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Seasonal and year-to-year dynamics of occurrence
frequency of the main food objects for haddock
and their stomach fullness degree in the Barents Sea

by
Antipova, T.V., Ponomarenko, I.Ya.
&
Yeragina, N.A.

Abstract

On the basis of systematization and summary of the long-term data on field analyses of the stomach contents of 235 136 specimens of haddock taken from different areas of the Barents Sea the seasonal, local and annual variations in occurrence frequency of demersal animals, capelin and euphausiids in haddock food and their stomach fullness degree (or stomach fullness index) were observed.

The most intensive feeding of haddock on demersal animals is registered in the second half of the year, on capelin - in March-April, on krill - in June-July.

The most intensive haddock feeding (the highest average index of stomach fullness) takes place in March, the second peak in feeding refers to July, the third one - to September.

The frequency of Echinodermata occurrence in haddock feeding in 1957-1966 and 1967-1976 increased compared to that of 1947-1956. The occurrence frequency of molluscs, capelin and euphausiids in the last ten years compared to those of the previous decades slightly decreased, but of worms - did

^{x/} PINRO, M u r m a n s k, USSR.

not almost changed.

The tendency to the inverse correlation between the average annual values of occurrence frequency of Echinodermata and molluscs, capelin and euphausiids, i.e. the animals related between each other by the relation "predator - prey" has been revealed.

Résumé

Les résultats systématisés et généralisés des recherches en mer, effectuées pendant plusieurs années, sur le contenu stomacal de 235136 eglefins des régions différentes de la mer de Barents ont servi de base à l'examen de la variation de la fréquence saisonnière, locale et annuelle des animaux benthiques, des capelans et des Euphausiidae, en tant qu'objets de nutrition de l'eglefin, et de la réplétion stomacale de ce dernier.

L'engraissement des eglefins, dû surtout aux animaux benthiques, a lieu au cours du deuxième semestre de l'année, dû aux capelans - en mars et en avril, dû aux Euphausiidae Hyperiidæ - en juin et en juillet. La réplétion de l'eglefin (l'indice moyen de réplétion stomacale) atteint son maximum en mars, la deuxième pointe de la réplétion a lieu en juillet, la troisième - en septembre.

La fréquence des Echinodermes en tant qu'objet de nutrition de l'eglefin s'est accrue en 1957-1956 et en 1967-1976 par rapport à 1947-1956. La fréquence des mollusques, des capelans et des Euphausiidae a un peu diminué la dernière décennie par rapport aux décennies précédentes; par contre la fréquence des annélides n'a presque pas varié.

On a relevé la tendance au rapport inverse entre les données moyennes annuelles sur la fréquence des Echinodermes et des mollusques, des capelans et des Euphausidae, faisant partie de la nourriture des eglefins, c'est-à-dire des espèces qui sont dans les rapports du "rapace" et de la "proie".

During several decades the Polar Research Institute (PINRO) carried out the observations on haddock (*Melanogrammus aeglefinus* L.) feeding in different areas of the Barents Sea. For the period since 1947 throughout 1977, 235 136 haddock stomachs were investigated by a field analysis method. Comparatively small part of these materials was used in a set of papers aimed at revealing the relationships between feeding and behaviour of haddock in diurnal, seasonal and annual aspects (Novikova and Mikhailovich, 1963; Novikova, 1965; Sonina, 1969; Antipova, 1967, 1971).

The aims of the present paper are to systematize and summarize all the data available on field analyses of haddock feeding, to reveal, on their basis, the local, seasonal and year-to-year variations in haddock feeding indices and occurrence frequency of the main food objects and to determine some regularities in these variations.

Material and methods

All data on field analyses of haddock feeding caught with bottom trawl in the southern Barents Sea during the

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cruises of the research, scouting and, partially, commercial vessels for the period since 1947 throughout 1977 have been used in the paper.

The volume of material by years, months and areas is given in Table 1.

A field analysis of feeding is considered to be the most popular type of biological analysis of commercial fishes undertaken at sea. Only the length measurements are the most numerous. Usually, the content of 25 haddock stomachs taken by bottom trawl is analysed. However, not less than 100 specimens of haddock are analysed for feeding while taking the age samples from the biggest catches.

The field analysis of haddock feeding consisted in visual quantitative assessment on stomach fullness degree due to 5 indices scale (0, 1, 2, 3, 4) with determination and enumeration of food components. On the basis of feeding field analyses data on sample, area, season, year and etc., an average index of stomach fullness and occurrence frequency of separate food objects (the relation between a number of stomachs, in which a given object was found and total number of stomachs analysed, contained food, in %) were estimated. The first index was used for evaluation of quantitative character of haddock feeding (their amount of food in the stomach), the second one - for judging what percentage of fishes investigated fed on any of food objects.

Results

In accordance with the literary data different demersal

animals constituted the main food for the Barents Sea haddock during the greatest period of the year, however, in some seasons and in separate areas the fish (chiefly, spawning capelin and their eggs) and euphausiids descending after spawning into the near bottom layers of the sea can play a considerable role in haddock feeding (Dekhtereva, 1934; Zatsepin, 1939; Petrova-Grinkevich, 1944; Tseeb, 1958, 1960, 1964; Antipova, 1967, 1971).

Some authors stated that in the fifties-sixties the significance of capelin and euphausiids in the food ration of haddock had been increased compared to those of the thirties but the importance of benthos had been decreased (Tseeb, 1958; 1960; Sonina, 1969). This was the explanation for increase of the growth rate of the Barents Sea haddock, their fatness and variations in migrations in the fifties-sixties (Sonina, 1969).

Judging by summarized results of analysis of stomachs content of haddock the most ordinary food objects for this fish in the southern Barents Sea for the last 30 years were Echinodermata, occurred in 32.6% of stomachs analysed, worms (20.8%), molluscs (19.5%), Ctenophora (18%), euphausiids (13.9%) and capelin (8.9%). The food objects above-mentioned with small displacements by places dominated during all three comparable decades: 1947-1956, 1957-1966, 1967-1976 (Table 2).

Demersal animals are mostly often eaten by haddock in the second half of the year: Echinodermata - in October-December, worms and molluscs - in August-September. Seasonal

minimum of haddock feeding with benthos is observed in February-April (Fig.1). The occurrence frequency of capelin in haddock stomachs is the highest during the period of mass capelin spawning - in March-April (32.0 - 40.8%). Euphausiids are mostly often eaten by haddock in the period of post-spawning descending of crustaceans into the near bottom layers of the sea - in June-July (35.0 - 39.4%). From July to December the occurrence frequency of euphausiids in stomachs decreases, that is probably related to reduction of crustaceans abundance caused by the intensive feeding by fishes. A comparative analysis of seasonal variations in the occurrence frequency of capelin and euphausiids in cod and haddock stomachs in the southern Barents Sea shows a considerable similarity of curves (Fig.2). However, the occurrence frequency of capelin in cod stomachs in all months of the year is higher than that of haddock. In spring euphausiids more often occurred in haddock stomachs, but in the rest months - in cod stomachs. Apparently, in spring the haddock, more than cod, migrate to upper water layers, where the spawning euphausiids concentrate at that time.

Well-defined seasonal character is also typical for feeding of haddock on Ctenophora: their maximum occurrence frequency is marked in January-March with peak in February (see Fig.1). In this period of the year Ctenophora, as Kamshilov, M.M. stated (1961), are observed in the near bottom water layers.

Seasonal maximum of stomachs fullness for haddock falls to March, the period of the most intensive feeding on capelin. The second peak of haddock feeding is in July (the

period of predominant feeding on euphausiids), the third one - in September (the period of feeding on benthos). The percentage of fishes with empty stomachs is the lowest in September-October and in March, the highest - in November-January and in April (see Fig.1).

Seasonal dynamics of occurrence frequency of the most important food objects of haddock by separate groups of areas is reflected in Tables 3-5^{x/}. The highest frequency of Echinodermata occurrence (mainly, Ophiurozoidea), is observed in the coastal and western areas, of worms (mainly, Polychaeta) - in the central and eastern areas, of molluscs (mainly, Lamellibranchiata) - in the eastern and coastal areas. Mostly often capelin is eaten by haddock in the coastal areas, euphausiids (mainly, *Thysanoessa inermis* and *Th. raschii*) - in the coastal and central ones. According to average indices of stomachs fullness the feeding conditions of haddock in the western areas of the sea almost in all months of the year are worse than those in the coastal, central and eastern areas. In spring haddock feed most intensively in the coastal areas, in summer - in the coastal and central areas, in autumn - in the eastern areas.

The analysis of the long-term data on haddock feeding shows that in spite of some stability of benthos feeding, the significance of the main groups of bottom animals in their feeding does not retain constant (Fig.3).

^{x/} the chart of the areas allocation is represented in the former papers (Ponomorenko, I.Ya. and Yaragina, 1978, 1979).

The most sharp year-to-year fluctuations effect the occurrence frequency of Echinodermata. In the forties-fifties it was considerably less than the long-term mean (excluding 1947 and 1955), and in the sixties-seventies in most cases it exceeded the long-term mean and was maximum in 1964, 1970 and 1975. In recent years a fairly accurate periodicity of maximum and minimum frequencies of Echinodermata occurrence in the haddock stomachs was observed: the maximum ones repeated each 5-6 years, the minimum ones - each 8 years. It can be assumed, that an increase of Echinodermata significance in the haddock feeding in the sixties-seventies is related with the predominance of the samples taken from the western and coastal areas in these years, where the biomass of Echinodermata is higher, than that of the central and eastern areas. However, the analysis of materials only by western and coastal areas shows the same tendency to increase of occurrence frequency of Echinodermata in the haddock stomachs in the sixties-seventies. It permits to conclude that in the sixties-seventies, compared to the forties-fifties, the abundance of Echinodermata increased.

The occurrence frequency of molluscs in the haddock stomachs fluctuates also by years, maximum values were registered in 1948-1949, 1955, 1961-1962 and 1971. No accurate periodicity of maximum frequencies was defined. As it is seen from Fig. 3 the occurrence frequency of molluscs in haddock food on the space of the most part of 30 years period is in the anti-phase in relation to occurrence frequency of Echinodermata. Probably, this is explained by the fact, that Echinodermata are the predators in relation to molluscs. Therefore,

with the increase of Echinodermata abundance, the abundance of molluscs decreases. The anti-phase of the year-to-year variations in the occurrence frequency of Echinodermata and worms is also observed (Fig.3).

Year-to-year variations in the occurrence frequency of worms in haddock food are less vividly expressed than those for Echinodermata and molluscs. Apparently, the abundance and biomass of worms are not under the influence of considerable annual fluctuations.

The relations between the annual variations in occurrence frequency of the mentioned groups of demersal animals in haddock food and annual variations of near bottom water temperatures were not able to reveal.

The comparison of the data on the field analyses of haddock feeding in the southern Barents Sea by decades (1947-1956, 1957-1966, 1967-1976) showed, that the occurrence frequency of Echinodermata in haddock stomachs in the second and third decades had been increased, of molluscs in the third decade had been decreased, of worms - had not almost changed (see Table 2). The reduction of the molluscs significance in the haddock feeding in the last decade is to a considerable extent related with displacement of their areal into the western and coastal regions, where molluscs' biomass compared to that of the eastern regions was not high.

The average annual frequency of capelin occurrence in haddock stomachs fluctuates within very extensive limits - from less than 1% in 1948 and 1964 to 40% in 1960 (Fig.4). Maximum frequencies of occurrence of capelin in haddock stomachs, as

well as in cod stomachs had a 10-11 years periodicity (Ponomarenko, I.Ya. and Yaragina, 1978) and fall to 1960-1961 and 1971. Besides, a 5-6 years periodicity for maximum frequencies of capelin occurrence in haddock stomachs during the seasons of the most intensive capelin feeding (February-April) is observed. These maximum frequencies took place in 1954, 1960-1961, 1966 and 1971 (Fig.4). Year-to-year amplitude of frequency fluctuations of capelin occurrence in haddock stomachs in the season of intensive capelin feeding is extremely high: from 79% in 1954 to 0.8% in 1948.

In contrast to cod (Ponomarenko, I.Ya. and Yaragina, 1978) in the last decade the frequency of capelin occurrence in haddock stomachs somewhat decreased, compared to those in two previous decades (see Tables 2-6).

An accurate relationship between the frequency of capelin occurrence in haddock stomachs in separate years and heat content of the Barents Sea water masses in the same years was not able to determine ($r=0.20$). However, the highest peaks in frequency of capelin occurrence nevertheless correspond to the warm 1954 and 1960.

For recent years (1971-1976) data on abundance and biomass of the Barents Sea spawning capelin population obtained by the mathematical model by Allen's method (Seliverstov, Korytov, Shulga, 1977) are available. The comparison of these data with the frequency of capelin occurrence in haddock food in the period of the most intensive capelin feeding shows a good coordination of the curves (Fig.4).

Average annual frequency of euphausiids occurrence in had-

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dock stomachs also varies in fairly wide limits: from 3.8% in 1961 to 39.7% in 1957; maximum value exceeds the minimum one by 10 times (Fig.5). Frequency fluctuations of euphausiids occurrence from year to year are especially sharply pronounced in the period of intensive summer feeding of haddock on these crustaceans. Maximum values were observed in 1952, 1957, 1964, 1968-1969 and 1976, the minimum ones - in 1961 and 1971. The minimum values repeated each 10 years. An accurate periodicity of maximum values and their relationships with temperature conditions in separate years were not revealed. It can be only noticed, that almost all the maximum values correspond to the years close to the temporary ones due to the thermal conditions.

The relationship between the results of annual autumn-winter euphausiids assessment (Drobysheva, 1979) and their occurrence frequency in haddock feeding in summer next year was not determined.

At the same time as for cod, there was revealed the inverse correlation between average annual occurrence frequencies of capelin and euphausiids in haddock stomachs (Fig.6). It can be explained by the fact, that in the years of great capelin abundance, the latter intensively feeds on euphausiids in spring months and by summer the abundance of these crustaceans sharply decreased, they more rarely occur in haddock stomachs. Apparently, just therefore an accurate relationship between the results of euphausiids assessment in autumn and results of cod and haddock feeding on these crustaceans in summer next year (Ponomarenko, I.Ya. and Yaregina, 1979) was not revealed.

In the last decade (1967-1976) the frequency of euphausiids occurrence in haddock food, compared to those in the previous decades, decreased (see Tables 2-6). It is seen from the data both on the southern Barents Sea in total and separate areas (Tables 2-6, Figs. 5, 6):

Average indices of stomachs fullness of haddock in the last decade also reduced, the percentage of fish with greatly full stomachs (index 4) decreased, but percentage of fish with empty stomachs increased, particularly, in the period of autumn feeding on benthos (Fig. 7). This is greatly conditioned by the fact that because of climatic conditions and size-age population composition variations, haddock rarely migrate to the richest with benthos south-eastern Barents Sea areas. Food resources in these areas are not completely used by haddock.

However, in January-March the average indices of stomachs fullness of haddock in the last decade were higher than those in the previous decade, and in February - higher, than those in both previous decades (see Fig. 7). This is the evidence of earlier intensive haddock feeding on capelin in the last decade in relation to earlier and predominantly more western approaches of spawning capelin.

Conclusions

1. Summary of the long-term results of the field analyses of stomachs contents of 235 136 haddock specimens taken from different areas of the Barents Sea showed, that in 1947-1976 the mostly often observed food objects for haddock were Echi-
nodermata (occurrence frequency - 32.6%); worms (20.8%);

molluscs (19.5%); Ctenophora (18%); euphausiids (13.2%); and capelin (8.9%). These food objects with small displacements in their places were predominant in all comparable decades: 1947-1956, 1957-1966, 1967-1976.

2. Demersal animals have the maximum significance in haddock feeding in the second half of the year; the minimum one - in February-April.

Capelin is eaten by haddock since February throughout May, maximum feeding is observed in March-April. The percentage of haddock fed on capelin in all months is less than that of cod.

The haddock feeds on euphausiids the whole year around, but most of all, in June-July, minimum feeding is observed in October-January. In February-April the percentage of haddock fed on euphausiids is higher, than that of cod, and in the rest months it is lower.

3. Haddock feeding (average index of stomach fullness) is the highest in March, the second peak of feeding is in July, and the third one - in September. The lowest percentage of fish with empty stomachs is in September-October and in March, the highest one - in April and December-February. In spring the average indices of stomachs fullness of haddock are the highest in coastal areas, in summer - in coastal and central, in autumn - in eastern areas. In the western areas of the sea the average indices of stomach fullness in all months are practically the lowest.

4. The greatest frequency of Echinodermata occurrence in haddock stomachs is registered in the western and coastal

areas, of worms - in central and eastern ones, of molluscs - in eastern and coastal ones. Capelin is mostly often found in haddock food in the coastal areas; euphausiids - in the coastal and central areas.

5. The occurrence frequency of the main food objects for haddock are subjected to considerable year-to-year fluctuations. The fluctuations of occurrence frequency of capelin and euphausiids are the most sharp, and as for the demersal animals the fluctuations of occurrence frequency of Echinodermata are also the most sharp.

A tendency to inverse relationship between average annual values of occurrence frequency of food animals, related between each other by ratios "predator - prey": Echinodermata and molluscs, capelin and euphausiids has been revealed.

6. The occurrence frequency of Echinodermata in the recent two decades (1957-1966 and 1967-1976) increased, of molluscs in the last decade decreased; of worms - almost did not vary.

The occurrence frequency of capelin and euphausiids in the last decade somewhat reduced compared to that of two previous decades.

7. Average indices of stomachs fullness of haddock in 1967-1976 almost in all months were lower than those in the previous decades, and percentage of fishes with empty stomachs were the highest. Reduction of average indices is particularly sharply expressed in the period of predominant feeding of haddock on benthos.

8. In accordance with the displacement of haddock areal

to the west, rich food resources of the south-eastern areas.
of the sea are almost not used by haddock.

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Table I

Number of haddock stomachs taken from different areas
of the Barents Sea and analysed by months

Years	Jan.	Feb.	March	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Western areas												
1947-1956	664	1326	1049	2041	1212	505	1110	360	183	431	358	321
1957-1966	5023	6323	4352	7936	7402	1726	1693	1213	2233	1930	3056	4638
1967-1976	7425	7905	4925	7678	11903	5354	2385	1838	1479	2237	4297	4000
Coastal areas												
1947-1956	44	130	261	11	826	1163	122	80	276	820	201	146
1957-1966	387	1297	1193	1377	5357	1882	2298	5216	2660	2816	2249	1409
1967-1976	1559	529	584	1349	7133	3287	3992	2550	1837	2099	1275	1425
Central areas												
1947-1956	389	455	43	465	124	150	128	41	20	456	383	187
1957-1966	523	230	135	-	546	240	106	1644	655	775	1480	1138
1967-1976	1477	85	240	-	746	1886	3050	1538	505	1245	1640	2305
Eastern areas												
1947-1956	46	-	-	-	-	-	500	914	1570	1221	567	383
1957-1966	-	-	-	-	-	-	-	3000	3257	1946	798	4
1967-1976	1	-	-	-	-	-	1818	2322	1271	175	322	295
the southern Barents Sea in total												
1947-1956	1143	1911	1353	2517	2162	1818	1860	1395	2049	2928	1509	1037
1957-1966	5933	7850	5680	9313	13305	3848	4097	11073	8805	7467	7583	7489
1967-1976	10462	8519	5749	9027	19503	10527	11245	8248	5295	5756	7981	8025
1977	976	1816	56	639	2017	450	601	629	1039	849	580	727

Food content of haddock taken in the southern
Barents Sea in 1947-1976 (due to data on field
analyses of feeding)

Food objects	: Frequency of occurrence , %			
	1947-1956	1957-1966	1967-1976	1947-1976
Echinodermata	17,3	31,9	35,3	32,6
Worms	18,8	18,2	22,8	20,8
Molluscs	23,1	20,1	15,1	19,5
Bottom crustaceans	2,5	1,5	1,9	1,8
Shrimps	2,1	2,5	3,6	2,9
Amphipoda	3,2	3,7	3,7	3,6
Other benthos	7,0	3,7	4,0	4,1
Ctenophora	17,4	18,1	18,7	18,0
euphausiids	11,3	18,8	11,2	13,9
Capelin	11,1	10,5	6,6	8,9
Herring	1,5	1,3	0,0	0,8
Young cod	0,8	0,5	0,0	0,4
Young haddock	0,1	0,3	0,0	0,2
Other fishes	3,0	2,5	2,3	2,5
Digested food (species are not determined)	2,1	1,5	1,1	1,3

Table 3

Seasonal variations in occurrence frequency (%) of the main food objects and haddock stomach fullness index in the waters of the Barents Sea

Months/years	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Average for I-XII
Echinodermata													
1947-1956	3,5	9,0	14,9	9,0	29,7	38,6	34,2	50,9	57,6	27,2	10,9	25,2	25,2
1957-1966	43,5	16,2	15,1	26,2	33,9	15,5	13,0	44,9	42,7	54,6	48,0	64,6	34,8
1967-1976	46,7	23,5	18,7	22,2	41,9	42,5	42,4	22,1	46,1	42,8	57,8	61,2	39,0
1947-1976	43,0	19,5	16,9	22,0	38,2	35,3	30,3	36,4	44,6	46,0	51,5	61,6	
Molluscs													
1947-1956	3,5	4,0	1,0	2,5	6,1	22,6	5,5	7,0	10,7	15,2	6,7	16,5	8,4
1957-1966	9,0	2,5	2,9	5,9	10,0	5,1	9,6	25,5	27,0	16,2	29,8	16,6	13,3
1967-1976	8,9	2,4	2,6	4,7	13,6	18,8	18,1	16,4	13,4	10,0	12,0	12,2	11,1
1947-1976	6,8	2,9	2,7	5,2	12,5	16,2	12,8	19,4	22,3	14,0	21,2	16,0	
Worms													
1947-1956	1,8	2,4	2,9	1,0	7,7	14,8	44,8	31,6	32,3	22,7	10,9	6,8	15,0
1957-1966	13,5	4,5	4,6	7,5	8,9	9,7	11,3	18,3	24,4	19,7	29,6	20,4	14,4
1967-1976	16,1	4,9	6,0	9,4	18,3	27,5	25,1	21,5	19,9	17,2	17,4	22,4	17,1
1947-1976	14,4	4,5	5,1	7,3	14,2	22,1	25,2	21,6	23,4	18,9	21,8	20,8	
Capelin													
1947-1956	0,2	2,8	22,9	64,0	4,5	1,1	9,1	0	0	0	0	0	8,7
1957-1966	0,3	6,1	31,2	40,9	18,1	3,5	4,4	0	1,9	0	0,1	0	8,9
1967-1976	2,1	9,1	22,6	28,7	4,0	3,8	1,6	3,1	0,5	0,4	0,0	0,5	6,4
1947-1976	1,3	7,4	26,0	39,4	11,7	3,5	4,4	1,3	1,4	0,2	0,1	0,2	
Benthic crustaceans													
1947-1956	6,1	13,3	13,4	5,8	22,5	28,3	9,0	5,1	1,9	4,8	0,4	3,9	9,5
1957-1966	4,9	13,6	13,4	15,4	25,1	58,3	33,6	16,7	8,0	3,6	7,4	3,1	16,9
1967-1976	3,2	6,6	13,6	11,6	12,0	9,3	15,2	2,9	6,3	5,2	1,8	1,9	7,5
1947-1976	4,0	9,8	13,5	12,4	17,5	23,2	20,0	9,3	7,2	4,5	4,1	2,6	
Average index of stomach fullness													
1947-1956	1,28	1,13	1,79	1,88	1,11	1,10	1,56	1,94	1,82	1,52	1,16	1,13	1,45
1957-1966	0,96	1,05	1,30	1,20	1,12	1,40	1,40	1,15	1,43	1,00	1,15	1,04	1,18
1967-1976	1,11	1,32	1,61	1,02	1,03	0,96	0,97	0,64	0,83	0,97	0,95	0,86	1,02
1947-1976	1,06	1,19	1,49	1,20	1,07	1,07	1,24	0,96	1,22	1,04	1,04	0,96	

Table 4

Seasonal variations in occurrence frequency (%) of the main food objects and haddock stomach fullness source in the coastal waters of the Barents Sea

Months/years	I	II	III	IV	V	VI	II	VII	IX	X	XI	XII	Mean for I-XII
<i>Schistocephala</i>													
1947-1956	0	27,7	9,4	0	15,6	22,3	1,0	33,3	53,2	40,5	53,2	12,6	22,4
1957-1966	36,4	20,2	13,6	17,3	35,4	12,7	15,2	37,3	43,3	72,5	67,9	59,4	35,9
1967-1976	51,9	14,1	22,7	26,8	42,7	33,3	26,5	31,3	53,0	54,7	55,6	73,4	40,5
1947-1976	47,4	19,0	15,6	20,8	37,8	25,0	21,6	35,4	47,1	61,9	63,4	64,4	
<i>Pollicipes</i>													
1947-1956	0	4,0	3,4	0	11,7	25,9	1,9	30,7	28,6	31,4	28,8	42,1	17,4
1957-1966	10,7	4,2	1,9	4,0	20,1	6,6	35,4	39,7	53,9	45,3	30,6	15,7	22,3
1967-1976	6,8	0	1,4	8,8	19,7	7,3	17,7	33,0	25,8	26,0	14,9	15,2	14,7
1947-1976	8,1	3,0	2,2	6,2	20,0	10,2	25,4	38,7	43,5	32,0	26,3	17,4	
<i>Worms</i>													
1947-1956	0	28,7	1,3	0	8,0	18,3	1,0	20,0	39,5	25,5	53,2	37,9	19,4
1957-1966	11,8	4,7	8,8	6,6	20,0	10,7	23,7	26,6	30,6	24,3	19,6	29,0	18,0
1967-1976	19,9	4,9	8,0	30,7	24,3	15,2	17,8	30,1	22,1	39,4	20,5	32,9	22,1
1947-1976	17,7	6,4	7,6	15,7	21,4	14,3	19,8	27,6	28,3	29,6	20,9	31,3	
<i>Capelin</i>													
1947-1956	0	2,0	80,9	55,6	28,2	2,5	12,6	0	0	0	0	0	15,1
1957-1966	0	46,7	66,9	55,2	20,9	7,0	0,8	0,5	0	0	0,1	0	16,5
1967-1976	0,3	18,9	40,6	19,6	3,2	2,1	3,0	0	0,2	0,5	1,3	0,3	7,5
1947-1976	0,2	35,8	61,5	41,7	13,6	3,7	2,4	0,3	0,1	0,2	0,4	0,1	
<i>Euphausiids</i>													
1947-1956	10,7	16,8	12,3	44,4	17,9	48,1	64,5	41,3	0	6,3	4,5	2,1	24,1
1957-1966	13,2	15,8	9,4	24,6	19,0	57,5	57,1	27,3	16,8	6,4	13,8	5,3	22,2
1967-1976	6,0	6,1	16,1	16,4	17,9	45,5	44,8	29,5	7,2	4,9	9,3	3,4	17,3
1947-1976	7,6	13,1	11,6	21,6	18,3	49,7	50,3	28,2	12,6	5,9	11,9	4,2	
Average index of stomach fullness													
1947-1956	1,09	1,29	2,62	2,00	1,66	1,21	1,76	2,19	1,45	1,45	1,27	1,31	1,61
1957-1966	1,36	1,73	2,25	1,69	1,37	1,45	1,47	1,34	1,66	1,45	1,57	1,36	1,56
1967-1976	0,97	2,22	1,79	0,69	1,08	1,36	1,36	1,25	1,01	1,05	0,99	1,28	1,25
1947-1976	1,05	1,84	2,17	1,19	1,24	1,36	1,41	1,32	1,40	1,31	1,35	1,33	

Table 5

Seasonal variations in occurrence frequency (%) of the main food

objects and haddock stomach filling in the central waters of the Barents Sea

Year/years	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Mean for I-XII
Echinodermata													
1947-1956	20,0	18,1	0	12,1	67,0	0,8	11,9	2,7	0	22,0	33,3	22,4	17,5
1957-1966	37,0	17,9	15,2	-	44,4	10,1	9,8	9,2	11,8	45,0	33,4	47,2	25,5
1967-1976	40,9	10,2	5,3	-	26,6	32,6	23,5	19,0	28,9	36,3	42,2	46,5	28,4
1947-1976	37,0	17,1	8,0	12,1	37,5	27,9	22,4	14,0	17,8	36,2	37,9	45,5	
Molluscs													
1947-1956	27,1	14,8	0	8,6	24,5	3,9	29,7	10,8	0	14,3	17,8	9,6	13,4
1957-1966	9,0	8,9	21,4	-	50,1	4,5	11,8	15,2	20,2	21,3	15,3	10,1	17,1
1967-1976	11,7	0	0,6	-	26,3	17,2	11,6	11,7	20,0	18,2	20,1	10,6	13,5
1947-1976	14,5	11,2	7,7	8,6	35,9	15,1	13,4	13,9	20,2	19,7	16,7	9,8	
Worms													
1947-1956	20,0	21,5	0	4,2	9,4	3,9	24,7	5,4	38,9	29,2	33,3	20,8	17,6
1957-1966	26,5	23,9	24,1	-	37,4	16,7	9,8	22,3	22,6	40,6	35,3	32,6	26,5
1967-1976	41,8	18,6	5,9	-	55,3	35,5	36,3	48,3	32,9	43,2	57,4	43,6	38,1
1947-1976	35,0	21,8	11,4	4,2	43,9	31,2	34,8	35,0	26,7	39,7	33,4	39,5	
Caprellin													
1947-1956	0	6,3	86,0	74,1	1,9	8,6	0	0	5,6	0	0	0,8	15,3
1957-1966	0,3	10,4	36,6	-	0,2	7,6	1,0	1,0	0,6	0,2	0	1,1	5,4
1967-1976	6,9	50,8	10,7	-	0,6	3,3	3,1	2,4	0,3	0,4	0,2	0,7	7,2
1947-1976	4,3	13,2	29,7	74,1	0,7	4,1	2,9	1,7	0,6	0,3	0,1	0,5	
Euphausiids													
1947-1956	7,6	5,6	4,7	8,4	4,7	64,8	47,5	24,3	44,4	20,4	2,4	0	19,6
1957-1966	9,6	1,5	3,6	-	1,8	55,6	69,6	29,9	50,5	10,6	12,8	2,8	22,6
1967-1976	0,4	0	0	-	4,4	26,5	34,7	10,5	2,8	2,2	1,0	0,7	7,6
1947-1976	3,7	3,7	1,9	8,4	3,4	32,4	36,6	20,1	32,9	8,3	4,9	0,7	
Average index of stomach fullness													
1947-1956	0,99	1,05	2,78	2,08	1,95	1,44	1,56	1,80	1,90	1,67	1,12	1,18	1,63
1957-1966	1,20	1,09	1,89	-	1,68	1,64	2,23	0,98	1,87	1,30	1,23	0,97	1,46
1967-1976	0,95	1,27	1,40	-	1,36	1,37	1,26	1,13	0,81	1,04	0,97	1,14	1,15
1947-1976	1,01	1,09	1,70	2,08	1,53	1,40	1,38	1,06	1,42	1,24	1,11	1,09	

Table 6

Seasonal variations in occurrence frequency (%) of the main food objects and haddock stomach fullness degree in the eastern waters of the Barents Sea

Months/years	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Mean for I-III
<i>Echinodermata</i>													
1947-1956							0	5,7	5,4	1,0	10,4	2,8	4,2
1957-1966							-	15,7	21,2	33,8	15,2	-	17,2
1967-1976							6,2	9,4	8,9	34,7	36,7	32,3	21,4
1947-1976							4,9	11,8	15,1	23,7	17,8	17,9	
<i>Molluscs</i>													
1947-1956							47,8	63,1	60,3	31,7	63,6	21,1	47,9
1957-1966							-	67,9	67,1	54,0	26,7	-	43,1
1967-1976							41,5	50,8	44,2	54,2	31,8	28,1	41,6
1947-1976							45,8	61,5	62,5	45,2	39,5	25,5	
<i>Worms</i>													
1947-1956							5,4	15,7	44,8	33,9	10,4	46,7	26,1
1957-1966							-	40,4	42,3	32,5	40,1	-	31,7
1967-1976							20,3	29,0	34,4	39,6	52,6	54,7	36,4
1947-1976							17,2	32,4	41,5	33,4	43,9	51,2	
<i>Capelin</i>													
1947-1956							0	0	0,3	0,2	0	0	0,1
1957-1966							-	0,1	0,3	0	0	-	0,1
1967-1976							9,5	0	1,0	0	0,4	0	1,6
1947-1976							7,5	0,1	0,4	0,1	0,1	0	
<i>Euphausiids</i>													
1947-1956							4,8	5,8	0,6	0	0	2,0	2,2
1957-1966							-	2,3	2,5	0,6	2,8	-	2,1
1967-1976							25,1	6,6	3,8	0	0,8	0	6,0
1947-1976							20,8	4,4	2,2	0,5	1,5	1,2	
Average index of stomach fullness													
1947-1956							1,23	1,76	1,28	1,78	1,58	1,15	1,46
1957-1966							-	1,39	1,64	1,34	1,81	1,25	1,49
1967-1976							1,26	1,52	0,94	1,27	1,59	1,36	1,33
1947-1976							1,25	1,49	1,40	1,50	1,69	1,25	

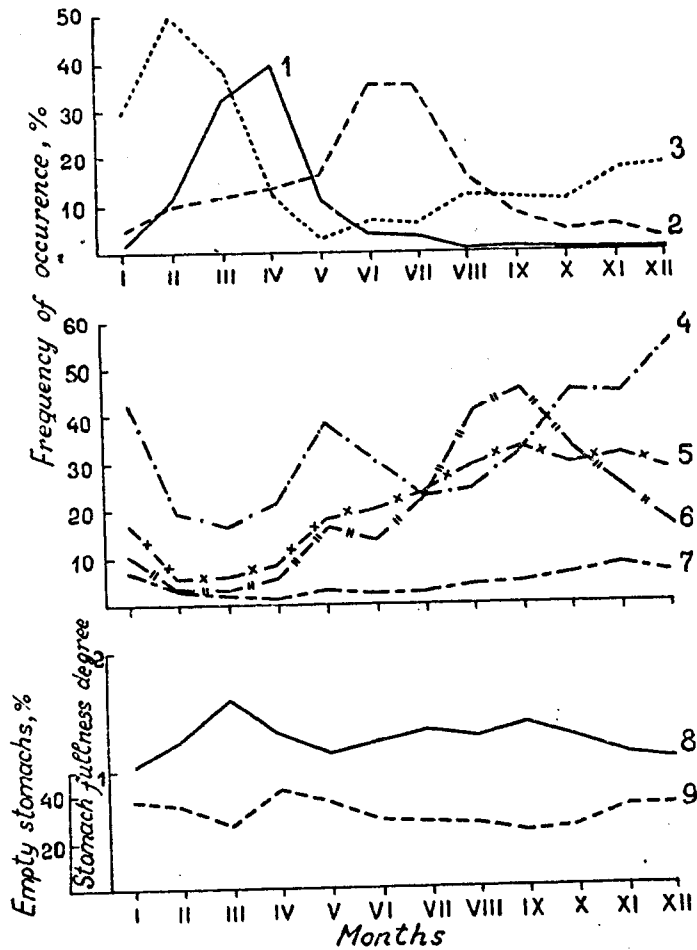


Fig. 1 Seasonal variations of occurrence frequency of capelin (1), euphausiids (2), Ctenophora (3), Echinodermata (4), worms (5), molluscs (6), other benthos (7) in haddock stomachs, of average index of stomach fullness (or degree) (8) and percentage of fishes with empty stomachs (9) in the southern Barents Sea due to the long-term data.

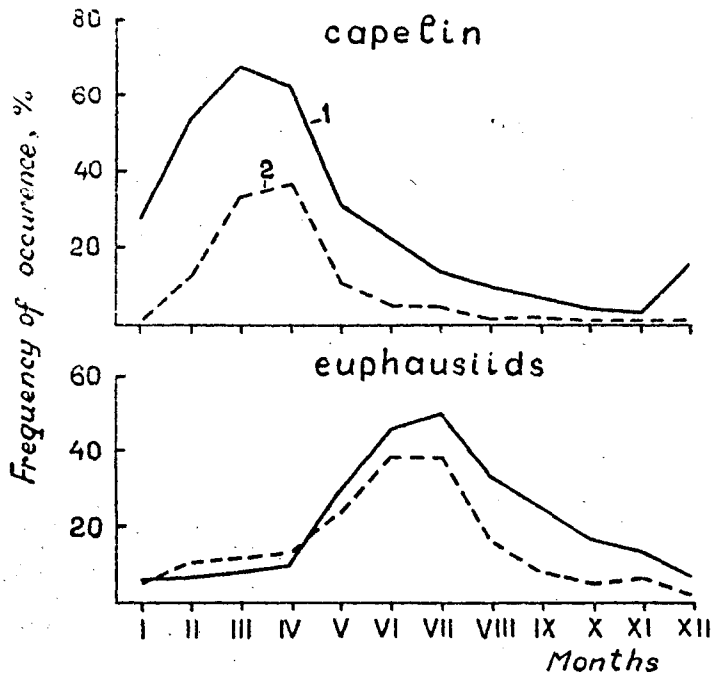


Fig.2 Seasonal variations of occurrence frequency of capelin (top) and euphausiids (bottom) in stomachs of cod (1) and haddock (2) due to the long-term data.

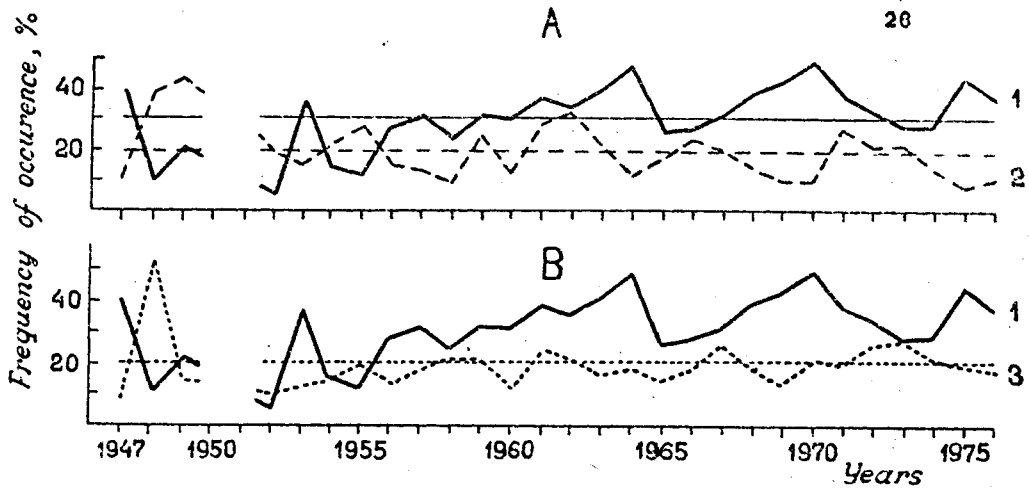


Fig. 3 Annual variations of occurrence frequency of Echinodermata (1), molluscs (2) and worms (3) in haddock stomachs. The long-term means of corresponding indices are designated by thin horizontal lines.

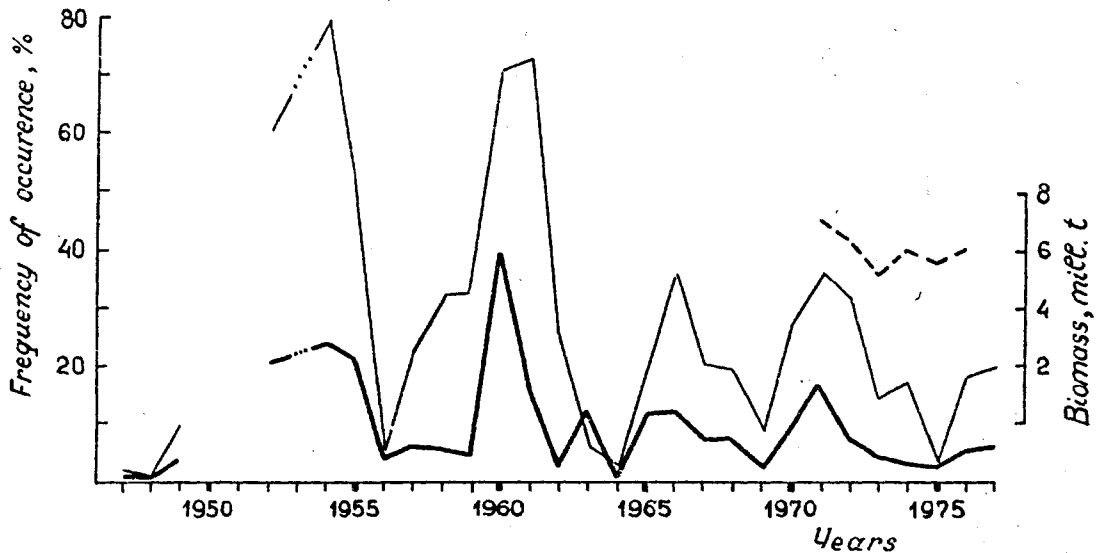


Fig. 4 Occurrence frequency of capelin in haddock stomachs in the southern Barents Sea per year on the average (thick line) and for the feeding period in February-April (thin line) and capelin biomass estimated by the mathematical model due to Allen's method (B. Iivertov et al., 1977) (dashed line).

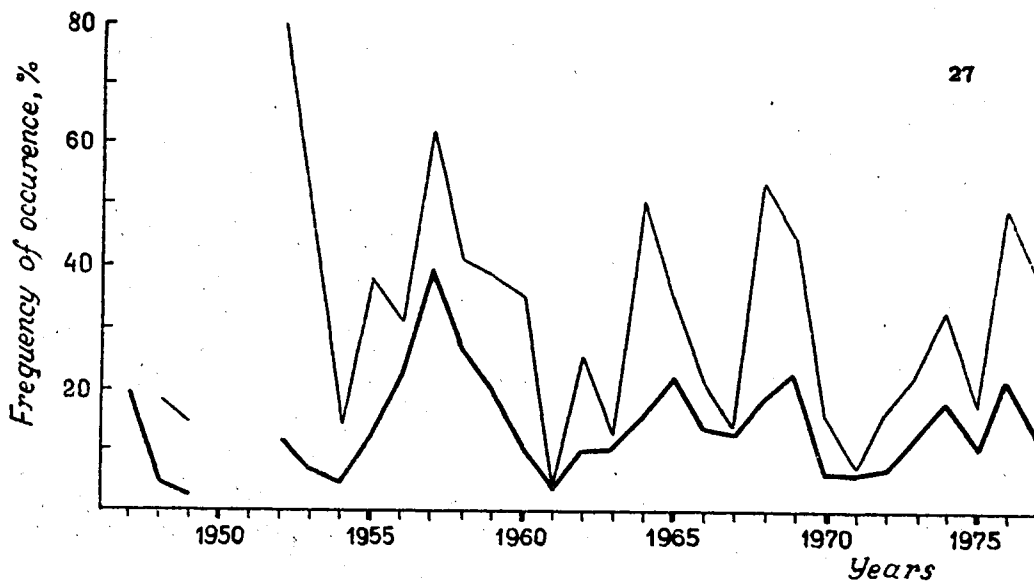


Fig.5 Occurrence frequency of euphausiids in haddock stomachs from the southern Barents Sea per year on the average (thickline) and the feeding period in June-August (thin line).

Fig.6 Year-to-year variations of occurrence frequency of capelin (solid line) and euphausiids (dashed line) in stomachs of cod (top) and haddock (bottom) in the southern Barents Sea.

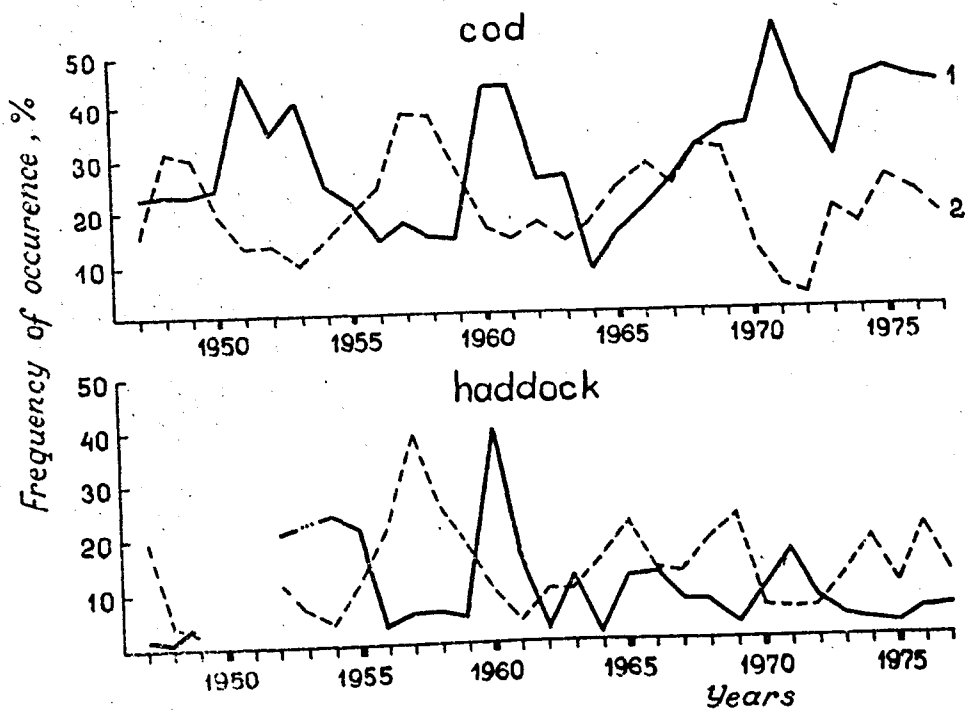


Fig.7 Average indices of haddock stomach fullness, percentage of fishes with index 4 and percentage of fishes with empty stomachs in the southern Barents Sea by months for three decades: solid line - 1937-1976, dashed line - 1957-1966, dotted line - 1947-1956.

