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Feeding of Greenland Halibut (*Reinhardtius hippoglossoides*) in 3LMNO
NAFO Regulatory Area Divisions (Northwest Atlantic), 1991-94

by

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ABSTRACT

Feeding of Greenland halibut in Flemish Pass and Newfoundland's Grand Bank slope (3LMNO NAFO divisions) was studied from on board commercial fleet analysis, from June 1991 to December 1994. Percentage of empty stomachs from 625 165 specimens and frequency of occurrence of prey from 18 527 stomachs, were used to evaluate feeding intensity and importance of prey groups.

Examination revealed increasing feeding intensity with size. The emptiness percentage varies with depth, in a directly proportional way, in specimens of less than 60 cm, and is inversely proportional in those of over 70 cm. A smaller percentage of empty stomachs was found in females than in males, upwards of the length of first maturity of the latter, as well as a decreasing feeding rate as females become reproductively active.

Analysis of frequency of occurrence of main prey groups indicated a change in Greenland halibut feeding at 60 cm in all divisions, a change which supposes a fall in consumption of crustaceans and molluscs, an increase in fish and offal, and an increase in prey species size. The difference between divisions is due to the consumption of *Mallotus villosus* by specimens of less than 60 cm in divisions 3NO. There are also significant changes with depth at around 1000 m in the diet of *Reinhardtius hippoglossoides* of less than 60 cm, bringing about a substitution of capelin for decapod cephalopods. At great depths squid have a similar role in the diet of Greenland halibut to that played by capelin on the continental shelf. The variation of the prey species is related to their distribution. Offal are an extra provision of food introduced by fishing activity, making up the second most important prey group in specimens of over 60 cm.

INTRODUCTION

Greenland halibut (*Reinhardtius hippoglossoides*) is the target species of the Spanish freezer fleet which fishes in deep waters in the NAFO area, representing over 60% of the total catch (Gil *et al.*, 1997). The feeding of this species has been studied since almost the beginning of the fishery, as it has the interest that few studies of the diet of this species at depths of over 1000 m have been made.

Data from the fishery in 1992 on Greenland halibut feeding, provided the basis for a preliminary study (Rodríguez-Marin *et al.*, 1995), which is now extended to cover a period of four years.

MATERIAL AND METHODS

The study area was Flemish Pass and the slope that surrounds Newfoundland's Grand Bank in the NAFO Regulatory Area (NAFO Divisions 3L, 3M and 3NO), where the commercial bottom

trawl fleet fishes. By means of observers on board Spanish commercial ships, two kinds of sampling were carried out, the first of which consisted exclusively of determining length, sex, state of sexual maturity and state of stomach, empty or full, for each specimen. This first sampling was carried out from July 1991 to December 1994, with a total of 625 165 specimens (Table 1). From this data the emptiness index, the percentage of empty stomachs against the total was obtained, and was used as a measure of feeding intensity.

For the analysis of stomach contents, a second sampling was carried out from May 1992 to December 1994, and a total of 18 527 stomachs containing food were analyzed (Table 2). In each haul a maximum of 100 Greenland halibut were randomly sampled. Size and sex were determined for each specimen. Stomach contents were analyzed on board. The waste products from fish processing, mainly heads and tails of Greenland halibut, and heads, tails and alimentary tracts of grenadiers, were included in the category of offal (Saila, 1983).

The frequency of occurrence method was used to characterize fish feeding, $FO = N_p/N_t * 100$, where N_p is the number of stomachs with a specific prey, and N_t is the total number of stomachs containing food analyzed.

To study Greenland halibut feeding, the following variables were taken into consideration: length, sex, maturity, depth, NAFO division and month of the year. The minimum size of each category was, in both samplings, 50 stomachs. To infer whether significant differences exist between frequencies, the Chi-square test was used ($df=1$).

RESULTS

Feeding intensity

The average percentage of stomachs which were empty (%E) is 68%. Significant differences appear between NAFO Divisions ($P < 0.001$) with a minimum value of 65% in Division M, and the maximum value of 70% in Division L. Significant differences are also found in feeding intensity between length groups, with a %E of 73% in specimens of less than 30 cm, and 35% in those of over 90 cm (Table 3).

To study the influence of sex on feeding intensity, the emptiness index by 10 cm length groups and sex was represented through time (Figure 1). It can be seen that there is no difference in specimens of less than 40 cm, and in the 40-49 cm group females begin to show a significantly lower percentage of empty stomachs ($P < 0.001$), the difference becoming greater as length increases. To check whether the maturing process of females influences their feeding intensity, the emptiness index of females of over 69 cm, the maximum length at first maturity estimated for this species in this area (Junquera and Saborido-Rey, 1995), was compared with the percentage of females in a maturing and spawning state, stages 2 and 3 according to a four point scale (Junquera and Zamarro, 1994), throughout the year (Figure 2). A significant correlation was found ($r = 0,39$, $P < 0,01$).

Depth affects the emptiness index of the different length groups in a different way, while in specimens of less than 60 cm a significant fall ($P < 0.001$) is seen in the percentage of empty stomachs with depth. In specimens of over 69 cm the opposite trend appears, and the group of 60-69 cm would be one of transition (Table 4).

In Table 4 and Figure 3 it is clearly seen that at the same depth, large specimens have a greater feeding intensity than smaller ones. Annual rhythms are not observed, and the same trends are found for all length groups and all depth strata through time (Figure 3).

Diet composition

Frequency of occurrence of main prey groups by division and size (Figure 4) shows that a change comes about in Greenland halibut feeding at 60 cm in all divisions. This change represents a fall in consumption of crustaceans and molluscs, and an increase in fish and offal. Divisions 3NO are the only ones in which the frequency of occurrence of fish is constant in all length groups.

Taking the length of 60 cm as a reference to divide the total length distribution, NAFO Division (Table 5) and depth (Table 6) were taken into account. There are about 60 prey items in the diet of *Reinhardtius hippoglossoides* (Table 5), although the diversity of prey taxa undoubtedly increases with sampling intensity, specimens of less than 60 cm present a greater number of preys than the larger ones.

Influence of NAFO division

Cephalopods are the most important prey group in specimens of less than 60 cm in divisions 3L and 3M, while fish are in Greenland halibut of over 60 cm in these two divisions and in the two length groups of the divisions 3NO (Table 5). This difference between divisions is due to the consumption of *Mallotus villosus* by specimens of less than 60 cm in divisions 3NO. Offal is the second most important prey group in Greenland halibut of over 60 cm in all divisions. Decapod crustaceans make up the third most important prey group in those of less than 60 cm in 3LM and the second in Division 3NO. The cannibalism rate in division NO is significantly higher ($P < 0.001$) in specimens of less than 60 cm with respect to the other two divisions, while division M is that which presents the lowest rate ($P < 0.01$) in specimens of over 60 cm.

Influence of depth

There is a change in the diet of specimens of less than 60 cm from 1000 m depth (Table 6). This change represents a significant increase ($P < 0.001$) in the consumption of cephalopods and a significant fall ($P < 0.001$) in that of fish. The composition of fish species also varies with depth. The frequency of occurrence of macrurids, mainly *Coryphaenoides rupestris*, increases with length and with depth, as happens in the case of other prey species, such as *Gaidropsarus sp.* and *Urophycis sp.* The opposite occurs in the case of small sized prey species, such as *Mallotus villosus* and Myctophids. Decapod crustaceans are important at less than 800 m in both length groups, their importance diminishing as depth and length increase. The frequency of offal do not present significant variations with depth.

DISCUSSION

We have found several factors which influence feeding intensity. In first place it increases with length of Greenland halibut, confirming the results obtained by Rodriguez-Marín *et al.* (1995). It must be taken into account that as length increases, the proportion of females and the number of specimens found at greater depth increase, parameters (sex and depth) which, as we have already seen, also influence feeding intensity. The greater inter and intra specific competition for preys in smaller specimens with respect to larger ones, and a shorter time of digestion of prey, small invertebrates, by specimens of smaller size, must also have an influence on this trend. Secondly, feeding intensity varies with depth in an inversely proportional way in specimens of less than 60 cm, and is directly proportional in those of over 70 cm. This may be due to the availability of prey, with respect to their size and their distribution. The different trend of the emptiness index with depth as a function of size may explain the discrepancies found in the bibliography (Chumakov and Podrazhanskaya, 1986; Bowering and Lilly, 1992; Pedersen and Riget, 1993). Variation in feeding intensity with depth must take length into account, as Rodriguez-Marín *et al.* (1995) propose.

Thirdly, there are differences between sexes. In the length group of 40-49 cm and upwards, males present a lower feeding intensity than females throughout the year. These differences in feeding intensity between sexes occur in other Pleuronectiformes, such as *Limanda limanda* (Lozan, 1992) and may be due to the fact that it is in this length group that males begin to mature (Kovtsova and Nizovtsev, 1985; Serebryakov *et al.*, 1992). This may lead one to think that maturity brings with it a fall in feeding rate in males, which could cause an increase in the natural mortality rate of this sex, as postulated by De Cárdenas (1996). Fourthly, there is a relationship between the percentage of mature females and their feeding intensity from 69 cm throughout the year, in such a way that when the gonads of the females are maturing or spawning, that is to say, when there is greater reproductive activity, their feeding rate declines. This relationship has been found in other fish, such as capelin (Winters, 1969) and herring (Iles, 1984).

As Bowering and Lilly (1992) also found, there is a clear dietary change between specimens both smaller and larger than 60 cm of Greenland halibut. This change is characterized by an increase in the mean size of the prey. Specimens smaller than 60 cm feed mainly on squids such as *Illex coindetii*, small fishes such as *Mallotus villosus*, Myctophids, *Serrivomer beanii* and *Nezumia bairdi*, and shrimps. On the other hand, the prey of specimens greater than 60 cm are more voluminous, the fish *Coryphaenoides rupestris*, *Macrurus berglax*, *Antimora rostrata*, octopus and offal. It is obviously in this group where the highest cannibalism rate appears. Offal, mainly in the form of Greenland halibut heads, are largely consumed in every NAFO Division and at every depth stratum, mostly by large individuals due to their greater mouth size. They are an extra provision of food introduced by fishing activity (Rodríguez-Marín *et al.*, 1995). A change in feeding behaviour during ontogeny, with fish becoming more prevalent in the diet of Greenland halibut is somewhat common in other non-specialist fishes, and is an advantage due to the greater energy content of fish preys (Bromley, 1991).

The main difference in the diet composition between NAFO divisions 3NO and 3LM is due to the substitution of capelin for squids in Greenland halibut feeding of less than 60 cm. It is precisely the frequency of occurrence of the cephalopods in division 3LM which is unusual with respect to that found in other studies, where the diet is dominated by two large groups: fish and crustaceans, mainly

Pandalus borealis (Haug and Gulliksen, 1982; Chumakov and Podrazhanskaya, 1986; Bowering and Lilly, 1992; Pedersen and Riget, 1993). There are significant changes with depth at around 1000 m. in the diet of *Reinhardtius hippoglossoides* of less than 60 cm, where there is a substitution of capelin for decapod cephalopods. At great depths squid have a similar role in the diet of Greenland halibut to that played by capelin on the continental shelf (Rodríguez-Marín *et al.*, 1995). The composition of fish species also varies with depth, and species such as *M. berglax*, *C. rupestris*, *A. rostrata* and *Gaidropsarus* sp. increase with depth in the diet of specimens both larger and smaller than 60 cm. This is due to the fact that the consumption of these prey species is intimately associated with their distribution.

Thus, we have a well known element in the optimum exploitation of feeding resources, in the availability of prey, with respect to the prey length-predator length/mouth size relationship, and their distribution.

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Table 1. Number of stomachs analyzed, by division, depth and year, to obtain the emptiness index.

DIVISION	DEPTH	YEAR				TOTAL
		91	92	93	94	
L	<800 m	3522	15256	1675	9106	29559
	800-999 m	15296	58207	22453	18938	114894
	1000-1199 m	32828	54596	19142	11538	118104
	>1199 m	3980	26841	5101	4581	40503
M	<800 m	1438	1791	0	0	3229
	800-999 m	4897	8059	4293	3497	20746
	1000-1199 m	57077	54381	8755	15849	136062
	>1199 m	40566	24630	954	4878	71028
NO	<800 m	1465	1128	4101	6869	13563
	800-999 m	0	7979	16672	14626	39277
	1000-1199 m	77	5591	11888	9073	26629
	>1199 m	0	326	5159	6086	11571
TOTAL		161146	258785	100193	105041	625165

Table 2. Number of stomachs containing food analyzed by NAFO Division, depth and year.

DIVISION	DEPTH	YEAR			TOTAL
		92	93	94	
L	<800 m	1244	227	62	1533
	800-999 m	1724	1993	219	3936
	1000-1199 m	729	2074	409	3212
	>1199 m	135	643	132	910
M	<800 m	85	0	0	85
	800-999 m	72	211	92	375
	1000-1199 m	305	664	925	1894
	>1199 m	58	108	206	372
NO	<800 m	0	233	138	371
	800-999 m	405	1603	500	2508
	1000-1199 m	261	1749	571	2581
	>1199 m	7	321	422	750
TOTAL		5025	9826	3676	18527

Table 3. Emptiness percentage (%E) by size group. *P* is the probability that each %E is not different between consecutive size groups, ***=*P*<0.001; *=*P*>0.01.

SIZE (cm)	<30	30-39	40-49	50-59	60-69	70-79	80-89	>90
%E	72,6	74,0	76,8	69,6	53,4	43,6	37,2	34,7
<i>P</i>		*	***	***	***	***	***	*

Table 4. Emptiness percentage (%E) by size group and depth. *P* is the probability that each %E is not different between consecutive depth strata. ***=*P*<0.001; **=0.01>*P*>0.001; *=0.05>*P*>0.01; ns = non significant.

		SIZE					
DEPTH		<40	40-49	50-59	60-69	70-79	>79
< 800	%E	67,7	66,4	61,0	55,4	52	
	<i>P</i>	***	***	***	ns	ns	
800-999	%E	73,6	73,5	67,1	54,9	49,1	42,3
	<i>P</i>	***	***	***	*	**	ns
1000-1199	%E	79,2	80,6	72,3	56,0	46,4	38,8
	<i>P</i>	**	ns	ns	***	***	***
>1199	%E	81,3	80,8	67,4	48,0	37,6	32,9

Table 5. Prey items expressed as frequency of occurrence by length group and NAFO Division, + indicates presence but percentage <0.5.

PREY TAXA	NAFO DIVISION	L		M		NO	
	SIZE (cm)	<60	>59	<60	>59	<60	>59
<i>Nemichthys scolopaceus</i>		+	+	-	-	-	-
<i>Serrivomer beanii</i>		0.7	+	+	+	0.6	+
<i>Synaphobranchus Kaupi</i>		+	-	-	-	+	-
Gadidae unidentified		+	-	+	-	-	-
<i>Gadus morhua</i>		+	0.8	+	-	+	+
<i>Gaidropsarus sp.</i>		+	1.5	+	1.5	-	+
<i>Merluccius bilinearis</i>		-	-	-	-	-	+
<i>Urophycis chesteri</i>		+	+	-	+	-	-
<i>Urophycis sp.</i>		+	1.4	+	1.9	+	+
<i>Coryphaenoides rupestris</i>		2.3	6.2	7.7	22.0	3.6	8.1
Macrouridae unidentified		2.5	5.4	3.3	5.4	3.6	10.2
<i>Macrourus berglax</i>		0.9	3.8	1.3	2.3	0.8	2.3
<i>Nezumia bairdi</i>		3.5	1.9	3.0	2.0	3.1	3.9
Total Macrouridae		9.2	17.3	15.2	31.7	11.2	24.5
<i>Antimora rostrata</i>		0.5	2.7	1.6	6.7	1.5	6.9
Fish larva		-	-	+	-	+	-
<i>Lophius americanus</i>		-	-	-	+	-	+
<i>Melanocetus sp.</i>		+	-	-	-	-	-
<i>Lampadena speculigera</i>		+	+	-	-	-	-
Myctophids unidentified		0.9	+	1.0	0.5	+	-
Paralepididae		+	-	+	+	-	-
<i>Notacanthus chemnitzii</i>		+	+	+	+	-	+
Pisces unidentified		19.6	17.7	15.2	15.9	18.3	21.7
<i>Ammodytes sp.</i>		+	-	-	-	+	+
<i>Anarhichas spp.</i>		+	+	-	-	-	-
<i>Cottunculus sp.</i>		-	+	-	-	-	-
<i>Cyclopterus lumpus</i>		-	-	-	+	-	-
<i>Chiasmodon niger</i>		+	-	+	-	-	-
<i>Sebastes spp.</i>		+	1.9	-	0.5	+	0.8
<i>Lycodes sp.</i>		+	1.2	+	0.8	+	+
<i>Petromyzon marinus</i>		-	+	-	-	-	-
<i>Glyptocephalus cynoglossus</i>		+	+	-	-	+	0.6
<i>Hippoglossoides platessoides</i>		+	+	-	-	+	1.3
<i>Reinhardtius hippoglossoides</i>		+	4.5	+	2.3	1.2	4.2
Pleuronectiformes unidentified		-	+	-	-	+	+
<i>Alepocephalus sp.</i>		+	+	-	-	+	+
<i>Chauliodus sloani</i>		+	-	-	-	+	-
<i>Mallotus villosus</i>		2.6	+	+	-	21.1	0.8
<i>Raja radiata</i>		+	-	-	-	-	-
Rajidae unidentified		-	-	-	-	+	-
Sharks unidentified		-	+	-	-	-	+
<i>Centroscyllium fabricii</i>		+	-	-	-	-	+
TOTAL FISH		35.8	51.5	35.1	62.4	55.0	62.3

Table 5 (cont.). Prey items expressed as frequency of occurrence by length group and NAFO Division, + indicates presence but percentage <0.5.

PREY TAXA	NAFO DIVISION		L		M		NO	
	SIZE (cm)		<60	>59	<60	>59	<60	>59
Amphipoda			+	-	-	-	0.7	-
Hyperidea			-	-	-	-	+	-
Copepoda			+	-	-	-	-	-
Crustacea unidentified			0.6	-	0.6	+	1.1	+
Brachyura unidentified			+	-	-	-	-	-
<i>Hyas sp.</i>			+	+	+	-	-	-
Decapoda unidentified			12.7	1.9	4.6	+	9.6	0.8
<i>Acanthephyra pelagica</i>			+	-	+	-	+	-
Caridea unidentified			0.5	+	+	-	+	-
Natantia unidentified			5.1	1.2	3.0	0.5	8.3	2.3
<i>Pandanus borealis</i>			0.5	+	-	-	2.0	0.5
<i>Pasiphaea tarda</i>			+	-	-	-	0.6	+
Penaeidea unidentified			-	-	-	-	+	-
<i>Plesiopenaeus edwardsianus</i>			+	+	-	-	-	-
Total Natantia			6.6	1.5	3.4	0.5	11.3	2.8
TOTAL CRUSTACEA			20.4	3.5	8.6	0.9	22.8	3.7
Bivalvia			+	-	-	-	-	-
Cephalopoda unidentified			27.6	5.2	25.9	2.6	11.7	4.3
Decapoda unidentified			6.1	0.7	10.7	1.1	5.3	2.4
<i>Illex coindetii</i>			6.6	1.2	12.3	2.3	2.4	1.0
Octopoda			0.9	1.3	1.1	0.8	1.0	3.0
Gastropod			+	-	+	+	+	-
Mollusca unidentified			+	+	+	+	+	+
TOTAL MOLLUSCA			41.2	8.6	50.2	7.1	20.6	10.7
Echinodermata unidentified			+	-	-	-	+	-
Echinoidea (Reg. and Ireg.)			-	-	+	+	-	-
Cnidaria			+	-	-	-	-	-
Scyphozoa			+	+	+	-	-	+
Ctenophora			-	-	-	-	-	+
Polychaeta			+	-	-	-	+	-
Ponifera			+	-	-	+	-	-
Unidentified			2.7	4.4	3.5	3.3	0.8	+
Ship debris			+	+	-	+	+	+
TOTAL OTHER			2.9	4.7	3.7	3.7	1.0	0.6
OFFAL			5.7	40.4	6.4	35.9	4.1	31.3
TOTAL No. OF STOMACHS			7664	1928	1661	1064	4257	1953
TOTAL No OF PREY TAXA			48	31	26	23	33	29
MEAN DEPTH			991		1086		1022	

Table 6. Prey items expressed as frequency of occurrence by length group and depth stratum. + indicates presence but percentage <0.5.

PREY TAXA	DEPTH (m)		800 - 999		1000 - 1199		> 1200	
	SIZE (cm)		<60	>60	<60	>60	<60	>60
<i>Nemichthys scolopaceus</i>			-	+	0.5	+	-	-
<i>Serrivomer beanii</i>			1.3	-	0.7	+	+	+
<i>Gadus morhua</i>			+	-	+	+	+	0.8
<i>Gaidropsarus</i> sp.			+	-	+	0.6	+	1.0
<i>Urophycis chesteri</i>			-	-	-	-	+	+
<i>Urophycis</i> sp.			-	-	+	0.8	+	0.7
<i>Coryphaenoides rupestris</i>			+	-	1.6	5.5	5.5	10.1
Macrouridae unidentified			0.8	-	2.3	5.2	4.2	7.3
<i>Macrourus berglax</i>			+	-	1.0	3.2	1.1	3.0
<i>Nezumia bairdi</i>			1.9	8.5	4.7	4.2	2.7	2.4
Total Macrouridae			3.2	8.5	9.6	18.1	13.4	22.8
<i>Antimora rostrata</i>			+	-	0.7	5.0	1.5	5.4
Myctophids unidentified			+	2.1	0.7	+	0.7	+
<i>Notacanthus chemnitzii</i>			-	-	+	0.5	+	+
<i>Ammodytes</i> sp.			0.5	-	+	-	+	+
<i>Sebastes</i> sp.			+	2.1	+	1.0	+	1.1
<i>Lycodes</i> sp.			+	-	+	+	+	0.9
<i>Hippoglossoides platessoides</i>			-	-	+	2.1	+	+
<i>Reinhardtius hippoglossoides</i>			+	2.1	0.7	2.8	0.7	4.7
<i>Mallotus villosus</i>			9.7	2.1	13.3	0.5	2.9	+
Pisces unidentified			26.8	44.7	18.6	22.4	16.1	18.7
Other fish			+	-	+	+	+	+
Chondrichthyes			-	-	+	-	+	+
TOTAL FISH			42.7	61.7	45.8	56.2	37.5	57.7
Amphipoda			1.5	-	+	-	-	-
Hyperidea			+	-	-	-	-	-
Copepoda			+	-	+	-	-	-
Brachyura			-	-	+	-	+	+
<i>Acanthephyra pelagica</i>			0.5	-	+	-	+	-
Caridea unidentified			-	-	0.8	+	+	0.7
Natantia unidentified			2.4	2.1	5.3	1.4	7.3	1.6
<i>Pandalus borealis</i>			+	-	0.7	0.5	1.4	+
<i>Pasiphaea tarda</i>			+	-	0.5	-	+	0.6
Penaeidea unidentified			-	-	-	-	+	-
<i>Plesiopenaeus edwardsianus</i>			+	-	+	-	+	-
Total Natantia			3.6	2.1	7.4	2.0	8.9	1.9
Decapoda unidentified			18.3	10.6	11.9	1.4	7.7	1.1
Crustacea unidentified			0.6	-	0.6	+	0.8	+
TOTAL CRUSTACEA			24.3	12.8	20.2	3.4	17.7	3.1
<i>Illex coindetii</i>			1.3	-	6.5	1.4	7.5	1.5
Decapoda unidentified			2.0	-	6.1	1.5	8.0	1.5
Octopoda			+	2.1	+	0.8	1.6	1.9
Cephalopoda unidentified			32.9	6.4	17.1	3.4	23.5	4.7
Bivalvia			-	-	+	-	-	-
Gastropod			+	-	+	-	+	-
Mollusca unidentified			-	-	+	+	+	+
TOTAL MOLLUSCA			36.6	8.5	30.5	7.2	40.6	9.8
TOTAL OTHERS			1.2	4.3	2.9	5.3	2.3	2.7
OFFAL			2.6	27.7	5.8	36.2	6.1	36.3
TOTAL No STOMACHS			1941	47	5806	1015	4837	2849
NUMBER OF PREY TAXA			28	9	41	30	39	27

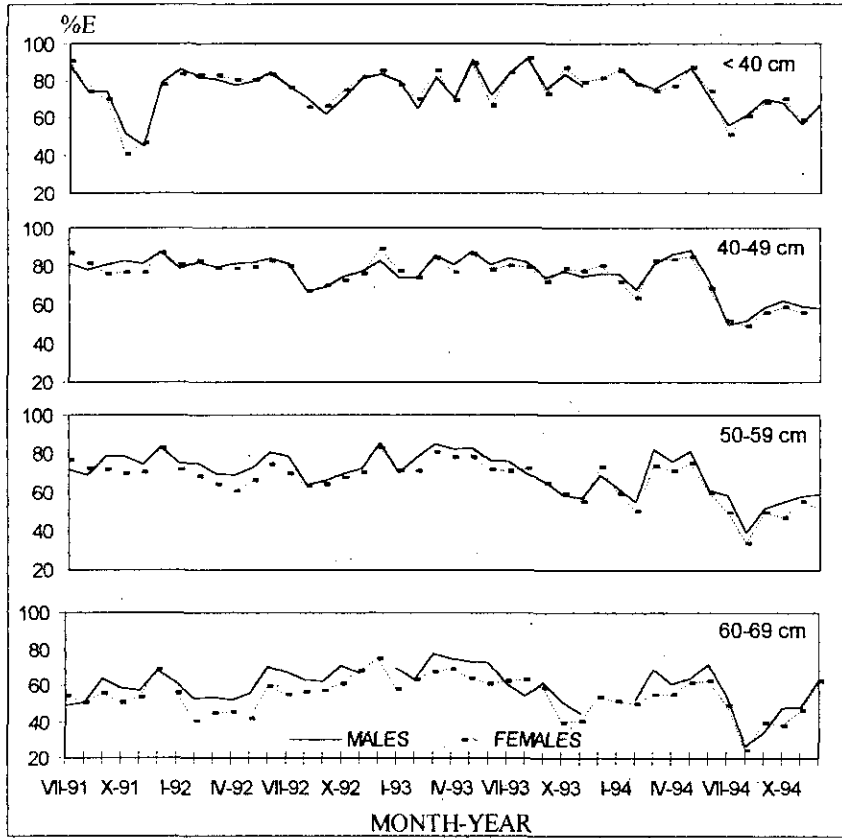


Figure 1. Emptiness percentage (%E) through years by length group (cm) and sex.

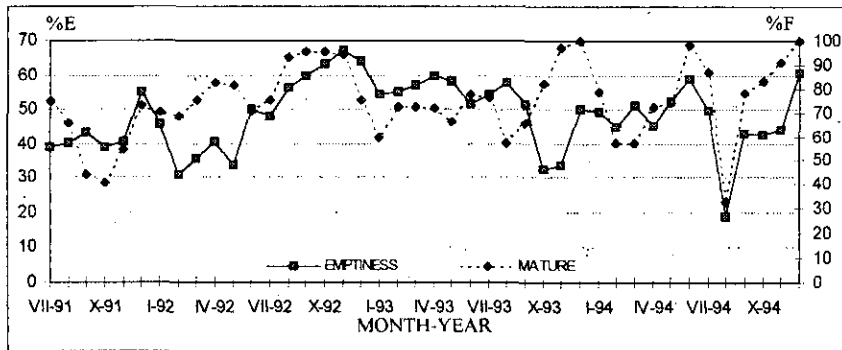


Figure 2. Emptiness (%E) and maturity (%F) percentage of females over 69 cm.

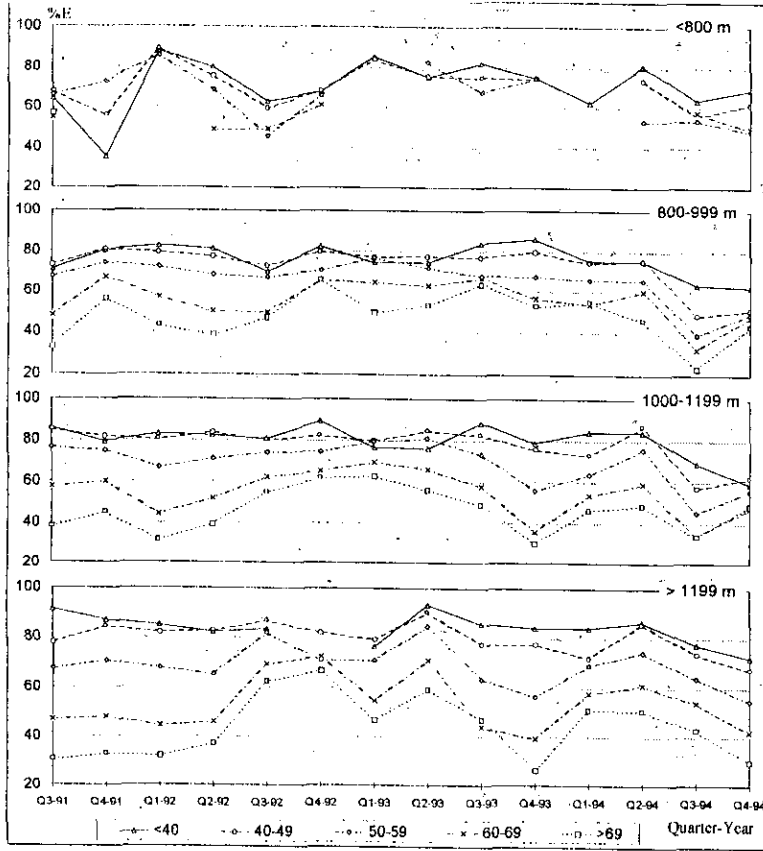


Figure 3. Emptiness percentage (%E) trough years by depth (m) and length group(cm).

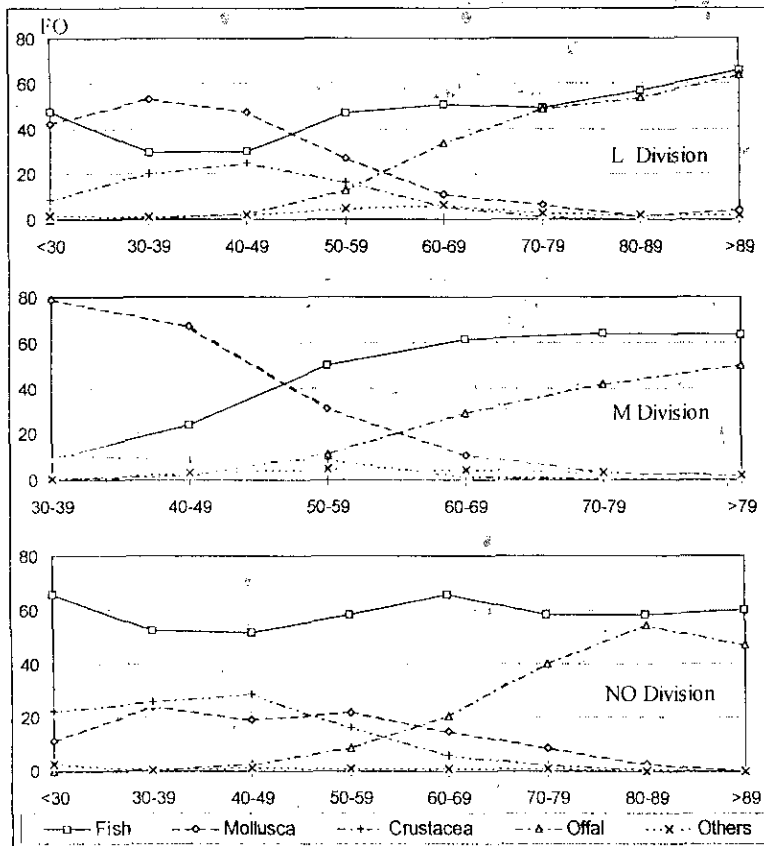


Figure 4. Greenland halibut main prey groups by length group (cm) and NAFO Division, expressed as frequency of occurrence (FO).