TROPHIC RELATIONSHIPS AND FEEDING-DEPENDENT GROWTH IN THE NORTH-EAST ARCTIC COD

by

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ABSTRACT

The North-East Arctic cod is the major top predator in the Barents Sea food chain and it is involved in close predator-prey relationships with a large number of commercial species. The impact of predation on such prey species as capelin, redfish, young gadoids and shrimps was clearly indicated by the estimated values of their consumption by cod in 1984-1989.
The natural mortality of capelin and shrimp due to cod predation was comparable to (or,in some years, even higher than) the fishing mortality rate. In addition to an adverse effect the overfishing exerts on populations of marine organisms it also leads to inadequacy of traditional food for predators (e.g. cod). With this in view stock assessments and catch predictions should be made with due regard to the ratio between predation-caused and fishing mortalities of prey species. Predation of cod on young gadoids and redfish is particularly heavy during the period preceding the prey recruitment to commercial stocks, which results in low abundance of recruits, particularly when no other food is available for the predator.

INTRODUCTION

Rational exploitation of biological resources in the Barents Sea demands a comprehensive knowledge of trophic relationships to be employed in the multispecies mathematical models. The North—East Arctic cod is one of the most abundant species in the Barents Sea and adjacent waters of the Norwegian and Greenland Seas which governs interspecific relations in the Barents Sea ecosystem. Feeding studies of the Barents Sea cod have been in progress since the 1920s (Zenkevich and Brotskaya, 1931).

As a result of long-term investigations data were obtained on food spectra of cod of different size, on seasonal, local and year-to-year changes in feeding and on routes of feeding migrations (Zatsepin and Petrova, 1939; Wiborg, 1949; Sysoeva, 1958; Ponomarenko, 1968, 1973; Ponomarenko and Yaragina, 1978, 1979 and 1984, and others) as well as on daily rations of cod both in natural and controlled conditions (Karpevich and Bokova, 1936, 1937; Tarverdieva, 1962; Novikova, 1962, 1965; Orlova et al., 1989 and Braaten, 1984).

However, the development and implementation of a mathematical model of the multispecies fishery demands accurate annually- collected quantitative data on size and age composition of preys from stomachs of predators of different age to be broken down by feeding grounds and seasons as well as information on the geographical and size-dependent availability of preys and energy requirements and seasonal and annual rations of predators.

In view of the necessity of such information a joint PINRO—IMR stomach content database has been being developed since 1984 and a program of cooperation in the field of studies of commercial stock interactions in the Barents Sea was worked out in 1988. The present paper summarizes some results of the above-mentioned investigations and provides a general concept of studies of cod trophic relationships.

MATERIAL AND METHODS

Use was made of data on cod stomach contents which were collected during numerous cruises of the PINRO and IMR research vessels in 1984-1990 and entered into the joint database which contains the results of analyses of 27 550 cod stomachs. The methods of stomach sampling and treatment and of data recording and processing were similar to those used within the framework of the Stomach Sampling Project for the North Sea (Anon., 1980a, 1980b and 1981; Westgård, 1982 and Mehl, 1986). More detailed information on the methodology and data distribution by years, seasons, areas and age-groups of cod is presented by Mehl and Yaragina (1992). The quantitative assessment of cod feeding was made on the basis of data on the average daily weight of the food bolus of an individual at a definite age (size) for a given quarter of the year. The predation was calculated using the following formula:

$$D_{s,a} = \sum_{b} \frac{R_b \cdot \delta_{sab} \cdot \beta_b \cdot \overline{N}_b \cdot 91.25}{w_{s,a}}$$

where

- $D_{s,a}$ is quarterly consumption of prey species s at age a, thousand individuals;
- R_b is average quarterly stomach weight of predator at age b, g;

- δ_{sab} is proportion of prey species s age group a in stomach content of predator at age b;
- β_b is proportion of food bolus for predator at age b digested daily
- $\overline{N_b}$ is average annual abundance of predators at age b, thousand individuals;
- 91.25 is the number of days in a quarter
- $w_{s,a}$ is average weight of prey species s at age a, g.

The annual consumption by cod of each of the prey species was calculated by summing up the quarterly values. Age-length keys were used to convert prey size to prey age. Data on the abundance and biomass of the cod stock were taken from Reports of the ICES Arctic Fisheries Working Group (Anon, 1988, 1989).

The model of gastric evacuation in cod given by Mehl (1989) was used. The proportion of food digested daily varied from 1.124 in 1-year olds to 0.168 in individuals at the age of 7 years and older.

Age-frequency distribution and other parameters which are indicative of the interaction of preys with the North-East Arctic cod were determined using the multispecies VPA as modified by Pope (1979). The method involves a generalized standard VPA with reference to several species and with account taken of predator-prey relationships.

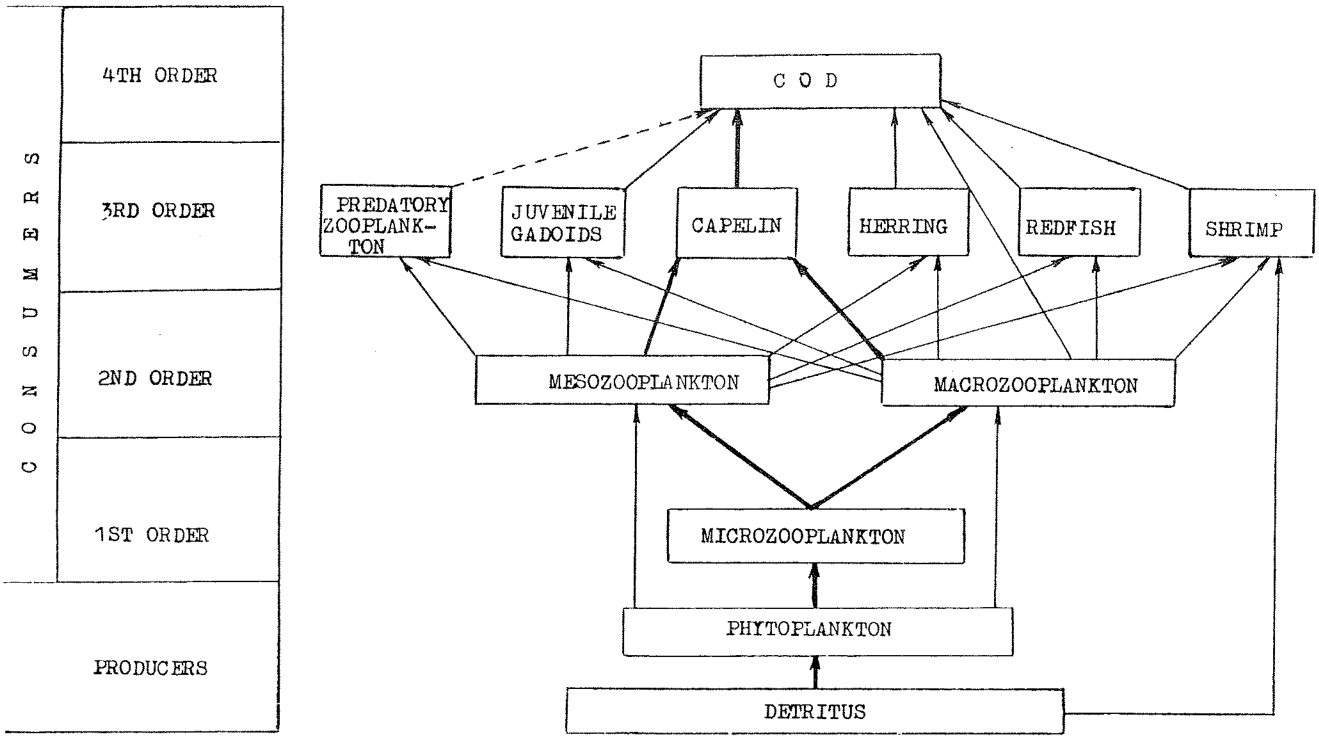
RESULTS AND DISCUSSION

Since the Barents Sea lies in high latitudes the species diversity is not as high as that in the southern seas, which is true for almost all ecological groups of the food web, i.e. phytoplankton, zooplankton, nekton and benthos. A high degree of dominance of individual species is a typical feature of the Barents Sea, e.g. Calanus finmarchicus constitutes 80-90% of the mesozooplankton biomass (Degtyareva, 1979), and Thysanoessa inermis and Th. raschii are dominant species in macrozooplankton (Drobysheva, 1967).

Out of 150 species (Andriyashev, 1954 and Rass, 1965) a total of 20-25 are commercially important. Capelin, herring, polar cod and redfish are the most abundant pelagic plankton-eaters whereas among predators the highest abundance is shown by cod and Greenland halibut and the mass benthos-eaters are haddock, catfish and long rough dab.

The central trophic links are easily distinguishable in the Barents Sea ecological groups to comprise dominant species through which the major part of energy is transferred (Fig.1). Since only few species are dominant in the ecosystem and the natural annual fluctuations in the abundance are fairly high the trophic relationships between the Barents Sea hydrobionts are unstable, particularly at the highest trophic levels, namely, in consumers of the 3rd and 4th orders which are subject to anthropogenic effects. A large amount of food which is produced by one link of the food web (meso- and macrozooplankton) can remain unutilized by the next trophic link (capelin) due to a decrease in the abundance (caused by man-induced effects or poor year classes) and, consequently, the traditional pattern of energy transfer appears to be disturbed and food is either consumed by fast-developing predatory zooplankton (e.g. ctenophores) or settled on the bottom as organic remnants.

Figure 1 Main food webs in the Barents Sea ecosystem.



The situation can differ from year to year. The food requirements of a trophic link may not be met due to collapse in the mass development of forage organisms or severe competition for food, which is accompanied by a reduction in condition factor and fat content, inhibited growth and maturation, and an increase in starvation-induced mortality in species from the next trophic link. The process of changing over to feeding on other preys takes some time during which the pattern of feeding migrations is being changed accordingly, e.g. the decrease in capelin abundance during the 2nd half of the 80s resulted in the development of cannibalism in cod and in switching over to feeding on shrimp, small-size redfish and haddock. Besides, despite the small cod stock size which usually implies a reduction in the species range cod performed long-distance migrations to the eastern areas of the Barents Sea to feed on small non-commercial species (Lumpenidae, sculpins and eelpout) as well as on polar cod and benthos.

Age dynamics of cod trophic relationships

Food spectrum of cod is characterized by a high species diversity. The analyses of stomach contents have revealed a total of 200 food items, however, the bulk was formed by 20-25 species whereas the rest were recorded occasionally. Cod feed on nekton, plankton and benthos. Food habits show age variations. Newly-hatched larvae do not feed during the first 5-7 days and they live at the expense of the yolk sac reserve, which is followed by a change to active feeding on copepod eggs and nauplii and on phytoplankton during the earliest life (Tilseth et al., 1987). Growing larvae consume larger food organisms, such as Calanus (early and then late copepodite stages) and young euphausiids (Sysoeva, 1964 and 1973). Euphausiids are the major food item of fry at the late pelagic stage (Baranenkova et al., 1964). After a downward migration in autumn the fry begin to feed on benthic and demersal species (Kuchina, 1932; Wiborg, 1949 and Ponomarenko, 1979) of the orders Polychaeta, Decapoda, Amphipoda and Cumacea whereas the role of pelagic organisms diminishes. Based on data provided by Mironova (1956) the food spectrum of cod shows fundamental changes during the first 2 years of life with the major transformations falling on the second year.

Fish (capelin, herring, polar cod, and sandeel, as well as young gadoids and long-rough dab, and some others) form the average of 70% of the food bolus of cod exceeding 30 cm in size (Zatsepin and Petrova, 1939; Orlova et al., 1988 and Mehl, 1986). Cod is an active predator for which fish is always the preferable food. The results of experiments on live food preference in cod and haddock have shown that cod as opposed to haddock preferred mobile food organisms irrespective of the nutritive value which was frequently lower than that in less mobile forms, such as polychaetes (Astaf'eva, 1967, a and b).

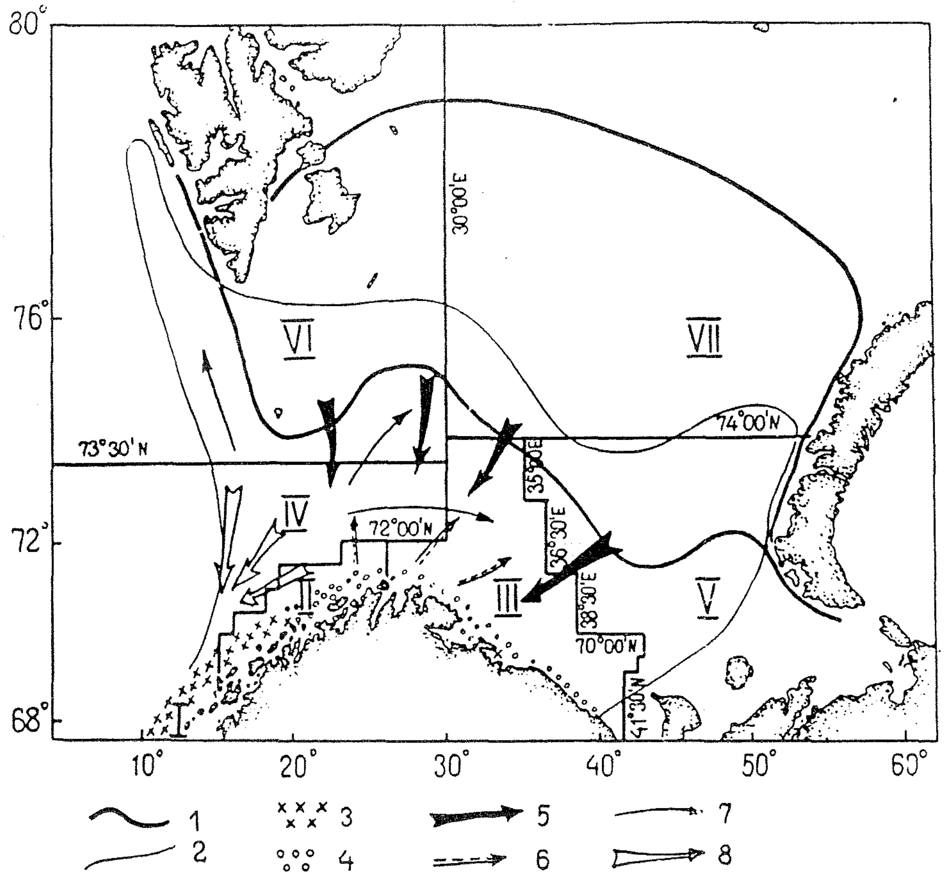
Pelagic crustaceans of the order Euphausiacea and of the family Hyperiidae, nectobenthic shrimps of the genus Pandalus and bottom crustaceans are essential food items for cod. The food habits are similar in cod 30 to 70-80 cm in size with no significant differences in the ratio of different food items. The share of small organisms such as amphipods and euphausiids shows a somewhat decrease with the fish age. In cod longer than 80 cm fish form the bulk of food with preference given to young cod up to 30-34 cm in size as well as to haddock and long rough dab (Orlova et al., 1989).

Seasonal dynamics of cod trophic relationships.

The cyclicity in the functioning of the plankton community which is responsible for not less than 80% of the terminal production is a typical feature of the Barents Sea which is located in high latitudes (Zenkevich, 1963 and Marti and Martinsen, 1969). The mass development of phyto- and zooplankton occupies a short period of time in spring and summer, which determines the seasonality of feeding migrations in the Barents Sea fishes and, primarily, in plankton-eaters. A number of species of the Barents Sea biota are passive or active migrants, which should be taken into account in trophological studies since migrations contribute to both overlap and divergence in ranges of preys and predators.

The North—East Arctic cod is an active migrant. Mature individuals perform 1500 miles long annual spawning migrations to the Lofoten area. The major feeding grounds are confined to the southern part of the Barents Sea and to the Bear Island and Spitsbergen areas. The northward and eastward feeding migrations start in May when currentinduced heat advection takes place. In search for food cod can migrate to water layers where the temperature is close to or even below 0° C.

Figure 2 Distribution and migrations of cod and capelin in the Barents Sea. 1 — capelin distribution area, 2– cod distribution area, 3 — cod spawning area, 4 — capelin spawning area, 5 — capelin spawning migration, 6 — capelin post-spawning migation, 7 — cod feeding migration, 8 — cod spawning migration; I-VII: sea areas as established in the PINRO-IMR cooperation.



The spring, summer and autumn peaks in feeding are recorded in cod in the southern part of the Barents Sea. In February and March the major food item is capelin which perform spawning migration to the Norwegian and Murman coasts (Fig.2). The ranges of capelin and immature cod overlap and the cod which is named by fishermen a "capelin cod" ("loddetorsk" in Norwegian) migrate coastward. This is the most important feeding period of cod when the highest values of stomach fullness are recorded as compared to the rest part of the year. Cod consume 54% of the annual diet in February and March (Orlova et al., 1988). The original data indicate that the total consumption of capelin by cod in 1984 - 1988 was about 3.6 million tonnes. Of this, about 1.8 million tonnes (50 %) and 1.2 million tonnes (30 %) of capelin were consumed by cod in the 1st and 2nd quarters of the year respectively (Table 1). A high fat content (up to 6-7% as compared to the annual average of 5%) is recorded in cod fed on capelin (Ponomarenko, 1970 and Yaragina, 1989), which is indicative of an increase in the energy depot. In June cod start to feed on post-spawning euphausiids which are brought with the currents to the shallows in the southeastern part of the Barents Sea to perform downward migration to off-bottom layers. Cod schools migrate to these areas to feed on euphausiids.

Table 1 Biomass of capelin consumed by cod in 1984-1988, 1000 tonnes.

Year	Quarter				Total
	I	II	III	IV	
1984	237.7	529.0	41.6	4.3	812.6
1985	1178.2	54.8	261.4	70.2	1564.6
1986	342.5	453.5	52.9	67.5	916.4
1987	43.6	77.8	12.8	14.8	149.0
1988	26.3	81.4	79.8	0.0	187.5
Total	1828.3	1196.5	448.5	156.8	3630.1

According to Mantejfel (1960) "the annual migrations of cod and haddock to the areas where euphausiids move to near-bottom layers are to be regarded as a kind of adaptation of cod aimed at obtaining food at the least energy costs under specific conditions of the water body".

The Barents Sea cod is characterized by seasonal variations in the length of the food chain which comprises 5-6 links in winter and not more than 3 in summer (Drobysheva, 1990) to provide a direct energy transfer from the lowest trophic level to the highest one.

Cod feed mainly on polar cod, young cod and various non- commercial fish species and benthic organisms, such as crabs, mollusks and worms.

The pink shrimp Pandalus became an essential food item of cod in the 80s, particularly in autumn and winter when cod stick to deep-sea wintering layers which are penetrated by warm currents. The maximum overlap of distribution areas of cod and shrimp is observed during this period and the shrimp accessibility increases. Similar situation takes place with regard to cod feeding on young redfish.

No detailed literature data are available on the seasonal dynamics of feeding and migrations of cod in the Bear Island and Spitsbergen areas and the reference material comprises fragmentary information on food spectrum of cod during individual months (Robertson, 1932; Brown and Cheng, 1946; Fender, 1958 and Berger, 1968). With this in view a brief outline of cod feeding migration in this area is given below. The feeding migration starts when the influx of warm water is recorded and it extends northward along the Spitsbergen shelf and northeastward to Hopen Island and the Perseus Rise. The migration starts in June - July to continue up to October - November when cod shoals reach the marginal areas of the range (Fig.2). The peak of feeding falls on summer and autumn. Euphausiids form the bulk of cod food in shallows in June-July whereas capelin is the major food item in July-October. Cod migrate northward and northeastward to follow capelin which perform feeding migration. During cold years cod do not migrate far to the north and to the east and some divergence between the distribution of cod and capelin is observed.

It is worth noting that the traditional seasonal feeding pattern can differ from year to year as dependent on food availability and the feeding periods can show variations accordingly. The Barents Sea cod appear to be evolutionary adapted to reconstructions in the food spectrum against both seasonal and interyear background.

Interyear dynamics of trophic relationships in cod.

Information from the joint database assists both in theoretical studies and in long-term catch predictions. With this aim the annual consumption by cod of such important commercial species as capelin, shrimp, redfish as well as of young cod and haddock was estimated (Table 2). Significant year- to-year fluctuations were revealed in consumption by cod of different food items, which seemed to be related to the unstable trophic relationships recorded in the 2nd half of the 80s and caused by dramatic changes in the abundance of capelin which used to be the major food of cod. To establish options of fishery management a model of the "predator-prey" type which describes interactions between 2 species was used. A model of cod fishery management with account taken of cannibalism and a model of regulation of capelin and shrimp fisheries with allowance made for cod predation were developed for the Barents Sea.

Table 2 Consumption by cod of commercial species 1984–1989, 1000 tonnes

Food Items	Year					
	1984	1985	1986	1987	1988	1989
Capelin	800	1560	900	150	188	480
Cod	6	55	41	25	10	1
Haddock	47	70	100	16	41	1
S. mentella	220	70	200	300	70	80
Shrimp	690	570	380	290	110	160

Young cod below 34 (occasionally up to 39) cm are recorded in stomachs of adults, i.e. cod individuals at the age of 0+ - 3 years are most vulnerable to cannibalism-caused mortality (M2). The M2 rate decreases with the fish age (Table 3) to show a reduction by 1 order (10 or more times) with every 3 years of the fish life. The comparison between M2 and M1 (the rate of natural mortality due to reasons other than predation) shows that M2 is always higher at the age of 0+. However, $M2 < M1$ after the age of 2 years, i.e. the highest rate of predation is recorded in young individuals at the age of 0+ and 1 year. The estimates have shown that the M2 rates vary from year to year and the annual consumption by adults of young individuals in 1984-1989 corresponded to the abundance of a year-class of medium strength at the age of 3 years (Table 4). In individual years (e.g. in 1986) the rate of cannibalism is so high that significant errors can be introduced into stock assessments and catch predictions in case no allowance is made for it. The situation is usually observed when the abundance of traditional food items decreases sharply as it was the case in 1986-1987 when capelin abundance reduced considerably and, besides, comparatively strong year-classes of cod (the age of 0+ - 1 year) appeared from which abundant recruitment is expected.

Table 3 Natural mortality rates of the North—East Arctic cod at the age of 0 - 3 years due to cannibalism (M2) and to other causes (M1) in 1984 - 1989

Age	M1	M2					
		1984	1985	1986	1987	1988	1989
0	0.12	0.28	0.48	0.51	0.31	0.30	0.00
1	0.10	0.05	0.11	0.25	0.38	0.35	0.00
2	0.09	0.04	0.01	0.04	0.07	0.10	0.00
3	0.08	0.02	0.01	0.01	0.03	0.04	0.00

Table 4 Cannibalism - caused mortality of cod at the age 0 - 3 years in 1984 -1989, in million individuals.

Age	Year					
	1984	1985	1986	1987	1988	1989
0	188	339	344	255	233	2
1	43	56	111	147	186	10
2	13	12	17	23	27	-
3	4	4	6	10	13	-
Sum 0 -3	248	411	478	435	459	12

The recent data on predation of adult cod on the young individuals as well as the generalized VPA with account taken of cannibalism have allowed for estimatinge potential cannibalism-caused mortality rate and for introducing substantial amendments into cod catch predictions for 1987- 1988. The original preliminary estimates using the "cod-capelin" model have indicated a continuous decrease in the capelin biomass since 1975 (Table 5) down to 2.1 million tonnes in 1985. Cod has been exposed to inadequacy of the major food item since 1984. Even in case capelin fishery had been banned in 1983 the species biomass would not have reached the level required for adequate cod nutrition. At the cod abundance sufficient to provide the catch of about 800 thousand tonnes (which is possible at the spawning stock biomass of 1200 thousand tonnes) the average catch of capelin should be close to 500 thousand tonnes at an average stock size of around 6 million tonnes.

The results of estimates based on a two-species ("cod-shrimp") model suggest an over-exploitation of commercial shrimp stock in 1984-1987 (Table 6), and the 1991 and 1992 exploitation rates were determined with account taken of cod predation on shrimp and of the necessity to keep the shrimp stock at the present level, i.e. close to $F = 0.15$.

Table 5 Biomass (B2), catch (C2) and fishing (F2) and natural (M2) mortalities of capelin.

Year	B2, million tonnes	C2, million tonnes	F2	M2
1971	10	1.3	0.58	0.24
1972	12	1.4	0.53	0.27
1973	14	1.4	0.93	0.37
1974	13	1.1	0.99	0.39
1975	15	1.4	0.45	0.27
1976	14	2.6	0.43	0.27
1977	14	3.4	1.32	0.22
1978	10	2.1	1.35	0.25
1979	9	2.0	1.34	0.27
1980	8	1.4	1.24	0.22
1981	8	1.9	1.24	0.24
1982	7	1.6	0.70	0.28
1983	6	1.9	1.65	0.34
1984	4	1.1	0.40	-
1985	2	1.0	1.26	-

Table 6 Fishing mortality of shrimp in 1980 -1990.

Year of fishery	Age				Mean
	2	3	4	5	
1980	0.03	0.20	0.21	0.37	0.20
1981	0.02	0.10	0.12	0.18	0.10
1982	0.02	0.08	0.4	0.38	0.15
1983	0.03	0.19	0.16	0.52	0.22
1984	0.04	0.21	0.28	1.06	0.40
1985	0.06	0.41	0.29	0.90	0.41
1986	0.66	0.84	0.85	0.21	0.64
1987	0.67	0.73	0.83	0.22	0.61
1988	0.02	0.07	0.09	0.30	0.12
1989	0.08	0.16	0.21	0.25	0.17
1990	0.03	0.15	0.19	0.26	0.16

CONCLUSIONS

Cod is the most abundant predatory species and a top predator in the trophic chain of the Barents Sea. It exerts a strong impact upon other commercial species through trophic relationships. Cod performs long-distance migrations throughout the Barents Sea due to which it can affect marine organisms in all parts of the range. Underestimation of quantitative aspects of the impact of cod predation on commercial stocks may cause errors in catch predictions. With this in view it is recommended that the development of the multispecies model of the Barents Sea be continued by elucidating theoretical models and increasing the accuracy of both field data on fish feeding and estimates of annual food requirements.

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