83 \cdot 10^{-4}$	2.47	0.97
March	$1.08 \cdot 10^{-3}$	3.47	0.97
Nov. - Dec.	$4.79 \cdot 10^{-3}$	3.12	0.98
March	$8.49 \cdot 10^{-3}$	3.09	0.99
July	$4.43 \cdot 10^{-3}$	3.78	0.96
Oct. - Nov.	$9.06 \cdot 10^{-3}$	2.95	0.97
March	$3.52 \cdot 10^{-3}$	3.26	0.97
September	$1.05 \cdot 10^{-4}$	2.99	0.94
November	$2.23 \cdot 10^{-3}$	3.36	0.98
Febr. - March	$4.03 \cdot 10^{-3}$	3.26	0.96
June - Sept.	$7.04 \cdot 10^{-3}$	3.12	0.93
Oct. - Dec.	$4.16 \cdot 10^{-3}$	3.16	0.96

b) Regional variations. The material sampled in 1980 and 1981 has been used to evaluate regional variations in the quantity of stomach content. The material sampled prior to 1980 was excluded since the number of stomachs from each area was considered insufficient, particularly in the lower and the upper predator length range.

The results are given in Tables 9-10 and illustrated in Fig. 8. The range of the parameters a and b was somewhat narrower than observed with respect to the seasonal variations. However, a similar inverse relation-

Apparently, there was no clear, consistent regional difference in the stomach content throughout the period 1980-81. In most seasons the quantity of stomach content was somewhat smaller in the NE-area than in the NW- and E-areas. On the average, however, this difference was hardly significant (Table 10).

The coefficient of determination was clearly somewhat lower at the regional level (Table 10) than at the seasonal level (Table 8). This is most likely due to the more limit-

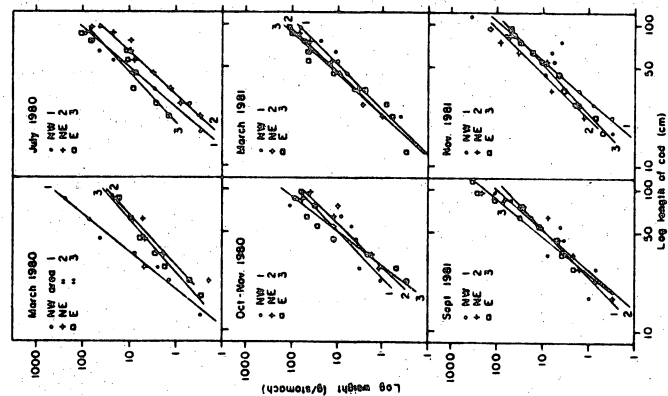


Fig. 8. Regional variation in the average quantity of the stomach content of cod (grams per stomach) in relation to length (cm) by seasons in 1980-81 (Tables 9 and 10).

ed number of stomachs analysed with respect to areas than with respect to seasons.

3) Prey size preference

The prey size preference of cod was analysed on the basis of material sampled in 1980 and 1981. The size of the prey has been quantified as the average weight of individual prey (Fig. 9) as well as in terms of the length distribution of each prey species or prey group (Figs. 10-11).

Obviously, the prey size range increased greatly with increasing predator length (Fig.

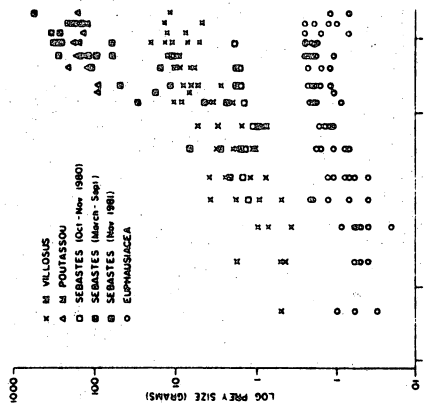


Fig. 9. The average weight (grams) of principal prey in relation to length (cm) of cod.

9). The lower limit of the prey size range was only slightly higher in the largest predator length groups than in the smallest ones, whereas the upper limit was approximately three orders of magnitudes higher.

The size of the various most important prey in relation to predator length was quite different. The size of the relatively small Euphausiacea increased only slightly with predator length. This was also the case for the much larger *M. pouasou* which were mainly consumed by the larger predators (Fig. 9). The length distribution of this prey was mainly in the length group 30-34 cm (Fig. 11).

The size of *M. villosus*, on the other hand, increased roughly linearly with predator length (Fig. 9). In general, the length distribution of this prey showed a gradual shift with increasing predator length, from the smallest 0- and I-group prey (around 5 cm) over to the largest II- and III-group prey (around 15 cm). Medium sized I and II-group *M. villosus* were observed less

TABLE V
The quantity of the stomach content of cod (grams per stomach) with respect to predator length groups, seasons and areas. Length groups where less than 20 stomachs were analysed are omitted

Season (Month and year)	Area	Predator length group (cm)											
		10-14	15-19	20-24	25-29	30-34	35-39	40-49	50-59	60-69	70-79	80-89	90-129
March	NW	0.3	1.4	2.5	7.9	42.7	—	—	70.0	—	—	—	—
	NE	—	0.2	5.2	1.9	4.9	—	—	—	—	—	—	—
July	NW	—	0.3	0.5	1.7	2.9	6.1	—	9.6	—	—	—	—
	NE	—	—	0.5	2.8	9.1	—	—	—	—	—	—	—
Oct. - Nov.	NW	—	0.3	0.8	1.3	3.0	7.8	—	—	—	—	—	—
	E	—	1.4	2.7	8.3	7.6	10.6	—	—	—	—	—	—
March	NW	—	1.1	3.3	2.3	4.0	5.1	—	—	—	—	—	—
	NE	—	0.3	1.2	1.7	12.9	12.3	—	—	—	—	—	—
September	NW	—	0.3	0.5	2.1	2.5	27.7	—	—	—	—	—	—
	E	—	0.4	2.8	4.6	6.1	10.0	—	—	—	—	—	—
November	NW	—	0.3	0.6	0.8	3.4	12.2	—	—	—	—	—	—
	NE	—	1.0	2.8	3.4	9.1	13.9	—	—	—	—	—	—
March	NW	—	0.3	0.7	0.7	2.2	4.6	—	—	—	—	—	—
	NE	—	0.3	0.7	0.7	2.2	4.6	—	—	—	—	—	—
September	NW	—	0.3	0.3	0.8	1.6	9.2	—	—	—	—	—	—
	E	—	1.3	2.1	6.4	4.4	8.4	—	—	—	—	—	—
November	NW	—	0.5	0.7	1.7	3.4	4.3	—	—	—	—	—	—
	E	—	—	—	—	—	—	—	—	—	—	—	—

TABLE 10

Power function regression coefficients (a and b) and coefficient of determination (r^2), describing the average weight of the stomach content (grams per stomach) of cod in relation to predator length (cm) by seasons and areas

Season (Month and year)	Area	a	b	r^2
March	NW	$1.83 \cdot 10^{-3}$	3.70	0.98
	NE	$1.88 \cdot 10^{-3}$	2.62	0.67
July	NW	$1.84 \cdot 10^{-3}$	2.65	0.96
	NE	$8.37 \cdot 10^{-3}$	3.58	0.94
Oct. - Nov.	NW	$1.22 \cdot 10^{-3}$	3.28	0.96
	NE	$2.11 \cdot 10^{-3}$	2.83	0.87
September	NW	$7.28 \cdot 10^{-3}$	3.01	0.76
	NE	$2.37 \cdot 10^{-3}$	3.20	0.89
November	NW	$1.23 \cdot 10^{-3}$	4.05	0.94
	NE	$3.74 \cdot 10^{-3}$	3.16	0.95
March	NW	$2.97 \cdot 10^{-3}$	3.32	0.99
	NE	$2.34 \cdot 10^{-3}$	3.41	0.94
September	NW	$1.12 \cdot 10^{-3}$	2.88	0.86
	NE	$1.21 \cdot 10^{-3}$	3.45	0.92
November	NW	$4.51 \cdot 10^{-3}$	3.79	0.94
	NE	$5.77 \cdot 10^{-3}$	3.56	0.86
March	NW	$5.78 \cdot 10^{-3}$	3.15	0.92
	NE	$1.20 \cdot 10^{-3}$	2.85	0.99
1980-81	NW	$3.68 \cdot 10^{-3}$	3.20	0.86
	NE	$3.12 \cdot 10^{-3}$	3.19	0.87
—	E	$2.38 \cdot 10^{-3}$	3.33	0.91

The size of *Sebastes* in relation to predator length was more complex since it differed with seasons, and, apparently, also with respect to years. In the period March-September the relationship between prey size and predator length (Fig. 9) resembled that of a power function (slope 3.8). In October-November 1980 the size of *Sebastes* prey was virtually constant for predators of the length range 20–99 cm, i. e. approximately 1–2 grams (Fig. 9) or 5–7 cm (Fig. 10) which is 0-group *Sebastes*. In this season *Sebastes* was the most important prey of cod of the middle size classes (Fig. 3). One year later, however, the size of *Sebastes* was similar for predators up to 80 cm in length whereupon it changed abruptly to a size of 200–300 grams (Fig. 9). The length distribution of the prey changed from 4–7 cm in the predator length range 40–79 cm to prey length of 6–36 cm, (mainly about 20 cm) in the predator length range 80–129 cm (Fig. 10). In this season (November 1981) *Sebastes* provided the bulk of the food for the largest predators, whereas it was of no importance for the smaller cod (Fig. 3).

These differences in the length distribu-

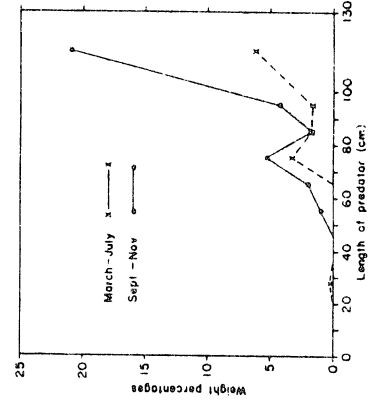


Fig. 12. Average weight percentages of *Gadus morhua* as food for cod in March-July and September-November 1980–81 in relation to predator length (Tables 1–V).

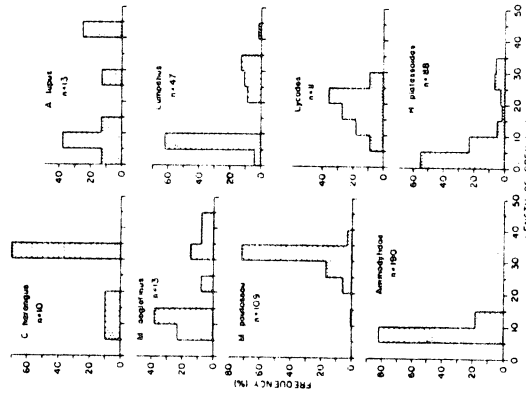


Fig. 11. The length distribution (%) of important fish prey irrespective of length of cod. The number of prey measured is given by n. Based on material sampled in 1980–81.

frequently in the stomachs (Fig. 10). However, the length distribution was also characterized by some seasonal differences. In March the smallest 1-group prey were a significant part of the diet of virtually all length groups, whereas in October-November the smallest 0-group individuals were hardly consumed by predators larger than 80 cm. Furthermore, in March the larger *M. villosus* were consumed by predators 30–39 cm and larger, whereas in October-November this hardly occurred until in the predator length group 60–69 cm. Thus in March prey of its entire length range was found in the stomachs of most predator length groups, whereas in October-November prey of such a broad length spectrum was recorded only for predators of relatively narrow length range.

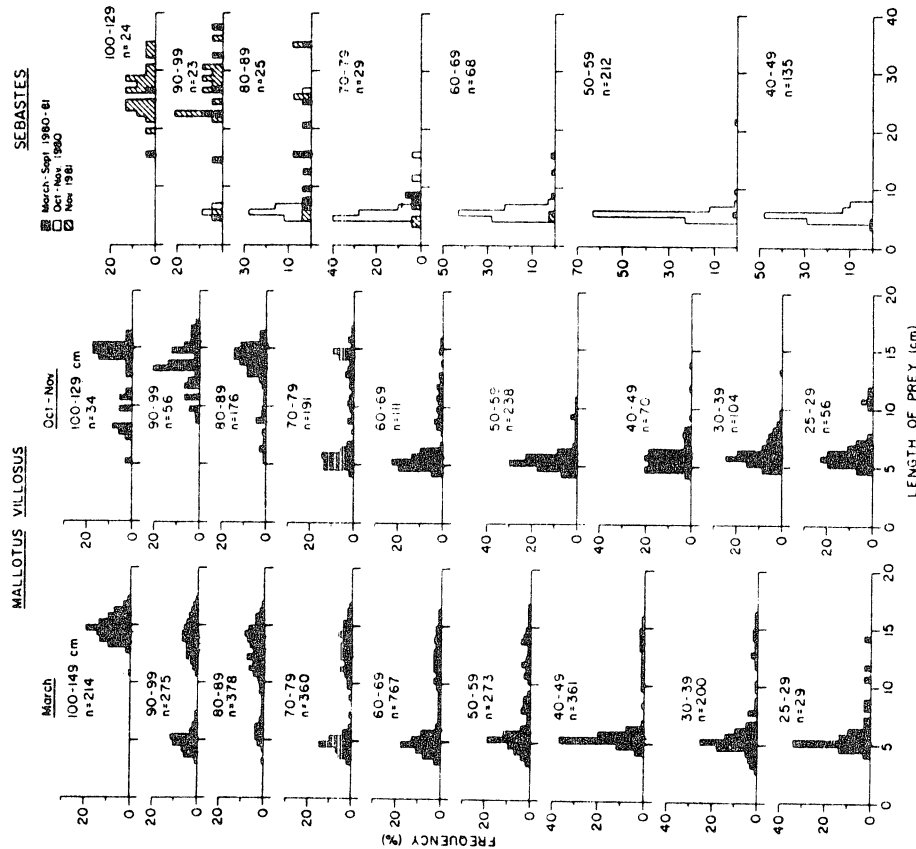


Fig. 10. The length distribution (%) of *M. villosus* and *Sebastes* with respect to length groups (cm) of cod. The number of prey measured is given by n. Based on material sampled in 1980–81. In the text the smallest *M. villosus* around 5 cm are referred to as 0- and 1-group in March and October-November respectively and the largest prey around 15 cm as 11- and 111-group.

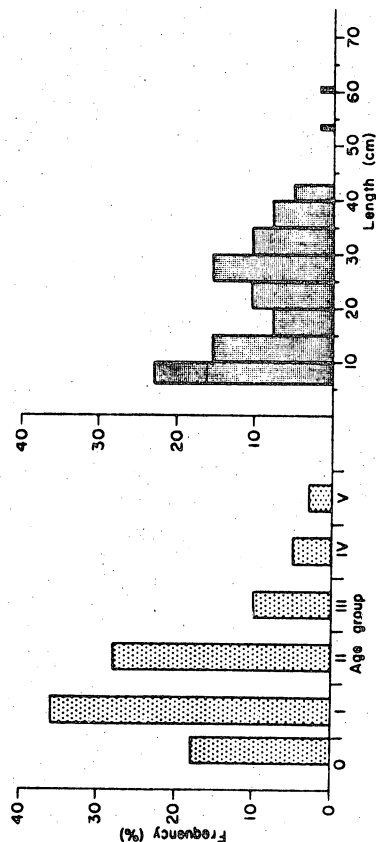


Fig. 13. Age and length frequency distribution (%) of *Gadus morhua* as food for cod in 1980-81.

tion of *Sebastes* and in the amount consumed by cod in different years, indicate a considerable variability in the amount of the particular size or age groups of *Sebastes* available. In fact, compared to the situation in 1970-79, the distribution area of 0-group *Sebastes* on the continental shelf area north and east of Iceland was unusually extensive in August 1980, whereas in August 1981 0-group *Sebastes* were not recorded there at all (Vilhjálmsen and Magnússon 1980, 1981). On the other hand, the narrow predator length range in which 0-group *Sebastes* were of outstanding importance as food in October-November 1980, indicates a rather sensitive predator — prey size relationship.

The length distribution of other fish prey species (Fig. 11) shows that their length does not exceed 50 cm. In most cases the prey length is below 10 cm. An exception to this is the length distribution of *M. pourtaussou*, which were mainly consumed by cod off the east coast during summer, i. e. during the post-spawning migration of the prey to the feeding grounds off the eastern and north-eastern coasts of Iceland.

4) Cannibalism

The occurrence of cannibalism is an interesting feature in the feeding of cod, particularly because of its potential impact on stock-recruitment relationships.

As shown in Fig. 3 cannibalism occurs occasionally. However, it is subject to considerable variations with respect to seasons as well as predator length (Fig. 12). In the period March-July cannibalism was recorded amongst predators 70-130 cm in length and one *G. morhua* (0.3%) was found in the predator length group 25-29 cm. By weight the amount of cannibalism was in the range 1.7-6.2%, and thus unimportant even in the largest predator length group. In the period September-November, on the other hand, cannibalism was somewhat more pronounced among predators 50-99 cm in length, and for the largest predators (> 100 cm) greatly increased cannibalism (21%) was recorded. Thus, cannibalism is apparently rather limited among Icelandic cod, except among the very largest predators in autumn and early winter.

The length distribution of the *G. morhua*

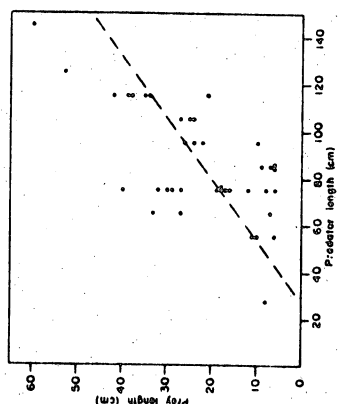


Fig. 14. Length of *Gadus morhua* (cm) as food for cod in 1980-81 in relation to predator length (cm).

prey is mostly confined to fish smaller than 40 cm, while the largest prey measured 61 cm in length (Fig. 13). The bimodal length distribution with peaks around 10 cm and 25-30 cm indicates the frequent occurrence in autumn and early winter of 0-group prey and I- and II-group prey respectively constituting more than 80% of this particular prey.

As indicated in Fig. 14 the length of *G. morhua* in relation to predator length is highly variable, especially in the predator

length range 60-79 cm. The general trend is, however, characterized by an increasing prey length with increasing length of the predator.

THE FOOD OF HADDOCK

1) The food composition

The main features of the seasonal and year to year variations in the food of haddock in 1976-81 are shown in Fig. 15. In general benthic prey were the dominating food in all seasons throughout the period, with only a few exceptions such as November 1976 and March 1977. Occasionally, nektonic prey were consumed in considerable quantities, especially in March. Usually, however, these prey were not predominant in the diet. Planktonic prey were also from time to time of considerable importance as food, especially in 1980 and 1981. Shrimps, on the other hand, were negligible as food for haddock.

The food composition in 1980 and 1981 is shown in more detail in Fig. 16. Polychaeta were an important prey in all seasons, especially in summer and early winter. Ophiuroidea and other Echinodermata were also a greater part of the diet in these seasons, particularly for the larger predators. In late

TABLE 11

The quantity of the stomach content of haddock (ml per stomach in 1978; grams per stomach in 1979-81) with respect to predator length groups and seasons. Length groups where less than 20 stomachs were analysed are omitted (see Table 5).

Season (Month and year)	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	100-109
June - July ... 1978	—	—	—	—	—	2.2	5.5	10.0	—	—	—	—
December ... 1978	—	0.2	—	1.2	—	2.5	3.8	6.5	11.9	27.0	—	—
March ... 1979	—	0.1	—	1.4	—	3.3	4.7	8.3	—	—	—	—
Nov. - Dec. ... 1979	—	0.2	—	0.6	—	2.1	4.1	8.0	10.8	—	—	—
March ... 1980	—	—	—	—	0.3	1.3	4.4	3.7	2.8(1)	—	—	—
July ... 1980	—	—	—	—	0.4	0.8	1.9	6.6	12.4	11.1	8.5	—
Oct. - Nov. ... 1980	0.1	—	0.3	0.4	—	0.4	1.5	3.0	3.9	12.2	20.0	—
March ... 1981	0.1	0.2	—	—	—	0.6	1.0	2.6	4.7	—	—	—

¹⁾ Length group 50-59 cm.

²⁾ Length group 70-99 cm.

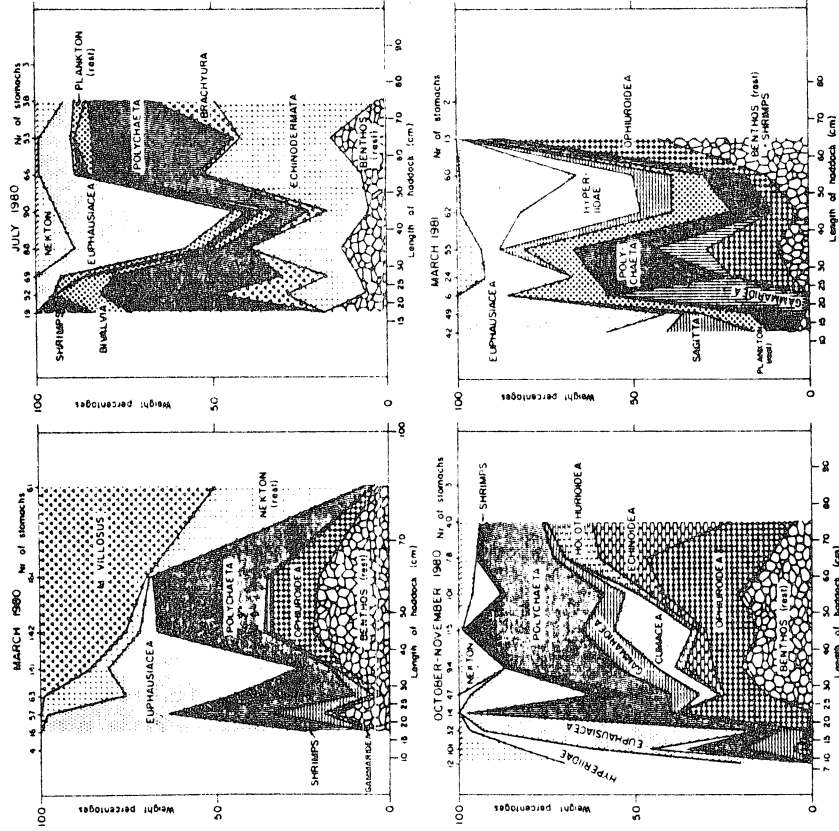


Fig. 16. The composition of the food of haddock (weight percentages) in relation to predator length (cm) in March, July, October-November 1980 and March 1981 (Tables VII-X).

ing predator length, whereas one year later this and other fish prey were hardly consumed at all.

The available results demonstrate the great importance of benthic prey groups as the principal food of haddock in Icelandic waters. Zooplanktonic prey is usually most

winter (March), on the other hand, Euphausiacea were more predominant in the food of haddock, mainly in the smaller length groups. Similarly, *M. villosus* of the spawning migration (12-17 cm in length) were a dominating prey in late winter 1980, showing increasing importance with increas-

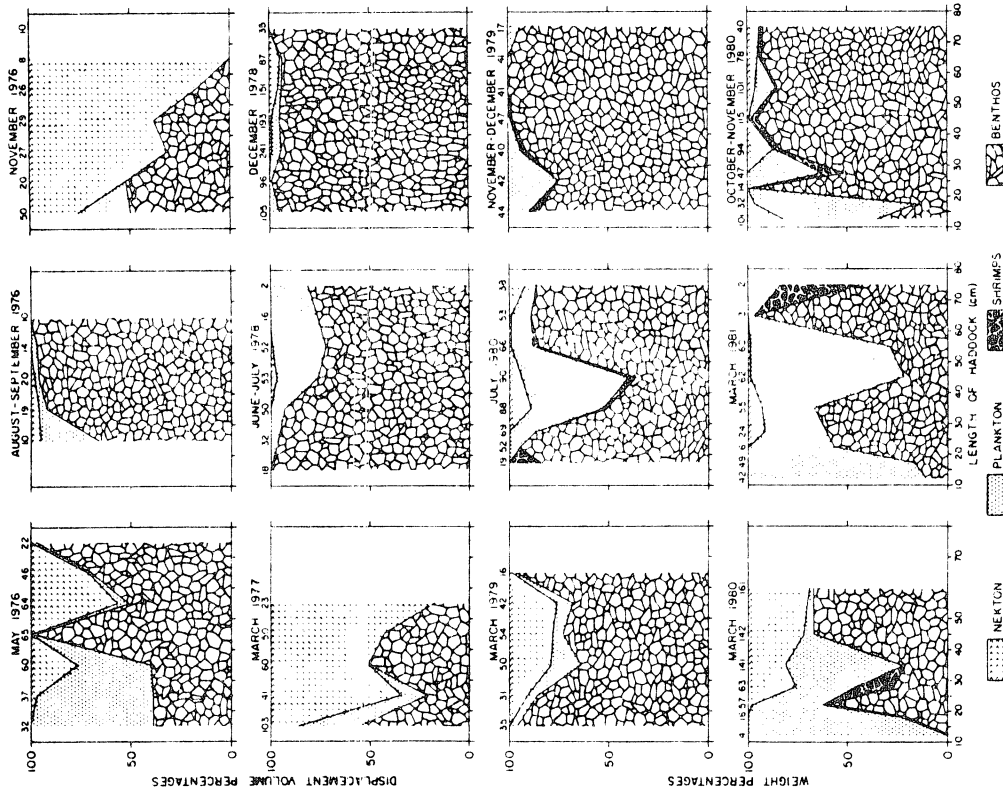


Fig. 15. The composition of the food of haddock (weight or volume percentages) in relation to predator length (cm) at different times during 1976-81, on the basis of ecological grouping of the prey. Shrimps were recorded as benthos prior to November 1977. The number of stomach analysed in each predator length group is given at the top of each illustration.

TABLE 12

Power function regression coefficients (a and b) and coefficient of determination (r^2), describing the average volume or weight of the stomach content of haddock (ml (1978) or grams (1979-81) per stomach, empty stomachs included) in relation to predator length (cm) by seasons.

SEASON (Month and year)	a	b	r^2
June - July 1978	$2.21 \cdot 10^{-4}$	2.65	0.99
December 1978	$9.42 \cdot 10^{-4}$	2.84	0.99
March 1979	$2.04 \cdot 10^{-3}$	3.29	0.95
Nov. - Dec 1979	$8.15 \cdot 10^{-3}$	2.84	0.99
March 1980	$4.48 \cdot 10^{-4}$	2.32	0.76
July 1980	$6.10 \cdot 10^{-3}$	2.91	0.89
Oct. - Nov 1980	$6.01 \cdot 10^{-3}$	2.86	0.96
March 1981	$1.26 \cdot 10^{-4}$	2.59	0.99
March 1979-81	$1.01 \cdot 10^{-4}$	2.73	0.88
June - July 1978, 1980	$9.96 \cdot 10^{-4}$	2.81	0.89
Oct. - Dec 1978-80	$6.39 \cdot 10^{-3}$	2.89	0.97

sumers. Seasonal and year to year variations in the food seem to depend mainly on the occurrence in March of *M. villosus* and other fish as prey for the larger predators. This results in a decreasing importance of benthic prey, particularly Echinodermata.

2) Stomach content quantity

Material sampled in 1978-81 has been used to evaluate the quantity of the stomach content in relation to the length of haddock (Fig. 17, Tables 11-12).

Seasonal variation in stomach content was rather limited (Fig. 17, a and b). Variations between years were particularly pronounced in March, but relatively small in other seasons (Fig. 17, c-e). On the average the quantity of the stomach content was similar in different seasons (Fig. 17, f).

Thus, the quantity of the stomach content ($\bar{W}$ in grams per stomach) in relation to predator length (L) can be adequately described by a single expression, based on the entire material sampled in June-July 1978 through March 1981:

$$\bar{W} = 8.6 \cdot 10^{-5} \cdot L^{2.8}$$

$$r^2 = 0.92$$

THE FOOD OF SAITHE — COMPOSITION AND QUANTITY

The results based on the material sampled in 1980 and 1981 are shown in Fig. 18. The food of saithe was clearly dominated by three prey groups: Euphausiacea were of particular importance in the smaller length groups. With increasing predator length this prey gave way to *M. villosus* which in turn were replaced by Cephalopoda in the largest length groups.

The average weight of the stomach content can be related to predator length by a power function, which has a somewhat higher exponent than observed for the other gadoids. However, because of the limited number of stomachs analysed this result should be regarded as preliminary.

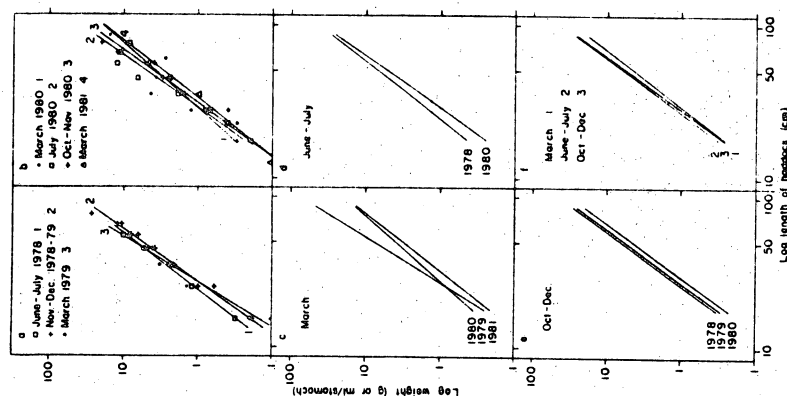


Fig. 17. The relation between the average quantity of the stomach content of haddock (ml (1978) or g (1979-81) per stomach) and predator length (cm), with respect to seasonal variations in 1978-81 (a and b), year to year variations in March (c), June-July (d) and October-December (e) and with respect to average seasonal variations over the period 1978-81 (f) (Tables 11 and 12).

important for the smaller predators, and since 1980 has become increasingly crucial also for larger haddock. As far as predation on other fish is concerned the larger haddock can be classified as facultative fish con-

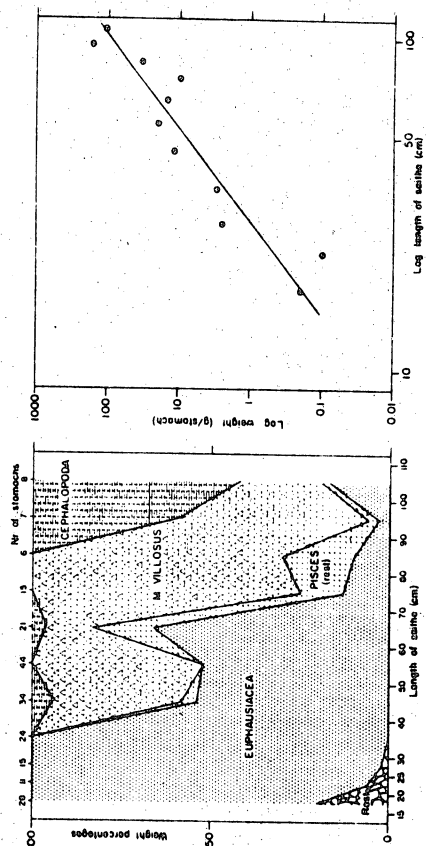


Fig. 18. The composition of the food of saithe (weight percentages), and the average weight of the stomach content (grams per stomach) in relation to predator length (cm).

The available material, although limited, demonstrates the highly pelagic nature of saithe, preying mostly on zooplanktonic animals in the juvenile phase, and gradually shifting over to pelagic fish and Cephalopoda as its length increases.

THE FOOD OF CATFISH

1) The food composition

The major prey groups consumed by catfish in 1980 and March 1981 are shown in Fig. 19. Benthic prey provided the bulk of

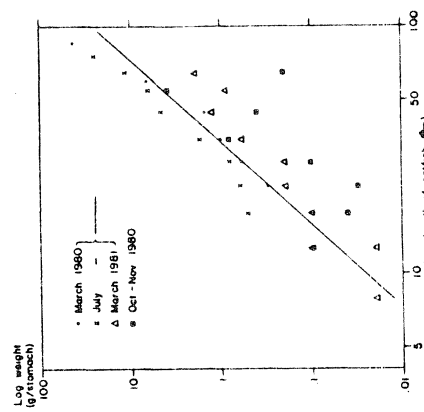


Fig. 20. The average weight of the stomach content of catfish (grams per stomach) in relation to predator length (cm) by seasons in 1980-1981. $W = 2.6 \cdot 10^{-5} L^{1.0}$ ($r^2 = 0.86$).

THE FOOD OF REDFISH

1) The food composition

Except for the smallest redfish length groups Euphausiacea were during all seasons in 1980 clearly of greatest importance as redfish prey (Fig. 21). In March 1981, however, Euphausiacea were important as food only for the largest predators. Large Calanoida, especially *C. finmarchicus*, *C. hyperboreus* and *Parachanna*, were the predominant food of the smaller redfish, particularly in late winter. Also, *Sagitta* were commonly recorded in the diet of most length groups in late winter. Nektonic prey, on the other hand, occurred in all seasons predominantly in the largest predator length groups.

Seasonal variations in the food composition of redfish thus seem to be rather insignificant, and mainly confined to a more pronounced occurrence of Calanoida in late winter instead of Euphausiacea.

One year later, however, fish prey were hardly recorded at all in the stomachs.

In October-November 1980 some nektonic animals became the predominant prey. In this season, the food composition was highly variable. This might be related to reduced feeding activity of the catfish in early winter as the result of tooth exchange (Jonsson, 1982).

Fig. 19 demonstrates the benthic nature of the diet of catfish in Icelandic waters, particularly the prominence of robust and relatively stationary animals of the benthic fauna. The largest catfish, however, might be classified as occasional fish consumers. The contributions of the different benthic prey to the food are clearly subject to considerable seasonal as well as year to year variations.

2) Stomach content quantity

The material sampled in 1980 and 1981 has been used to establish a relationship between the weight of the stomach content and the length of the catfish (Fig. 20).

The weight of the stomach content was similar in March and July 1980, although somewhat greater in the summer season. In October-November, on the other hand, the stomach content was significantly reduced and poorly related to predator length. As previously mentioned, this reduced feeding intensity is probably related to the tooth exchange in this season.

In March 1981 the level of the stomach content was considerably lower than in March 1980. This might be connected with the absence of *M. villosus* from the diet in 1981, whereas one year earlier this prey was predominant in the food of the largest predators.

Thus the food consumption of catfish is apparently characterized by pronounced seasonal as well as some year to year variations.

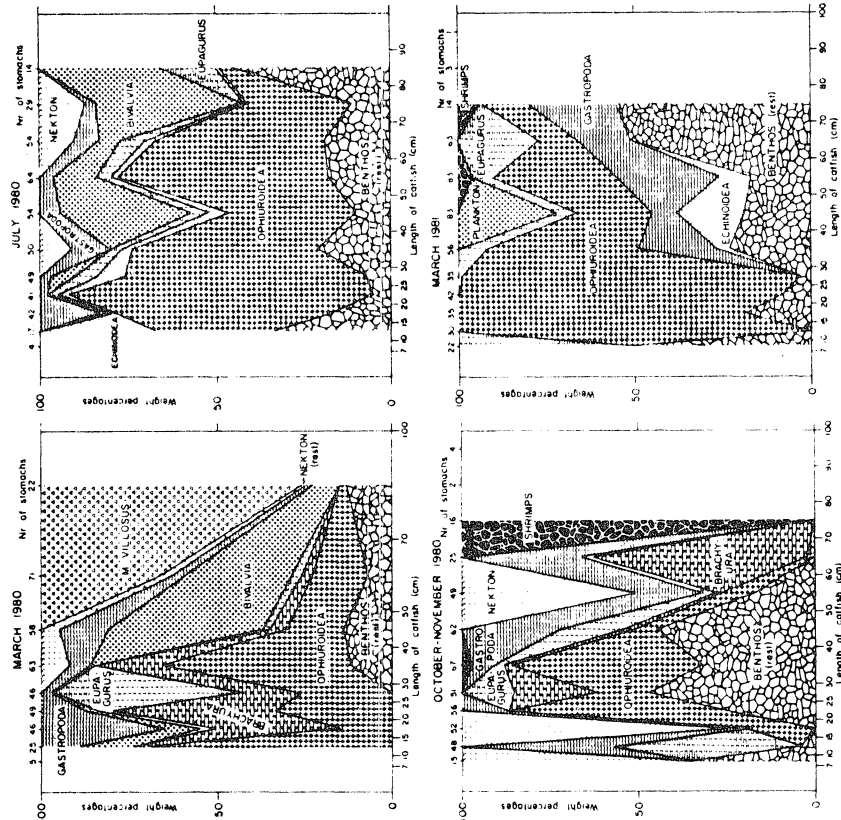


Fig. 19. The composition of the food of catfish (weight percentages) in relation to predator length (cm) in March, July, October-November 1980 and March 1981 (Tables XI-IV).

the food in all seasons, particularly Ophiuroidea. However, this prey became less important as the catfish increased in length. In the upper length range a variety of other benthic prey, Gastropoda, Euphausiacea, Bivalvia and Brachyura were recorded in com-

parable amount although somewhat variable with respect to seasons.

In March 1980 the spawning migrants of *M. villosus* increased in importance with increasing length of the predator and were the predominant food for the largest catfish.

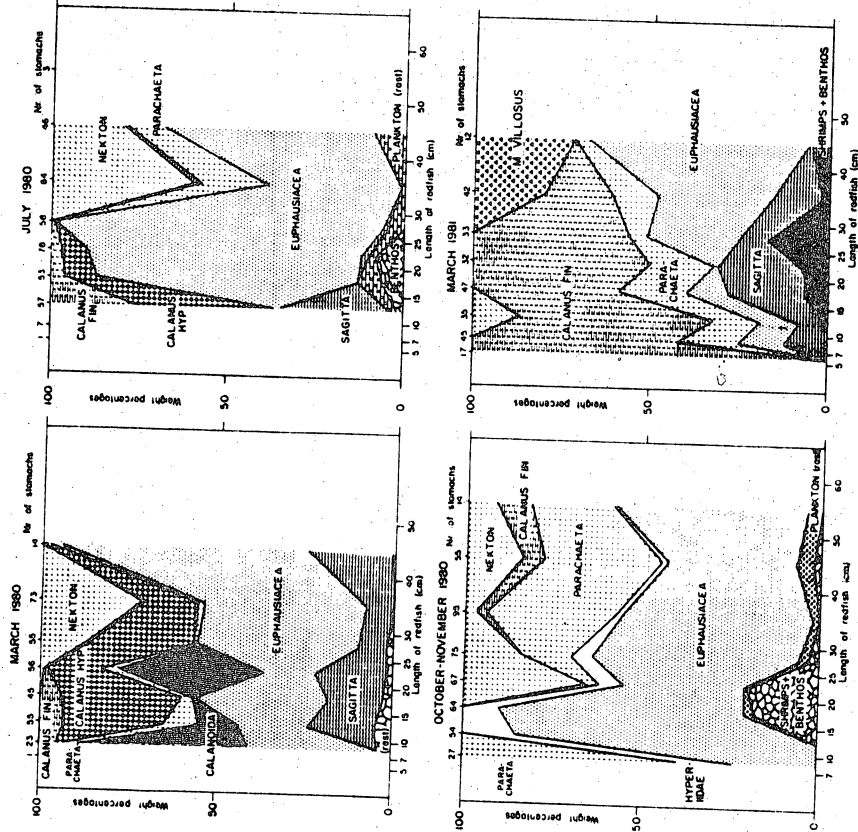


Fig. 21. The composition of the food of redfish (weight percentages) in relation to predator length (cm) in March, July, October-November 1980 and March 1981 (Tables XV-XVIII).

Obviously, zooplanktonic prey provide the bulk of the food of redfish in Icelandic waters. From the point of view of trophic ecological status this fish species should, therefore, be classified as "pelagic" rather than "demersal" as usually done.

2) Stomach content quantity

Based on material sampled in 1980-81, Fig. 22 illustrates the relationship between the average weight of the stomach content of redfish and its length. There are small seasonal or year to year fluctuations in the

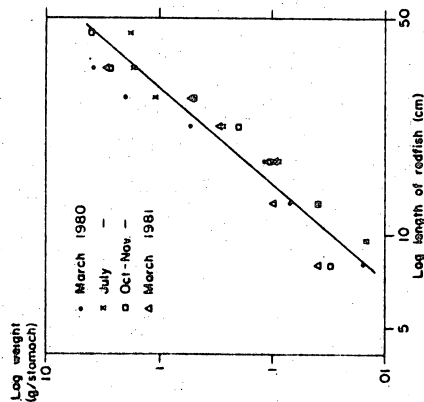


Fig. 22. The average weight of the stomach content of redfish (grams per stomach) in relation to predator length (cm) by seasons in 1980-81: $W = 2.04 \cdot 10^{-1} L^{2.2}$ ($r^2 = 0.90$).

level of the stomach content. Therefore, the quantity of the stomach content in relation to predator length is adequately described by a single power expression.

THE FOOD OF LONG ROUGH DAB

1) The food composition

Fig. 23 stresses the great importance of Ophiuroidea as the food of long rough dab in all seasons in 1980, particularly for the larger fish. However, in March 1981 the proportion of this prey had clearly decreased in the diet. In addition to Ophiuroidea various prey groups contributed a great deal to the diet in the different seasons. Thus, in March 1980, Gammaridea were predominant in the stomachs of predators of intermediate length and Polychaeta in the smallest length groups in July 1980. In October-November 1980, on the other hand, additional food was provided by O-group *G. morhua* and Polychaeta, and in March 1981 by *M. villosus* and Euphausiacea. The nek-

tonic prey were the more predominant food of the larger predators, whereas Euphausiacea and other planktonic prey were preferably consumed by the smaller predators.

The food of long rough dab in Icelandic waters is obviously primarily of benthic origin and the most important prey (Ophiuroidea) shows limited seasonal variations. However, the other prey groups show considerable seasonal and year to year variations. Since fish prey occasionally constitute an appreciable part of the diet, long rough dab should be classified as a facultative fish consumer. The predation on O-group *G. morhua* is of particular interest since this might to some extent influence the recruitment of the cod stock.

2) Stomach content quantity

On the basis of the material sampled in 1980-81 the relationship between the weight of the stomach content and the length of the long rough dab has been established (Fig. 24). The quantity of the stomach content was comparable in all seasons except in October-November 1980. In this season the stomach content was greatly reduced in the two largest predator length groups and, consequently, poorly related to predator length. Apparently, this discrepancy cannot be related to abnormal changes in the food composition of long rough dab in this season (Fig. 23). Nevertheless, it seems appropriate to describe the relation between the quantity of the stomach content and predator length by two equations, one representing the more intense feeding during late winter and summer, the other the reduced feeding intensity in early winter.

THE FOOD OF PLAICE — COMPOSITION AND QUANTITY

The results based on the material sampled in 1980 and 1981 are shown in Fig. 25. With the exception of the smallest length group,

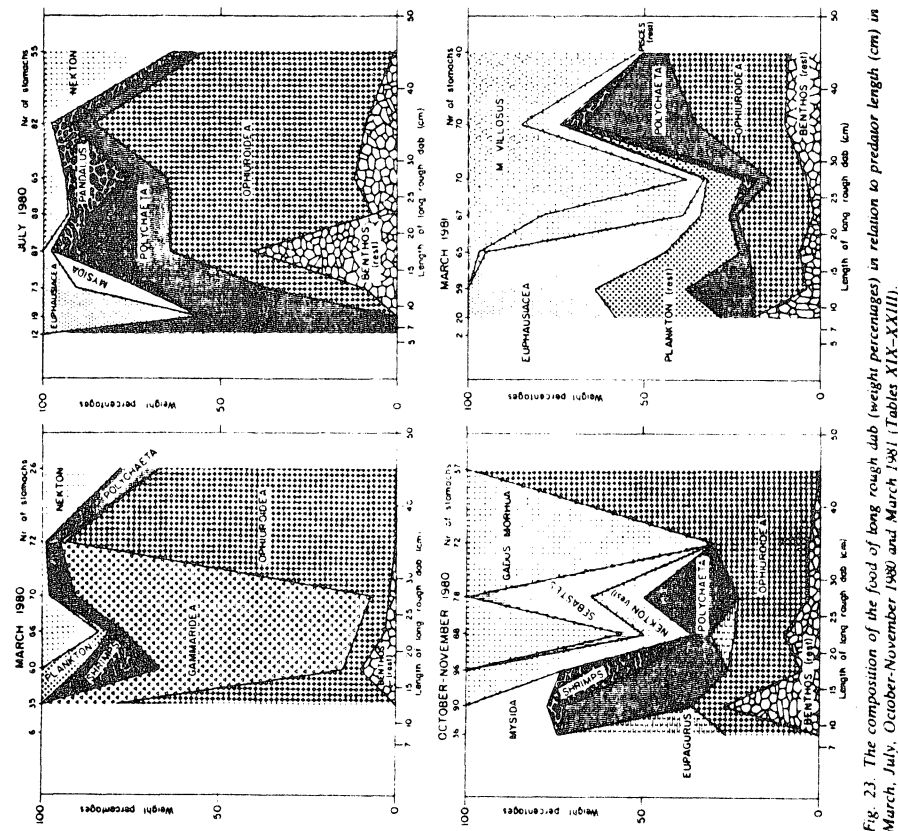


Fig. 23. The composition of the food of long rough dab (weight percentages) in relation to predator length (cm) in March, July, October-November 1980 and March 1981 (Tables XIX-XXIII).

where Ammodytidae were the exclusive prey, Polychaeta and Bivalvia provided virtually the complete diet of all length groups. Accordingly, the plaice in Icelandic waters could be classified as a heavy benthic predator. The average weight of the stomach con-

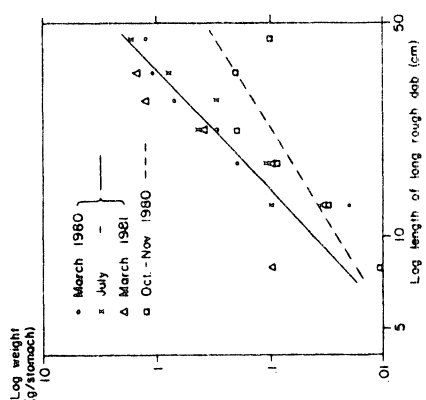


Fig. 24. The average weight of the stomach content of long rough dab (grams per stomach) in relation to predator length (cm) by seasons in 1980-81 $W = 1.26 \cdot 10^{-4} \cdot L^{2.5}$, $r^2 = 0.81$ (late winter and summer); $W = 5.34 \cdot 10^{-4} \cdot L^{1.7}$, $r^2 = 0.65$ (early winter).

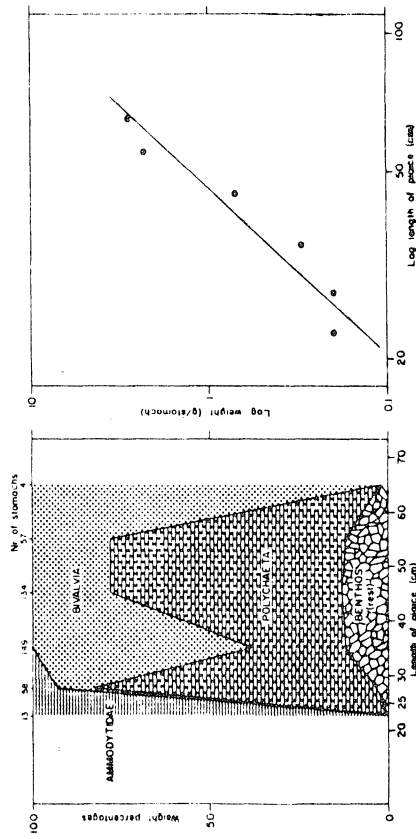


Fig. 25. The composition of the food of plaice (weight percentages), and the average weight of the stomach content (grams per stomach) in relation to predator length (cm): $W = 2.23 \cdot 10^{-5} \cdot L^{2.8}$. Based on material sampled in 1980 and 1981 (Table 6).

DISCUSSION FEEDING HABITS

In the qualitative descriptions by Faber (1829) and Samundsson (1926) cod were generally classified as voracious and unselective predators. Samundsson, however, noted the variability of the food with respect to seasons, regions and age or length of the cod. Later publications, on the other hand, have demonstrated the preference of cod for Pisces and Crustacea as food, as well as the shift in the food composition from Crustacea to Pisces with increasing length of the cod (Meschkat 1936, Brown and Cheng 1946; Rae 1968; Falsson 1980 a). The results of these investigations on the feeding habits of cod in Icelandic waters are, thus, in general agreement with the present work. Other aspects of the feeding habits, e.g. the weight of the stomach content or the prey size, have not been previously evaluated in Icelandic waters.

In earlier publications (Samundsson 1926; Thompson 1929; Oskarsson 1944;

Brown and Cheng 1946; Friðriksson and Timmermann 1950; Ingimarsson 1974; Pálsson 1980 a) the haddock in Icelandic waters has generally been classified as a benthic feeder. The particular preference of haddock for Ophiuroidea, Polychaeta and Bivalvia has been recorded as well as the occasional consumption of Pisces. Thus, previous results on the feeding habits of haddock in Icelandic waters are generally consistent with the present conclusions.

As regards the other fish species considered in the present paper, only qualitative descriptions of their food in Icelandic waters are hitherto available (Faber 1829; Sæmundsson 1926). In general, they are in agreement with the results here presented.

Investigations on the feeding habits of cod in the northwest Atlantic (Langton and Bowman 1980), around Newfoundland (Minet and Perodou 1978), in the North Sea (Daan 1973) and in Icelandic waters (this paper) have demonstrated considerable degree of similarity. In all regions Pisces yield roughly $\frac{1}{10}$ of the food and Crustacea roughly $\frac{1}{10}$, whereas benthic prey do not exceed $\frac{1}{10}$ of the food by weight. Exceptions from this pattern have been recorded in the southwestern Gulf of St. Lawrence (Wainwood 1981) and in the Baltic (Amiz 1974 and 1978; Uzars 1975) where Crustacea yield approximately $\frac{1}{2}$ of the food and Pisces only $\frac{1}{4}$, whereas the proportion of benthic prey is considerably greater than in the other regions. However, certain regional differences occur with respect to Pisces: In the northwest Atlantic and in the Baltic Clupeidae are recorded as the principal fish prey. *M. villosus* are found to be the most important fish prey in Icelandic as well as Newfoundland waters, whereas in the North Sea Gadidae are the predominant fish prey. In all regions, on the other hand, a more or less clear change in food composition is recorded from Crustacea to Pisces with increasing length of the cod.

The feeding habits of haddock have been

studied quantitatively in some regions of the northwest Atlantic (Wigley 1956; Kohler and Fitzgerald 1969; Langton and Bowman 1980) and in the North Sea (Ritchie 1937). These investigations along with the results presented in the present paper demonstrate the general benthic nature of the feeding habits of haddock. Approximately $\frac{1}{2}$ of its food is of benthic origin, mainly Echinodermata and Polychaeta, whereas Crustacea and Pisces yield respectively roughly $\frac{1}{4}$ and $\frac{1}{10}$ of the food.

Stomach analyses of saithe in the northwest Atlantic (Steele 1963; Langton and Bowman 1980) and in Icelandic waters (this paper) reveal a general similarity in the feeding habits of these fish. In both regions the food consists almost exclusively of Crustacea, mainly Euphausiacea, and Pisces in comparable proportions.

Feeding studies of redfish in the Gulf of St. Lawrence (Steele 1957) and in the Newfoundland Area (Lambert 1960) as well as in Icelandic waters (this paper) demonstrate the pelagic nature of the feeding habits of this fish in all of these regions.

A comparison of the feeding habits of long rough dab on the Grand Bank of Newfoundland (Pitt 1973) and in Icelandic waters (this paper) shows that in both regions major prey groups such as Ophiuroidea and *M. villosus* are of comparable importance as food. In the Grand Bank region, however, benthic prey amount to $\frac{1}{4}$ of the food and Pisces to $\frac{1}{10}$, whereas in Icelandic waters the relative importance of these prey groups is the reverse. In the Gulf of Maine and adjacent waters, on the other hand, (Langton and Bowman 1981) Echinodermata alone yield $\frac{1}{10}$ of the food whereas the proportion of fish is negligible.

INTERACTIONS BETWEEN COD AND *M. VILLOSUS*

In view of the important role of *M. villosus* as food for the Icelandic cod, as well as

the importance of both of these fish stocks in ecological and economical context, it seems appropriate to discuss some aspects of their interaction.

Perhaps the most important question regards the functional relationship of the cod predation on *M. villosus*. Estimates of the abundance of *M. villosus* by acoustic methods have demonstrated a drastic decline in the stock size, from 1000–1500 thousand metric tons in 1979 to 200–400 thousand tons in 1981 (Vilhjálmsen and Reynisson 1982). On the other hand, the relative amount of *M. villosus* in the food of cod has not been found to decline in this period, since with respect to *M. villosus*, the food composition was remarkably similar in 1979 and 1981, particularly in the autumn season. In March 1980, an exceptionally high proportion of the food was due to *M. villosus* (Figs. 2 and 3).

Furthermore, the average quantity of food per stomach of cod did not show a declining trend during 1979–81 (Fig. 7). On the contrary, the level of the stomach content in February–March was lowest in 1979, and in October–November it was somewhat higher among the larger cod in 1981 than in both 1979 and 1980. However, in the NW-area in November 1981 considerably reduced stomach content was recorded for cod of the length range 60–79 cm (Fig. 8). At that time the proportion of *M. villosus* in the food was only 1% by weight, and considering the time of year the proportion of Hyperiidæ and Euphausiacea was exceptionally high: 32% and 53% in length groups 60–69 cm and 70–79 cm respectively. In these same length groups the proportions of *M. villosus* were 57% and 66% in the NE-area and 40% and 43% in the E-area. In November 1981 most of the migrating *M. villosus* were located in a relatively limited area off the NE-coast, and the total size of the mature stock was estimated to be 400 thousand tons (Vilhjálmsen and Reynisson 1982). It therefore seems likely that the

small amount of *M. villosus* in the stomach content of cod in the NW-area in November 1981 is related to reduced availability and declining stock size of *M. villosus*.

These findings suggest that the predation of cod upon *M. villosus* generally does not depend on the size of the prey stock itself, as long as it remains above some minimum level. The predatory impact would thus rather be a function of the size of the cod year classes which mainly prey on *M. villosus*. However, there are some indications that the stock size of *M. villosus* was below this minimum level in November 1981.

An interesting feature of the food composition of cod is the occurrence of definite peaks or maxima at different predator lengths. (Fig. 3). Generally, these peaks were more typical for fish prey, particularly for *M. villosus* in early winter. This prey reached peaks of maximum weight percentage values in virtually identical predator length groups in October–November 1980 and in November 1981, i.e. in length groups 7–9, 25–29 and 70–79 cm (1980), and in length groups 10–14, 25–29 and 70–79 cm (1981). This suggests some kind of size or age specific predator-prey relationship.

The smallest cod prey only occasionally upon *M. villosus*, although in early winter this prey contributes significantly to their food. It seems that the *M. villosus* maximum in cod length groups 7–9 and 10–14 cm is a result of an accidental consumption of the relatively large prey, rather than its size specific suitability.

As demonstrated in Fig. 10 the length distribution of *M. villosus* for October–November is characterized by two different distribution patterns with respect to predator length. Among cod 20–59 cm in length there is a clear preference for 0-group *M. villosus* (around 5 cm in length). In the larger length groups of cod the prey is relatively evenly distributed over its entire length range, and, apparently, most evenly distributed in the length group 70–79 cm. The

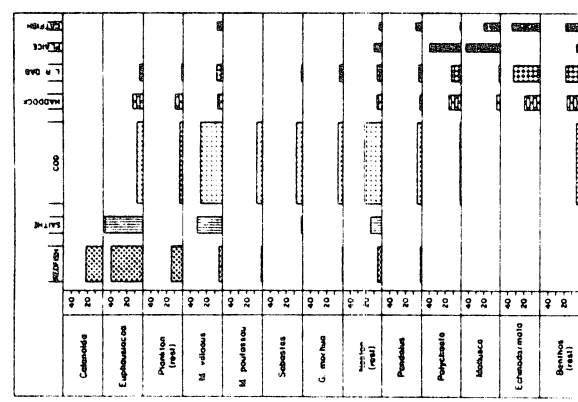


Fig. 26. Trophic ecological relationships. The average weight percentages of prey groups in 1980-81 for the different predator species. The relative size of each prey group is indicated by the width of the respective columns.

maximum of *M. villosus* in cod length group 25-29 cm might be related to a size specific suitability of the 0-group as prey for this particular length group of cod. On the other hand, the maximum of *M. villosus* in the food of predators 70-79 cm in length might be explained by the apparent ability of these predators to prey successfully on all length/age groups of *M. villosus*.

In late winter the maxima of *M. villosus* in the food were much more pronounced, occurred in cod of smaller lengths, and in March 1980 (Fig. 3) they included most cod length classes. Even in the smaller length groups of cod (Fig. 10) the length distribution of *M. villosus* in March was characterized by mature II- and III-group prey. It seems likely that *M. villosus* with fully matured gonads of up to about 20% of their body weight must be considerably retarded in their locomotive reactions. As a consequence this prey would be more vulnerable to predation during the spawning season than at other times of the year.

Apparently, the great importance of *M. villosus* as food of cod may be linked to various physiological and biological interrelations between the predator and the prey. In this context the size of the predator and the prey in relation to each other, as well as the condition of the prey are likely to be of importance. These factors may be the most obvious ones governing the interactions between these fish species. However, there are presumably other factors which must be considered. Furthermore, it would be expected that other predator-prey interactions, e. g. that of cod and Euphausiacea, are regulated in a comparable way.

GENERAL TROPHIC RELATIONSHIPS

The trophic relationships of the predators and their prey are demonstrated in Fig. 26. Redfish are characterized by their pronounced preference for zooplanktonic prey,

summer to the waters off the east and north-east coasts. Furthermore, the predation of cod on pelagic 0-group *Sebastes* in early winter off the north coast depends on the transportation of the prey into these waters by the anticyclonic current along the north coast of Iceland. Cannibalism is more pronounced among cod than the other predator species.

The remaining species are preferably benthic feeders, although most or all of them might be classified as occasional or partial fish consumers. Polychaeta and Echinodermata are the prey groups most preferred by these predators. This could indicate interspecific competition of these predators for such animals. This might, however, be avoided or reduced by differing preference with respect to a prey species.

Euphausiacea, *M. villosus*, *Pandalus* and Polychaeta were consumed by most of the predators investigated. In view of the size of the predator stocks as well as their prey preferences, Euphausiacea and *M. villosus* are likely to be most affected by the predation. However, this will to a great extent depend upon the actual size of the prey populations.

The trophic ecological status of the cod is emphasized by three important features: Firstly, the cod stock is by far the largest demersal fish stock on the Icelandic fishing grounds. Secondly, the cod preferably prey on other fish species, of which the most preferred ones are subject to extensive commercial exploitation in Icelandic and international waters. And finally, the average food consumption of cod in relation to predator length is apparently greater than that of the other predator species (Fig. 27). By virtue of these features the predation of cod is of paramount interest, generally as a part of the trophic ecological relationships in Icelandic waters and specifically because of the role of cod as a "competitor" in the exploitation of commercial fish stocks.

As a consequence, the predation of cod is of major importance in modelling fish

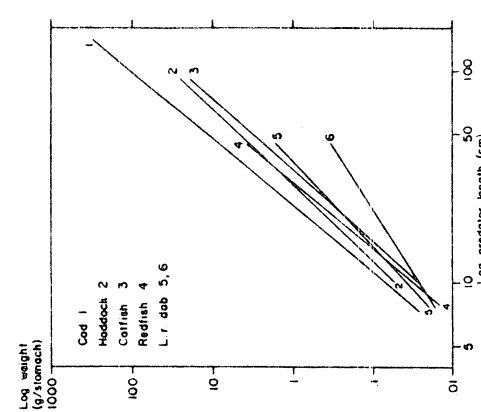


Fig. 27. Interspecific comparison of the average weight of the stomach content (grams per stomach) in relation to predator length (cm). Cullfish data from October-November 1980 excluded.

species interaction in Icelandic waters. The relevant predator-prey interactions of commercially exploited fish stocks seem to involve relatively limited number of species. Thus, the predation of cod upon *M. villosus*, *M. poulaou*, *Sebastes*, *G. morhua* and *Pandalus* includes the most important interactions. By considering also the predation upon *M. villosus* and *Pandalus* by the predators in Fig. 26 as well as the predation of long rough dab on *G. morhua*, all relevant predator-prey relationships would be included.

It remains the challenge of further research to evolve a suitable model to quantify the predator-prey interactions involved, and, thereby, to add a new dimension to marine science and fisheries management.

ACKNOWLEDGEMENTS

This project has been carried out with the invaluable cooperation and assistance of several members of the staff of the Marine Research Institute, Reykjavík, in particular Sigurður Guðjónsson, Sigmar Steingrímsson and Helgi Guðmundsson who worked on the analyses of the stomach samples.

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- Gunnar Hilmarrsson edited the programs for the computerized data processing and Sigurður Gunnarsson has drawn all figures.
- Albert Stefánsson, Gisli Ólafsson and Sigurður Gunnarsson worked at the sampling of the material at sea. Finally, the author would like to thank the crews of the research vessels "Bjarni Sæmundsson" and "Hafþór" for their efforts during the sampling of the material.
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TABLE IV
The food composition of cod in March 1981.

Prey group	Predator length group (cm)															Aver. age
	7-9	10-14	15-19	20-24	25-29	30-39	40-49	50-59	60-69	70-79	80-89	90-100	100-109	110-119	120-129	
Cephalopoda	—	—	—	—	—	1	2	1	3	2	1	1	1	—	1	
Clupea harengus	—	—	—	—	—	—	—	1	1	1	—	—	—	—	—	
Malibus villosus	—	4	3	19	19	62	88	62	60	51	34	3	—	—	27	
Myctophidae	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	
Gadus morhua	—	—	—	—	—	—	—	—	5	—	—	27	—	—	2	
Pollachius virens	—	—	—	—	—	—	—	—	—	—	7	4	—	—	1	
M. aeglefinus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
M. poussou	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	
Trisopterus esmarkii	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Ammodytidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Anarhichas lupus	—	—	—	—	—	—	—	—	—	—	—	11	—	—	—	
Lumpenidae	—	15	1	2	2	—	—	—	—	—	—	—	—	—	1	
Lycodes	—	—	—	—	—	—	—	—	2	1	2	—	11	—	1	
Sebastes	—	—	—	—	—	—	—	—	—	5	27	17	52	—	7	
H. platessoides	—	10	3	—	—	—	—	—	—	—	—	2	—	—	—	
Heterosomata	—	1	—	—	—	—	—	—	—	—	—	—	6	—	1	
Pisces unidentified	—	7	1	10	5	—	—	3	7	2	16	—	100	—	10	
Nekton Total	—	4	25	14	20	36	72	89	71	81	92	91	94	100	59	
Ctenophora	—	—	—	—	4	—	—	—	1	—	—	—	—	—	—	
Scyphozoa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Calanus finmarchicus	12	16	10	1	3	2	—	—	—	—	—	—	—	—	3	
Calanus hyperboreus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Parachaeata	—	1	—	2	1	5	1	—	—	—	—	—	—	—	1	
Metridia	43	—	—	—	—	—	—	—	—	—	—	—	—	—	3	
Mysida	—	2	1	1	1	—	—	—	1	—	—	—	—	—	—	
Hyperidae	—	—	—	1	2	3	1	3	4	—	—	—	—	—	1	
Euphausiacea	30	20	45	47	33	11	2	2	7	3	2	4	—	—	14	
Sagitta	—	1	—	2	2	3	8	—	—	—	—	—	—	—	1	
Plankton Total	84	40	56	54	42	28	12	4	13	8	2	4	1	—	23	
Pandanus	16	1	6	2	8	1	5	5	7	4	2	—	—	—	4	
Skrinks unidentified	—	3	—	—	—	—	—	—	5	3	1	1	—	—	2	
Skrinks Total	16	1	3	6	3	24	5	6	10	10	5	2	—	—	6	
Anthozoa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Pragipoda	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Gastropoda	—	5	—	—	—	—	—	—	—	—	—	—	—	—	—	
Bivalvia	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Polychaeta	—	22	4	5	13	7	8	—	1	—	—	—	—	—	4	
Cumacea	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Isopoda	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Gammaridea	33	12	11	12	4	1	—	—	1	1	—	—	—	—	5	
Anomura	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Eupagurus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Brachyura	—	—	5	9	—	—	—	—	—	3	—	2	—	—	1	
Holothuriidea	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	
Asteronidea	—	—	—	—	—	—	—	—	—	—	—	—	4	—	—	
Ophiuroidea	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Benthos Total	—	55	16	26	34	11	10	1	7	2	—	2	5	—	11	

TABLE III
The food composition of cod in October - November 1980.

[illegible]

'1) *Melanogrammus aeglefinus*.

TABLE VI
The food composition of cod in November 1981.

Prey group	Predator length group (cm)															
	7-9	10-14	15-19	20-24	25-29	30-34	35-39	40-49	50-59	60-69	70-79	80-89	90-99	100-129	Average	
Cephalopoda	—	—	—	—	—	—	—	—	6	1	1	—	—	—	1	
Clupea harengus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Mallotus villosus	—	42	11	10	42	36	20	34	51	64	57	41	7	32	32	
Myxophyceae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Gadus morhua	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
M. aeglefinus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
M. pourtaussou	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Ammodytidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Lumpenidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Lycodes	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Sebastes	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Iceland bicornis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Arctiellus europaeus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
H. platessoides	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Heterosomata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Pisces unidentified	—	9	1	5	20	21	26	15	29	23	18	13	18	15	15	
Nekton Total	—	51	13	16	69	62	55	68	87	91	96	93	100	61	61	
Hyperidae	—	—	1	1	1	1	4	4	1	1	1	1	—	—	—	
Euphausiacea	—	35	24	35	10	6	7	6	5	1	1	—	—	—	10	
Plankton unidentified	100	14	44	23	4	19	10	1	—	—	—	—	—	—	17	
Plankton Total	100	49	69	59	15	25	22	11	6	2	2	5	—	—	28	
Pandalus	—	39	15	7	4	7	7	7	3	5	1	1	—	—	4	
Shrimps unidentified	—	—	3	4	3	2	7	1	1	—	—	—	—	—	2	
Shrimps Total	—	—	5	19	10	6	14	8	3	5	1	1	—	—	6	
Polychaeta	—	—	3	1	2	3	5	4	1	—	—	—	—	—	2	
Gammaridea	—	—	10	6	4	3	3	1	—	—	—	—	—	—	2	
Benthos unidentified	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Benthos Total	—	—	13	7	7	7	10	14	4	2	2	1	—	—	5	

TABLE V
The food composition of cod in September 1981.

Prey group	7-9	10-14	15-19	20-24	25-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99	100-129	Average age
	Predator length group (cm)													
Cephalopoda	—	—	—	—	—	—	3	*	*	*	1	*	*	*
Gonostomatidae	—	—	—	—	—	—	—	—	—	—	—	—	—	*
Steropterychiidae	—	—	—	—	—	—	—	*	*	—	—	—	—	*
Clupea harengus	—	—	—	—	—	—	—	4	—	—	4	12	2	2
Mallotus villosus	—	—	12	—	—	8	12	10	4	16	13	13	1	7
Myctophidae	—	—	—	—	—	—	—	—	—	*	*	*	—	*
Cladus morhua	—	—	—	—	—	—	—	—	—	12	3	*	28	3
M. aeglefinus	—	—	—	—	5	—	—	*	—	—	—	—	—	*
M. poutassou	—	—	—	—	—	—	—	—	—	4	24	27	31	7
Molva dypterygi	—	—	—	—	—	—	—	—	—	—	—	—	—	*
Ammodytidae	—	—	15	—	—	—	2	1	1	1	*	*	1	2
Anarhichas lupus	—	—	—	—	—	—	—	1	—	*	2	6	—	1
Lumpenidae	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Gymnelis viridis	—	—	1	1	*	2	1	3	1	*	*	*	—	*
Lycodes	—	—	—	—	—	—	—	—	—	—	—	—	—	*
Sebastes	—	—	—	—	—	*	—	*	3	11	4	7	1	2
Triglopus pingelli	—	—	—	2	—	—	*	—	—	—	—	—	—	*
Agonidae	—	—	—	—	—	—	—	*	2	*	*	*	—	*
H. platessoides	—	—	—	5	9	5	*	—	*	*	*	1	3	2
H. hippoglossus ¹⁾	—	—	—	—	—	—	—	—	—	—	—	—	—	*
Heterosomata	—	32	5	7	1	2	1	*	*	4	3	*	*	4
Pisces unidentified	—	—	1	11	14	8	32	24	9	24	30	30	33	17
Nekton Total	—	32	18	40	30	23	54	40	22	73	86	98	99	47
Hyperipidae	6	—	*	*	2	4	8	9	3	1	*	*	*	3
Euphausiacea	—	—	11	12	1	6	8	16	34	14	5	1	*	8
Plankton unidentified	94	4	9	6	7	2	8	6	4	1	*	*	1	22
Plankton Total	100	4	19	18	8	10	19	32	50	21	7	1	1	21
Pandalus	—	20	24	16	28	55	7	3	3	2	1	*	*	12
Shrimps unidentified	—	—	2	11	18	4	3	4	12	*	4	*	*	5
Shrimps Total	—	20	27	27	45	59	10	7	15	2	4	*	*	17
Polychaeta	—	23	16	9	5	4	10	8	4	1	*	*	*	6
Gammaridea	—	7	16	4	5	2	2	1	2	*	*	*	*	3
Benthos unidentified	—	15	4	1	6	2	5	11	8	3	2	1	*	4
Benthos Total	—	44	36	14	17	8	18	20	13	4	2	1	*	14

1) Hippoglossus hippoglossus.

TABLE VIII
The food composition of haddock in July 1980.

Prey group	Predator length group (cm)										Average
	15-19	20-24	25-29	30-39	40-49	50-59	60-69	70-79	80-89		
Cephalopoda	—	—	—	4	5	—	1	3	—	1	
Mallopus villosus	—	—	—	—	—	1	—	—	—	—	
Pisces unidentified	—	—	—	7	1	—	—	5	—	1	
Nekton Total	—	—	—	11	6	1	—	8	—	3	
Nudibranchia	—	—	—	2	—	—	—	—	—	—	
Mysida	—	—	—	—	—	—	—	—	—	—	
Hyperidae	—	—	5	2	3	1	1	1	—	—	
Euphausiacea	—	5	7	31	50	10	9	3	1	13	
Sagitta	—	—	1	—	—	—	—	—	—	—	
Plankton Total	—	5	13	36	54	11	10	6	1	15	
Pandalus	16	—	—	2	3	1	—	—	—	3	
Shrimps unidentified	—	—	—	—	—	2	—	—	2	1	
Shrimps Total	16	—	—	2	4	3	—	—	2	3	
Anthozoa	—	—	—	—	—	—	—	—	—	—	
Nemertini	18	—	—	2	—	—	—	—	—	—	
Priapulida	—	—	—	—	—	—	—	—	—	—	
Loricata	2	1	—	—	—	—	—	—	—	—	
Gastropoda	2	1	6	1	—	—	3	1	18	3	
Bivalvia	11	13	9	4	5	1	5	1	—	5	
Sipunculida	—	—	5	—	—	—	—	—	—	1	
Polychaeta	55	35	48	8	9	30	40	18	48	32	
Cumacea	—	—	—	—	—	—	—	—	—	—	
Isopoda	—	—	—	—	—	—	—	—	—	—	
Gammaridea	—	1	1	1	3	1	1	1	—	1	
Eupagurus	—	—	—	—	1	2	8	—	—	—	
Brachyura	—	20	13	—	—	5	1	2	18	7	
Pycnogonidae	—	—	—	—	—	—	—	—	—	—	
Holothuriidea	—	12	—	1	3	17	9	9	—	6	
Echinoidea	—	—	4	9	2	13	4	24	—	6	
Asterosidea	—	—	—	2	—	—	—	—	—	—	
Ophiuroidea	—	11	5	15	7	16	13	14	—	9	
Tunicata	—	—	—	—	—	—	—	—	29	3	
Benthos Total	84	95	87	50	36	85	89	86	97	79	

TABLE VII
The food composition of haddock in March 1980.

Prey group	Predator length group (cm)									
	10-14	15-19	20-24	25-29	30-39	40-49	50-59	70-99	Average	
Cephalopoda	—	—	—	11	0	—	—	—	1	
Mallopus villosus	—	—	0	1	14	24	30	50	15	
Gadus morhua	—	—	—	—	—	—	—	2	0	
Ammodytidae	—	—	—	—	1	—	0	5	1	
Heterosomata	—	—	—	—	—	0	0	1	0	
Pisces unidentified	—	—	1	12	5	5	1	35	7	
Nekton Total	—	—	2	24	19	28	31	93	25	
Nudibranchia	—	—	—	—	3	—	—	0	0	
Calanoida	—	—	—	0	0	0	—	—	—	
Mysida	—	1	1	—	0	0	0	—	—	
Hyperidae	100	—	0	0	0	0	1	0	13	
Euphausiacea	—	76	34	30	55	5	1	0	25	
Sagitta	—	—	—	—	—	—	—	0	—	
Plankton Total	100	77	35	30	59	5	2	0	38	
Pandalus	—	—	18	0	0	0	0	0	2	
Shrimps unidentified	—	2	4	0	1	0	1	0	1	
Shrimps Total	—	2	4	19	1	0	1	0	3	
Anthozoa	—	—	—	—	—	—	0	—	0	
Nemertini	—	—	2	—	—	—	0	0	0	
Loricata	—	—	—	—	—	—	0	0	0	
Gastropoda	—	—	2	—	—	1	1	0	1	
Bivalvia	—	—	1	0	0	2	1	0	1	
Sipunculida	—	—	—	0	0	1	1	—	—	
Polychaeta	—	16	23	17	8	30	32	3	16	
Ostracoda	—	—	—	—	—	0	0	—	—	
Cumacea	—	2	4	1	1	2	0	—	1	
Isopoda	—	—	0	0	0	1	0	—	0	
Gammaridea	—	—	16	5	1	2	1	0	3	
Nephrops	—	—	—	—	—	0	0	1	—	
Anomura	—	—	7	0	0	—	3	—	1	
Eupagurus	—	—	0	—	—	0	2	1	0	
Brachyura	—	1	3	2	1	0	0	—	1	
Tanaidacea	—	—	—	—	—	0	0	0	—	
Pycnogonidae	—	—	—	—	—	0	0	—	—	
Holothuriidea	—	—	—	—	3	6	3	—	1	
Echinoidea	—	—	—	—	4	8	8	1	3	
Asterosidea	—	—	—	—	—	—	—	—	—	
Ophiuroidea	—	2	2	3	2	12	14	1	5	
Tunicata	—	—	—	—	—	0	0	—	—	
Fish eggs	—	—	—	—	—	0	0	—	—	
Benthos Total	—	21	59	27	21	67	67	6	34	

TABLE X
The food composition of haddock in March 1981

Prey group	Predator length group (cm)										
	7-9	10-14	15-19	20-24	25-29	30-39	40-49	50-59	60-69	70-79	Average
Cephalopoda	—	—	—	—	—	—	—	1	—	—	*
Mallotus villosus	—	—	—	—	3	—	—	*	—	—	*
Gadus morhua	—	—	—	—	—	6	1	—	—	—	1
M. aeglefinus	—	—	—	—	5	1	*	—	—	—	1
Ammodytidae	—	—	—	—	8	7	1	1	—	—	2
Sebastes	—	—	—	—	—	—	—	—	—	—	—
H. platessoides	—	—	—	—	—	—	—	—	—	—	*
Heterosomata	—	—	—	—	—	—	—	—	—	—	—
Pisces unidentified	—	—	—	—	—	—	—	—	—	—	—
Nekton Total	—	—	—	—	—	—	—	—	—	—	—
Foraminifera	—	—	—	—	—	—	—	—	—	—	—
Nudibranchia	—	—	—	—	—	—	—	—	—	—	—
Calanus finmarchicus	—	—	5	29	*	6	3	1	—	—	5
Paracheta	—	6	8	—	—	5	14	6	—	—	5
Mysida	—	—	—	—	—	5	3	—	—	—	1
Hyperidae	—	17	5	—	*	*	34	16	*	4	9
Euphausiacea	—	42	59	14	25	5	17	33	1	12	23
Sagitta	—	25	5	—	—	7	9	11	1	—	6
Plankton Total	—	89	83	43	31	26	77	70	3	16	48
Pandalus	—	—	—	—	—	1	*	—	—	40	5
Shrimps unidentified	—	4	1	—	—	—	—	3	—	—	1
Shrimps Total	—	4	1	—	—	1	*	3	—	40	6
Anthozoa	—	—	—	—	1	1	—	—	2	—	*
Nemertini	—	—	—	—	—	—	—	—	—	—	*
Prapauia	—	—	—	—	—	—	—	—	12	—	1
Loricata	—	—	—	—	1	—	—	—	—	—	*
Gastropoda	—	—	—	—	—	—	—	—	4	—	1
Scaphopoda	—	—	—	—	—	—	—	—	—	—	*
Bivalvia	—	—	—	—	*	2	2	*	2	—	1
Sipunculida	—	—	—	—	—	—	—	—	—	—	*
Polychaeta	—	5	12	—	37	23	11	11	7	20	14
Cumacea	—	—	—	—	—	4	*	*	—	—	*
Isopoda	—	—	—	—	3	1	*	—	—	—	*
Gammaridea	—	2	4	57	2	15	1	1	3	—	9
Anomura	—	—	—	—	—	—	—	—	—	—	*
Eupagurus	—	—	—	—	—	—	—	—	—	—	*
Brachyura	—	—	—	—	—	*	1	*	4	—	1
Pycnogonidae	—	—	—	—	—	—	—	—	—	—	*
Holothuriidea	—	—	—	—	—	—	—	—	—	—	*
Echinoidea	—	—	—	—	—	—	—	—	—	—	1
Ophiuroidea	—	—	—	—	—	16	20	7	6	44	24
Benthos Total	—	7	16	57	61	66	22	26	97	44	44

TABLE IX
The food composition of haddock in October - November 1980

Prey group	Predator length group (cm)										
	7-9	10-14	15-19	20-24	25-29	30-39	40-49	50-59	60-69	70-79	Average
Cephalopoda	—	—	—	—	—	*	—	—	—	—	*
Mallotus villosus	—	—	—	—	—	—	—	—	—	—	*
Gadus morhua	—	—	—	—	—	—	—	—	—	—	*
M. aeglefinus	—	—	—	—	—	—	—	—	2	—	*
Ammodytidae	—	—	—	—	—	*	*	*	*	*	*
Sebastes	—	—	—	—	3	—	—	—	—	6	1
H. platessoides	—	—	—	—	—	—	3	1	—	—	1
Heterosomata	—	—	—	—	—	—	1	*	—	—	*
Pisces unidentified	30	18	3	—	—	*	—	—	—	*	5
Nekton Total	30	18	3	—	—	13	1	4	5	6	7
Foraminifera	—	—	—	—	—	—	—	—	—	—	—
Nudibranchia	—	—	—	—	—	—	—	—	—	—	—
Paracheta	—	10	—	—	—	*	*	—	—	—	1
Mysida	—	—	—	—	—	*	1	*	—	—	*
Hyperidae	50	20	4	—	3	*	*	8	*	*	8
Euphausiacea	20	16	7	2	35	—	—	1	*	—	14
Sagitta	—	—	—	—	—	—	—	—	—	—	*
Plankton Total	70	47	27	2	38	1	1	10	1	*	23
Pandalus	—	3	2	—	10	1	2	1	1	1	2
Shrimps unidentified	—	—	—	—	—	*	1	—	—	*	*
Shrimps Total	—	3	2	—	10	2	3	1	1	2	2
Anthozoa	—	—	—	—	—	—	—	—	—	—	*
Octocorallia	—	—	—	—	—	—	—	—	—	—	*
Nemertini	—	—	—	—	—	—	—	—	—	—	*
Prapauia	—	—	—	—	—	—	*	2	*	*	*
Loricata	—	—	—	—	—	—	*	1	—	—	*
Gastropoda	—	—	—	—	—	—	4	1	2	2	*
Scaphopoda	—	—	—	—	—	—	—	—	—	—	*
Bivalvia	—	—	—	—	—	5	4	6	10	2	2
Sipunculida	—	—	—	—	—	1	1	*	6	—	1
Polychaeta	—	13	4	58	12	30	31	28	21	16	50
Alaudae	—	—	—	—	—	—	—	—	—	—	24
Cumacea	—	—	—	—	6	5	22	4	*	—	3
Isopoda	—	—	—	—	—	1	1	*	*	*	*
Gammaridea	—	—	—	—	—	—	—	—	—	—	*
Anomura	—	15	5	2	8	11	9	6	3	1	3
Eupagurus	—	—	—	—	—	—	—	—	—	—	6
Brachyura	—	3	—	—	—	1	8	3	2	1	2
Tanaidacea	—	—	—	—	—	*	*	1	*	1	2
Pycnogonidae	—	—	—	—	—	3	*	—	—	—	*
Holothuriidea	—	—	—	—	—	—	1	1	*	—	*
Echinoidea	—	—	—	—	—	*	3	2	3	10	13
Asteriidea	—	—	—	—	—	—	1	8	2	4	39
Ophiuroidea	—	—	—	—	—	—	—	—	—	—	*
Tunicata	—	3	—	38	12	8	15	21	35	18	41
Benthos Total	—	33	13	98	52	84	94	85	93	92	68

TABLE XI
The food composition of calfish in March 1980.

Prey group	Predator length group (cm)											Average
	7-9	10-14	15-19	20-24	25-29	30-39	40-49	50-59	60-69	70-79	80-89	
Mallotus villosus	—	—	—	—	—	—	—	34	74	—	—	12
Ammodontidae	—	—	—	—	—	—	—	2	—	—	—	1
Heterosomata	—	—	—	—	—	—	5	—	—	—	—	1
Pisces unidentified	—	—	—	—	—	8	—	1	—	—	—	1
Nekton Total	—	—	—	—	—	8	5	37	74	—	—	14
Pontifera	—	—	—	—	—	—	—	1	—	—	—	1
Octocorallia	—	—	—	—	—	—	—	—	—	—	—	—
Prisapulida	—	—	—	—	—	—	—	—	—	—	—	—
Gastropoda	—	11	35	13	3	6	14	4	2	10	—	10
Cyprina islandica	—	—	—	—	—	—	—	—	—	—	—	—
Bivalvia	—	15	10	3	—	1	44	30	8	12	—	12
Polychaeta	—	—	—	—	1	2	3	2	1	1	—	1
Isopoda	—	—	—	—	—	—	—	—	—	—	—	—
Gammaridea	—	—	—	—	—	—	—	—	—	—	—	—
Eupagurus	—	—	4	4	54	—	2	3	—	8	—	8
Brachyura	—	5	36	46	17	19	5	3	—	14	—	14
Bryozoa	—	—	—	—	—	—	—	—	—	—	—	—
Holothuroidea	—	—	—	—	—	—	—	—	—	—	—	—
Echinoidea	—	—	—	—	—	6	8	2	2	2	—	2
Asteroidea	—	—	—	—	—	2	1	1	—	—	—	—
Ophiuroidea	—	100	14	34	25	54	16	16	2	37	—	37
Tunicata	—	—	—	—	—	—	—	—	—	—	—	—
Fish eggs	—	—	—	—	—	—	—	—	—	—	—	—
Benthos Total	—	100	100	100	100	92	95	63	26	86	—	86
Quantity of stomach content (grams per stomach)	0.02	0.1	0.1	0.3	0.6	1.0	1.5	6.8	44.1	6.1	—	6.1

TABLE XII
The food composition of calfish in July 1980.

Prey group	Predator length group (cm)											Average
	7-9	10-14	15-19	20-24	25-29	30-39	40-49	50-59	60-69	70-79	80-89	
Cephalopoda	—	—	—	—	—	9	—	—	—	—	—	1
Gadus morhua	—	—	—	—	—	—	—	—	10	—	—	1
Trisopterus esmarkii	—	—	—	—	—	—	—	—	—	13	—	1
Nekton Total	—	—	—	—	—	9	—	—	10	13	—	3
Euphausiacea	—	—	—	—	—	—	—	—	—	—	—	—
Plankton Total	—	—	—	—	—	—	—	—	—	—	—	—
Octocorallia	—	—	—	—	—	—	—	—	—	—	—	—
Loricata	—	33	—	—	—	—	—	—	—	—	—	—
Gastropoda	—	—	17	2	3	11	6	4	7	3	22	7
Scaphopoda	—	—	—	—	—	—	—	—	—	—	—	—
Cyprina islandica	—	—	—	—	—	—	—	—	9	—	16	2
Bivalvia	—	—	2	—	7	—	37	12	6	41	34	13
Polychaeta	—	—	13	5	1	3	2	2	4	—	6	3
Balanidae	—	—	—	—	—	—	—	—	—	—	—	—
Isopoda	—	—	—	—	—	—	—	—	—	—	—	—
Gammaridea	—	—	—	—	—	—	—	—	—	—	—	—
Eupagurus	—	—	—	—	—	—	—	—	—	—	—	—
Brachyura	—	—	—	3	6	3	5	4	7	1	16	4
Bryozoa	—	—	—	—	2	10	5	8	4	2	—	3
Holothuroidea	—	—	—	—	—	—	—	—	—	—	—	—
Echinoidea	—	—	—	—	—	—	—	—	—	—	—	—
Asteroidea	—	33	1	3	8	3	6	2	3	1	1	6
Ophiuroidea	—	—	—	—	—	—	—	—	—	—	—	—
Benthos Total	—	100	100	100	100	91	100	100	90	87	100	88
Quantity of stomach content (grams per stomach)	0.03	0.1	0.5	0.6	0.8	1.7	4.6	6.3	11.4	25.3	33.3	7.7

TABLE XIV
The food composition of calfish in March 1981

Prey group	Predator length group (cm)													
	7-9	10-14	15-19	20-24	25-29	30-34	35-39	40-49	50-59	60-69	70-79	80-89	90-99	Average
Pisces unidentified	—	—	—	—	—	—	—	1	—	—	—	4	—	*
Nekton Total	—	—	—	—	—	—	—	1	—	—	—	4	—	*
Nudibranchia	—	—	—	—	—	—	—	27	—	—	—	—	—	2
Plankton Total	—	—	—	—	—	—	—	27	—	—	—	—	—	2
Pandanus	—	—	—	—	—	—	—	—	4	—	6	—	—	1
Shrimps unidentified	—	—	—	—	—	—	*	—	—	—	—	—	—	*
Shrimps Total	—	—	—	—	—	—	*	—	—	—	6	—	—	1
Octocorallia	—	—	—	—	—	—	—	1	*	—	—	—	—	*
Gastropoda	—	—	—	2	—	—	—	22	7	29	15	25	—	8
Scaphopoda	—	—	—	—	—	—	—	—	—	—	1	—	—	*
Cyprina islandica	—	—	—	—	—	—	—	—	—	—	42	—	—	3
Bivalvia	—	—	—	—	—	—	—	2	—	29	—	—	—	3
Polychaeta	—	—	—	—	—	—	—	16	*	5	1	3	—	2
Cumacea	—	—	—	—	—	—	—	—	—	*	—	—	—	*
Isopoda	—	—	—	—	—	—	—	—	—	—	—	—	—	*
Gammaridea	50	—	—	—	—	—	—	*	4	*	—	—	—	5
Anomura	—	—	—	—	—	—	—	—	—	—	1	4	—	*
Eupagurus	50	—	—	—	—	—	—	—	—	—	—	—	—	*
Brachyura	—	—	—	—	—	—	—	—	—	—	—	—	—	3
Echinoidea	—	—	—	—	—	—	—	—	—	—	—	—	—	3
Asterioidea	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Ophiuroidea	—	—	—	—	—	—	—	—	—	—	—	—	—	42
Fish eggs	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Benthos Total	100	100	100	100	100	100	100	73	96	100	94	96	—	88
Quantity of stomach content (grams per stomach)	0.02	0.02	0.1	0.2	0.2	0.2	0.6	1.3	0.9	1.9	1.0	13.1	—	—

TABLE XIII
The food composition of calfish in October - November 1980

Prey group	Predator length group (cm)													
	7-9	10-14	15-19	20-24	25-29	30-34	35-39	40-49	50-59	60-69	70-79	80-89	90-99	Average
Cephalopoda	60	—	—	—	—	—	—	—	—	—	—	—	—	5
Gadus morhua	—	—	—	—	—	—	—	—	2	—	—	—	—	*
Lumpenus + Lycoteles	—	—	75	—	—	—	—	—	1	—	—	—	—	6
Sebastes	—	—	—	—	—	—	—	—	47	—	—	—	—	4
Nekton Total	65	—	75	—	—	—	—	—	49	—	—	—	—	16
Pandanus	—	—	—	—	—	—	—	—	—	—	100	—	—	17
Shrimps Total	—	—	—	—	—	3	—	—	2	—	100	—	—	17
Anthozoa	—	—	—	—	—	—	—	—	—	—	—	—	—	*
Gastropoda	—	—	—	—	—	—	—	—	—	—	—	—	—	12
Bivalvia	—	—	—	—	—	—	—	—	—	—	—	—	—	2
Polychaeta	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Isopoda	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Gammaridea	—	—	—	—	—	—	—	—	—	—	—	—	—	3
Eupagurus	—	—	—	—	—	—	—	—	—	—	—	—	—	8
Brachyura	—	—	—	—	—	—	—	—	—	—	—	—	—	8
Holothuridea	—	—	—	—	—	—	—	—	—	—	—	—	—	6
Echinoidea	—	—	—	—	—	—	—	—	—	—	—	—	—	5
Asterioidea	—	—	—	—	—	—	—	—	—	—	—	—	—	14
Ophiuroidea	—	—	—	—	—	—	—	—	—	—	—	—	—	59
Benthos Total	35	100	25	100	100	97	100	49	100	—	—	—	—	—
Quantity of stomach content (grams per stomach)	1.4	0.1	0.04	0.03	0.1	0.8	0.4	3.9	0.2	0.3	—	—	—	0.4

TABLE XVI
The food composition of redfish in July 1980.

Prey group	Predator length group (cm)											Average
	5-6	7-9	10-14	15-19	20-24	25-29	30-39	40-49	50-59	60-69	70-79	
Cephalopoda	—	—	—	—	—	—	—	—	—	—	—	3
Mallotus villosus	—	—	—	—	—	—	—	—	—	—	—	1
M. pourtalesi	—	—	—	—	—	—	—	—	—	—	—	4
Ammodontidae	—	—	—	—	—	—	—	—	—	—	—	*
Sebastes	—	—	—	—	—	—	—	—	—	—	—	1
Pisces unidentified	—	—	—	—	—	—	—	—	—	—	—	*
Nefton Total	—	—	—	—	—	—	—	—	—	—	—	9
Scyphozoa	—	—	—	—	—	—	—	—	—	—	—	*
Calanus finmarchicus	—	—	—	—	—	—	—	—	—	—	—	4
Calanus hyperboreus	—	—	—	—	—	—	—	—	—	—	—	6
Parachaela	—	—	—	—	—	—	—	—	—	—	—	5
Metridia	—	—	—	—	—	—	—	—	—	—	—	*
Mysida	—	—	—	—	—	—	—	—	—	—	—	*
Hyperidiae	—	—	—	—	—	—	—	—	—	—	—	8
Euphausiacea	—	—	—	—	—	—	—	—	—	—	—	48
Sagitta	—	—	—	—	—	—	—	—	—	—	—	4
Plankton Total	—	—	—	—	—	—	—	—	—	—	—	75
Pandalus	—	—	—	—	—	—	—	—	—	—	—	*
Shrimps Total	—	—	—	—	—	—	—	—	—	—	—	*
Gammaridea	—	—	—	—	—	—	—	—	—	—	—	1
Decapoda larvae	—	—	—	—	—	—	—	—	—	—	—	3
Benthos Total	—	—	—	—	—	—	—	—	—	—	—	4
Quantity of stomach content (grams per stomach)	0.1	0.1	0.04	0.1	0.3	1.1	1.7	1.8	8.6			

TABLE XV
The food composition of redfish in March 1980.

Prey group	Predator length group (cm)											Average
	5-6	7-9	10-14	15-19	20-24	25-29	30-39	40-49	50-59	60-69	70-79	
Mallotus villosus	—	—	—	—	—	—	—	—	—	—	—	3
Pisces unidentified	—	—	—	—	—	—	—	—	—	—	—	2
Nefton Total	—	—	—	—	—	—	—	—	—	—	—	5
Scyphozoa	—	—	—	—	—	—	—	—	—	—	—	*
Calanus finmarchicus	—	—	—	—	—	—	—	—	—	—	—	3
Calanus hyperboreus	—	—	—	—	—	—	—	—	—	—	—	16
Parachaela	—	—	—	—	—	—	—	—	—	—	—	4
Metridia	—	—	—	—	—	—	—	—	—	—	—	*
Calanoida	—	—	—	—	—	—	—	—	—	—	—	12
Mysida	—	—	—	—	—	—	—	—	—	—	—	*
Hyperidiae	—	—	—	—	—	—	—	—	—	—	—	34
Euphausiacea	—	—	—	—	—	—	—	—	—	—	—	12
Sagitta	—	—	—	—	—	—	—	—	—	—	—	81
Plankton Total	—	—	—	—	—	—	—	—	—	—	—	81
Polychaela	—	—	—	—	—	—	—	—	—	—	—	*
Ostracoda	—	—	—	—	—	—	—	—	—	—	—	1
Gammaridea	—	—	—	—	—	—	—	—	—	—	—	*
Benthos Total	—	—	—	—	—	—	—	—	—	—	—	1
Quantity of stomach content (grams per stomach)	0.01	0.02	0.07	0.12	0.54	2.0	3.9	1.3				

TABLE XVIII
The food composition of reef fish in March 1981.

Prey group	Predator length group (cm)									
	5-6	7-9	10-14	15-19	20-24	25-29	30-39	40-49	Average	
Mallotus villosus	—	—	—	—	—	—	20	28	6	
Fishes unidentified	—	—	13	—	—	—	1	—	2	
Nekton Total	—	—	13	—	—	—	21	28	8	
Scyphozoa	—	—	—	—	2	—	—	—	*	
Calanus finmarchicus	100	56	55	41	50	44	19	—	46	
Parachaeta	—	17	13	19	18	5	13	4	11	
Mysida	—	—	—	—	—	—	*	—	*	
Hyperidae	—	—	—	6	2	—	1	4	2	
Euphausiacea	—	13	11	12	1	26	32	63	20	
Sagitta	—	12	8	22	24	8	14	1	11	
Plankton Total	100	100	87	100	97	82	78	72	90	
Pandalus	—	—	—	—	—	18	—	—	2	
Shrimps Total	—	—	—	—	—	18	—	—	2	
Scypharidea	—	—	—	—	—	—	—	—	*	
Benthos Total	—	—	—	—	3	—	1	—	*	
Quantity of stomach content (grams per stomach)	0.02	0.04	0.1	0.1	0.3	0.5	2.9	1.4		

TABLE XVII
The food composition of reef fish in October - November 1980

Prey group	Predator length group (cm)										Average
	7-9	10-14	15-19	20-24	25-29	30-39	40-49	50-59	60-69		
Mallotus villosus	—	—	—	5	1	*	12	—	2		
Myctophidae	—	—	—	—	—	—	3	8	1		
Gadus morhua	—	—	—	—	13	—	—	—	2		
Anmodyridae	—	—	—	—	—	1	—	—	*		
Sebastes	—	—	—	—	1	—	—	—	*		
Fishes unidentified	—	—	—	29	*	2	1	1	4		
Nekton Total	—	—	—	34	16	3	16	8	10		
Calanus finmarchicus	—	—	—	—	—	3	6	10	2		
Parachaeta	60	—	—	4	14	36	33	23	21		
Metridia	—	—	3	—	2	—	—	—	1		
Hyperidae	16	15	10	7	6	2	2	1	7		
Euphausiacea	24	85	69	34	58	54	36	54	52		
Sagitta	—	—	—	1	1	2	5	3	1		
Plankton Total	100	100	82	45	82	97	82	91	85		
Pandalus	—	—	—	20	2	—	2	—	3		
Shrimps unidentified	—	—	—	—	—	*	*	*	*		
Shrimps Total	—	—	—	20	2	*	2	*	3		
Gammaridea	—	—	18	—	*	—	—	—	2		
Benthos Total	—	—	18	—	*	—	—	—	2		
Quantity of stomach content (grams per stomach)	0.03	0.04	0.1	0.2	0.5	3.0	4.1	1.5			

TABLE XIX
The food composition of long rough dab in March 1980.

Prey group	Predator length group (cm)							
	7-9	10-14	15-19	20-24	25-29	30-39	40-49	Average
Mallotus villosus	—	—	—	—	—	—	21	3
Heterosomata	—	—	*	—	*	—	—	*
Pisces unidentified	—	—	—	16	2	1	1	3
Nekton Total	—	—	*	16	2	1	22	6
Mysida	—	—	4	—	*	—	—	1
Hyperidae	—	—	1	3	—	—	—	*
Euphausiacea	—	—	4	—	*	*	—	1
Sagitta	—	—	2	—	—	—	—	*
Plankton Total	—	—	11	3	*	*	—	2
Pandalus	—	—	22	—	—	*	—	3
Shrimps unidentified	—	—	1	—	—	—	*	*
Shrimps Total	—	—	22	—	—	*	—	3
Bivalvia	—	—	6	3	3	*	—	2
Polychaeta	—	—	—	4	7	4	11	4
Cumacea	—	—	—	—	—	*	—	*
Isopoda	—	—	1	—	*	*	—	*
Gammaridea	—	21	52	66	84	1	—	32
Brachyura	—	—	2	—	—	—	—	*
Ophiuroidea	—	79	5	8	5	94	67	37
Benthos Total	—	100	66	81	98	99	78	75
Quantity of stomach content (grams per stomach)	—	0.02	0.2	0.3	0.7	1.1	1.4	

TABLE XX
The food composition of long rough dab in July 1980.

Prey group	Predator length group (cm)									
	3-6	7-9	10-14	15-19	20-24	25-29	30-39	40-49	Average	
Mallotus villosus	—	—	—	—	—	—	—	31	4	
Lumpenus + Lycodes	—	—	—	—	2	4	—	—	1	
H. platessoides	—	—	—	—	4	—	1	—	—	
Pisces unidentified	—	—	—	—	2	2	1	4	1	
Nekton Total	—	—	—	—	7	6	2	36	6	
Mysida	—	—	18	—	*	—	—	—	2	
Hyperidae	—	—	—	—	—	—	—	*	*	
Euphausiacea	—	44	9	2	1	—	—	—	7	
Plankton Total	—	44	27	2	1	—	—	*	9	
Pandalus	—	—	4	9	5	18	6	4	6	
Shrimps Total	—	—	4	9	5	18	6	4	6	
Anthozoa	—	—	—	—	—	—	*	—	*	
Octocorallia	—	—	—	—	—	1	2	*	*	
Nemertini	—	—	10	—	—	—	—	—	1	
Gastropoda	—	—	3	—	1	3	—	—	1	
Scaphopoda	—	—	—	*	—	—	—	*	*	
Bivalvia	—	—	32	25	23	11	6	5	32	
Polychaeta	100	56	—	3	1	*	—	—	1	
Gammaridea	—	—	5	3	4	*	—	*	2	
Eupagurus	—	—	—	8	—	6	—	—	2	
Brachyura	—	—	1	17	*	—	*	—	2	
Pycnogonidae	—	—	—	—	—	—	—	—	*	
Bryozoa	—	—	—	—	—	—	—	—	*	
Echinoidea	—	—	—	—	—	—	—	—	*	
Ophiuroidea	—	—	28	23	57	53	77	54	36	
Benthos Total	100	56	69	89	87	76	92	60	79	
Quantity of stomach content (grams per stomach)	0.02	0.04	0.1	0.1	0.4	0.3	0.8	1.6		

TABLE XXII
The food composition of long rough dab in March 1981.

Prey group	Predator length group (cm)										
	5-6	7-9	10-14	15-19	20-24	25-29	30-39	40-49	Average		
Mallotus villosus	—	—	—	3	21	62	15	48	19		
Gadus morhua	—	—	—	—	—	2	1	—	*		
Lumpenidae	—	—	—	—	14	2	—	—	2		
Lycodes	—	—	—	—	11	—	1	—	1		
Sebastes	—	—	—	—	—	—	3	—	*		
H. platessoides	—	—	—	2	—	—	1	—	*		
Pisces unidentified	—	—	—	—	15	1	1	—	2		
Heterosomata	—	—	—	—	—	—	5	1	1		
Nekton Total	—	—	—	5	61	67	26	50	26		
Nudibranchia	—	—	—	—	—	—	1	—	*		
Mysida	—	9	25	—	—	1	*	—	4		
Hyperidae	—	11	—	—	*	—	—	—	1		
Euphausiacea	—	42	36	56	5	1	1	*	18		
Sagitta	—	11	—	16	7	10	—	—	5		
Plankton Total	—	72	62	72	13	11	2	*	29		
Pandalus	—	—	—	—	—	2	5	—	1		
Shrimps unidentified	—	—	—	—	—	2	—	—	*		
Shrimps Total	—	—	—	—	—	4	5	—	1		
Anthozoa	—	—	—	—	—	—	1	8	1		
Nemertini	—	—	—	—	—	—	2	—	*		
Priapulida	—	—	—	—	—	*	—	—	*		
Gastropoda	—	—	—	1	—	—	1	6	1		
Bivalvia	—	—	—	1	*	1	32	6	9		
Polychaeta	—	9	19	3	2	4	*	*	2		
Cumacea	—	9	—	4	—	—	—	—	*		
Isopoda	—	—	—	—	*	—	—	—	*		
Gammaridea	—	11	4	2	1	3	*	*	3		
Brachyura	—	—	—	—	*	—	—	—	*		
Pycnogonidae	—	—	—	—	—	—	—	—	*		
Asteroida	—	—	—	—	—	—	—	—	*		
Ophiuroidea	—	—	15	14	22	10	25	35	15		
Benthos Total	—	28	38	24	26	18	67	50	31		
Quantity of stomach content (grams per stomach)	—	0.1	0.03	0.1	0.4	1.3	1.5	1.5	1.5		

TABLE XXI
The food composition of long rough dab in October - November 1980.

Prey group	Predator length group (cm)										
	7-9	10-14	15-19	20-24	25-29	30-39	40-49	Average			
Cephalopoda	—	—	—	5	—	—	—	1			
Gadus morhua	—	—	—	44	—	70	—	16			
Lumpenus + Lycodes	—	—	—	—	5	—	—	1			
Sebastes	—	—	—	6	35	—	—	6			
H. platessoides	—	—	4	3	2	—	—	1			
Pisces unidentified	—	—	23	6	8	—	—	5			
Nekton Total	—	—	27	64	50	70	—	34			
Mysida	26	22	—	—	—	—	—	7			
Hyperidae	—	2	—	—	*	—	—	*			
Euphausiacea	—	—	—	*	—	—	—	*			
Plankton Total	26	24	—	*	—	—	—	7			
Shrimps unidentified	—	5	22	—	—	—	—	4			
Shrimps Total	—	5	22	—	—	—	—	4			
Priapulida	—	—	—	—	1	—	—	*			
Gastropoda	—	—	—	1	—	—	—	*			
Bivalvia	—	36	25	1	1	—	—	*			
Polychaeta	—	—	—	—	27	—	—	13			
Isopoda	—	—	—	—	—	2	—	*			
Gammaridea	—	17	4	5	—	—	—	4			
Eupagurus	48	—	7	—	—	—	—	8			
Brachyura	—	—	—	3	—	—	—	*			
Pycnogonidae	—	9	2	—	—	—	—	2			
Ophiuroidea	26	9	21	14	20	27	100	31			
Benthos Total	74	71	52	35	49	30	100	59			
Quantity of stomach content (grams per stomach)	0.01	0.03	0.1	0.2	0.3	0.2	0.2	0.1			

