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Spatial and Functional Structure of Cod Trophic Relations
on the Newfoundland Shelf in Spring-Summer Season

by

O. V. Gerasimova and S. A. Kuzmin
Polar Research Institute of Marine Fisheries and Oceanography (PINRO)
6 Knipovich Street, 183763, Murmansk, Russia

ABSTRACT

Data on the distribution, size-age composition and feeding of cod in NAFO Divs. 3KLNO in spring-summer seasons of 1987-1991 are summarized.

Cod of younger age have been distributed over the northeastern and eastern slopes of the Grand Bank, with growth they migrate towards the western slope, coastal areas and Central shallows.

The diet of cod from Div. 3K is dominated by shrimp, from Div. 3NO by sand eel, and from Div. 3L by crabs. Capelin is an important prey for cod in all areas. The distribution and biomass of the first three species do not show significant year-to-year variations; these species appear to dominate the cod food and provide sustained minimum food supply required for subsistence of the population. Distribution and stock size of capelin - mobile species with a short life cycle - exhibit considerable year-to-year variations, hence, conditions of cod feeding on capelin also change. These changes seem to be major reasons behind abrupt variations of yearly increments in cod during 1985-1991.

The paper gives summarized maps of the distribution of total biomass of cod, numbers of certain age groups, maps of cod feeding grounds and distribution of its major prey.

INTRODUCTION

Comprehensive research of feeding and food relations of cod over the Newfoundland shelf, done in the recent 30 years, has shown the complexity and diversity of cod trophic relations (Lilly, 1987). The ultimate goal of collection of such information is, obviously, a construction of model, that could allow, in particular, to forecast the response of cod population to changes in food availability. However, an attempt to incorporate all complex of relations involved would be a failure, because an important attribute of a working model is its simplicity. At present, the analysis of available information is needed, that could help to show the structure of trophic relations and present relations of cod as a structured system, having specific hierarchy of its components.

The present paper attempts to accomplish such analysis in the course of study of the relationship between the cod growth rate and status of food supply. This paper should be regarded as the first, rather tentative suggestion for a certain field of research.

MATERIAL AND METHODS

Data on the abundance, distribution, age-length composition and stomach content of cod from the Newfoundland shelf (NAFO Divs. 3KLNO), obtained in spring-summer season during PINRO survey for 1987-1991 are presented in the paper (Table 1).

Data on yearly increments of cod at age 2-12 were used to analyse variations of cod growth rates. Yearly increments were estimated as a difference in mean length of fish from the same cohort for two neighbouring years. Variations in

yearly increments are presented in per cent of mean value of this parameter for the given age group for 1985-1991.

Data on cod food composition were obtained from analysis for feeding of cod in field conditions, when 25 fish from catch were examined for size, sex, stage of gonads maturity, and main preys were registered in stomachs. Stomach fullness was estimated by 5-point scale, i.e. 0 - empty, 1 - poor fullness, 2 - mean fullness, 3 - full stomach, 4 - stomach walls are stretched. Frequency of prey occurrence in cod stomachs was estimated as a ratio of number of stomachs, containing a given prey to a total number of stomachs analysed.

When studying distribution peculiarities of cod at different age from each catch, abundance of fish with size similar to those of cod of the same age were estimated, and the values obtained were used on the map. A map of distribution of fish of size given was drawn for each year using interpolation. When drawing general map, mean values of the abundance for 5 years (1987 - 1991) in each point of standard grid (15'W x 10'N) were estimated.

The same methods were used for drawing the following maps:

1. A map of distribution of cod total biomass;
2. Maps of main feeding grounds of cod - by degree of stomach fullness;
3. Maps of cod feeding on shrimp, capelin, crabs and sand eel - by these species frequency of occurrence in cod food;
4. Maps of distribution of shrimp (Pandalus sp.), capelin (Mallotus villosus), crabs (Chionoecetes opilio, Hyas araneus), sand eel (Ammodites sp.) - by their abundance in by-catches during bottom surveys.

Such method of summarizing of the results allow to reveal a pattern of variations of the parameter analysed, however, absolute values of the parameter are somewhat reduced. (Fig. 1).

RESULTS.

1. Peculiarities of growth rate, age composition and distribution of cod in NAFO Divs. 3KLNO.

Considerable differences in growth rate, age composition and distribution of cod from Divs. 3KLNO are observed.

Fish at age 5-6 are dominated in Div. 3K (Bulatova et al., 1989; Kuzmin, 1992) (Fig. 2). Values of yearly increments compared to the long-term mean values in cod from all age groups vary synchronically, except for fish younger than 3 (Fig. 3). In this area cod appear to be a single concentration, which in some years can migrate as a whole unit to the west, north or south (Fig. 1). Depth range occupied by cod in Div. 3K is rather narrow - 310-340 m (Kuzmin and Tevs, 1991).

In Div. 3L cod at age 4-5 appear to be the most abundant, while according to the year-to-year dynamics of growth rate, the following age groups could be distinguished: a) younger than 3, b) age 3-5, c) age 6-7, d) older than 7. From year to year in spring-summer season in this area cod is distributed at 190-240 m depth and, as a rule, form concentrations in the west, near Newfoundland Island coast, as well as on the northern and northeastern slopes of the Grand Bank.

Cod at age up to 3 inclusive dominate in the south of the Bank in Divs. 3N and 3O with a relatively low abundance of cod at age 5-8, while cod at age older than 8 are more abundant than those from the northern areas. Values of yearly increments in cod at age 3-7 and at age older than 8 are observed to vary synchronically. In the southern Grand Newfoundland Bank cod occur in a wide depth range from 75 m to 340 m, with concentrations on the Bank slopes and shallows at depth up to 100 m.

The character of yearly increments variations in cod of different age relates, probably, to cod feeding peculiarities, since other parameters influence (i.e. temperature) would appear in synchronic variations of yearly increments in total cod stock. Hence, to make further analysis easy, cod stock on the Newfoundland shelf was subdivided by similarity of yearly increments variations into several age groups: 1) younger than 3, 2) Age 3-5, 3) Age 6-7, 4) Age 7-8, 5) older than 8.

Analysis of distribution of several cod age groups showed their similar distribution in Div. 3K, while in Div. 3L smaller cod was observed to be concentrated on the northeastern and eastern slopes of the Bank, and larger cod - in coastal areas. In Divs. 3NO main concentrations of cod younger than 8 are distributed over the slopes, i.e. smaller fish - on the eastern and southern slopes, while

larger fish - on the western one (Fig. 4). Cod at age 7-8 with the smallest quantities in Divs. 3NO, were distributed in a narrow section of the western slope approximately along 44°N - 53°W, while fish older than 8 occupied an extensive area of the shallows. As cod at age 7-8 as well as cod older than 8 are not numerous in Divs. 3NO and 3K, respectively, these age groups were combined and considered to be a single group.

2. Spatial structure of cod trophic relations in NAFO Divs. 3KLNO.

In spring-summer season the diet of cod from Div. 3K is dominated by shrimp and capelin, from Div. 3L - capelin and crabs, from Div. 3NO - capelin and sand eel (Table 2).

Shrimp (*Pandalus borealis*) appeared to be widely distributed in Div. 3K with the densest concentrations being observed at the western slopes of the Funk Island Bank (Fig. 5). In Div. 3L shrimp were mainly distributed over the northern and eastern slopes of Grand Bank, approximately up to 46°N. Cod fed on shrimp mainly in the vast area of Div. 3K (Fig. 6).

In spring-summer season capelin are widely distributed in Div. 3L with single concentrations being observed in Div. 3K, as well as dense concentrations - on the eastern and southern slopes in Divs. 3NO. The most intensive cod feeding on capelin is observed in Div. 3L with areas of high frequency of capelin occurrence in food of cod younger than 5 being distributed both in the coastal areas and on the northeastern slope. Large cod feed on capelin mainly in the coastal waters. Only small cod feed on capelin on the slopes in Divs. 3NO (Fig. 7).

Crabs in by-catches from a bottom trawl occurred mainly at depth above 300 m. On the southern Bank there were mixed concentrations of *Ch. opilio* and *Hyas* sp., while *Ch. opilio* dominated in the north. The main feeding grounds, where cod feed on crabs are the Funk Bank in the Div. 3K and an extensive coastal area in Div. 3L (Fig. 8).

Sand eel concentrations on the Newfoundland shelf are well pronounced at depth above 100 m in the central shallows of the Grand Bank. In the eastern shallows these concentrations are denser, probably, as a result of bottom structure (Winters, 1983). In this area, closer to the eastern slope, the main feeding grounds where cod feed on sand eel are registered, with smaller cod feeding on sand eel only in the north of the shallows (Fig. 9).

Areas of the most intensive cod feeding in spring-summer season could be isolated by variations in degrees of cod stomach fullness. For all fish, except for the smallest (younger than 3), these feeding grounds are observed in coastal areas, where cod feed on crabs and capelin running to spawn (Fig. 10). As for the largest cod, the area of its feeding on sand eel is well pronounced.

Areas of steady occurrence of cod from given age group for the whole period of observations are presented in these maps. Small cod constantly occur on the Funk Bank northern and western slopes, as well as on the northeastern and eastern slopes of the Grand Bank. Large cod form stable concentrations in the same areas, as well as in the coastal areas and in the Central shallows of the Grand Bank.

DISCUSSION

As it was pointed out above, capelin, shrimp, crabs and sand eel are the most important preys for cod on the Newfoundland shelf in spring-summer season. Summary frequency of these preys occurrence in fish stomachs varies from 60% in Divs. 3NO to 85% in Div. 3K. The weight percentage of these preys in cod food could be higher, as all these preys are relatively large.

Capelin is an important prey in cod feeding in all areas. Capelin is a very mobile species, which is able to migrate for spawning and feeding for a long distance. The total capelin stock with a short life cycle is closely related to certain year-class abundance, hence, exhibit considerable year-to-year variations. Recent observations showed the capelin stock on the Newfoundland shelf to decline more than 50 times from 1990-1991 (Rep. Sci. Coun., 1992).

Distribution of the three remained species is more stable, since they do not make extensive migrations during a year. Their life cycle is twice as long as that in capelin (Winters, 1983; Parsons et al., 1992), hence their stock size is more stable (Rep. Sci. Coun., 1992). The areas of intensive cod feeding on these preys cover the main part of the area surveyed, with distribution of cod stable concentrations evidently coinciding with these areas (Fig. 1, 6, 8, 9 for comparison).

It can be supposed, that these species, i.e. shrimp, crabs, sand eel appear to dominate cod food on the Newfoundland shelf, providing sustained minimum food supply required for subsistence of the population.

It will be correct to characterize capelin as a preferable prey, but not the main one, due to high instability of their stocks and distribution. Cod intensively feed on capelin nearly all the year round. Cod feeding migrations, in particular, their approach to the Newfoundland coast in spring and summer, relate to capelin (Lilly, 1987). Year-to-year variations in cod distribution and rather abrupt variations of its yearly increments are assumed to be determined, primarily, by the conditions for cod feeding on capelin in each specific year.

From this point of view we shall try to analyze reasons for year-to-year variations in growth rates of cod on the Newfoundland shelf. As it was mentioned above, character of yearly increments variations in cod at age 2-3 considerably differ from that of older fish from all three areas. Plankton crustaceans (copepods, euphausiids, hyperiids) appear to be predominant in small cod food. This seem to be a reason for cod distribution along the northeastern and eastern slopes of the Grand Bank, where plankton biomass is the highest (Plekhanova, Ryzhov, 1976). Insignificant range of variations in yearly increments values indicate, apparently, a stability in food supply.

Cod at age 3 reach 30-40 cm in length and begin to feed on capelin (Popova, 1962; Turuk, 1986; Lilly, 1987, 1989; Lilly, Rice, 1983). This change is gradual, i.e. growth rates of cod at age 3-5 in Div. 3L relate to abundance of small immature capelin from the northern and northeastern slopes of the Grand Bank, while those of cod above 7 - to abundance of large capelin running to spawn to the Newfoundland coast (Gerasimova et al., 1992). Peculiarities of distribution of cod from these age groups, presented in the paper, confirm the map earlier suggested.

The most intensive cod feeding on capelin in Div. 3K is observed in the second half of the year, when capelin at age 2+ and partially 3+ migrate for feeding to the north. It should be mentioned, that size composition of capelin migrating in this period appears to be more homogeneous than that in spring in Div. 3L, since considerable amount of large fish at age 4+ die after spawning, while juveniles at age 1+ are concentrated southwards in vicinity of the northern boundary of Div. 3L (Bakanev and Gorchinsky, 1985). This, probably, is regarded to be a reason for distribution similarity and synchronism of variations in yearly increments in cod from different age groups in Div. 3K.

The variations in yearly increments, probably, depend on localization of main capelin concentrations during summer-autumn feeding. Extention of capelin migrations for feeding to the north changes from year to year, i.e. the most intensive cod feeding on capelin was observed in Div. 2J in autumn 1985, while in autumn 1986 - in Div. 3K (Lilly, 1991). We should note, that similarity of variations in yearly increments in cod from Div. 3K and small cod from Div. 3L could be a result of fish migration from one division to another along the northeastern and eastern slopes to the sites of maximum capelin concentrations (Lear, 1986a).

As it was mentioned above, abundance of cod at age 4-7 in Divs. 3NO was abnormally low, meanwhile the closest trophic relations between capelin and fish of the same age from other areas are observed. Analysis of tagging allows to assume cod to migrate from the southern Grand Newfoundland Bank to Div. 3L along the western slope of the Bank and the coast (Lear, 1986b). Cod migrations from south to north along the coast, probably, relate to cod feeding on spawning capelin, as far, the peaks of capelin approaches for spawning shift precisely in this direction (Templeman, 1968).

As for cod older than 8, occurring in considerable amounts only on the southern Grand Newfoundland Bank, close trophic relations between cod and capelin are, probably, being lost (Fig. 11), that is also proved by different character of variations in growth rates being observed in the Central shallows. Sand eel become predominant prey for cod in the southern Grand Newfoundland Bank. However, sand eel stock on the Grand Bank is rather stable (Winters, 1983), while yearly increments in cod older than 8 sharply vary from year to year. The latter could be explained by the inaccurate data on size-age composition due to a low abundance of fish at age older than 8. However, in certain years, trophic relations between large cod from the southern Grand Bank and capelin, probably, exist. Some fragmentary data indicate large amounts of mature capelin to occur in stomachs of large cod from these areas in the end of June - beginning of July. Observations on large cod feeding on capelin juvenile are also done (Lilly, 1987).

CONCLUSIONS

The simplest classification of cod trophic relations, which can be divided into the secondary and main ones, and the latter - into stable and labile, is a result of the analysis reported. Stable relations provide the possibility of subsistence of this species population in the ecosystem, while labile ones determine cod growth rates and, hence, influence their fecundity and abundance of the population.

We suppose, that even such primitive systematization of the data obtained presents the certain base for further research and trophic relations modelling.

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Table 1 Dates of Research Ground Trawl Surveys
in NAFO Div. 3KLNO in 1987-1991

Division	3NO	3L	3K
1987	11.03-13.04	26.04-11.05	11.05-06.06
1988	17.03-06.04	07.04-23.04	24.04-08.05
1989	05.03-21.05	27.04-21.05	05.06-19.06
1990	05.04-26.04	26.04-23.05	01.06-18.06
1991	09.04-27.04	09.05-06.06	no data

Table 2 Frequency of occurrence of food objects in cod stomachs
(Spring-summer 1988-1991, Div. NAFO 3KLNO)

Region	3K					3L					3NO							
	87	88	89	90	91	Mean	87	88	89	90	91	Mean	87	88	89	90	91	Mean
Euphausiidea	2.4	1.9	0.5	0.6	n	1.4	5.6	3.1	10.4	1.7	0.6	4.3	3.6	3.2	3.8	2.2	2.7	3.1
Hyperiid	1.8	0.7	4.0	3.4	o	2.5	-	1.8	0.2	2.1	4.1	1.6	2.0	3.3	1.8	-	2.7	2.0
Gammaridea	4.1	-	0.5	1.5	d	1.5	3.7	7.9	10.7	19.8	14.8	11.4	2.1	1.4	4.5	3.6	10.7	4.5
Crabs	5.2	16.1	10.3	11.8	d	10.8	17.5	16.3	33.3	20.3	13.9	20.3	4.6	5.0	7.0	10.8	6.8	6.8
Shrimps	23.2	18.2	56.8	40.1	a	34.0	9.0	6.9	12.3	4.3	11.4	8.8	2.2	2.5	2.5	2.2	5.2	2.7
Gastropoda	0.3	0.1	0.1	0.1	t	0.2	1.8	0.2	1.0	4.7	3.8	2.3	0.8	0.6	1.4	1.8	0.9	1.1
Bivalvia	0.3	-	0.2	0.1	a	0.2	0.7	-	0.4	0.8	0.2	0.4	5.1	4.5	2.8	4.7	0.1	3.4
Polychaeta	2.2	1.5	0.9	2.3		1.7	1.8	1.7	2.1	8.5	3.1	3.4	2.2	1.0	1.0	0.7	2.8	1.5
Echinoderm.	1.8	0.3	0.5	0.6		0.8	0.7	2.3	1.4	0.5	0.7	1.1	1.1	2.1	1.5	-	2.5	1.5
Cephalopoda	0.3	-	0.3	0.1		0.2	-	0.3	0.3	0.2	0.6	0.3	0.2	1.1	0.5	-	0.5	0.5
Capelin	18.8	14.0	11.4	5.5		12.4	29.6	32.8	30.6	19.7	41.0	30.7	12.5	6.5	12.6	11.9	7.0	10.1
Sand lance	-	-	0.1	0.3		0.1	7.7	2.3	3.5	1.3	4.7	3.9	3.9	9.6	8.9	32.7	3.0	11.6
Polar cod	-	0.8	0.1	-		0.2	-	-	-	-	-	-	-	-	-	-	-	-
Redfish	0.1	0.1	-	0.1		0.1	-	-	0.2	0.2	0.6	0.2	0.6	1.9	-	0.7	0.6	0.0
Cod	-	-	-	0.4		0.1	-	-	0.1	-	0.5	0.1	0.1	0.1	0.1	1.8	1.9	0.8
Flat fishes	-	-	0.3	0.1		0.1	-	-	0.9	0.9	0.9	0.5	0.4	1.4	0.7	1.1	0.9	0.9
Empty stomachs,%	38.6	46.0	13.2	30.8		32.2	32.6	25.0	15.9	20.0	15.8	21.9	48.4	46.1	49.0	38.5	56.7	47.7
Total number of stomachs analysed, spec.	996	721	825	585		-	466	871	1845	1200	1072	-	1062	727	716	278	857	-

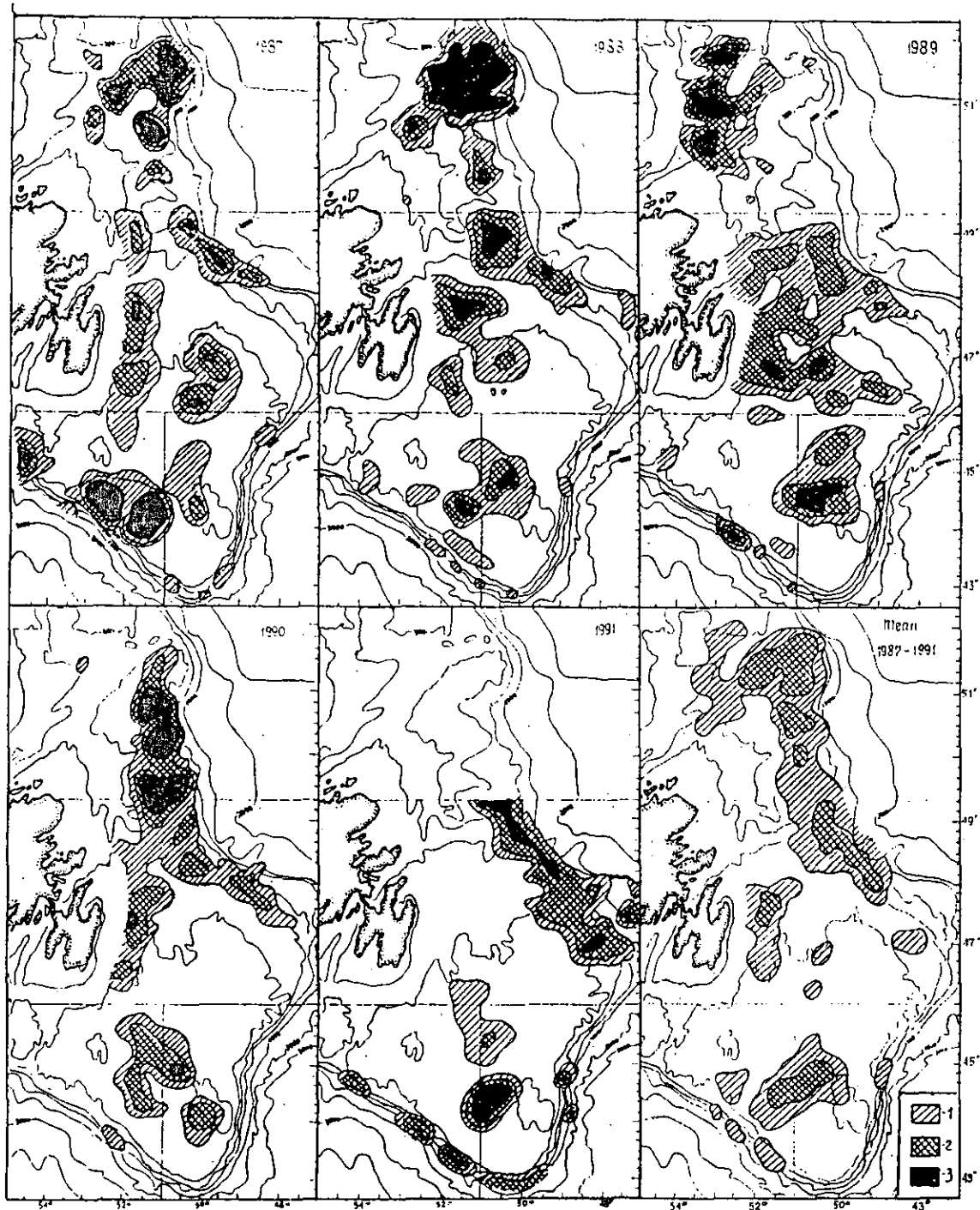


Fig. 1. Distribution of main concentrations of cod from the Newfoundland shelf in spring-summer season from 1987 to 1991.

1 - 100-200 kg/hour trawling; 2 - 201-500; 3- above 500

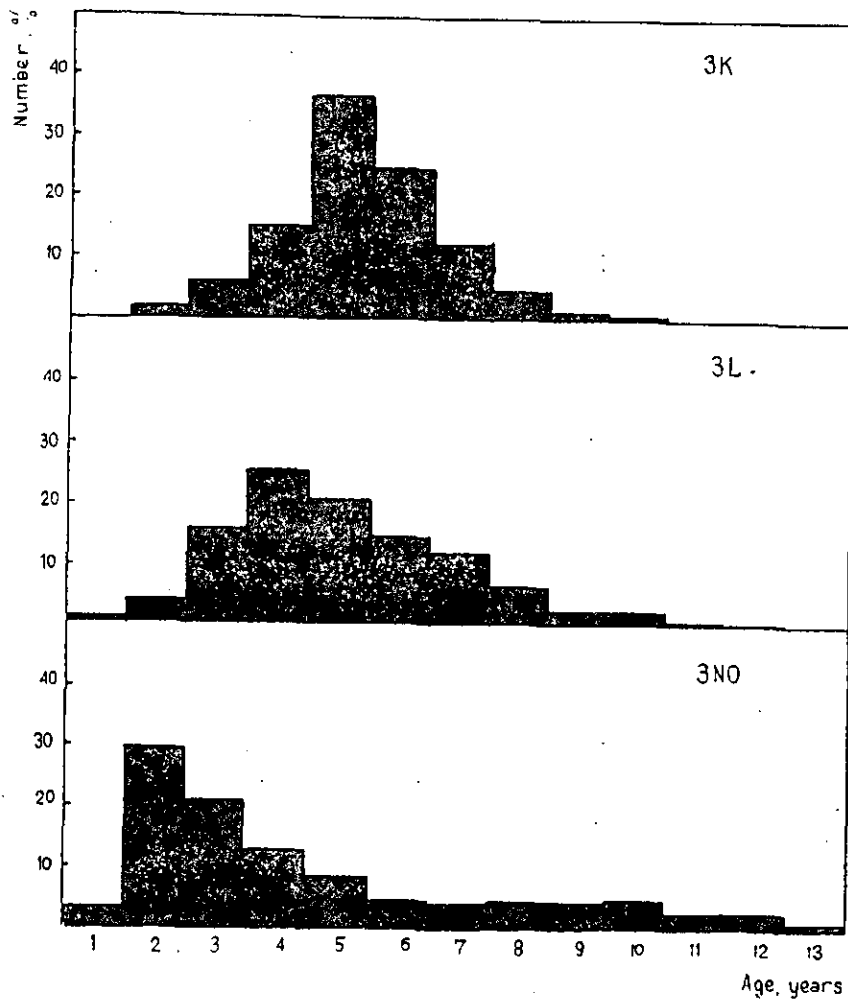


Fig. 2. Age composition of cod in NAFO Divs. 3K, 3L, 3NO by the data from 1987-1991 surveys.

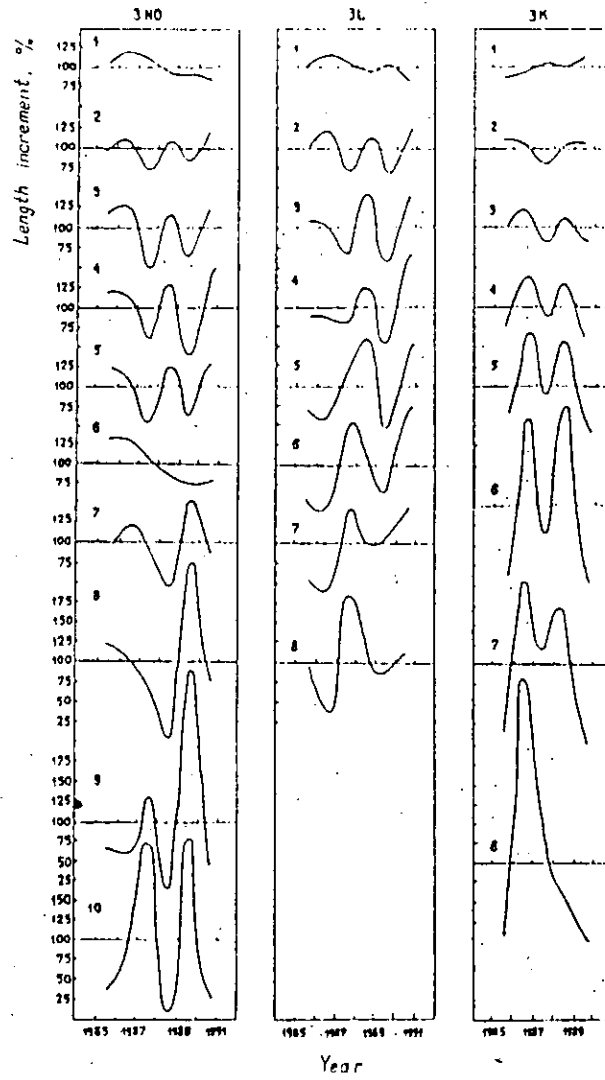


Fig. 3. Year-to-year dynamics of cod growth rate in NAFO Divs. 3KLNO (in % of mean yearly increments for 1985-1991).

1 - cod at age 2-3; 2 - age 3-4; 3 - age 4-5; 4 - age 5-6;
5 - age 6-7; 6 - age 7-8; 7 - age 8-9; 8 - age 9-10;
9 - age 10-11; 10 - age 11-12.

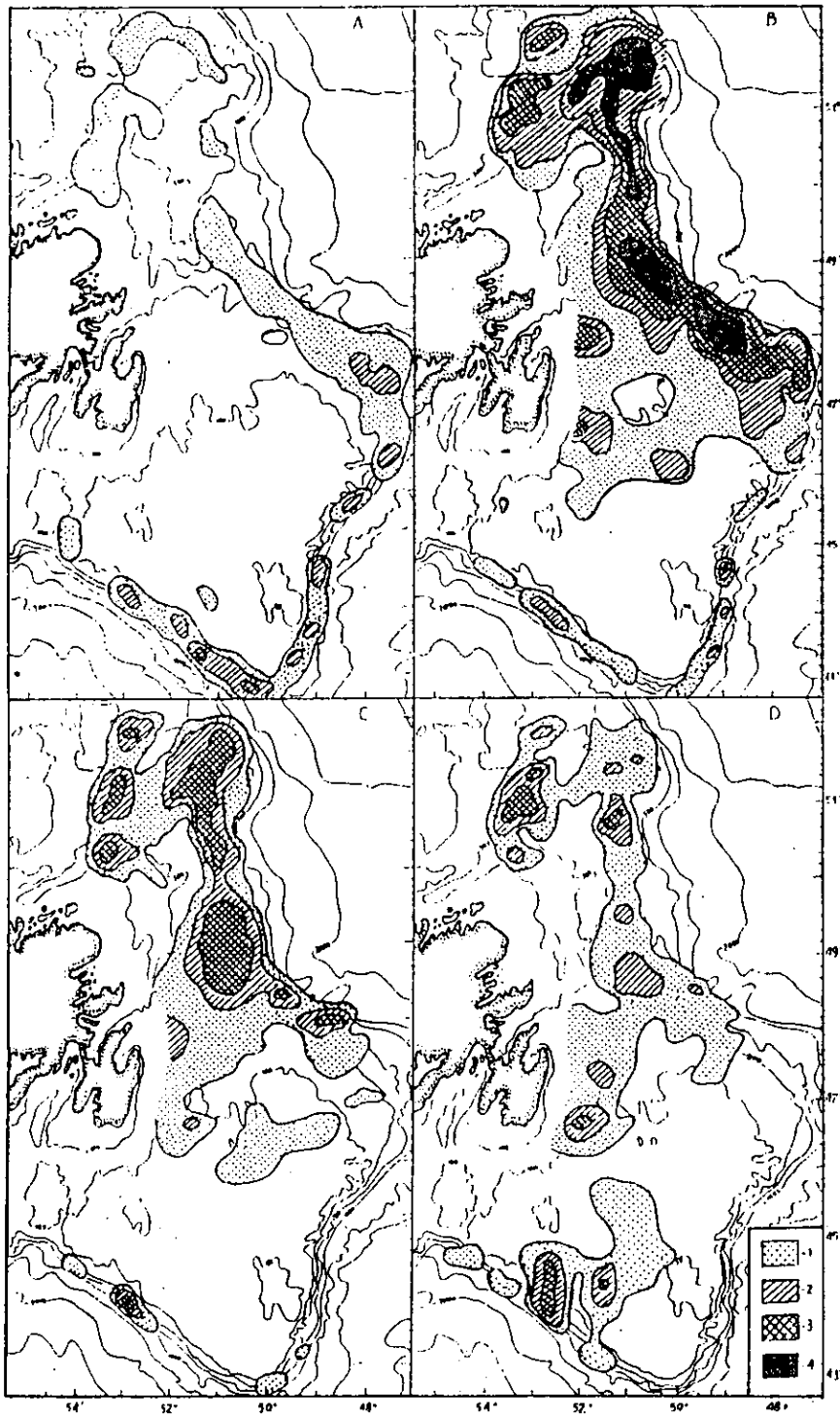


Fig. 4. Distribution of cod younger than 3 (A), age 3-5 (B), age 6-7 (C) and older than 7 (D) on the Newfoundland shelf by the data from surveys for 1987-1991.

1 - 1-10 fish per 30 minutes trawling; 2 - 11-25 fish; 3 - 26-50 fish; 4 - above 50 fish

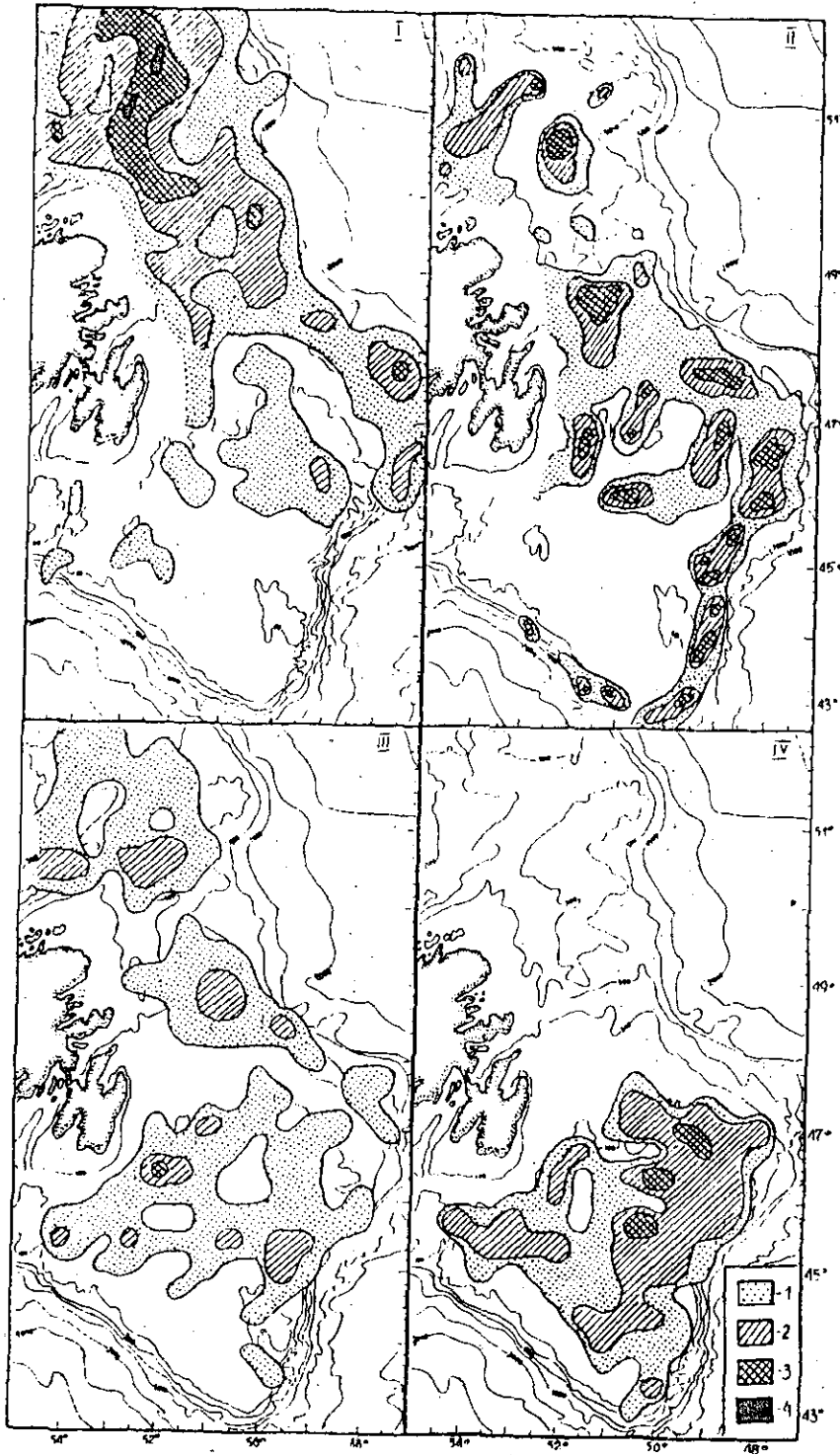


Fig. 5. Abundance of shrimp (I), capelin (II), crabs (III) and sand eel (IV) in by-catches during bottom surveys in NAFO Divs. 3KLNO in 1987-1991.

1 - single fish; 2 - tens; 3 - hundreds; 4 - thousands and more fish

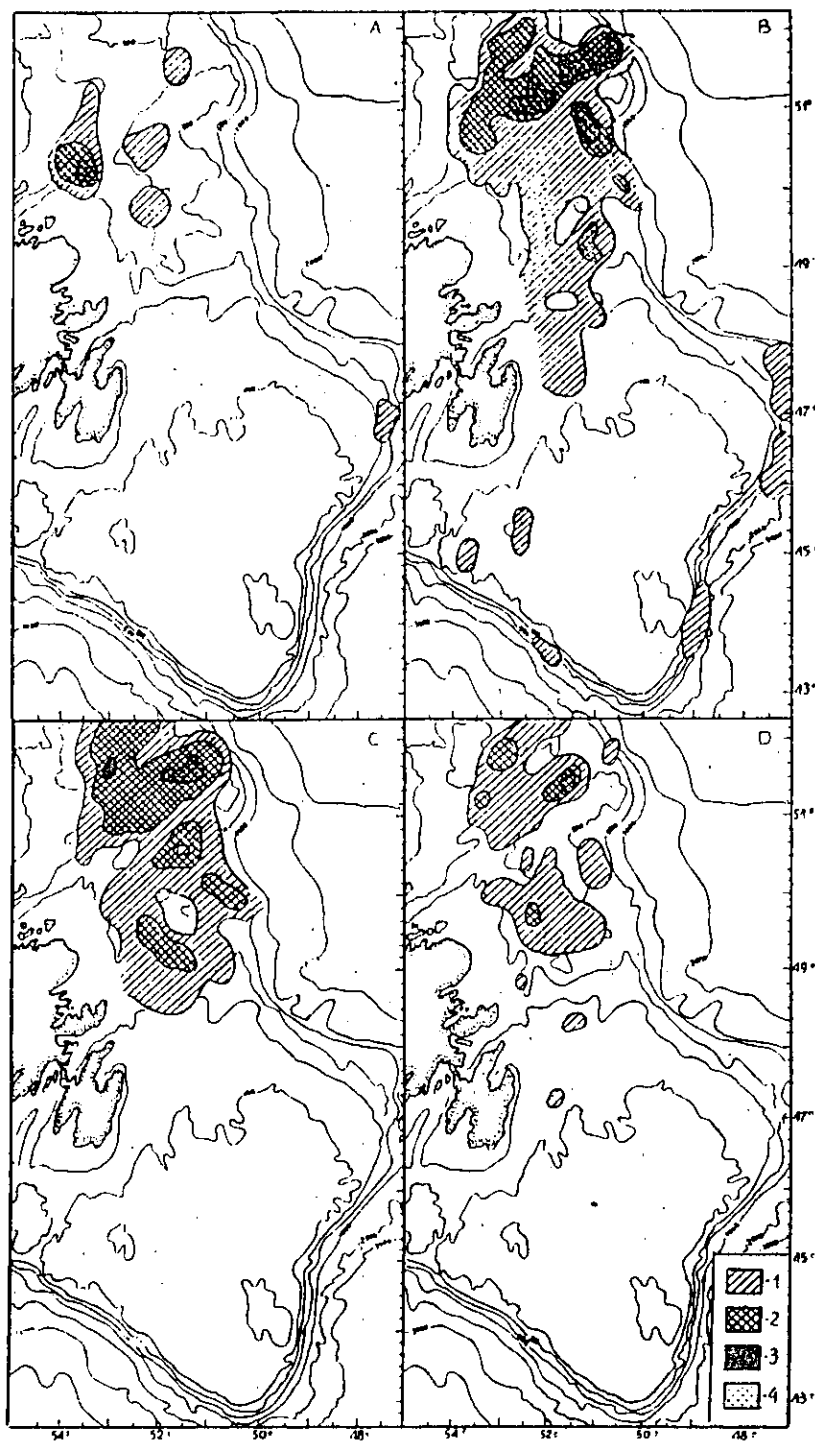


Fig. 6. Main feeding grounds where cod feed on shrimp: cod younger than 3 (A), age 3-5 (B), age 6-7 (C) and older than 7 (D) by the data from surveys for 1987-1991.
1 - frequency of shrimp occurrence in cod food - 10-25%, 2 - 26-50%
3 - 51-75%, 4 - areas, where cod feeding on shrimp were registered annually.

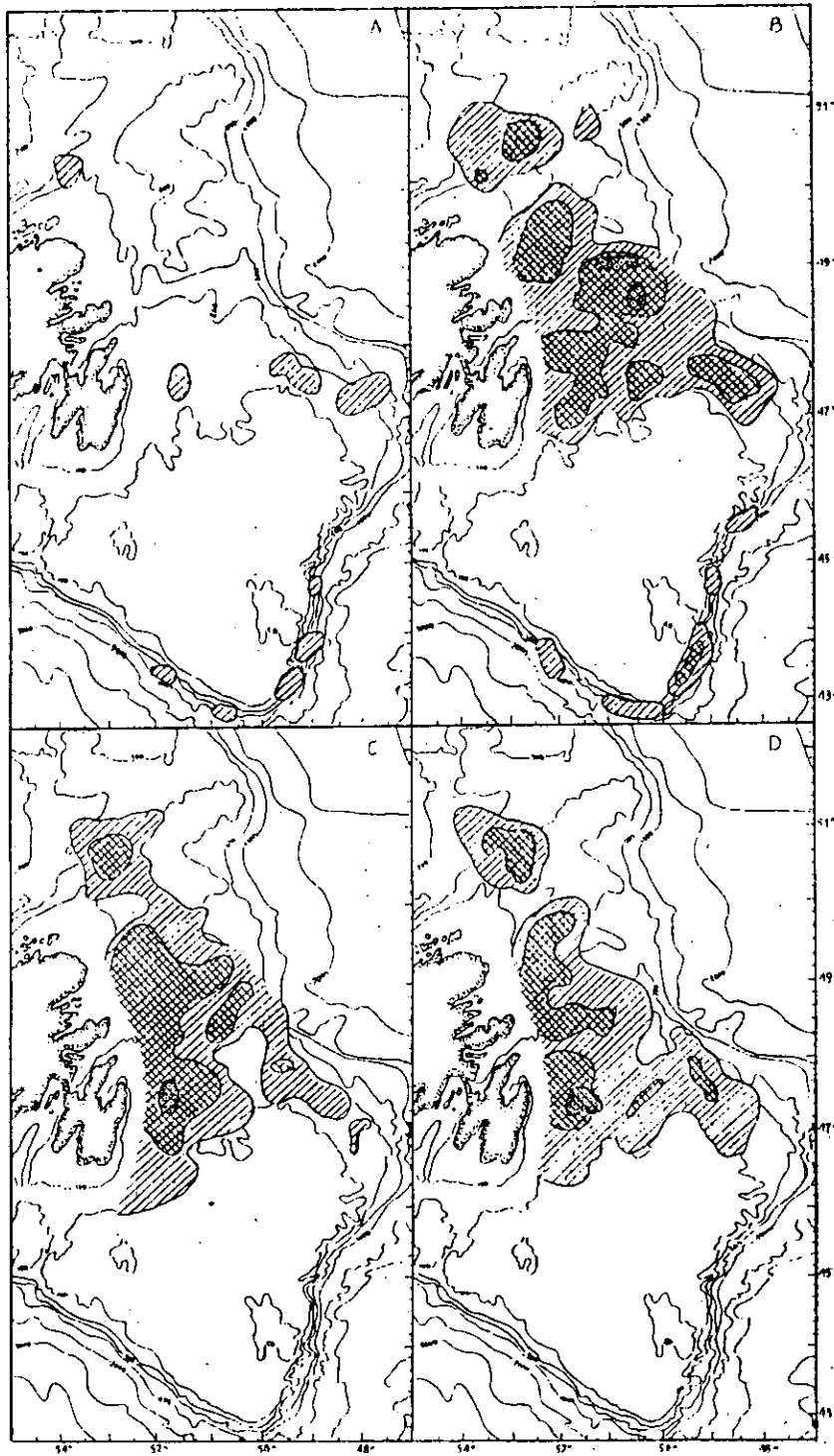


Fig. 7. Main feeding grounds where cod feed on capelin.
See Fig. 6 legend.

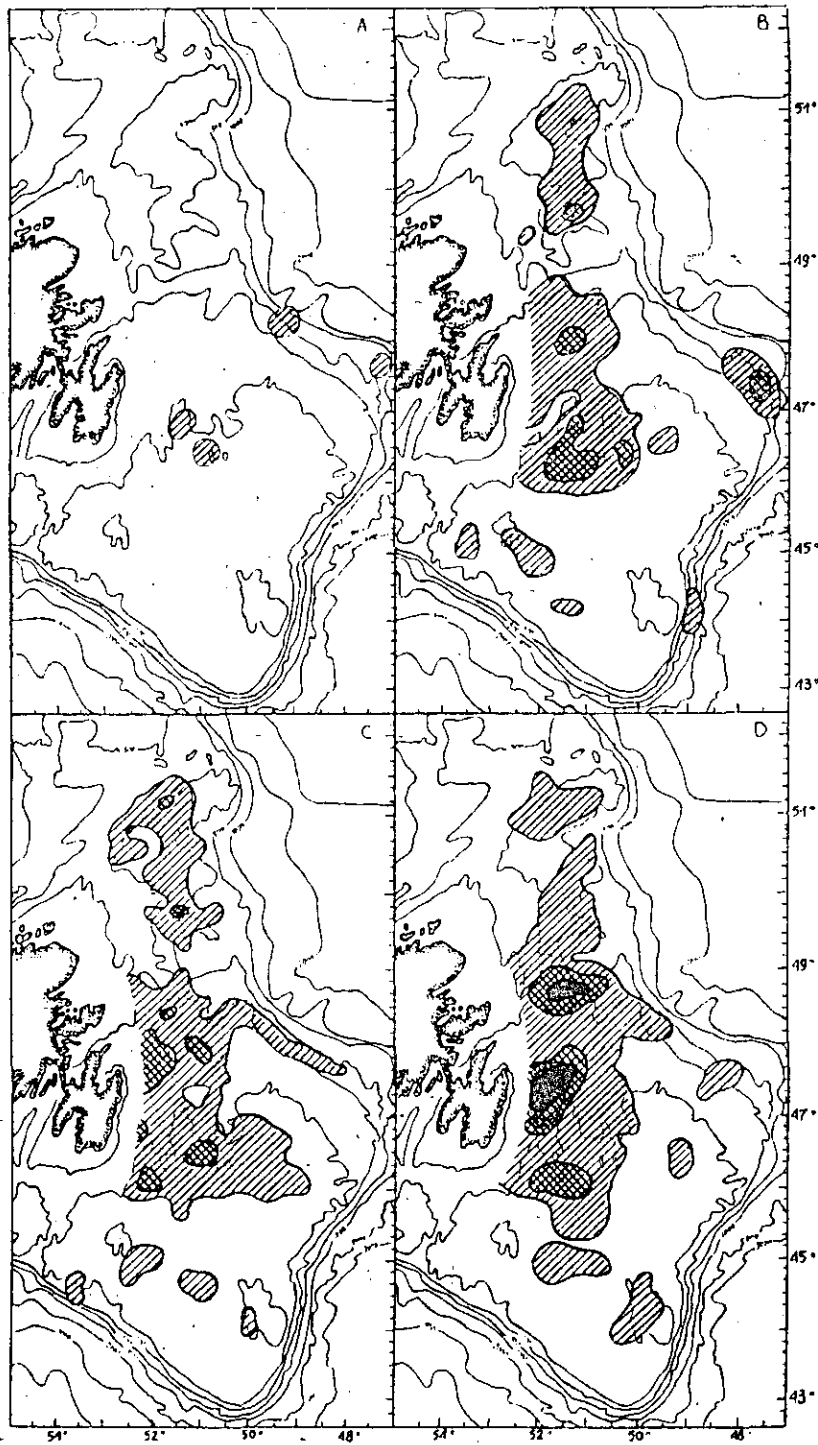


Fig. 8. Main feeding grounds where cod feed on crabs.
See Fig. 6 legend.

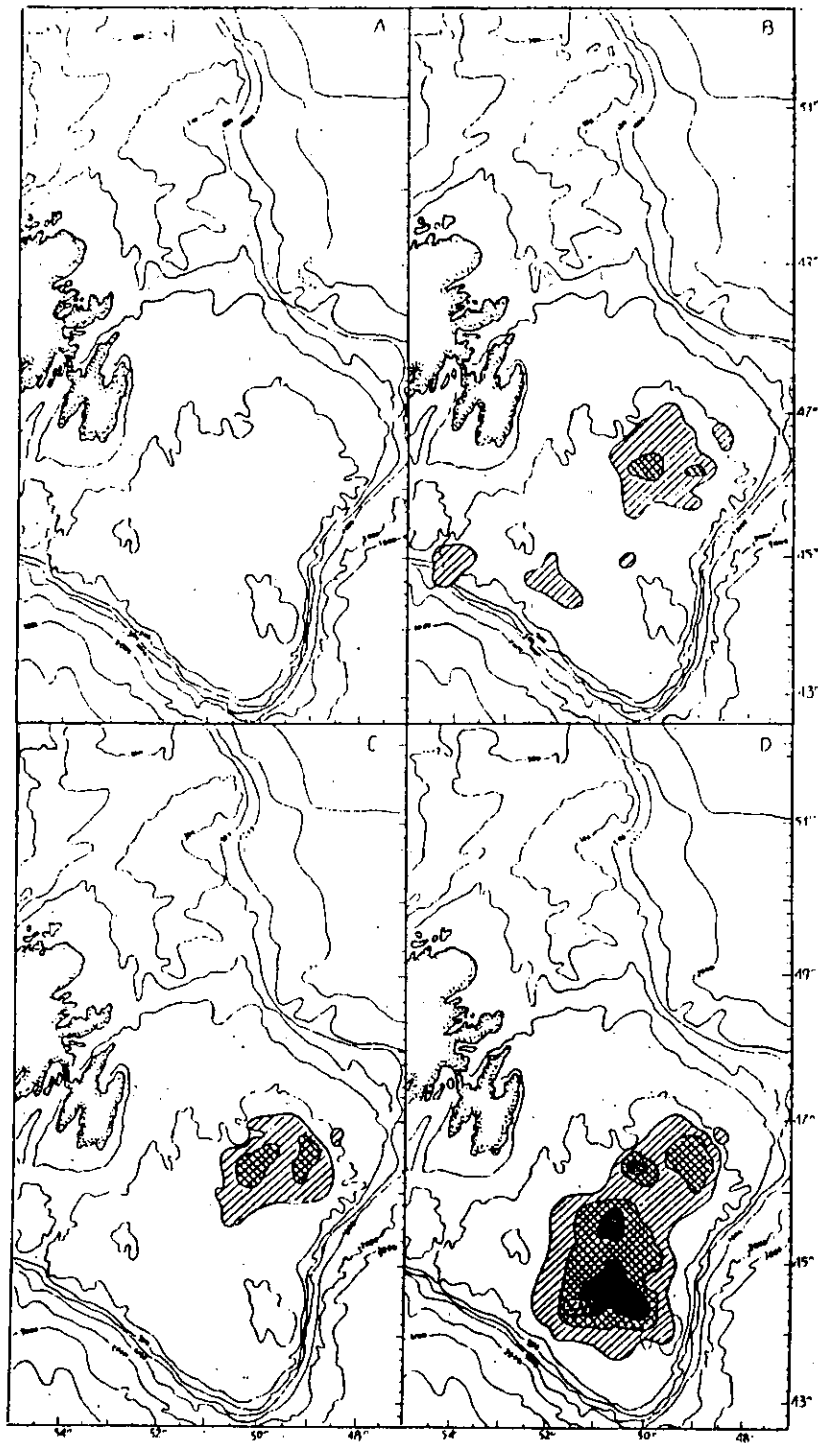


Fig. 9. Main feeding grounds where cod feed on sand eel.
See Fig. 6 legend.

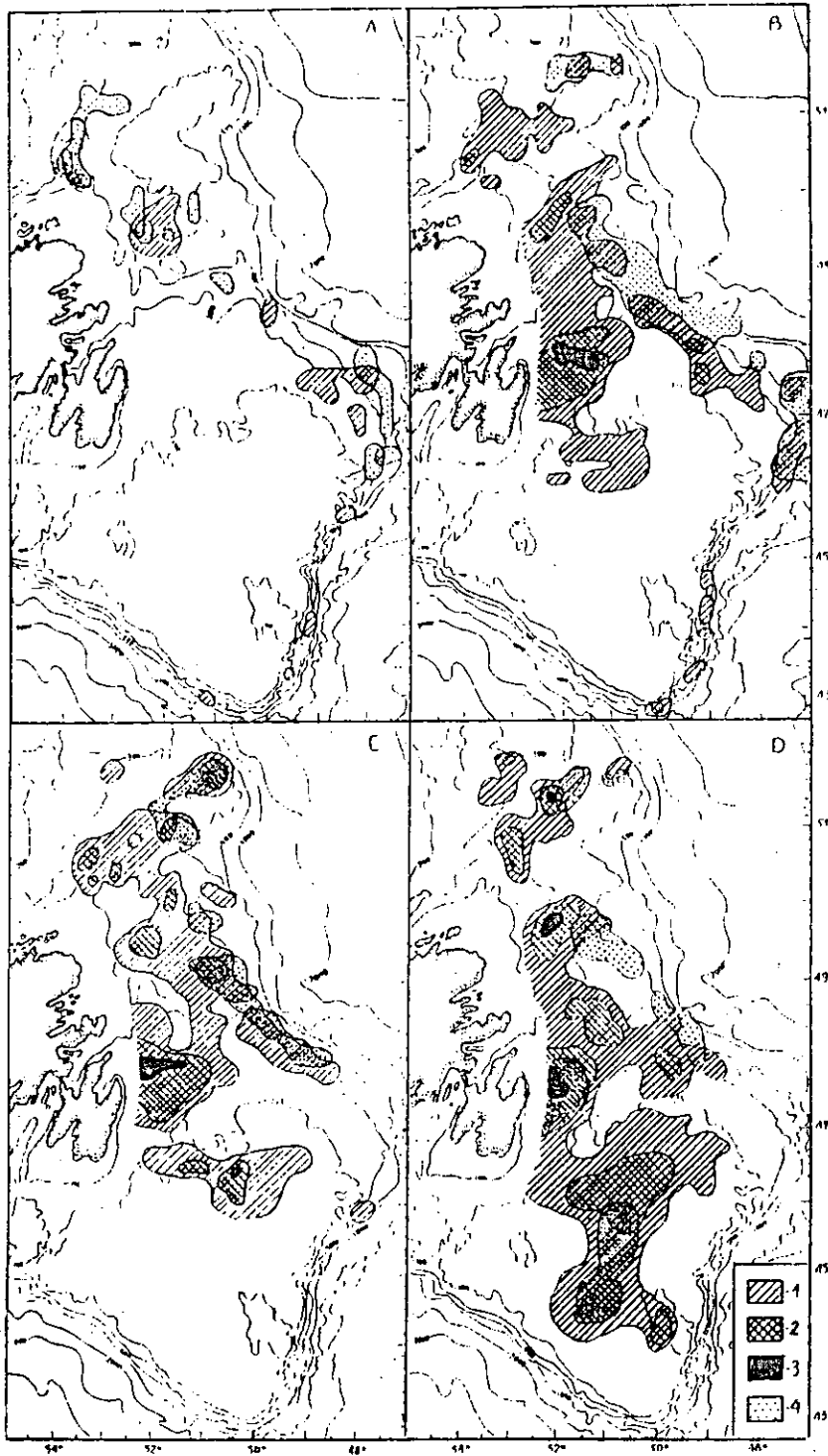


Fig. 10. Areas of intensive feeding of cod at age younger than 3 (A), age 3-5 (B), age 6-7 (C) and older than 7 (D) on the Newfoundland shelf in spring-summer season by the data from surveys for 1987-1991. 1-stomach fullness above 1 degree; 2-above 2 degrees; 3-above 3 degrees; 4-areas where cod at certain age occurred annually.

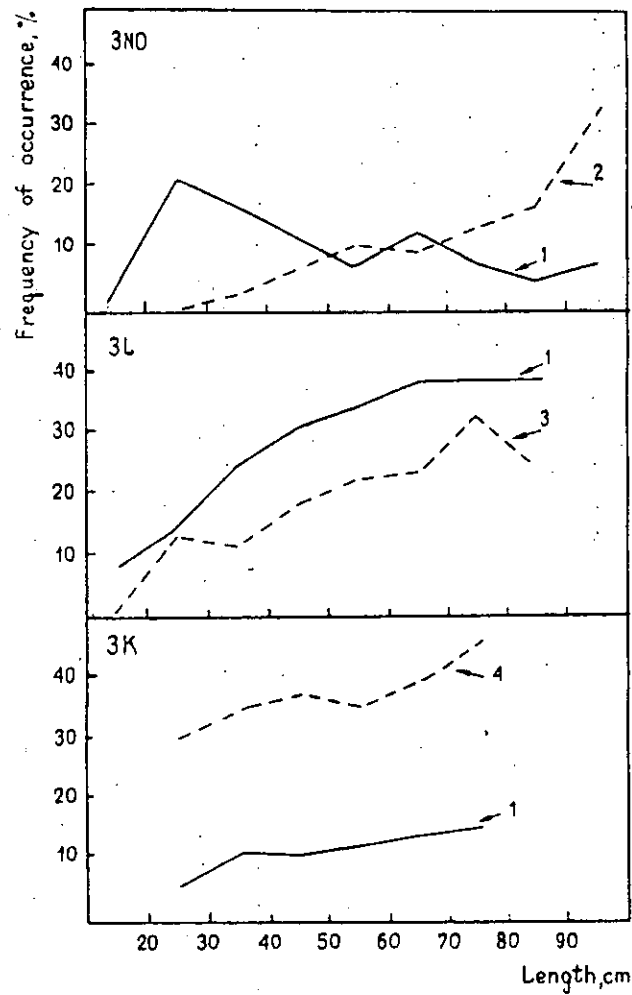


Fig. 11. Frequency of capelin (1), sand eel (2), crabs (3) and shrimp (4) occurrence in food of cod from different size groups (by the data from surveys in 1987-1991.