YEAR-TO-YEAR DYNAMICS OF TROPHIC LINKS OF THE MAIN COMMERCIAL FISHES IN THE BARENTS SEA AS INDICATING THE STATE OF ECOSYSTEM

by

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Functioning of the Barents Sea ecosystem is based on the energy transfer in the phytoplankton-zooplankton-pelagic fishes-cod trophic chain. Cod has a broad diet, feeding both on pelagic fishes – capelin, herring, polar cod, as well as seasonal concentrations of juvenile fish, shrimp, euphausiids and hyperiids. By feeding also on benthos (worms, mollusks, echinoderms, bottom amphipods) and other demersal animals including non-commercial fish species, cod is able to exploit a wide variety of the sea's food supply. However, cod predation has a great effect on commercial fish stocks. Abrupt fluctuations in cod food supply have large impact on its feeding behavior and the character of its migrations. Also, prey distribution influences the cod feeding cycle. The cod prey species and groups represent different geographic complexes; therefore, climatic fluctuations influence prey species abundance, distribution, and interactions. The interplay between climate, prey abundance and distribution, and interactions among prey species can be illustrated by the year-to-year dynamics of the historically observed cod feeding. In the end of the cold period in the 1920s, a high consumption of the polar cod was registered (Zenkevich and Brotskaya, 1931). This was connected to a very wide distribution of polar cod. However, in the cold 1960-1970s, due to the stock depression of polar cod (Shleinik, 1973), the polar cod almost completely disappeared from the cods diet. In the warm 1930s, "herring" and "capelin" years were alternating in cod diet (Zatsepin and Petrova, 1939), caused by year class variations and interactions between capelin and herring. Later, when a cold period (the 1960s) coincided with over-fishing of herring, the latter one was replaced by capelin (Ponomarenko and Yaragina, 1985) in the cods diet. In the cold years (the late 1970s-early 1980s), intensive feeding on capelin by cod accompanied by a reduced eastward migration by cod was recorded (Yaragina, 1984). Some of these particularities in cod feeding linked to climatic and hydrographic conditions and the prevalence of typical species (polar cod in the 1920s, herring – in the 1930s) have not been observed later.

When stocks of plankton-eating fish fluctuated, plankton food resources were redistributed between the different predator species. For instance, there was a recorded deficiency of euphausiids in the southern Barents Sea in the early 1950s owing to a considerable increase in the abundance of the main plankton consumers – capelin and cod, as well as the appearance of strong year-classes of herring (Shutova-Korzh, 1960). This deficiency was accompanied by cod starvation during several summer seasons (Grinkevich, 1957). Also there were alternating consumption of capelin and euphausiids by cod according to fluctuations in capelin abundance (Ponomarenko and Yaragina, 1990), and strengthening of food competition between capelin and polar cod for copepods and euphausiids in the northern Barents Sea in the early 1980s (Panasenko, 1990).

The trophic links abruptly changed in the middle of the 1980s, during the catastrophic depletion of the capelin stock coinciding with the increase in the cod stock owing to recruitment of cod from the strong 1983 year-class. Since that period, the cod food supply has been fluctuating, and these fluctuations have been intensified by climatic fluctuations and have led to irregularity in the traditional trophic links.

In this paper we will consider trophic in the Barents Sea by summarizing main findings from Russian studies on cod and capelin diet, condition and distribution, in relation to year-to-year variation in climate and prey abundance and distribution, with particular emphasis on the period from the late 1970s until present.

Material and methods

We used data obtained in the Bear Island-Spitsbergen area (ICES Subdivision IIb) (data from PINRO, literature and archive). These data include cod stomach content from 1984-2004 processed by quantity-weight (47384 ind.) and qualitative (over 400.000 ind.) methods. Capelin data (1979-1980) included 850 stomachs processed by quantity-weight methods and 4400 – by qualitative methods. Percentage by mass (m) (% of the stomach contents mass) and frequency of occurrence (f) (% of feeding fish) were used as feeding indices. Stomach fullness was visually determined using a five-point scale: 0, empty; 1, low fullness; 2, mean fullness; 3, full stomach; and 4, full stomach with walls stretched by food. An index of fullness was calculated as the stomach contents mass divided to the fish mass and multiplied by 10 000. Fish fatness was estimated by standard methods: of cod – by relative weight of liver, of capelin – by fat content in muscles (Lazarevsky, 1955). Distribution of cod and capelin aggregations was analyzed according to the distribution of catch data in the fishery areas. Long-term data were mainly used to estimate stock and distribution of the euphausiids in the Barents Sea (Anon., 1988; Anon., 1996).

Results and discussion

During the last twenty-thirty years significant fluctuations of the pelagic fish stocks were registered in the Barents Sea. Fluctuations were most typical for capelin, which, being the object of fishery, simultaneously served as the main food item for cod and other animals. Therefore, the capelin stock status was more often than other pelagic fish stocks, characterized by negative tendencies. The typical feature was alternating periods of a short-term recovery and a new reduction in the capelin stock (Fig.1). Accordingly, a relative index of cod food supply (the number of capelin per cod) reached 2.500-3.400 in the late 1970s – early 1980s, then significantly fluctuated till 1999 and only rose in periods of short-term capelin stock recovery (Fig.2). The minimal supply of cod by capelin was registered in 1995 (14 capelin per cod). Under those conditions, accessibility of food items for cod became deciding for its condition and migrations. Under periods of capelin deficiency, cod started migrating to the north-west (the Bear Island-Spitsbergen area) more regularly. We shall consider in detail trophic relations of cod and capelin in this area in the previous years and at present.

The cold years: 1976-1982

Despite a high extent of feeding area overlap between cod and capelin, there are certain limits to capelin accessibility for cod connected with temperature conditions. The supply and distribution of food for capelin is also of great importance for cod distribution.

Capelin feeding in the northwestern Barents Sea is related to the start of the season when copepod plankton is forming maximal biomasses. Capelin feeding is also dependent on the distribution of macroplankton. Transported and local species of euphausiids, forming maximal concentrations in the shallows, play an important role in capelin feeding at the beginning of summer, when the processes of plankton reproduction only begin. In some years feeding on euphausiids start already in June-July.

In the cold period (1976-1982), with a north and northeastern distribution of capelin (Røttingen and Dommasnes, 1985), and a favorable state of the capelin population, the food supply for capelin was at a high level. The good food supply was connected to a high density of euphausiids in these years due to combined concentrations of warm and coldwater species (Anon., 1988), low abundance of cod juveniles (the main capelin food competitor) and the existence of older capelin (Ushakov, 2000) which are able to reach the northern borders of feeding area early and use food resources of the arctic fauna. In most cases, the intensive consumption of euphausiids started in early August and was limited to the southern areas. In September-October, the area with capelin feeding on euphausiids widened northward to 76-77ºN, where euphausiids were consumed together with copepods. The copepods, though predominating by frequency of occurrence in capelin stomachs, had lower weight percent in the stomachs than euphausiids. In anomalous cold 1979, feeding on euphausiids was most prolonged in the Hopen Area (Fig.3). To the north of 77ºN, capelin did not feed on euphausiids, but consumed mainly copepods. In moderate 1980, in August-September, capelin having migrated northward to 77-78ºN, fed on euphausiids in the large area from the South Cape Deep to the Perseus Elevation (Fig.4). In 1980, weight percentage of euphausiids in capelin stomachs was very high: 58% in August, 62-96% in September-October, and 89% in November.

In the late 1970s capelin was characterized by a high level of fatness. In 1979, capelin mean fatness reached 12.9% in August, 18.1% in September and 16.7 % in October. This led to mass maturation of capelin (Oganesyan and Dvinin, 1988). In 1980, when the consumption of euphausiids by capelin was highest, capelin growth was the highest too (Gjøsæter, 1985). Capelin year class strength was moderate (1978, 1979) to strong (1976, 1977, 1980) (Anon., 1991). The capelin stock was heavily exploited despite that the stock was reduced already in 1981, owing to a decrease in the spawning stock, a decrease that continued and was particularly strong in 1983-1985 (Ushakov, 2000).

In those years (1976-1982), cod distribution did only to a minor extent overlap with capelin. Taking into consideration that small cod concentrations overlapped with capelin feeding on euphausiids to the north of 76ºN, in both anomalous cold (1979) and normal (1980) years (Fig.5, 6), one could assume that the lack of overlap of main aggregations of capelin and cod was not only caused by the limiting effect of low temperature on cod distribution. Probably another factor was more important, namely that there was a large supply of capelin in the western areas that favored that cod stayed there. It is also known, in that period, that cod had no feeding migrations eastwards. Due to intensive feeding on capelin, cod was characterized by a high fatness – 8-9% (Yaragina, 1984).

General warming with short-term periods of cooling: mid 1980s to late 1990s

With warming of the Barents Sea (the 1980s) and the change of capelin distribution (more south- and westwards) (Røttingen and Dommasnes, 1985) that coincided with the reduction in capelin stock size, cod started moving to the north more actively. Later, capelin stock variations, which, in their turn, were the reasons of the outbursts and drops of euphausiid abundance, had a great influence on the character of cod migrations, together the temperature conditions. In this warm period, the appearance of strong year-classes of cod and haddock was also observed. Thus, the total predation pressure on euphausiids became larger. As a result, in some periods, euphausiid concentrations were sharply reduced in the northwest and copepods started to dominate in capelin feeding.

In the periods of general warming in the Barents Sea, there were some well-pronounced periods of short-term cooling. These periods were radically different than the cold 1970s due to the sharp reductions in capelin abundance. First of all, the abundance of euphausiids increased, approaching the long-term mean in 1986-1988 in northwestern areas and exceeding it by 1.5-2 times in 1996 and 1998 (Anon., 1996). The outbreak of hyperiids abundance (consumers of *Calanus* and occupying the capelin food niche) was even more sudden and further enlarged the food supply of all the fishes (Orlova et al., 2003).

With the unstable supply of main prey species, the role of alternative prey became more important for cod. In the coldest years (1986-1987), when cod distribution was extremely westerly, cod fed on deepwater redfish, hyperiids, polar cod, non-commercial fishes, benthos, as well as shrimp. In less cold years (1996-1997), cod distribution was more southward. In 1996, cod consumed euphausiids from April to July. In the second half of the year cod started to feed intensively on hyperiids at the Perseus Elevation (Fig.7); making up more than 70% by weight in the diet of cod (Orlova et al., 2003) in the III-IV quarters. Despite a small increase in capelin abundance in those years, capelin constituted only 4-8% by weight of cods diet (Table 1). Only in 1998, when cod schools reached 77º30'N (Fig.8), and partly overlapped with feeding capelin aggregations, the percentage of capelin in cod diet rose to 15% by weight. That year, the percentage of shrimp was also high (more than 18% by weight).

In this period, generally warm and with capelin and euphausiids stocks fluctuations, cod migration behavior was not only determined by the environmental conditions and capelin supply, but also by an increase in cod abundance and a increase in percentage of elder fish in the population (Yaragina et al., 1996). The data for 1990-1992 are the most interesting. In those years cod was characterized by a northerly distribution. In the Hopen Area and the Perseus Elevation, large fish reached 78ºN-78º30'N. There, feeding areas of cod and capelin overlapped (Fig.9) leading to a high consumption level of the latter (36% by weight).

Cod fed regularly on shrimp similar to in the cold years (the 1970s). The consumption of shrimps usually was higher in the first half of the year, when capelin consumption was relatively poor (1990, 1992) or capelin was absent in the cod diet (1995). In 1995, the maximum frequency of shrimp occurrence (from 50 to 95%) was registered in the first half of the year, leading to more than 60% by weight (Orlova et al., 2003). The area of cod feeding on shrimps was, mainly, limited to western areas (Fig. 10) and, as shrimp was the main food item, when the local shrimp stock decreased after cod predation, large concentrations of cod migrated from area to area. Cod fed on shrimps in the Western Deep, on the slopes of the Bear Island and in the Hopen Area (April-June 1995) for the longest period. Later, in the year cod consumed shrimp regularly, but in smaller amounts, and euphausiids (August-September, November 1995), hyperiids (September-November 1995), and other invertebrates was important in cods diet this year. The weight percentage of shrimp in the cods diet made up over 11% in 1995 (Table 1).

Polar cod consumption by cod should be considered since the polar cod has a special importance in the annual life cycle of cod. Usually, consumption of polar cod by cod is connected with the final stage of cod feeding when water temperature decreases, and when cod growth finishes and the process of intensive accumulation of fat starts. Long-term data show large variability in the role of polar cod in cod feeding (Orlova, Oganin and Tereshchenko, 2001). In the second half of the 1990s, the consumption of polar cod by cod rose. This was caused by the reduction in capelin abundance and cooling of the Barents Sea. The consumption of juvenile polar cod by cod did not exceed 1-2% by weight, and for adult polar cod, it amounted to 14%. In the northwest, where cod fed on adult polar cod from the "western" component, the portion of the latter by weight reached 8% (Orlova et al., 2003).

The present: 1999-2004

The period from 1999 to 2004 was characterized by considerable reconstructions of the ecosystem structure of the Barents Sea. This was connected with stable warming and small increase in the stock size of most commercial species (Fig.1). The increase in capelin stock size was especially significant due to the appearance of strong year-classes in 1997-1999 and closed fishery in those years that led to an increase in percentage of older fish in the stock. In 2002-2003, capelin were distributed in the northern areas including the area of Frantz Josef Land, where capelin already in September fed on Atlantic and arctic species of copepods, euphausiids and hyperiids. Capelin reached a high fatness comparable to the one in the 1970s. However, in the following period, the stock was reduced again and, in 2004, it was 6 times lower compared to the maximum value in 2000 and 2001. In 1999-2004, the polar cod stock size also increased and the portion of mature fish in the population rose. This lead to an increase in the area of polar cod distribution. At the same time, in the Barents Sea, the immature herring abundance increased due to the appearance of moderate and strong year-classes (Krysov, 2002). Besides the Barents Sea traditional species, mass migration of blue whiting from the Norwegian Sea was observed. This was caused by the growth of its abundance owing to the appearance of strong 1999-2000 year-classes (Belikov et al., 2004).

In the considered years (1999-2004), euphausiids abundance was high despite an increase in plankton eater abundance due to the increase in warm-water species, especially *Meganyctiphanes norvegica* transported from the Norwegian Sea (Drobysheva et al., 2003).

On that background, new predator-prey interactions were formed. However, the main factor influencing fish feeding conditions, as before, was the abundance of the main prey species. The role of hydrographic conditions influencing overlap between predators and their potential preys was even more important than before.

The most favorable conditions for cod-feeding on capelin were in 1999-2002. In 1999, cod fed on capelin already in the cod wintering grounds in northwest. In that year, intensive capelin feeding was recorded from May-June to October (Fig.11), where capelin frequency of occurrence reached 65-90%. As a result, this year the maximum annual value of capelin in cod feeding was observed out of the years 1984-2004 – about 60% by weight (Table 1). In 2000, when the capelin stocks was at its maximum (over 4 x 10^6t), cod started feeding on capelin early (in February), however, the main consumption took place later (July-October), with a maximum level of feeding in the Hopen Area and the Perseus Elevation. Shorter feeding period of capelin compared to the previous year, led to lower level of consumption (about 19% by weight). In the other years (2001-2002), variation in accessibility of capelin and duration of capelin consumption in some areas caused fluctuations in capelin consumption (19-31% by weight, Table 1).

Despite the reduction in capelin abundance, the biomass of capelin consumed by cod was extremely high, amounting to 1.43-2.38 x 10^6t and remaining to be at the high level in 2003 and 2004 (Fig.12). Those values significantly exceeded the capelin catch (14 times in 1999, the other years, 3-4 times).

The area of polar cod feeding by cod expanded and extended from West Spitsbergen to the Perseus Elevation and Frantz Josef Land (Fig.13). Polar cod made up 6-18% by weight in northern areas, this was higher than in the southern part of the sea, where juvenile polar cod were consumed. In 2004, when capelin abundance decreased, in some areas (Perseus Elevations, Zuidkap Deep, Western Spitsbergen) polar cod practically substituted capelin in the diet of cod or was consumed by cod at the same level as capelin. That caused food competition strengthening between capelin and polar cod for food resources.

A wide distribution of blue whiting in the Barents Sea led to an increase in food competition between blue whiting and cod. In the Bear Island-Spitsbergen area, large blue whiting fed on capelin, polar cod and juvenile cod (these prey species amounted to 25-65% by weight in October-December 2003), as well as on euphausiids and hyperiids (Belikov, Sokolov and Dolgov, 2004). Fish were mostly consumed by blue whiting in West Spitsbergen, Bear Island Bank, and South Cape Deep, in areas with concentrations of feeding cod.

The blue whiting itself also started to occur more often in the cod diet. The widest distribution of blue whiting consumption by cod was recorded in 2002 (Fig.14), corresponding to the maximal biomass of blue whiting in the Bear Island-Spitsbergen area (around 145 x 10^3t). As a result, blue whiting made up about 10% by weight in the annual diet of cod, in the other years, it varied from 3% to 14% (Table 1).

Herring was not important in cod feeding in the Bear Island-Spitsbergen area. However, due to the shift of cod wintering borders eastwards, cod influence on concentrations of herring wintering in the central, coastal southeastern and even eastern areas strengthened. Mostly, it showed itself in 2003, when a high level of herring consumption was recorded from January to July, and then it was resumed in September (Fig.15). However, in that year, the portion of herring in the annual diet of cod did not exceed 9% by weight (Table 1).

Cod fatness changed according to the seasonal succession and the intensity of consumption of capelin and other important prey species. The prey species differ in accessibility and calorie content; capelin has high calorie content (2 kcal/g in raw weight), while the other abundant prey species (microplankton crustaceans, shrimps, polar cod) hardly reaches1 kcal/g. According to the significance of capelin in annual dynamics of cod feeding, the years from 1984 to 2004 can be grouped into two groups, characterized by the level and seasonal variations in cod fatness. The first group included the years with capelin percentage by weight of 15% and more in the cods diet (1984, 1990-1992, 1998-2000). In most cases, after a small reduction in fatness in May-July, an abrupt rise (to 8-9%) was registered in August-October and the level was high until December (Fig.15). The second group involved the years with percentage of capelin of less than 15% (1986-1988, 1993-1997).

In 2001-2003, with low level of capelin consumption, cod fatness was corresponding to that one of the second group of years. In January-July 2003, cod fatness value did not exceed 4-6% and, in August-September, it was reduced to 4-5%. Only in September, in the areas where cod fed on capelin, fatness steadily increased to 7-7.8%.

In 2004, cod from the Hopen Area had higher fatness even in December.

Conclusions

Structural changes in pelagic (plankton, nekton) communities of the Barents Sea and the interactions of the main commercial fish species caused different efficiency of the Barents Sea ecosystem functioning. From time to time, fishery made a significant contribution to the trophodynamics that, on the background of climatic variations had catastrophic consequences. It is exemplified by the disappearance of the Atlanto-Scandian herring, falling out of the ecosystem and cod diet for a long period (the late 1960s-early 1980s).

In the cold period (mid-1970s-the early 1980s), the conditions were favorable for capelin. Good conditions for feeding, a high rate of growth and reproduction provided a large capelin stock. This had several causes. With high capelin abundance, cod was provided well with capelin and did not make long migrations and was concentrating in the western areas. It resulted in a main separation of the feeding areas of cod and capelin in the northern areas and, respectively, a weak predator pressure by cod on capelin. The lack of the main food competitors of capelin also had a favorable effect on capelin feeding conditions. Fatness of both capelin and cod was high.

Over-fishing of capelin led to a collapse in the mid-1980s. With a low total abundance and an abrupt reduction in the proportion of older fish in the population, capelin did not use the feeding resources in the northern areas. Capelin deficiency, in its turn, conditioned poor feeding of cod and an increase in the consumption of euphausiids and hyperiids, i.e. cod and capelin became food competitors. In this period, where cod fed intensively on macroplankton, the food chain was short, and due to the low calorie content of e crustaceans, feeding on crustaceans could not compensate the cod energy consumption. As a result, cod fatness was low (less than 3%). Only in some periods, when capelin abundance recovered, the ecosystem came to the normal functioning regime (1990-1992) based on the ecologically efficient interactions of the key species: euphausiids (copepods) – capelin – cod.

In the stable warm period (1999-2004), plankton-eater food supply was stabilized because of a higher transport of warm-water euphausiids (and copepods, probably) and their wide distribution in the Barents Sea area. Also, the opportunity for fish using the food resources from the northern areas increased. Plenty of zooplankton favored migration and a wide distribution of blue whiting and polar cod, which increased in abundance in the Barents Sea. At the same time, in some local areas, the feeding areas of capelin and polar cod, as well as cod and blue whiting overlapped leading to the increased food competition being acknowledged in some cases by low fatness of those fish species.

Negative consequences for cod of food competition were compensated by a wide distribution in the warm years and a high accessibility of capelin and polar cod, as well as of herring wintering in the southeast and east. Cod fatness became higher when consuming these species. Blue whiting did not play a significant part in cod feeding, since blue whiting were, mainly, consumed by cod having completed the return from feeding migration, in the west (November-December). Euphausiids were stabilizing as a food supply for the plankton eaters in 1999-2004.

At present, the stock of capelin is close to the new collapse. With a high accessibility of capelin for cod in the warm years 1999-2004, capelin was under a great predation pressure. The impact of predation on the capelin stock was intensified by a fishing pressure that resembled the one in 1993-1995. It was absolutely different from the situation in the 1970s, when the predation pressure was practically absent. Presently, the influence of cod is greater than the fishery effect on capelin.

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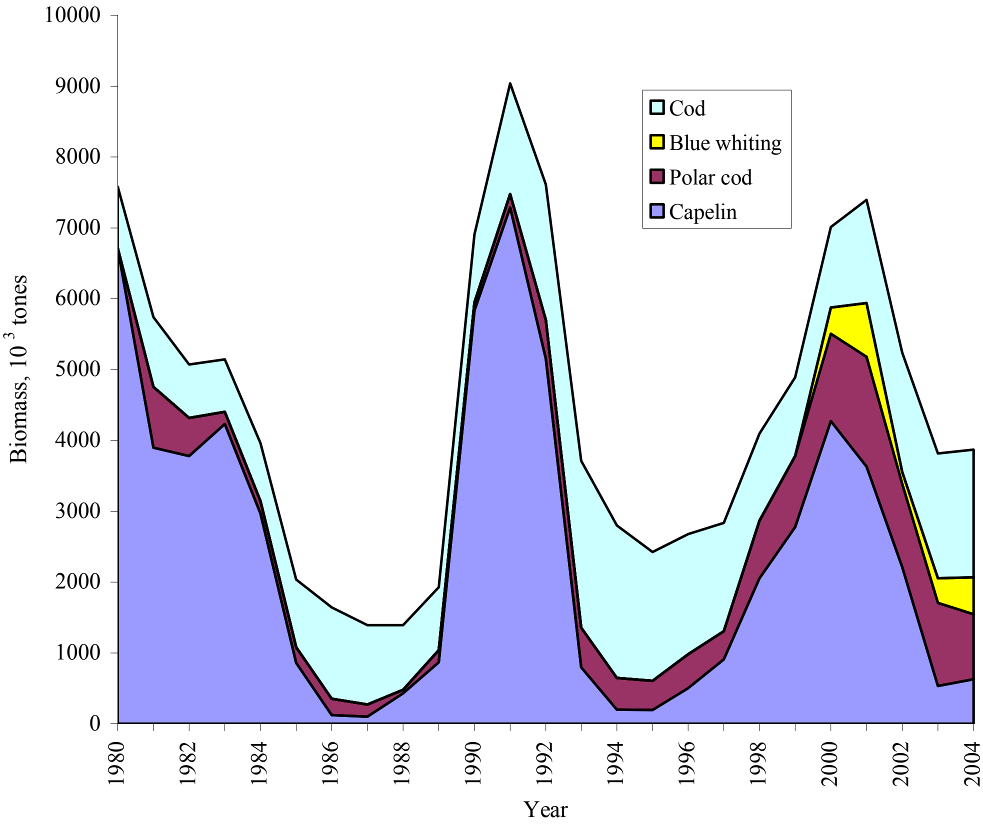

Fig. 1. Stocks dynamics of cod, capelin, polar cod and blue whiting in 1980-2004

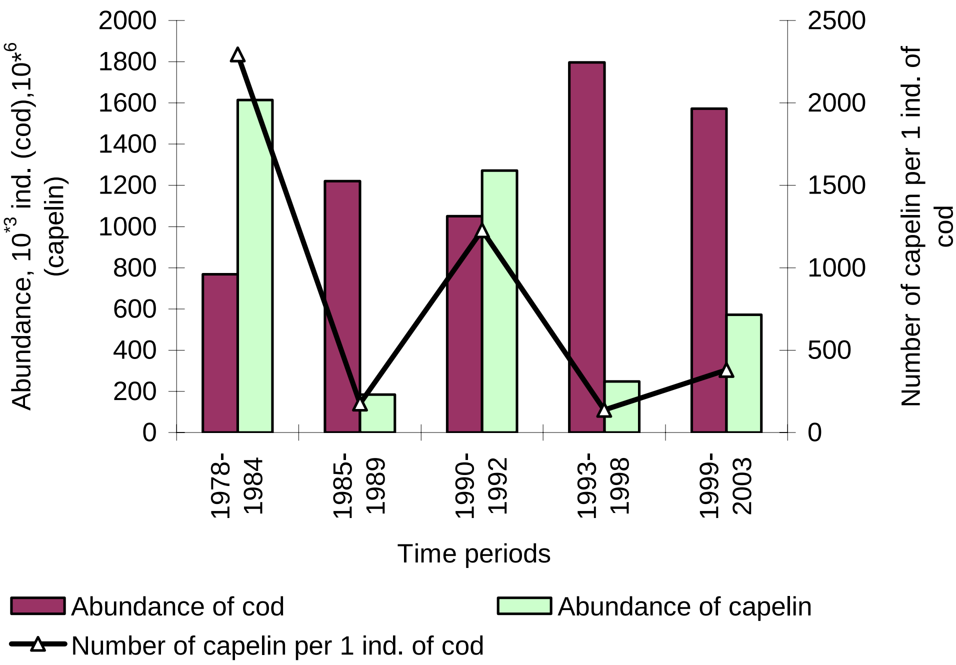

Fig.2. Stock dynamics and cod supply by capelin in the different time periods in 1978-2003

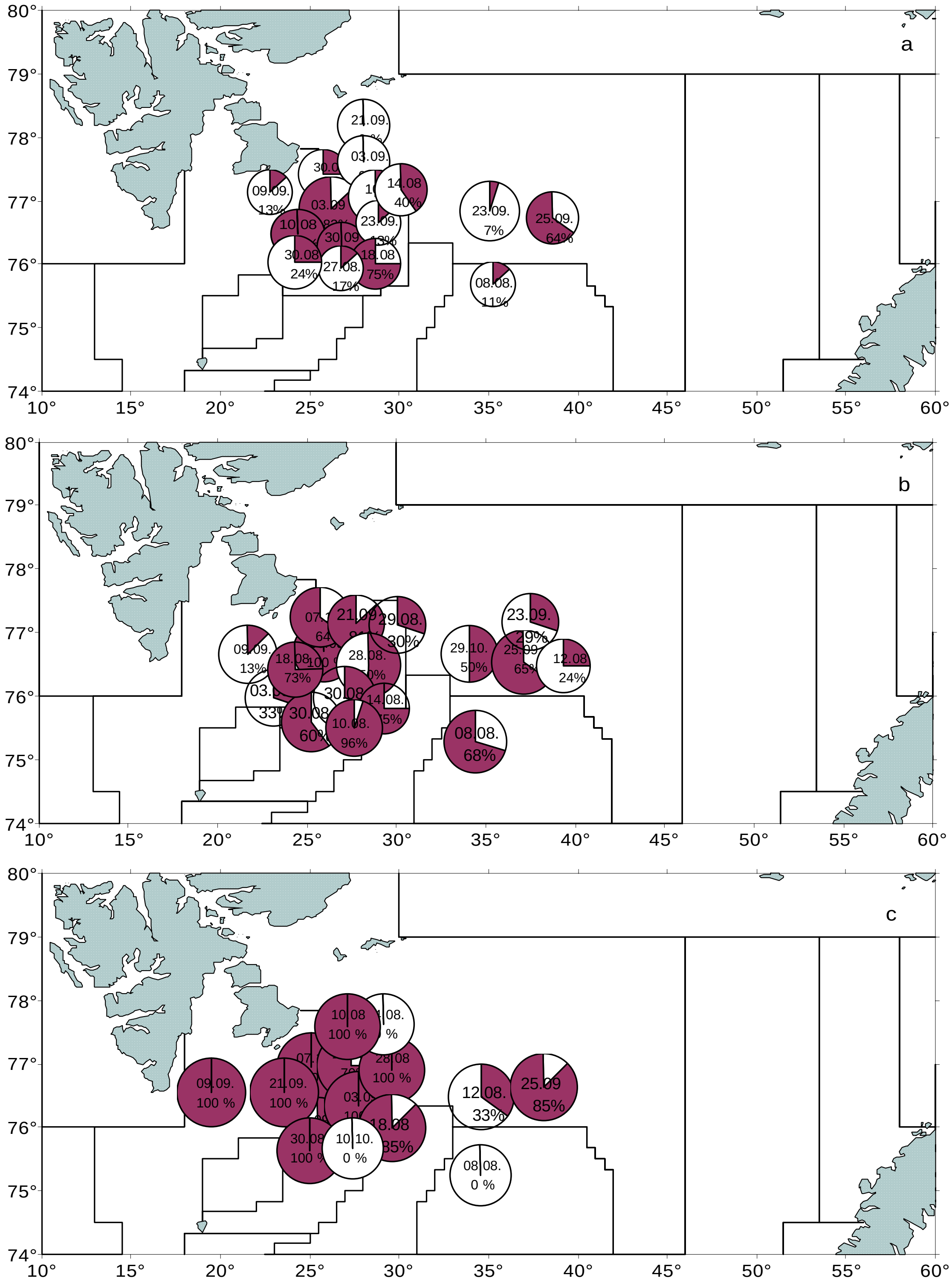

Fig. 3. Frequency of occurrence (%) euphausiids in stomachs of capelin by age 2 (a), 3 (b) и 4 (c) in August-Oktober 1979

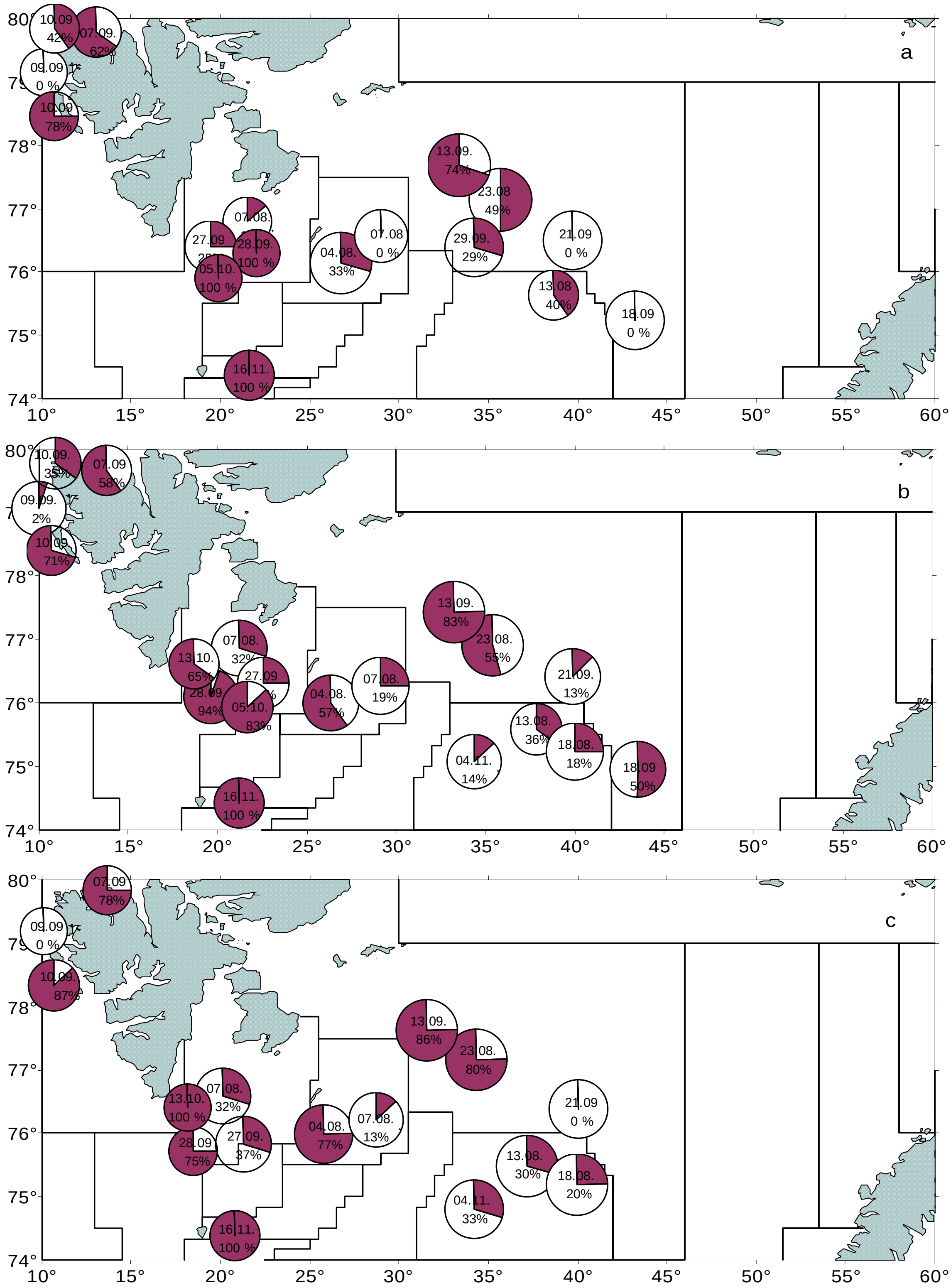

Fig. 4. Frequency of occurrence (%) euphausiids in stomachs of capelin by age 2 (a), 3 (b) и 4 (c) in August-November 1980

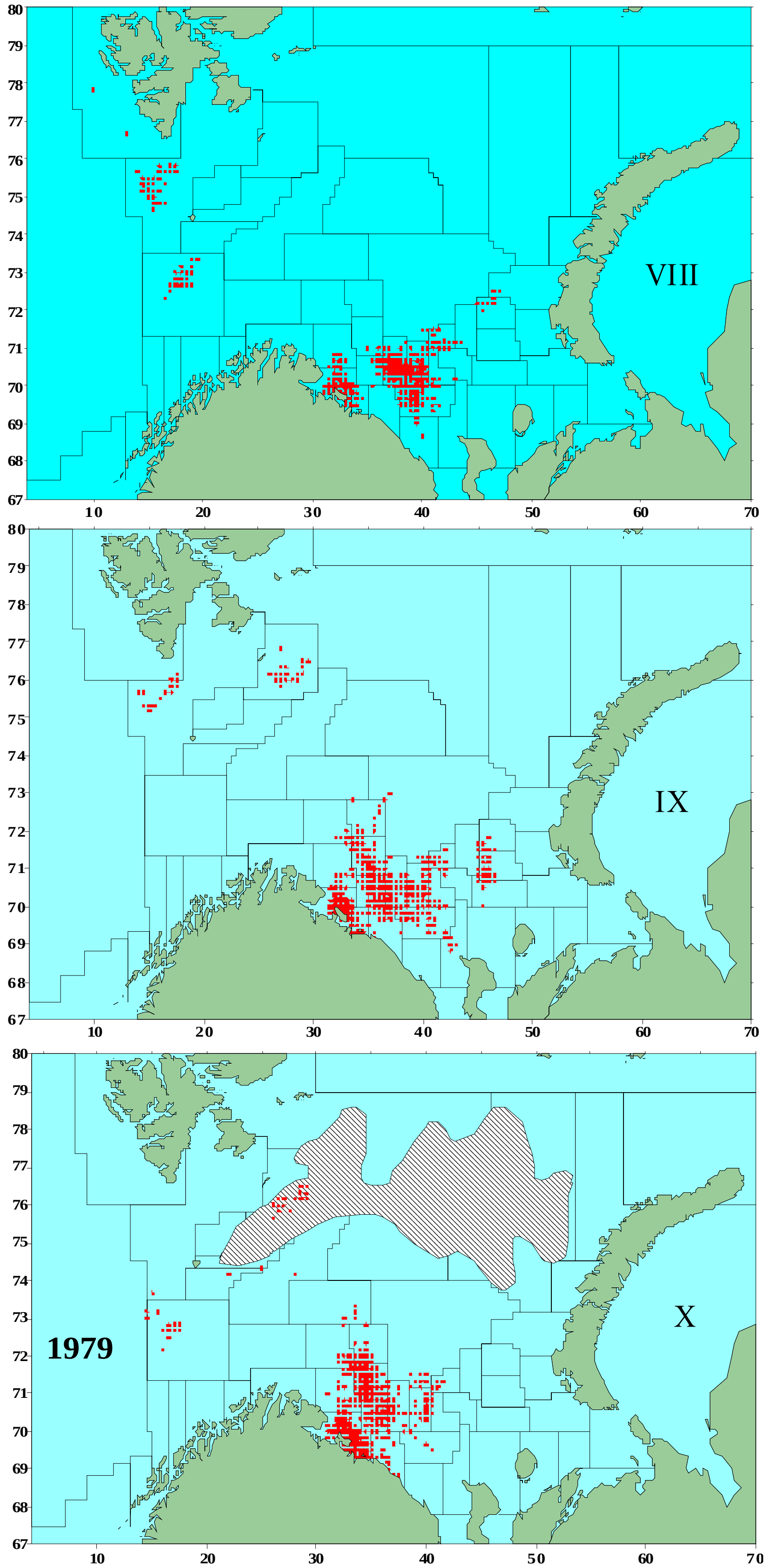

Fig.5. Distribution of cod (red color) and capelin (shading) aggregations in the Barents Sea in 1979

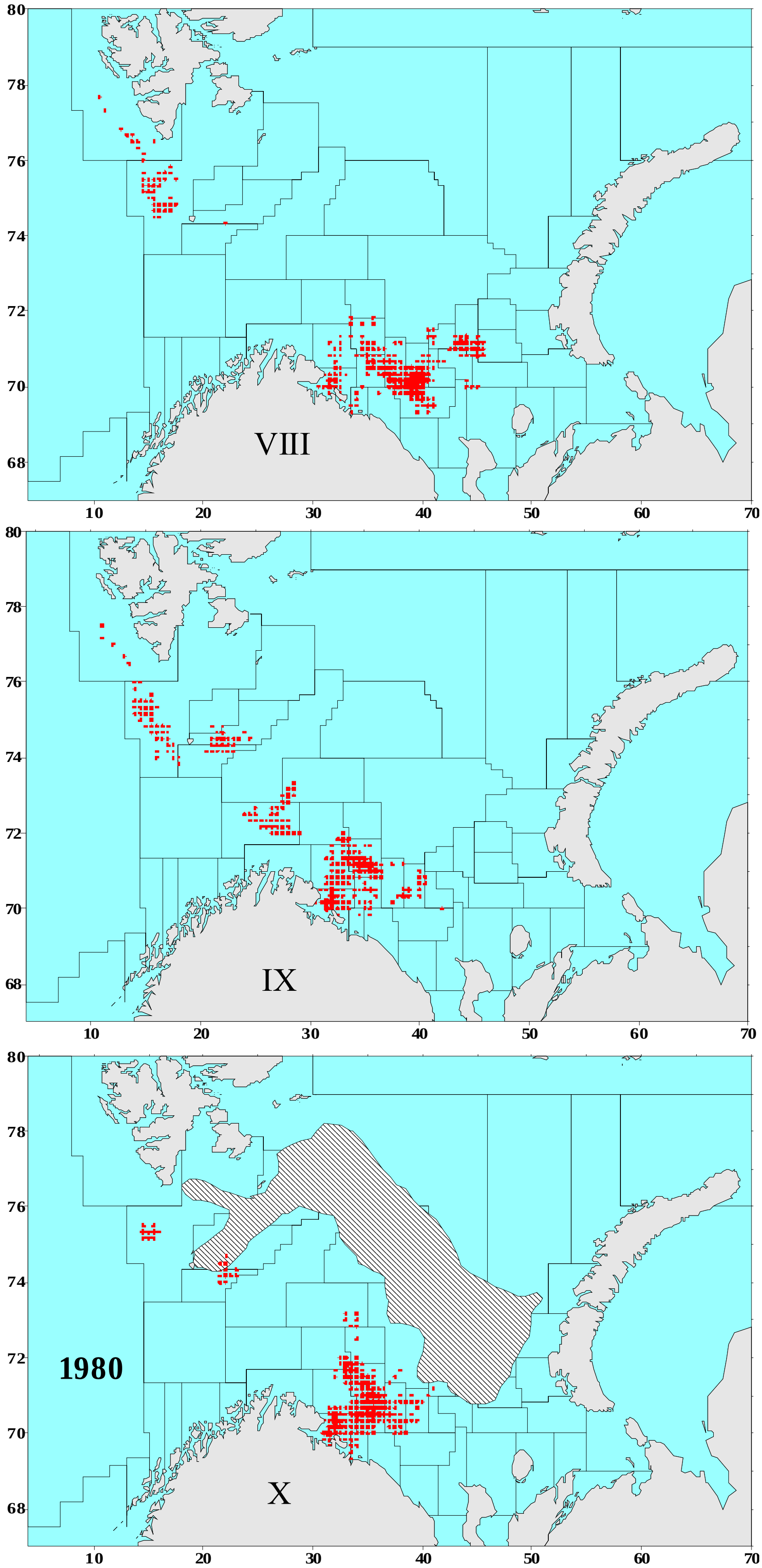

Fig.6. Distribution of cod (red color) and capelin (shading) in the Barents Sea in 1980

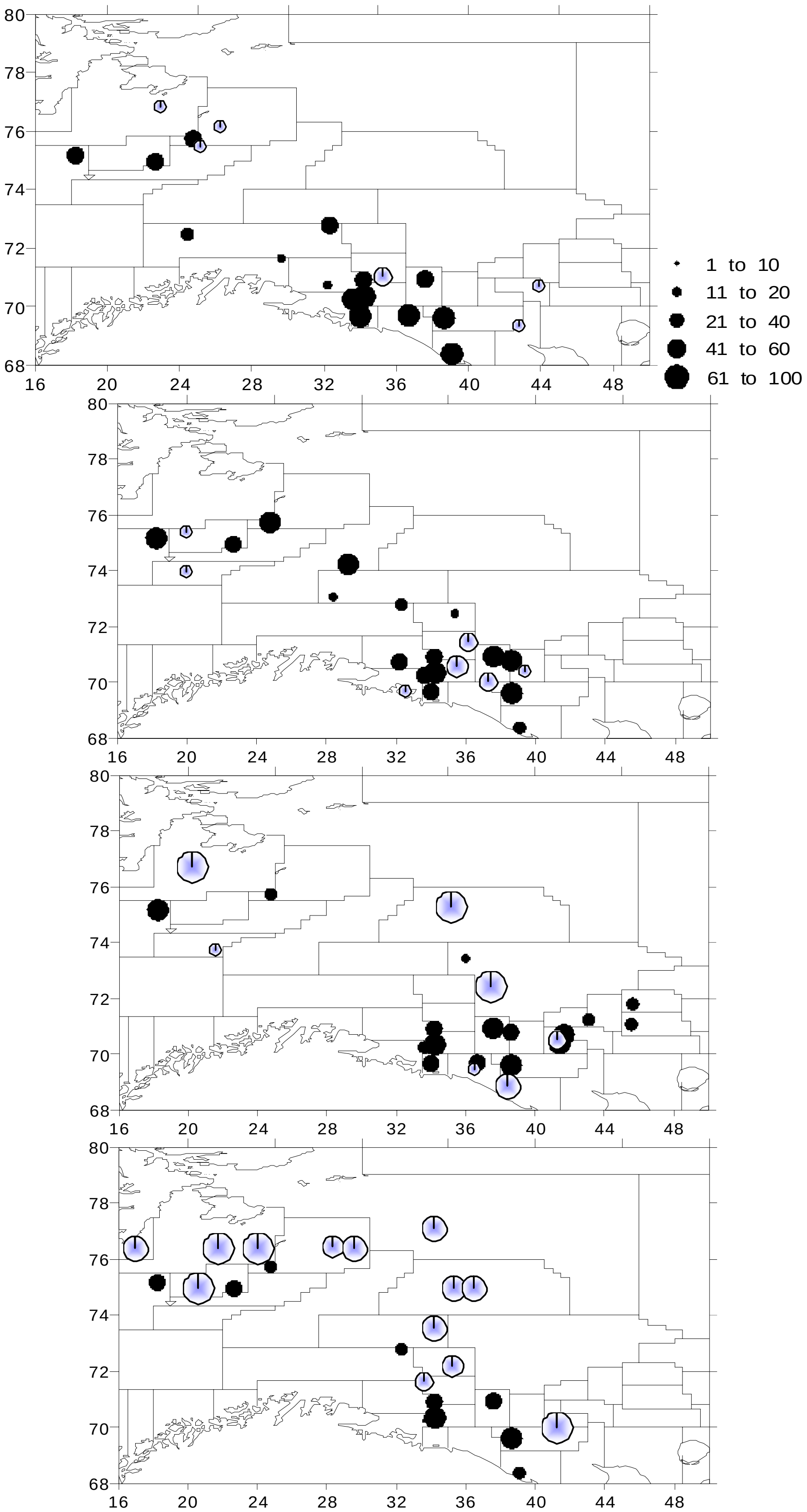

Fig. 7. Frequency of occurrence (%) euphausiids (black colour) and hyperiids (blue colour) in cod stomachs in June (a), July (b), August (c) and September (d) 1998

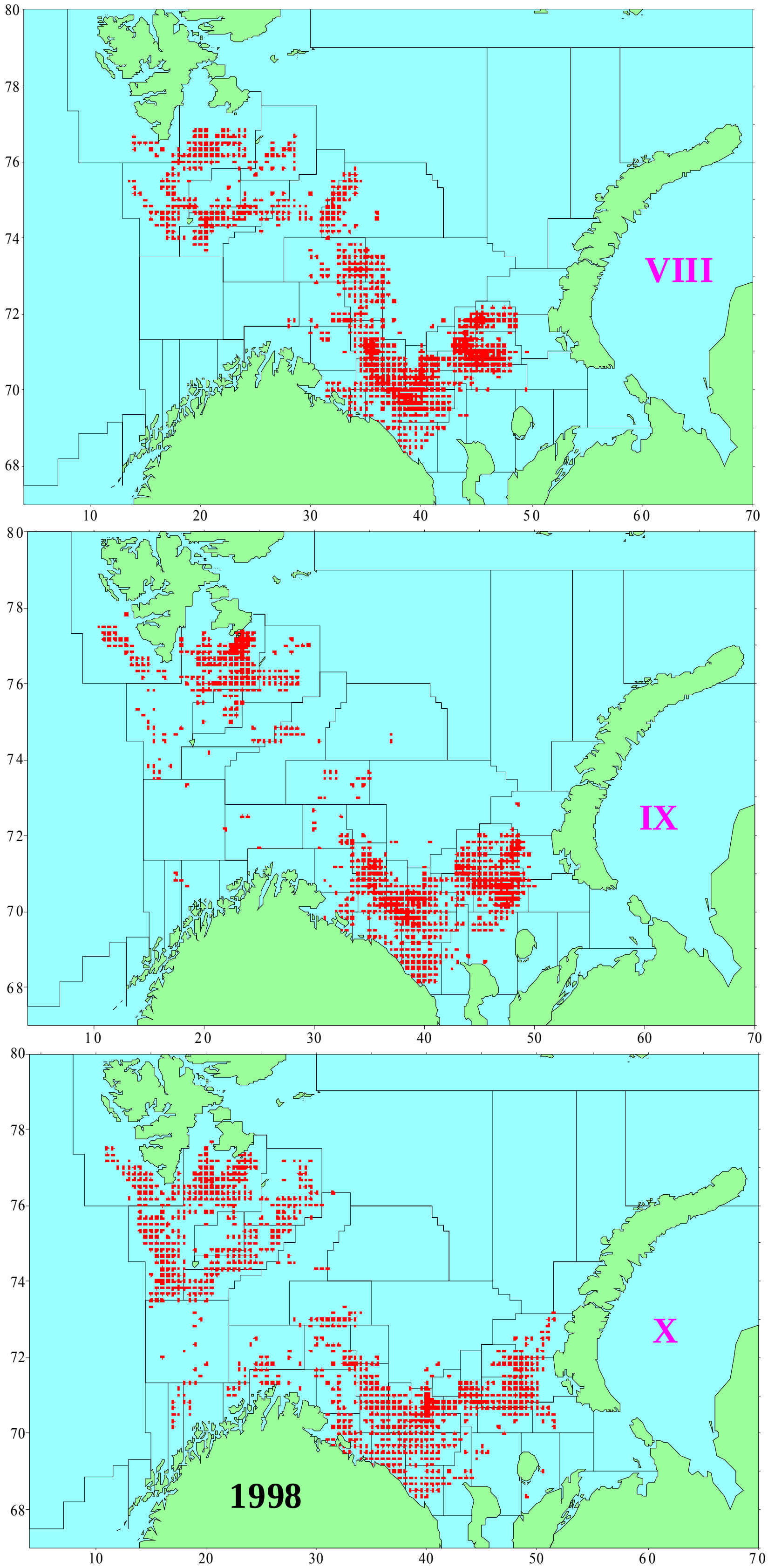

Fig. 8. Distribution of cod aggregations (red color) in the Barents Sea in August-October 1998

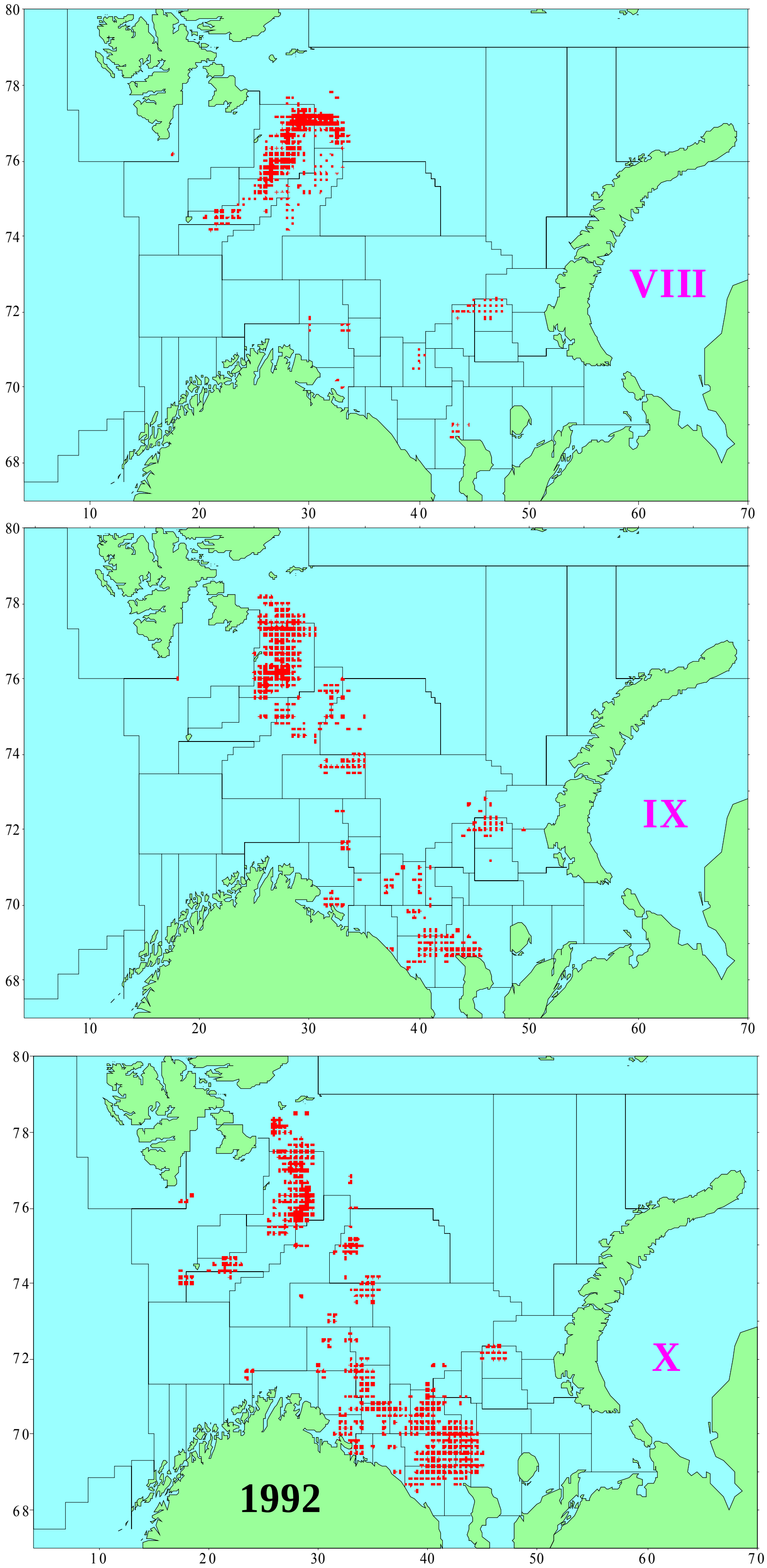

Fig.9. Distribution of cod aggregations (red color) in the Barents Sea in August-October 1992

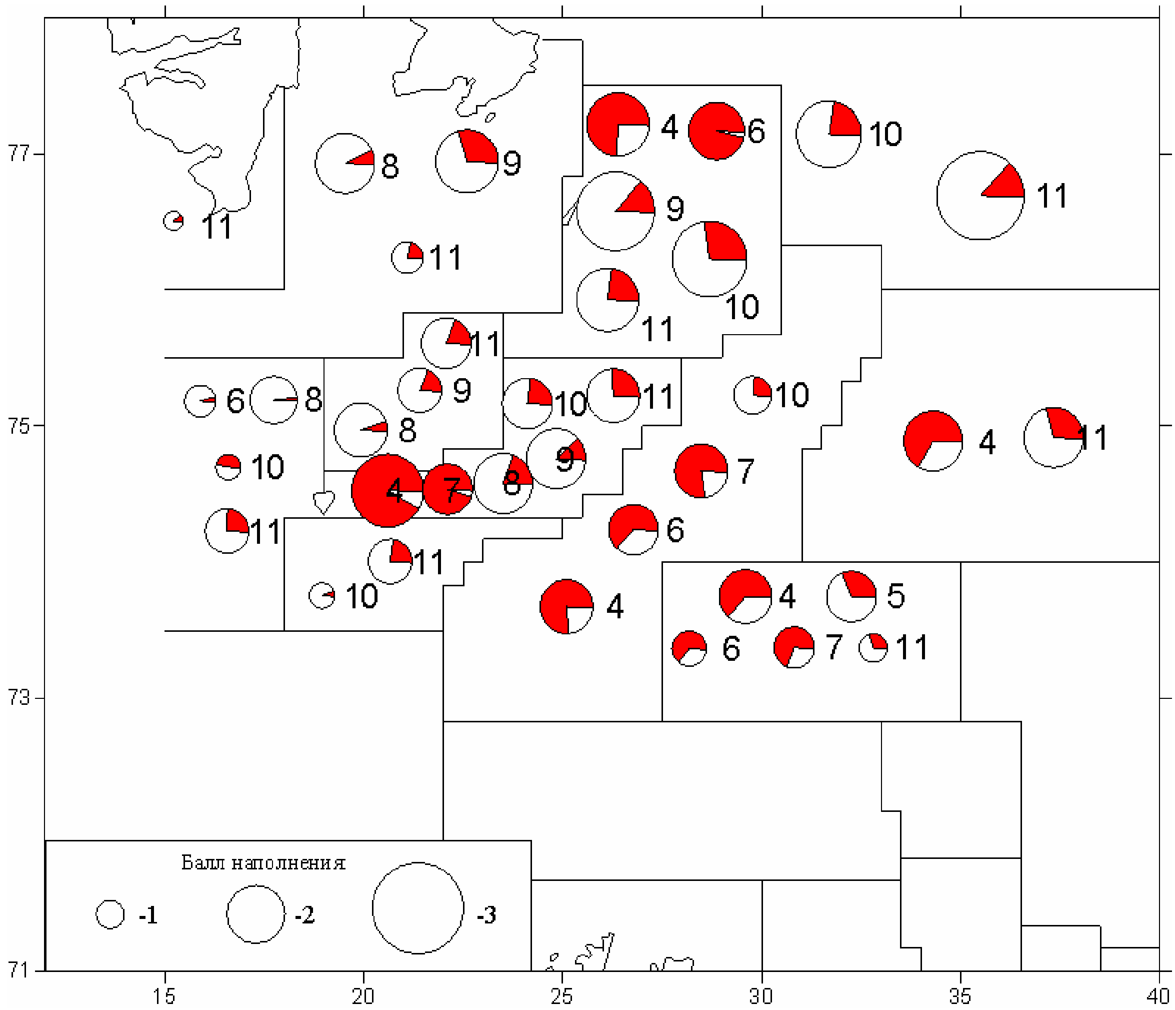

Fig. 10. Frequency of occurrence (%, red colour) shrimp in cod stomachs
in Barents Sea by months 1995 (ciphers show months)

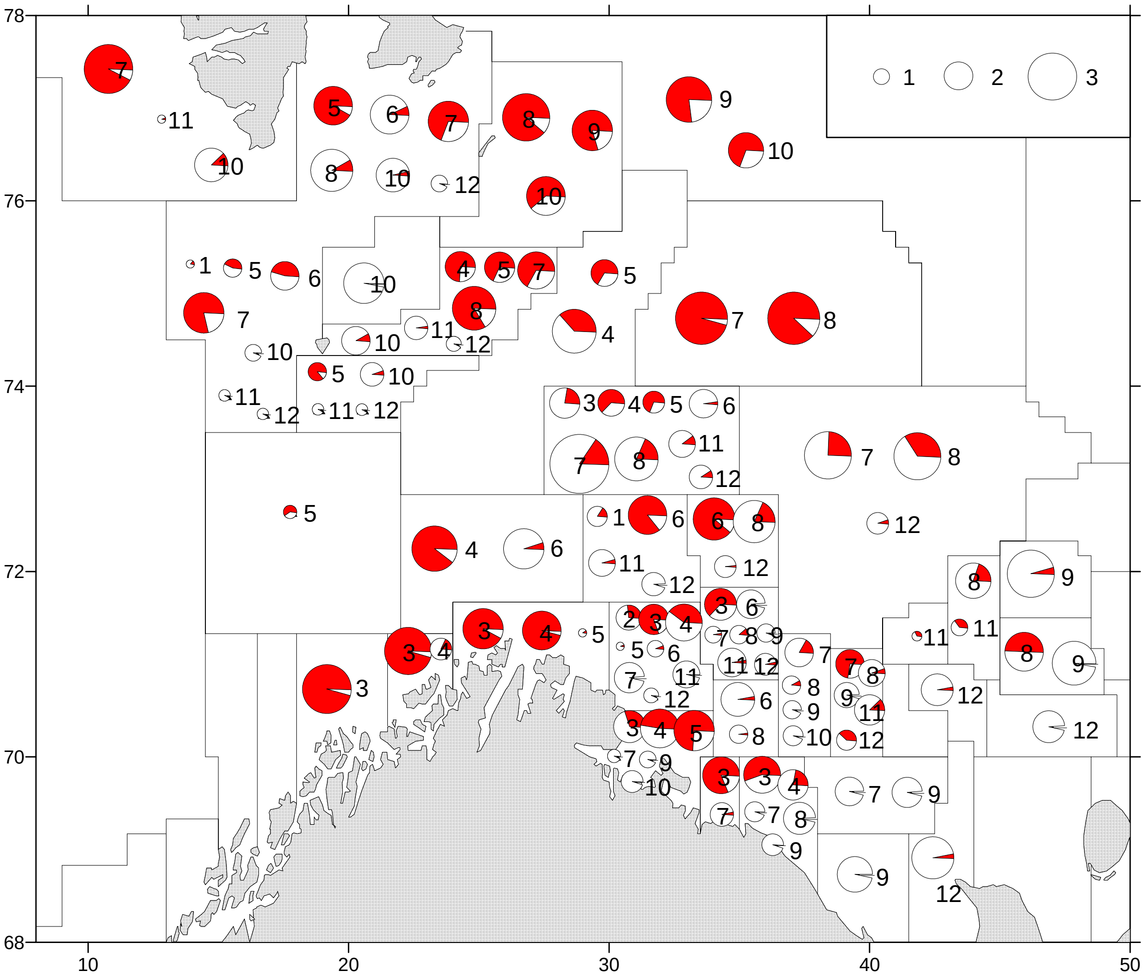

Fig. 11. Frequency of occurrence (%, red colour) capelin in cod stomachs
in Barents Sea by months 1999 (ciphers show months)

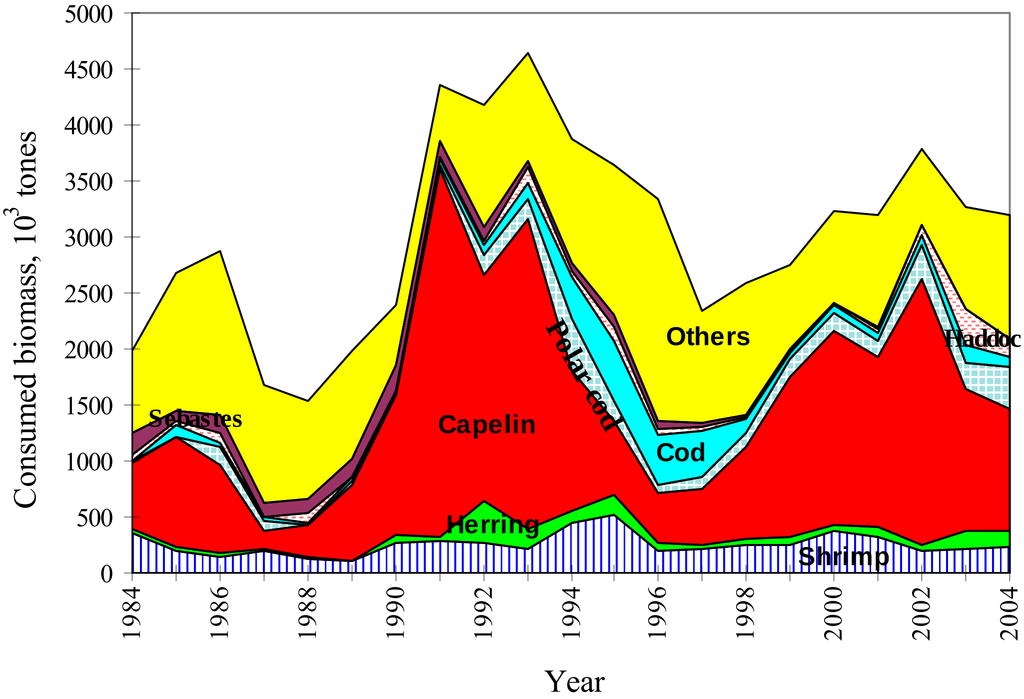

Fig. 12. Food consumed by cod in the Barents Sea in 1984-2004

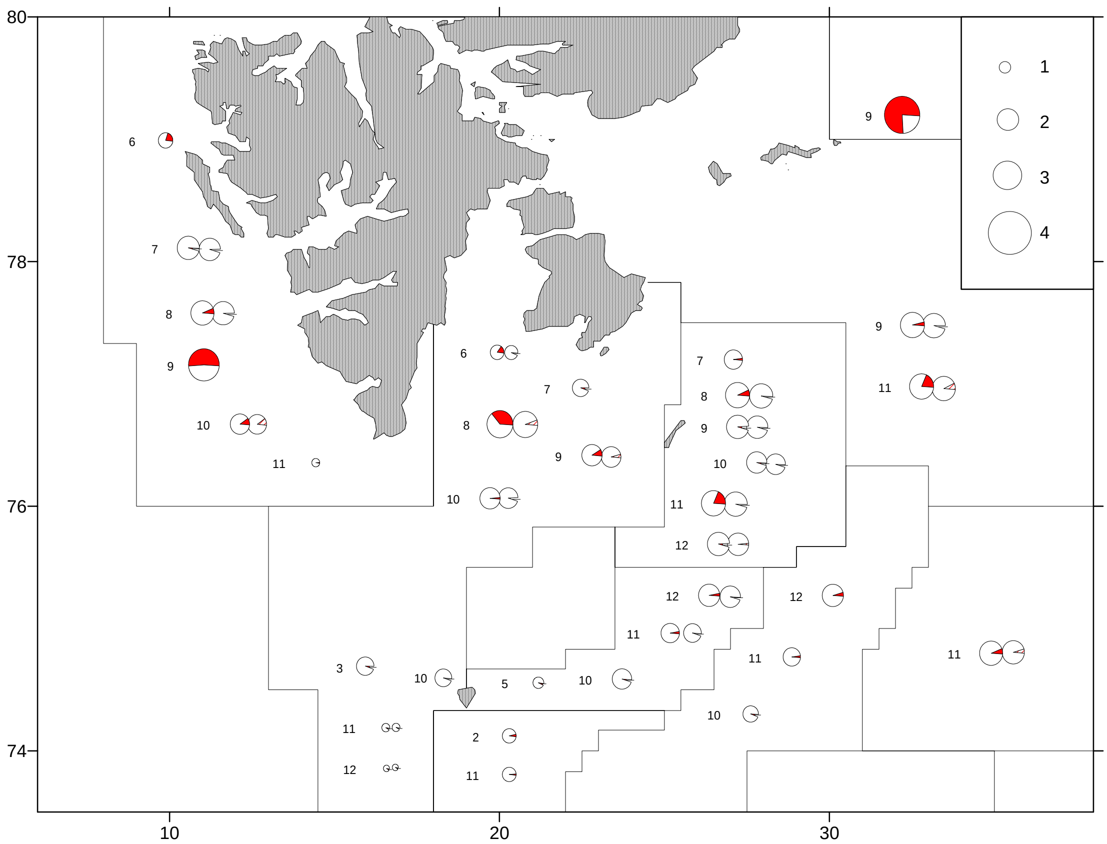

Fig. 13. Frequency of occurrence polar cod (red colour) and young polar cod (shading) in cod stomachs in Barents Sea by months 2001 (ciphers show months)

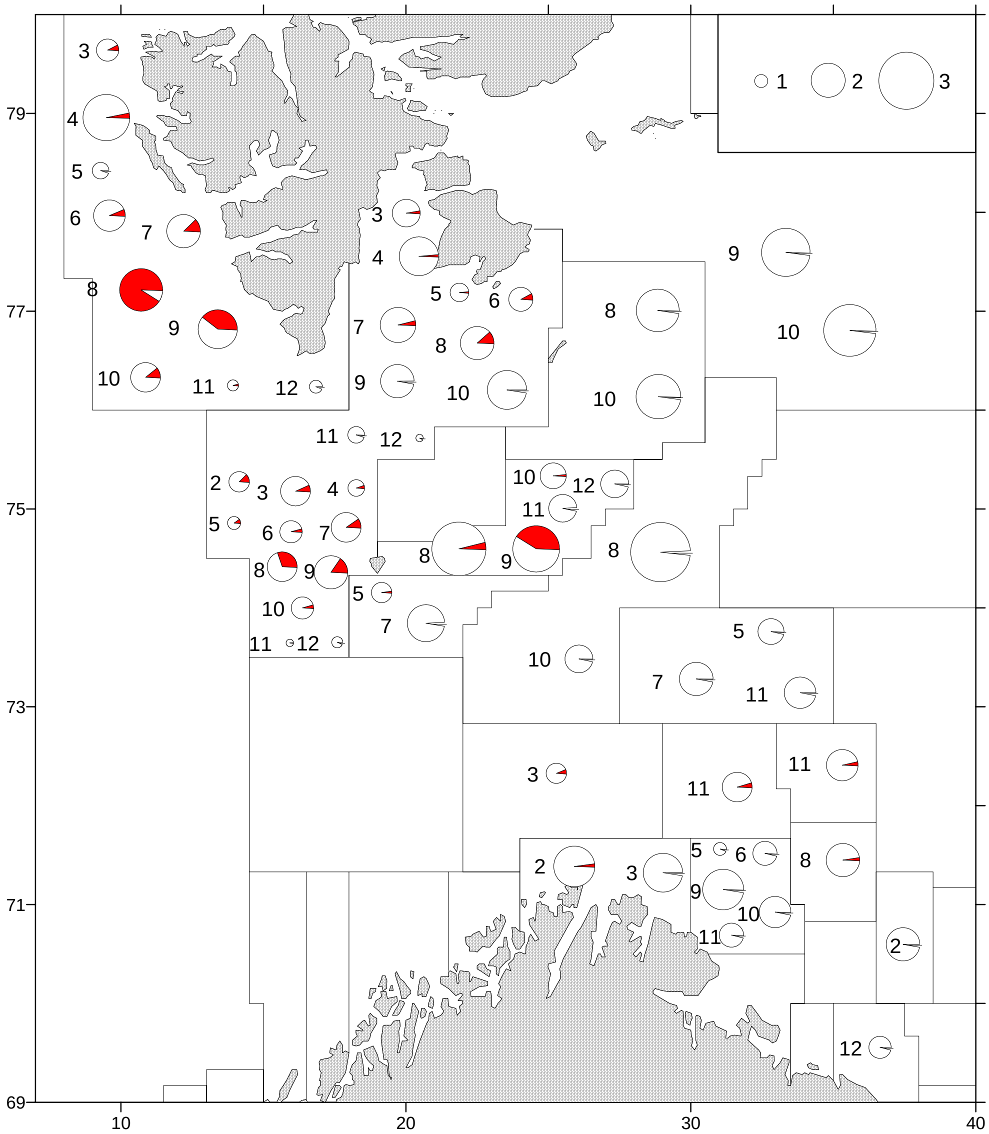

Fig. 14. Frequency of occurrence (red colour) blue whiting in cod stomachs in Barents Sea by months 2002 (ciphers show months)

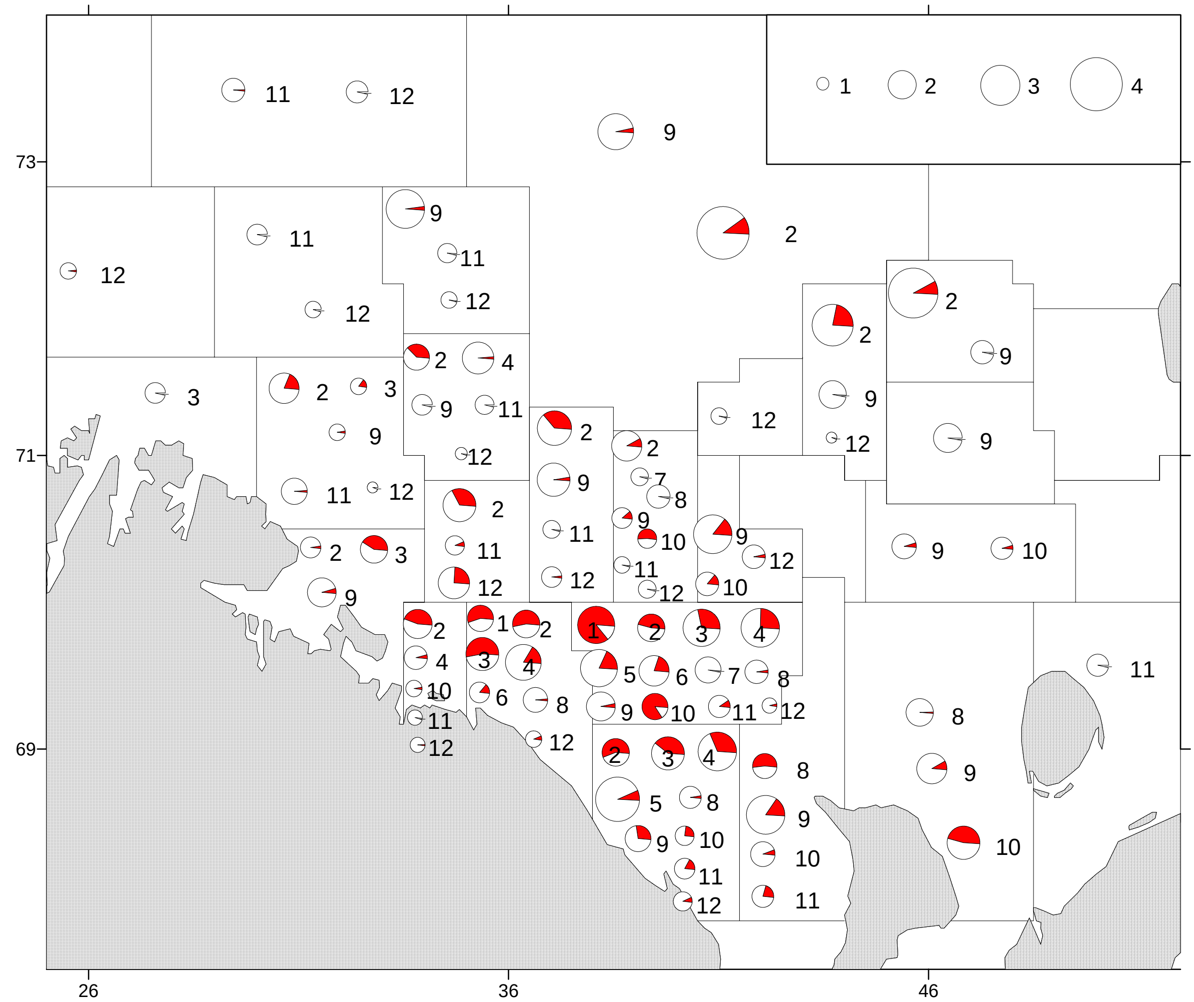

Fig. 15. Frequency of occurrence (red colour) herring in cod stomachs
in Barents Sea by months 2003 (ciphers show months)

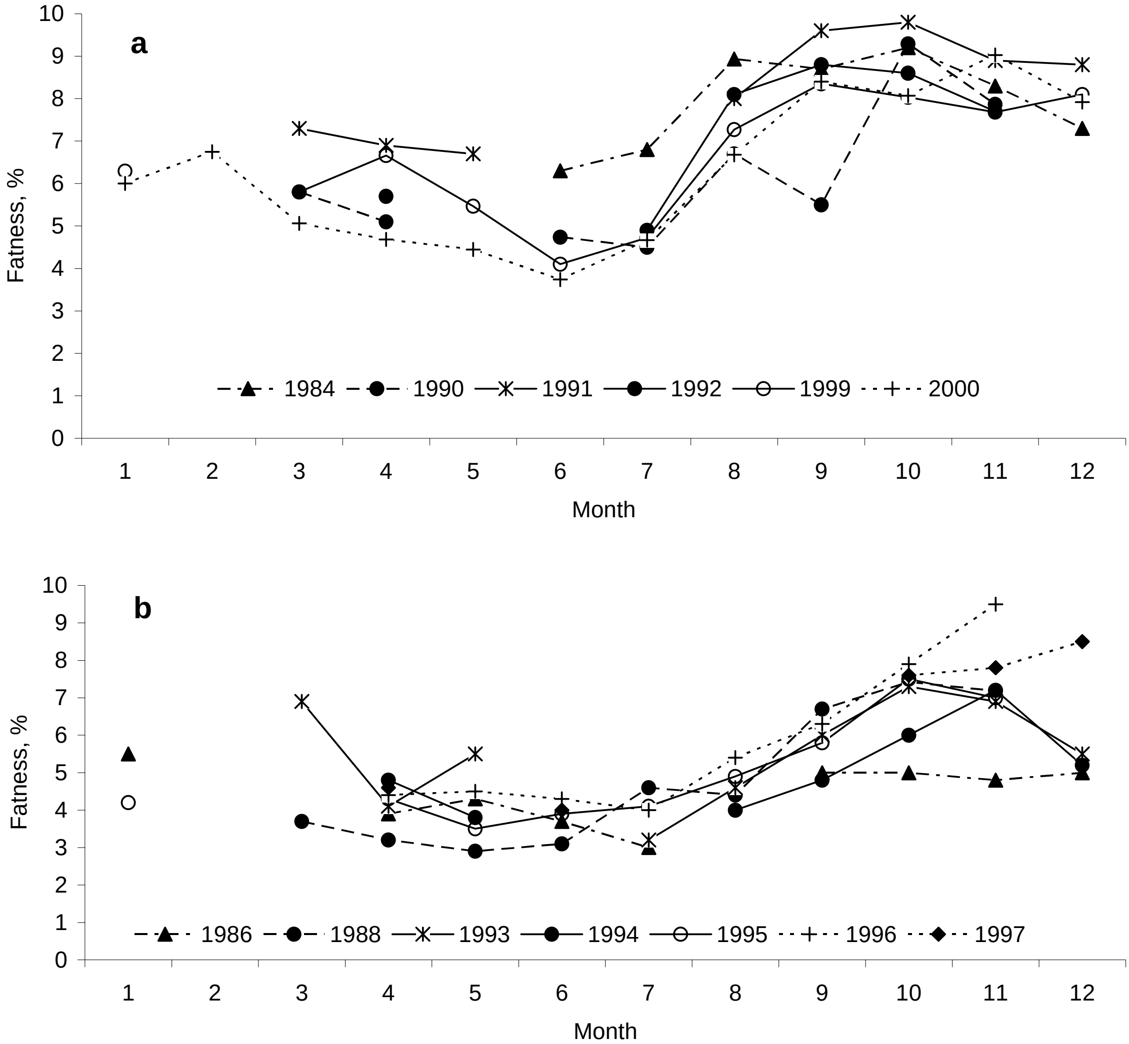

Fig. 16. Seasonal changes in cod fatness with high (a) and low (b) capelin supply

Table 1. Food composition of cod in the Bear Island-Spitsbergen area in 1984-2004, % of bolus weight

Food items	Years																				
	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
Hyperiids	9,80	28,00	28,47	24,84	3,81	13,90	1,24	0,83	0,29	5,89	9,69	7,38	27,38	3,97	8,88	2,69	9,39	2,82	0,82	5,01	6,25
Euphausiids	1,96	0,07	0,62	0,98	3,89	1,54	0,19	0,64	0,31	0,26	1,37	4,35	8,59	6,09	2,50	3,06	4,26	1,81	2,63	2,21	0,74
Northern shrimp	13,32	6,19	6,47	9,84	1,87	9,43	11,27	4,60	14,64	17,02	8,00	11,30	11,78	5,45	18,46	6,76	7,08	6,08	4,42	14,30	12,17
Herring	1,12	0,00	0,00	0,00	2,69	0,00	0,00	0,00	0,87	0,18	0,09	0,03	0,00	0,00	0,01	0,17	3,07	1,00	1,63	0,06	1,27
Capelin	6,68	20,37	8,24	5,09	12,92	24,08	40,77	64,21	36,19	6,41	4,32	1,57	8,15	4,26	14,62	58,82	18,61	19,22	31,15	22,71	11,16
Polar cod	0,00	0,00	14,75	6,97	0,00	0,28	0,35	0,55	6,37	14,57	6,23	5,68	0,82	0,10	8,04	1,91	6,86	8,51	17,69	6,25	20,64
Cod	0,04	2,11	2,45	1,61	0,00	0,00	0,28	1,17	1,18	1,76	6,54	17,12	17,53	38,70	17,26	6,76	9,37	13,24	4,63	5,46	4,13
Haddock	0,00	1,49	0,06	0,00	1,40	0,00	0,05	0,90	0,20	0,01	0,92	0,14	0,18	0,61	1,90	0,27	1,45	1,81	2,25	3,18	0,83
Norway pout	0,00	0,01	0,11	0,00	9,08	0,15	0,06	0,00	1,91	0,03	0,03	0,00	0,06	0,00	0,00	0,01	0,00	0,77	0,00	0,03	0,14
Blue whiting	0,14	2,28	0,00	0,00	0,00	0,00	0,32	0,38	0,00	0,00	0,00	0,03	0,05	0,77	1,50	0,57	2,42	14,23	9,95	6,02	4,26
Redfish	1,53	9,89	10,90	21,61	1,11	7,70	13,19	11,46	6,53	2,89	5,43	7,55	7,62	7,67	1,08	0,52	0,70	1,00	0,89	0,62	0,00
Wolffish	0,01	0,06	0,02	0,00	0,00	0,57	0,38	0,00	2,29	0,50	0,55	0,06	0,09	0,00	0,19	0,08	0,00	0,54	0,00	0,00	0,01
American plaice	1,85	3,14	1,79	0,76	0,62	1,11	2,31	0,96	1,54	14,56	3,42	1,51	1,83	4,22	1,05	0,31	2,64	4,40	1,08	2,60	3,16
Greenland halibut	0,00	0,00	0,08	0,00	0,00	0,00	0,00	0,00	0,00	0,12	0,01	0,00	0,00	0,00	0,00	0,00	0,01	0,42	0,04	0,00	2,81
Other fish	24,42	19,04	22,34	15,79	29,52	17,31	21,25	8,66	13,31	14,13	10,83	8,18	6,48	13,45	10,07	6,70	14,27	15,84	12,18	22,81	18,38
Other food	39,13	7,35	3,70	12,51	33,09	23,93	8,34	5,64	14,37	21,67	42,57	35,10	9,44	14,71	14,44	11,37	19,87	8,31	10,64	8,74	14,05

Total amount of stomachs	1002	1282	1858	2558	987	855	1804	1302	1510	1235	1625	2185	2422	1613	3528	4343	3152	5338	5757	1560	1471
Food items	Years																				
	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
Empty stomachs, %	16,1	18,4	13,2	13,4	10,8	3,9	7,6	10,2	15,6	18,9	12,5	12,7	12,0	26,8	29,3	23,0	17,3	27,8	25,9	31,3	30,2
Mean fullness.	2,8	2,8	3,0	2,2	2,8	3,1	2,9	3,2	3,1	3,2	3,1	3,1	2,9	2,2	2,2	2,4	2,5	2,6	2,6	2,0	2,2
Mean index of fullness.	186,9	180,9	222,9	169,3	184,3	226,9	314,6	181,8	211,6	171,6	154,4	176,5	169,8	134,9	168,8	252,9	217,1	205,0	235,9	197,9	156,2