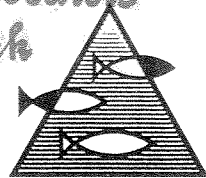


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INTERRELATIONS BETWEEN FISH POPULATIONS IN THE BARENTS SEA

Proceedings of the fifth PINRO-IMR Symposium
Murmansk, 12–16 August 1991

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Murmansk, 26-28 May 1986
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Edited by

Bjarte Bogstad and Sigurd Tjelmeland

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ERRATA

Interrelations between fish populations in the Barents Sea.

Proceedings of the fifth PINRO-IMR symposium, Murmansk 12 – 16 August 1991. Edited by Bjarte Bogstad and Sigurd Tjelmeland.

In A.M. Ajiad and T. Ya. Pushchaeva: The daily feeding dynamics in various length groups of the Barents Sea capelin, pp. 181–192, figures 1–4, 5A and 5B are missing. They are given in this errata, and should be included after page 192.

The editors

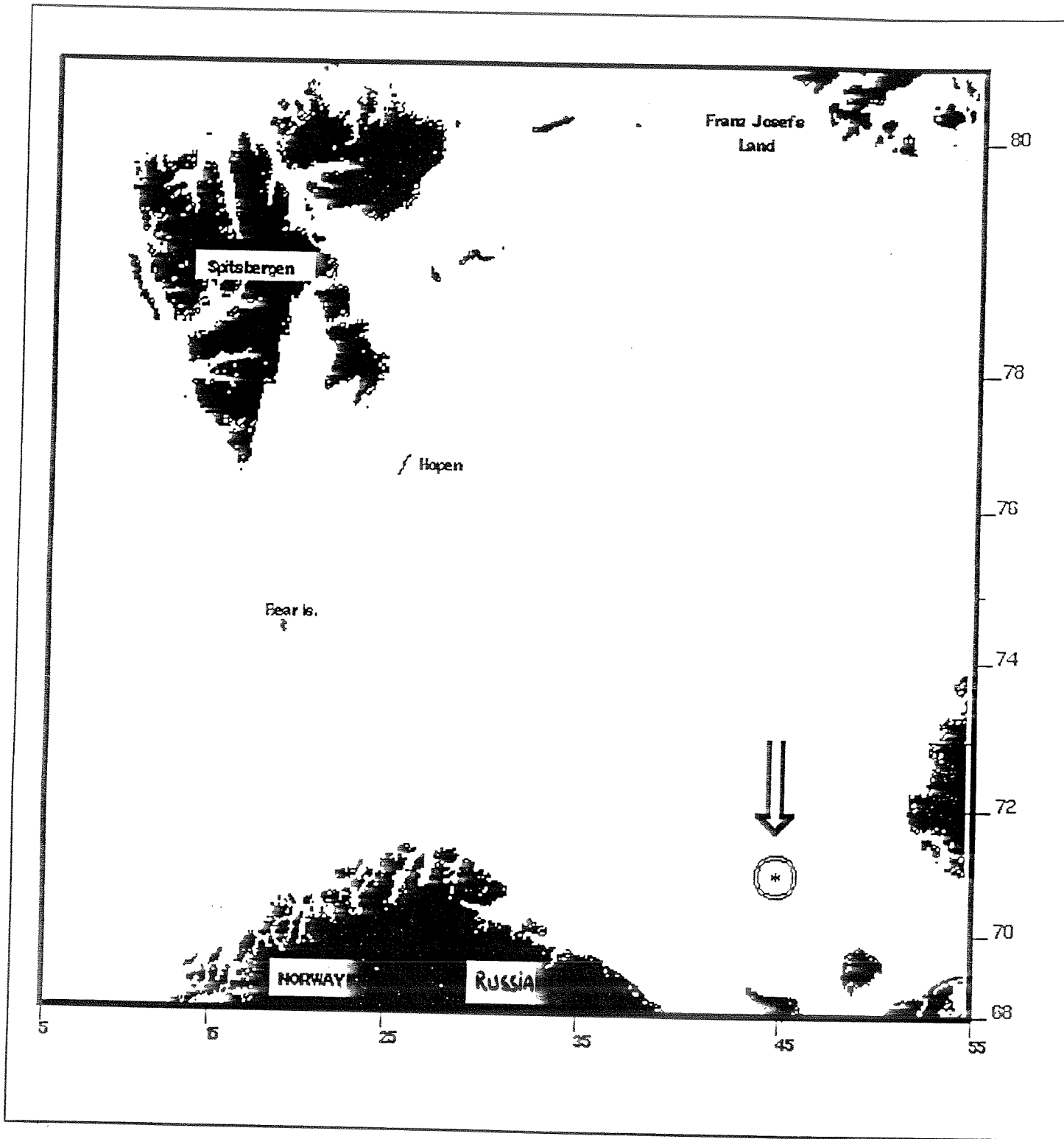


Fig.1

Figure 2

length -- weight relationship

length group 06-17.9cm, Males and Females

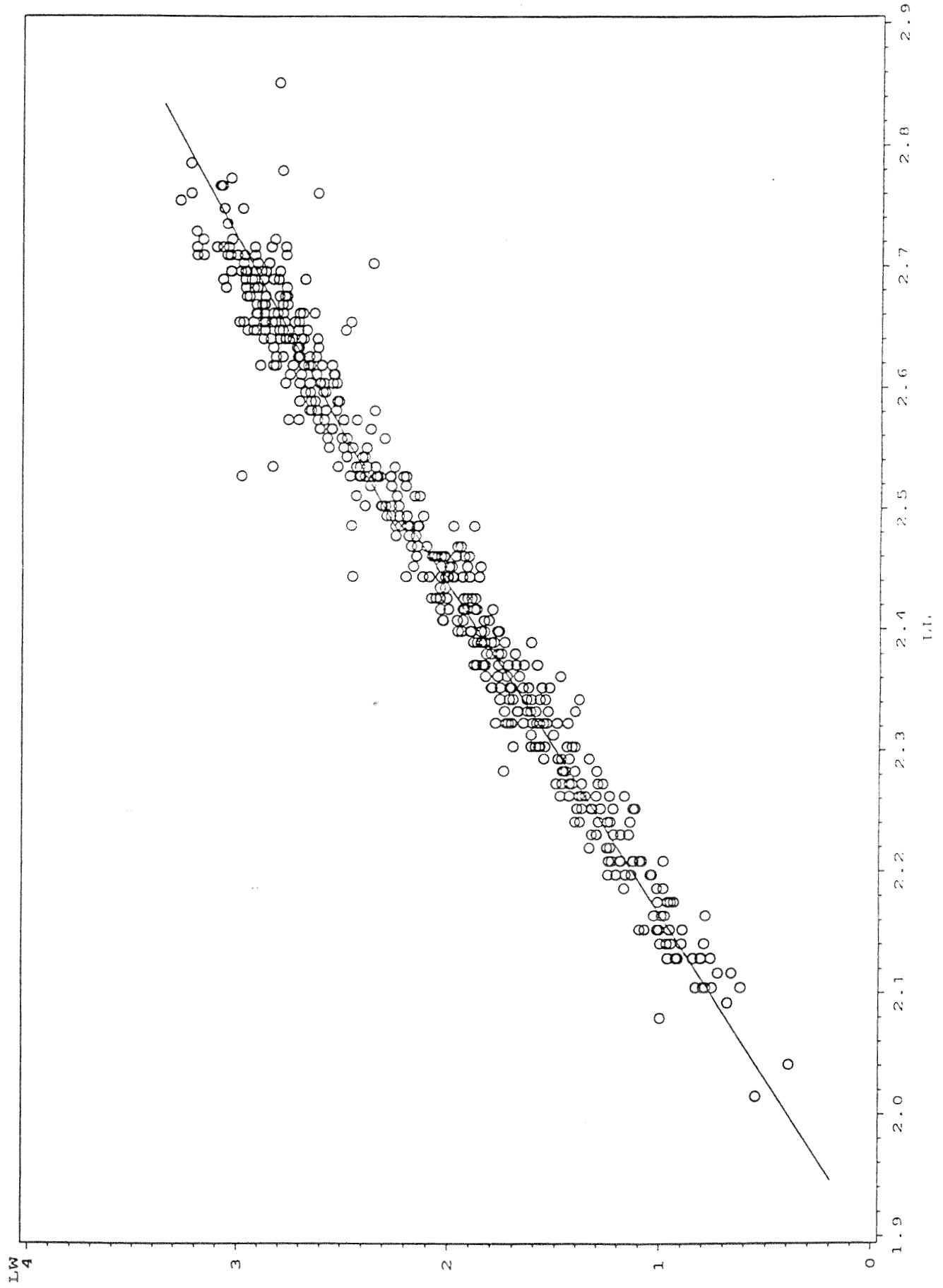
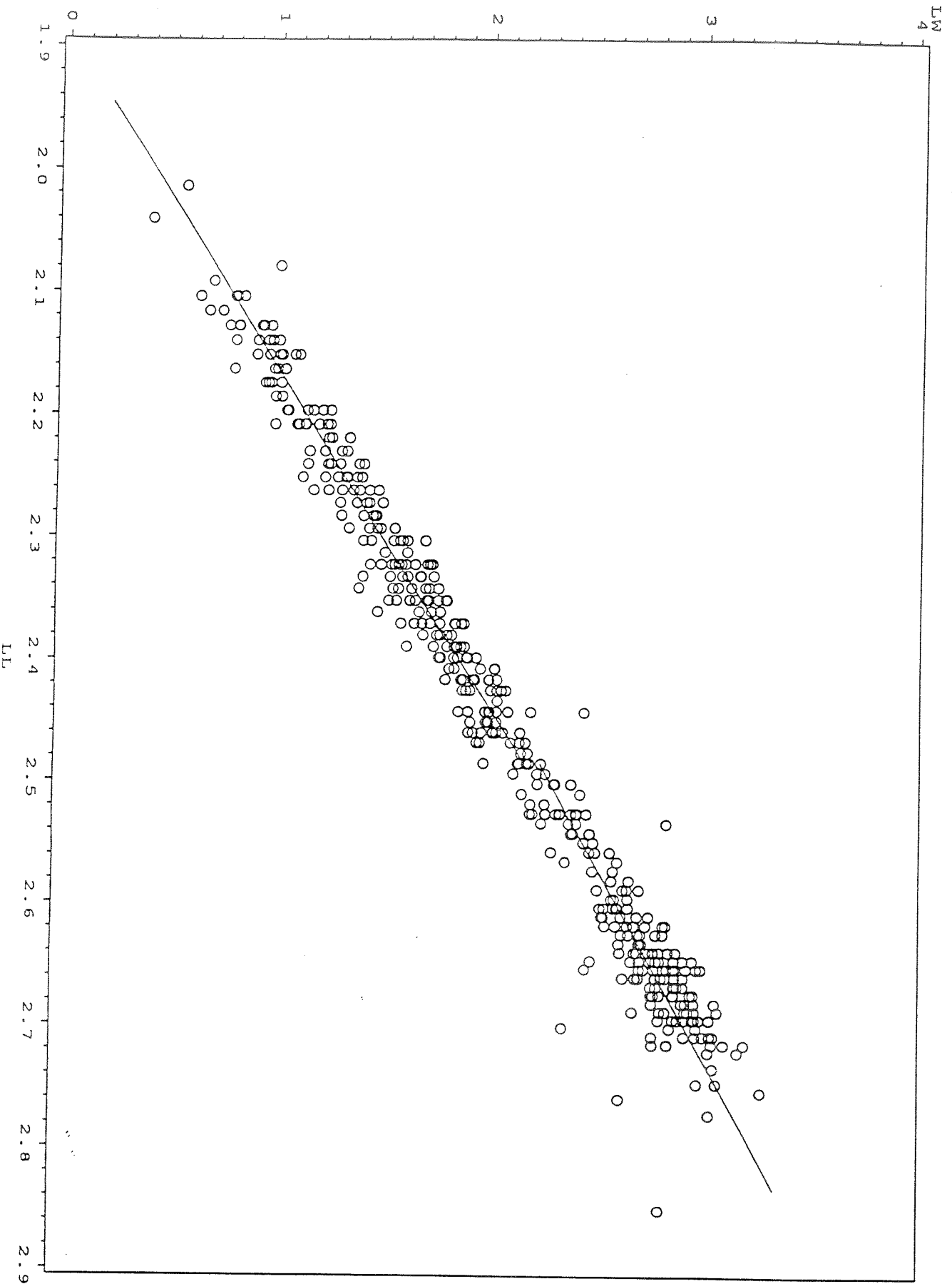


Figure 3
length — weight relationship
length group 06-17.9cm, Female



Gastric evacuation for capelin 6-17.9cm
(star=predicted, square=observed)

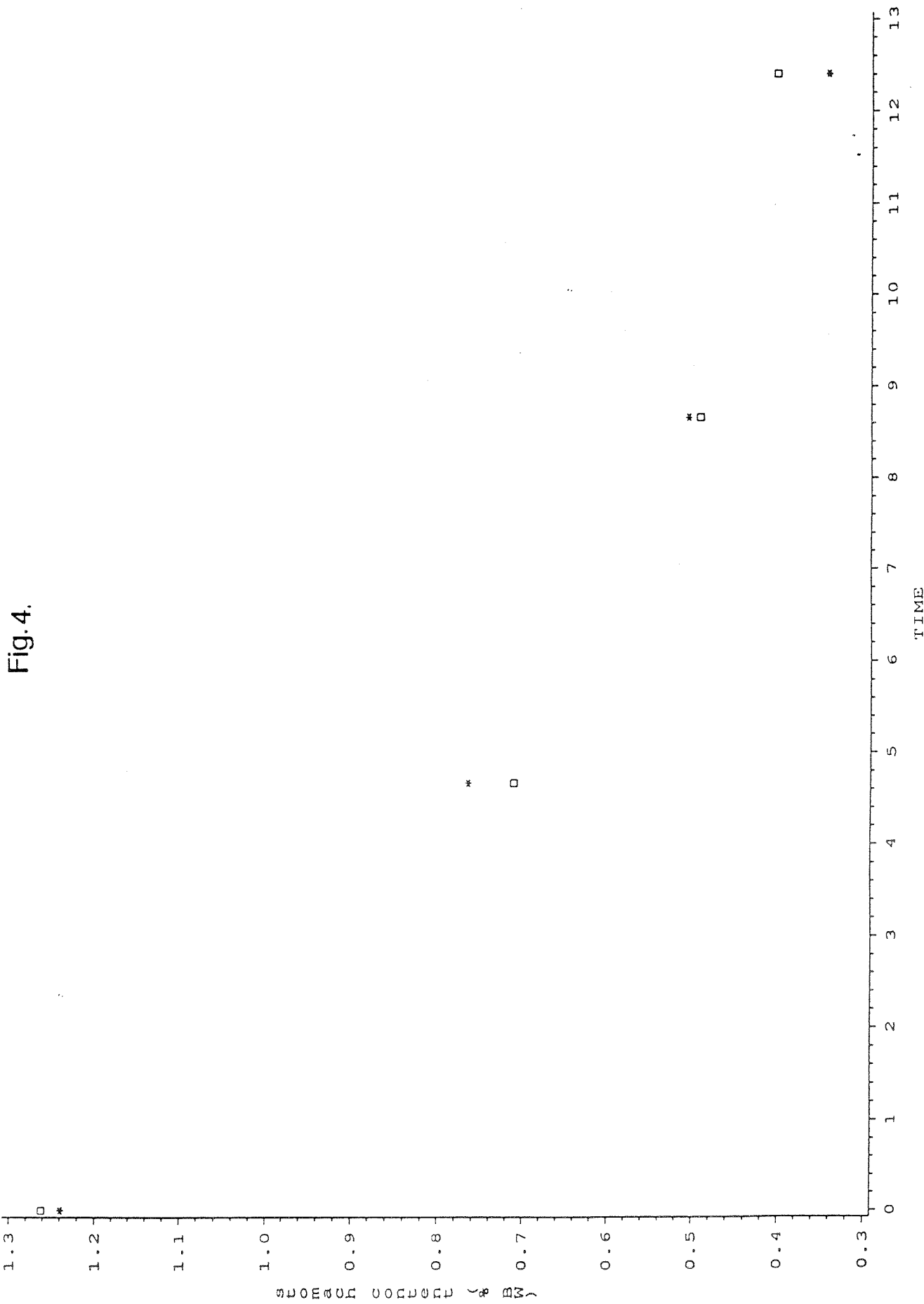


Fig.5a -- Length group 06--14.9 cm

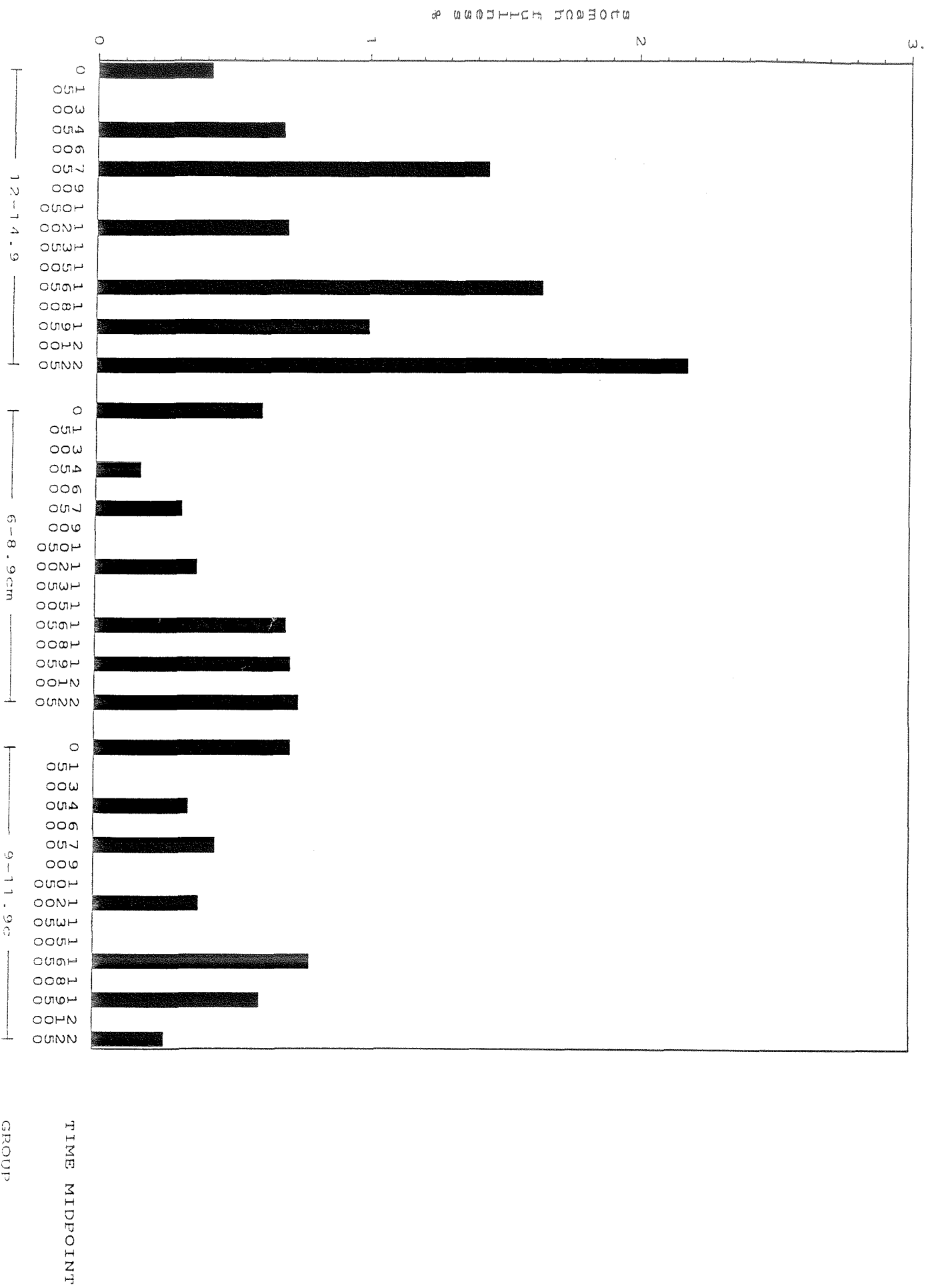
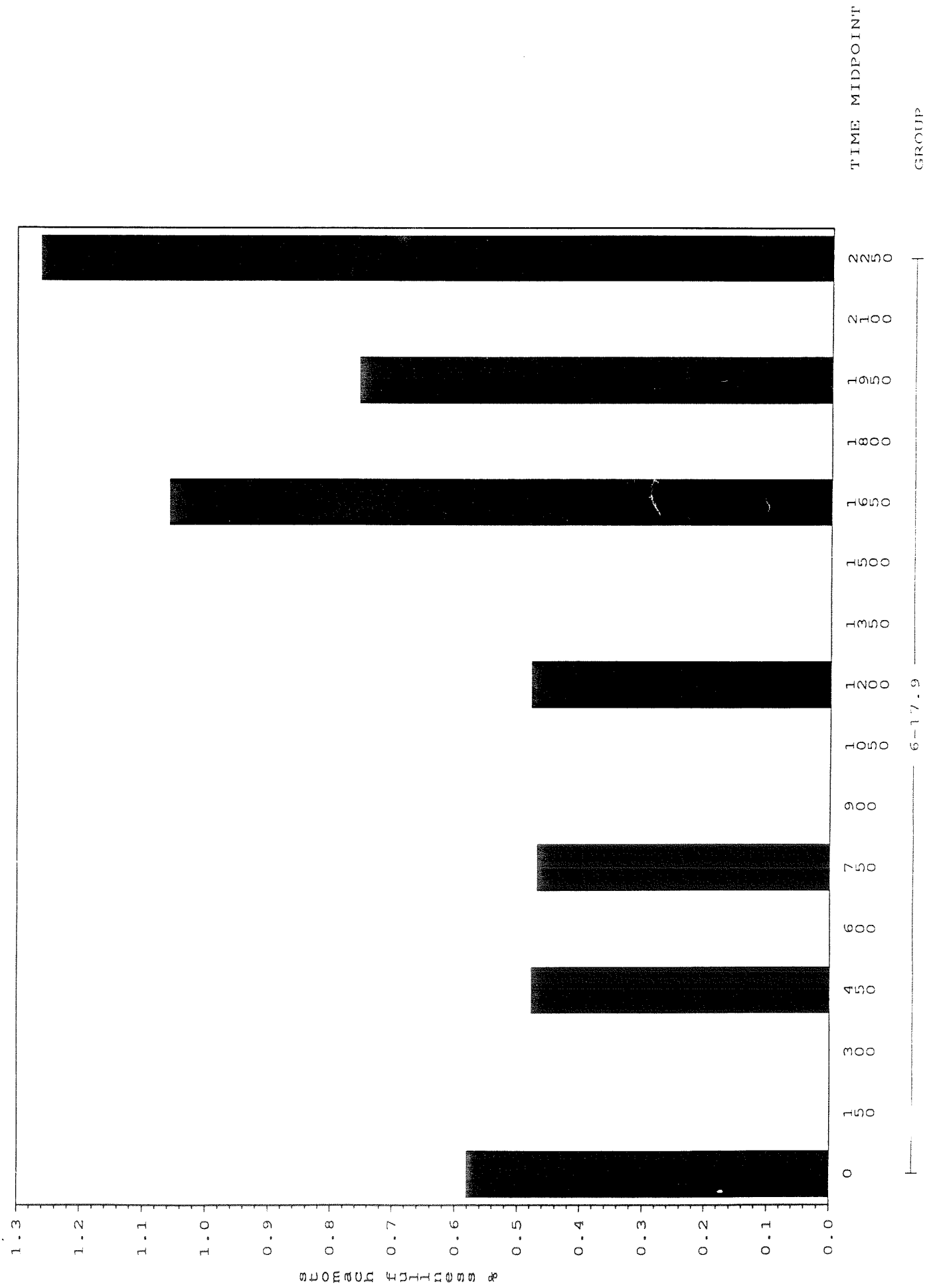


Fig.5b — Length group 06—17.9 cm



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PREFACE

The latest decade has seen a growing interest among fish managers of taking into account species interactions. The collapse of the Barents Sea capelin stock in the period 1983–1986 increased this interest and has led to a demand for the fish scientists to build interaction terms into the management models.

This symposium presents some of the research done in the joint PINRO-IMR programme "Interrelations between stocks of commercial marine organisms in the Barents Sea". The programme was started in 1985 and focused in its first years on the building of a joint stomach content data base. Based on this data base, the main features of the importance of the North-East Arctic cod in the Barents Sea ecosystem have been revealed in a number of papers by researchers from PINRO and IMR, some of the papers being presented at this symposium.

The work with the stomach content data is the basis for developing new models that may provide a better basis for management than the previous single-species ones. The cooperation between PINRO and IMR has not yet resulted in a joint model, although a number of different models exist on each side and are to a certain extent documented in these symposium proceedings.

The symposium is the fifth in a series of PINRO-IMR (formerly named Soviet — Norwegian) symposia dealing with important aspects of fish stocks and their environment in the North-East Atlantic.

As with earlier symposia, the papers have not been subject to peer reviews. The editors have made changes in order to clarify the content of the papers, and it was not always possible to check this with the authors.

In addition to this version in the English language, the contributions will also appear in a version in the Russian language published by PINRO, Murmansk.

The editors are greatly indebted to Tatjana Smolianova for her effective and encouraging help with the Russian manuscripts and to Jaime Alvarez for invaluable technical assistance.

Questions about multispecies research in the Barents Sea in general or about papers in these proceedings in particular may be sent by e-mail to: sigurd@imr.no.

Bergen, November 1992

The editors

METHODS AND RESULTS IN THE JOINT PINRO-IMR STOMACH SAMPLING PROGRAM

by

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ABSTRACT

In 1984 IMR started a stomach sampling program on cod (Gadus morhua) in the Barents Sea. The aim of the program was to provide the multi-species model with quantitative data on the cod's food selection. Later other species have been included in the investigations. In 1987 PINRO joined the program, and the two countries have almost identical methods for sampling at sea, laboratory analyses and computer registration of the data. Stomach data are exchanged annually on data medium and the two countries have built up identical stomach content data bases. The data base now contains information from more than 56000 individually analysed fish. 40000 of these are cod, and the majority (34000) are sampled from 1984 to 1990. A number of works are based on the stomach data base; describing the diet of several species and the cod stock's food consumption, comparing individual growth and food consumption in the cod stock and calculating mortality on several preys induced by cod.

INTRODUCTION.

In the beginning of the 1980's the work on a multispecies model for the Barents Sea was initiated at IMR. Cod (Gadus morhua) and capelin (Mallotus villosus) were the starting point for the building of the model (Mehl et al. 1985), and an essential requirement for the model were quantitative data on the cod stock's food selection. A stomach sampling program on cod started winter 1984, and a stomach content data base has been built up. Later, data on other species than cod have been included in the base.

International cooperation on the development of multispecies models are necessary (Mehl and Tjelmeland 1990). The fish stocks are managed by international agreements, and the resources needed for developing multispecies models exceeds what can be expected to be spent by one country. Especially, the data requirements are high. The stomach data must be extensive both in time and space, and the predators' main area of distribution should be covered several times of the year. To meet this requirement, an exchange program between IMR and PINRO on stomach content data was initiated in 1987. This paper describes the methods used in the joint stomach sampling program, as well as the present status of the joint stomach content data base. The result of some work based on the stomach data base are also referred.

METHODS

The methods used for sampling, stomach analysis, data recording and computer input are mainly the same as for the ICES "Stomach sampling project 1981" in the North Sea (Anon. 1974, 1980, 1981; Westgård 1982; Mehl 1986a; Christiansen 1987a; Tretyak et al. 1990). Samples have been collected onboard Norwegian and Russian research vessels during routine surveys in the Barents Sea and the Svalbard area (Fig. 1). The gears used are both pelagic and bottom trawl, but the bulk of the samples are taken by the latter. The reasons for this are several: cod is difficult to catch by pelagic trawl, there is not enough time available for pelagic trawling during a bottom trawl survey, the Russian vessels can only have one type of trawl ready for trawling at a time.

In the North Sea project a minimum of ten stomachs per statistical rectangle per quarter should be collected for each given predator length group. The sampling intensity in the Barents Sea has been adjusted to the two countries' survey programs in the area. On Norwegian surveys, the aim has been to collect up to ten stomachs of cod for each 10-cm length group on stations with other biological sampling (otoliths etc.). The trawl stations are randomly spread within each stratum of the investigated area, and the sampling continues over 24 hours per day. A portion of samples collected by PINRO for 1986 and 1988-1990 has been obtained in special cruises for observations over daily dynamics of fish feeding. In these cases the samples have been taken in the same area in definite intervals of time during a day or more (Tarverdieva and Yaragina 1989; Dolgov 1989; Dolgov and Yaragina 1990).

Fish which show evidence of regurgitation, are if possible replaced with non-regurgitating feeding fish. Onboard Norwegian vessels, each stomach is frozen separately as soon as possible after sampling. Data on the length, weight, sex, maturity stage and the number caught per trawl haul of each individual predator are recorded together with the station data. Age data are included later after the otoliths

are read and age determined. Onboard Russian vessels, the stomachs are preserved individually in 4 % formalin. In addition to the above mentioned data, the weight of the predator's liver is normally recorded.

In the laboratory the frozen stomachs are open as soon as practically possible. Fish prey and shrimps are identified to species level when possible, other prey is identified to species level when practical. Each recognizable prey species, genus, family or higher order are split into size-classes and damp dried on bibulos paper. Numbers and total wet weight, measured to the nearest milligram, are recorded for each size-class and prey category separately.

Since the Norwegian and Russian methods for sampling at sea and laboratory analysis were almost similar, it was decided to use the Norwegian data form (with some minor changes) for data recording. This was agreed upon during a meeting between Norwegian and Russian scientists in Murmansk 15 - 26 April 1987. An example of the dataform and coding instructions is given in Christiansen (1987a). 10-digit NODC species codes (Anon. 1984) are used for coding the predator and prey species. Mehl (1985) lists the species and codes that are most frequently used in the stomach program. Norway and Russian have slightly different codes for maturity stage, degree of stomach filling and degree of digestion (Table 1). In addition, the two countries have opposite codes for sex (1=male and 2=female in Russian, in Norway the other way around). During the meeting it was decided to leave it this way in the data base and to convert the scales to match each other in the computer programs retrieving data from the data base. Attempts were made to install the IMR stomach program system on PINRO computers, but this failed. Back in Bergen, the Fortran programs on the IMR Norsk Data computer were converted to MS-DOS (Alvheim 1987) and installed on a personal computer which later was lent to PINRO. During a meeting between Norwegian and Russian scientists in Bergen 7 - 18 December 1987 the stomach program system was demonstrated for the Russian scientists and they got some experience using the system. It was decided that the first exchange of stomach data on data medium (diskettes) should take place in Murmansk at the annual spring meeting in 1988.

Since 1988 stomach data have been exchanged annually, and both countries have built up identical data bases. The structure of the data base is described in Westgård (1982), Mehl (1986a), Alvheim (1987) and Christiansen (1989). Several computer programs have been developed for extracting information from the data base (Westgård 1982; Mehl 1986a, Alvheim 1987, Christiansen 1987b, 1989). The most commonly used program aggregates information over areas and time periods and produces a summary table for the specified predators diet after criteria given interactively on the screen (Christiansen 1989). The user has to specify time period, geographical area, predator species, predator size group or age group, prey size or not, taxonomic level on output and which stomachs to be included (all or only those with content). Other criteria have default values that can be changed: weight unit on output, time of the day to be included, depth interval, gear, weighting factor in aggregation procedure, nation and which predator age to be used (punched or calculated from an age/length key). The result file first gives information on the number of stations in the given area and time period with the specified predator, total number of stomachs, percentage empty, average filling degree, mean index of stomach fullness, relative index of fatness (if liver-weight data) and average predator weight. The following diet list gives information about each

prey category (mean values): weight per predator and weight percentage, number per predator and number percentage, weight of an individual prey item, frequency of occurrence, index of relative importance and the average weight percentage per stomach.

THE STOMACH DATA BASE.

Table 2 lists the present number of stomachs included in the data base by species and year. All together data from 56737 fish are now in the base. Cod contribute with more than 70 % of the stomachs (40512) and haddock (Melanogrammus aeglefinus) with almost 20 %. A smaller number of stomachs from capelin, herring (Clupea harengus), redfish (Sebastes spp.), blue whiting (Micromesistius potassou), polar cod (Boreogadus saida) and plaice (Pleuronectes platessa) are also included in the data base.

The cod stomachs are sampled from 1950 to 1990, but the bulk of them are from 1984 and onwards. Table 3 presents the number of cod sampled from 1984 to 1990 by year and quarter. The first and third quarter of the year are best covered with samples. All of the stomachs collected in 1990 are not yet analysed and included in the data base.

Fig. 1A-D show the geographical distribution of trawl stations with sampling of cod stomachs by quarter for the period 1984-1990. In the first quarter of the year the main area of distribution is well covered north to the ice edge, and almost 500 stations have been taken in the period. The second quarter is least sampled, and most of the 150 stations are taken during the Norwegian shrimp survey in the central Barents Sea. The sampling in the third quarter cover most of the Northeast Arctic cod stock's area of distribution at that time of the year. More than 400 stations have been sampled, many of them during the Russian-Norwegian multispecies survey. The last quarter of the year has the best coverage in the south-eastern part of the Barents Sea, where the major part of about 200 stations have been taken.

Table 4 presents the number of cod stomachs sampled by predator size group and year for the period 1984-1990. The size groups between 30 and 70 cm are best represented, but also the groups 20-29 cm and 70-79 cm are reasonably well covered. Few fish below 10 cm and over 80 cm are sampled. Although the sampling strategy has been to collect the same number of stomachs from the different size groups, strong year classes are better represented than weaker ones. In the table we can follow the 1983 year class from it enters size group 10-19 cm in 1984 and goes across the table to size groups 60-69 and 70-79 cm in 1989-90.

RESULTS.

This paper does not intend to present any new results by its own, but the result of some of the work based on the stomach data base is summarized in the following.

The cod's diet and consumption

The prey spectrum of cod is broad, and there are size related, spatial, seasonal and year-to-year variations in the diet (Mehl 1986b; Orlova et al. 1988, 1989, 1990a). The general trend is that crustaceans, mainly copepods, krill (Euphausiacea) and amphipods (Hyperiidae), are the dominant food of smaller cod and fish are the major prey of cod

larger than 25-30 cm. Capelin is the main fish prey, and is most important for medium-sized cod. Crustaceans such as deep sea shrimp (Pandalus borealis), amphipods and krill also are important for medium-sized cod. The largest cod prey more upon larger fish such as haddock, redfish (Sebastes spp.), blue whiting, flatfish (Pleuronectidae) and cod (cannibalism).

The diets of cod and haddock have been compared (Burgos and Mehl 1987), but the diet overlap was low except in spring and fall when smaller sizegroups of both species prey on krill. Observations on 2-day stations indicated the indices of food similarity for cod and haddock to vary during the day and the highest indices resulted from an occurrence of euphausiids in feeding spectra of these fishes (Dolgov and Yaragina 1990).

The Northeast Arctic cod stock's total consumption has been estimated by combining stomach content data for each agegroup with data on gastric evacuation and the number of cod in each agegroup (Mehl 1989; Bogstad and Mehl 1991). Capelin has made up the largest part of the total consumption, and the increasing cod stock in 1984-86 probably contributed to the quick depletion of the capelin stock. The consumption of capelin was lowest in 1987 and started to increase from 1988. Shrimp, redfish and amphipods have also contributed much to the cod stock's consumption. Herring, haddock and young cod have made up a minor part of the diet measured in biomass consumed, but measured in numbers consumed, the predation pressure must have been considerable on several year classes of these prey species during the mid 1980s. The cod stock has probably consumed a higher number of itself than what is recruited to the fishable part of the stock (3+) in an average year (Korzhev and Tretyak 1989; Mehl 1989; Skagen et al. 1990).

The consumption estimates are strongly dependent on the gastric evacuation model used in the calculation and may vary by a factor of 2.0 depending on the chosen model (Bogstad and Mehl 1990). This is too much when the consumption of some important prey species are of the same order of magnitude as the catch. The estimates are also dependent on the quality of the stomach content data and how representative the data are for the different components of the cod stock. The stomach content may vary for fish feeding pelagic and near the bottom (Ajiad 1990). The survey design will affect the precision of estimates of average stomach contents (Bogstad et al. 1991). Theoretical calculations made by Tretyak et al. (1990) showed that 50 stomachs from each 10-cm size group are necessary for obtaining statistically reliable data, characterizing feeding of cod in any month. The total yearly number of samples with allowance for 7 areas of the Barents Sea then increases to 20.000, which hardly can be achieved.

There seems to be a food availability dependent growth in cod (Ajiad et al. 1989). The cod partly compensated the loss of capelin by preying more intensively on other food items. But change of qualitative food composition was followed by variations in seasonal growth of cod (Yaragina 1989; Orlova et al. 1990b). Scarce quantities of capelin, apparently influence upon the maturation of cod due to efficiency of feeding and variation in growth rate of cod (Orlova et al. 1990b). Total annual consumption and individual growth was dramatically reduced, and average fish weight decreased by about 50 % in most age groups from 1985 to 1988 (Mehl and Sunnanå 1990). Because the quotas are in tonnes, more fish than expected were caught. This together with the increased cannibalism caused management problems (Mehl 1991).

The diet of other fish species

The diet of a few other species has also been described based on data from the stomach data base. Haddock is a less ichthyophagous predator than cod and prefer more benthic preys including echinoderms, gastropods, bivalves and polychaetes (Burgos and Mehl 1987). The diet of polar cod, an opportunistic feeder, consist primarily of amphipods (Parathemisto spp.), copepods (Calanus spp.) and krill, the composition varying from region to region (Ajiad and Gjørseter 1990).

Stomach data in multispecies models

The main purpose for the stomach sampling program has been to provide the multispecies model for the Barents Sea with data on the cod's food selection. The data are used in connection with the parameter estimation of the predation equations in the model. The model has been used to calculate the mortality on mature capelin induced by cod (Tjelmeland 1987; Bogstad and Tjelmeland 1990, 1992). The obtained mortalities range from about 0.5 to 2.0, and vary from year to year depending on changes in the cod stock and in the environment.

The stomach data have also been used in a spreadsheet system to do a transparent multispecies analysis of the Barents Sea and Norwegian coast (Bax et al. 1990). Output from the spreadsheet showed discrepancies between the biomasses estimated from surveys and commercial fishery statistics on the one hand, and losses in biomass estimated via food habits and catch data, on the other.

Stomach data on cod have been essential when VPAs modified for cannibalism are made (Skagen et al. 1990; Korzhev and Tretyak 1989). These works show that cannibalism has been considerable during the second half of the 1980s, and such informations must be taken into account when prognosis are made.

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Table 1 Russian and Norwegian codes for maturity stage, degree of stomach filling and degree of digestion

| Maturity stage | | Stomach filling | | Digestion | |
|----------------|--------|-----------------|-------|-----------|-------|
| IMR | PINRO | IMR | PINRO | IMR | PINRO |
| 0 | I,II | 1 | 0 | 1 | 1 |
| 1 | III,IV | 2 | 1 | 2,3 | 2 |
| 2,3 | IV-V | 3 | 2 | 4,5 | 3 |
| 4 | V | 4 | 3 | | |
| 5 | VI | 5 | 4 | | |
| 6 | VI-II | 6 | 5 | | |
| 7 | - | | | | |

Table 2 Number of stomachs included in the PINRO-IMR stomach data base at 26 April 1991 by species and year.

| Year | Cod | Haddock | Capelin | Herring | Redfish | Blue W. | Pol. Cod | Plaic. |
|------|-------|---------|---------|---------|---------|---------|----------|--------|
| 1950 | 141 | | | | | | | |
| 1951 | 25 | | | | | | | |
| 1952 | 616 | | | | | | | |
| 1954 | 134 | | | | | | | |
| 1955 | 188 | | | | | | | |
| 1956 | 1005 | | | | 74 | | | |
| 1957 | 522 | | | | | | | |
| 1958 | 453 | | | | | | | |
| 1959 | 1028 | | | | | | | |
| 1960 | 186 | | | | | | | |
| 1973 | 174 | | | | | | | |
| 1975 | 199 | | | | | | | |
| 1980 | 608 | 241 | 125 | | | | | |
| 1981 | 408 | | | | | | | |
| 1982 | 833 | | 225 | | | | | |
| 1983 | | | 441 | | | | | |
| 1984 | 3731 | 593 | 636 | 998 | | | | |
| 1985 | 4153 | 1240 | 98 | 430 | | 21 | | |
| 1986 | 6044 | 1039 | 365 | 77 | | 103 | 208 | |
| 1987 | 5945 | 1006 | 50 | | | 228 | 488 | |
| 1988 | 5419 | 2296 | | | 110 | | 752 | 15 |
| 1989 | 6406 | 2224 | 728 | | | | 625 | 32 |
| 1990 | 2264 | 757 | | | | | | |
| SUM | 40512 | 9396 | 2668 | 1505 | 184 | 352 | 2073 | 47 |

Table 3 Number of cod stomachs sampled in the period 1984-1990 by quarter and year.

| YEAR | QUARTER | | | | SUM |
|------|---------|------|-------|------|-------|
| | 1 | 2 | 3 | 4 | |
| 1984 | 1087 | 346 | 1009 | 1289 | 3731 |
| 1985 | 1882 | 512 | 1271 | 488 | 4153 |
| 1986 | 1969 | 471 | 2952 | 652 | 6044 |
| 1987 | 1654 | 921 | 2045 | 1325 | 5945 |
| 1988 | 2513 | 252 | 1226 | 1428 | 5419 |
| 1989 | 2800 | 846 | 2497 | 263 | 6406 |
| 1990 | 1163 | 682 | 419 | | 2264 |
| SUM | 13068 | 4030 | 11419 | 5445 | 33962 |

Table 4 Number of cod stomachs sampled in 1984-1990 by predator sizegroup and year.

| Year | Predator sizegroup | | | | | | | | | | Total |
|-------|--------------------|-------|-------|-------|-------|-------|-------|-------|-------|-----|-------|
| | 0-9 | 10-19 | 20-29 | 30-39 | 40-49 | 50-59 | 60-69 | 70-79 | 80-89 | 90+ | |
| 1984 | 13 | 500 | 610 | 640 | 747 | 508 | 372 | 245 | 67 | 29 | 3731 |
| 1985 | 30 | 330 | 804 | 664 | 831 | 762 | 433 | 175 | 87 | 37 | 4153 |
| 1986 | 40 | 419 | 618 | 1111 | 1211 | 1344 | 1041 | 201 | 37 | 22 | 6044 |
| 1987 | 4 | 205 | 637 | 1004 | 1590 | 1164 | 910 | 350 | 59 | 22 | 5945 |
| 1988 | 3 | 44 | 358 | 979 | 1734 | 1644 | 558 | 204 | 54 | 23 | 5419 |
| 1989 | 12 | 141 | 287 | 724 | 1368 | 1842 | 1484 | 423 | 94 | 31 | 6406 |
| 1990 | 1 | 191 | 187 | 264 | 258 | 398 | 506 | 342 | 81 | 36 | 2264 |
| Total | 103 | 1830 | 3501 | 5204 | 7739 | 7662 | 5304 | 1940 | 479 | 200 | 33962 |

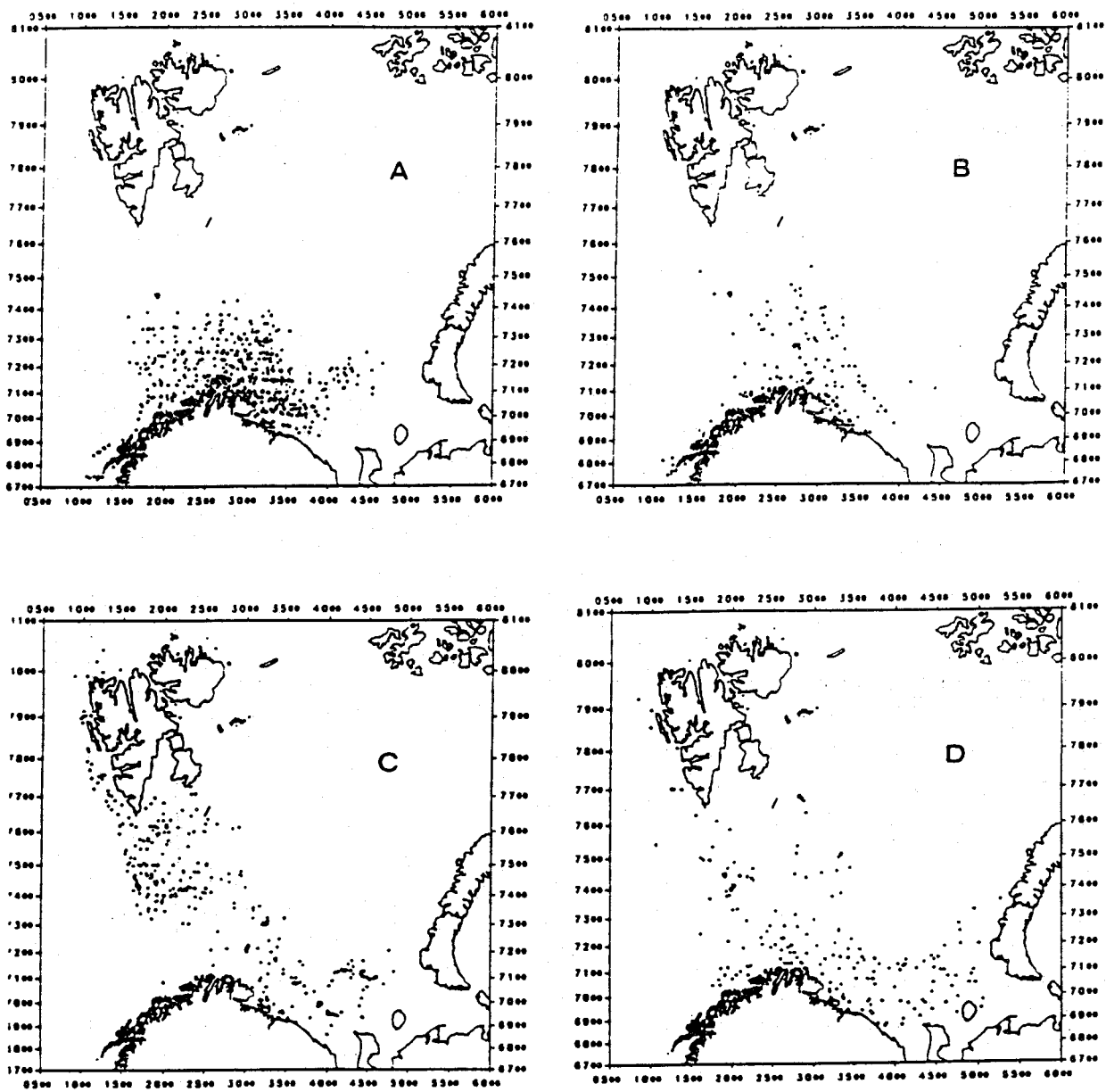


Figure 1: Geographical distribution of trawl stations with sampling of cod stomachs by quarter in 1984-1990. Q1 (A) = 497 stations, Q2 (B) = 149 stations, Q3 = 435 stations, Q4 = 221 stations.

TROPHIC GROUPS OF THE BARENTS SEA FISHES

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ABSTRACT

Based on the analysis of literature material trophic groups of fishes which are characterized by similar food habits were established with the aim of employing data on feeding of poorly-studied species in the Barents Sea ecosystem model and accounting for interspecific trophic relationships.

INTRODUCTION.

Feeding of an individual species and its trophic relationships with other components of a biocoenosis form the background of the Barents Sea multispecies fish model which has been developed by IMR and PINRO. However, up to now it is only material on feeding of cod, haddock and capelin which is adequate enough to be used in the model. Meanwhile, the neglect of trophic relationships can lead to regrettable results, which was the case with capelin in the mid-80s. With this in view at least a general concept of feeding of the Barents Sea fishes is needed to be applied in the model to species which are characterized by similar food habits (Larkins and Laevastu, 1987) and to provide a background for planning future research. The present paper attempts at identification of the above- mentioned trophic groups and of the degree of possible food competition (as a first approximation).

MATERIAL AND METHODS

Use was made of literature material and of the original results of quantitative and qualitative analysis of fish feeding which was performed at the Laboratory of the North European demersal fishes at PINRO. A list of the literature used is given in the Appendix. Out of about 150 species occurring in the Barents Sea (Andriyashev, 1954) feeding data are available on nearly 50 species. Despite the fact that information on quite a number of species is scarce and fragmentary it still allows for obtaining a general picture of feeding patterns. The following values were used as criteria of significance of a given group of food organisms in the feeding of a given fish species (mainly as percentage of food bolus weight or the frequency of occurrence): major food: > 50%, secondary food: 25-50%, additional food: 10-24% and occasional food: < 10%. The suggested classification is to be regarded as provisional and it was accepted due to inhomogeneity of the data available though traditional methods of assessment of food item significance have already been developed (e.g. Rosecchi and Nouaze, 1985).

RESULTS AND DISCUSSION

As a result of the analysis of feeding data the following groupings were established to include fishes which are characterized by similar feeding habits:

1. Plankton-eaters.

The bulk of food of planktophagous is formed by copepods, euphausiids and hyperiids. Within this group the following subgroups can be distinguished:

a) "pure" plankton-eaters (i.e. species which feed on plankton almost exclusively): herring, capelin, polar cod, Norway pout, sandeels, Triglops nybelini and Eumicrotremus spinosus;

b) species which are characterized by a fairly high proportion of benthic organisms (mostly amphipods) in their diet: Leptagonus decagonus, Liparis fabricii and Careproctus reinhardtii;

c) species in the feeding of which fish and shrimps play a very important part: Sebastes marinus and S. mentella.

To plankton-eaters belong also larvae and juveniles of fishes from other groups, such as pelagic one-summer old and juvenile cod, haddock, saithe, 3 catfish species and long rough dab.

2. Benthos-eaters

Polychaetes, echinoderms, small and large bottom crustaceans and mollusks are major food items of benthophagues. The following subgroups can be distinguished within the group to include species which feed mainly on

a) polychaetes and molluscs: plaice and flounder, Artediellus europaeus, Lumpenus medius, and Lycodes pallidus (+ echinoderms)

b) bottom crustaceans (mostly amphipods): Ulcina olriki, Lycodes agnostus, Myoxocephalus quadricornis (+ fish)

c) polychaetes and small bottom crustaceans: Raja fyllae (+ shrimps), Icelus bicornis, Triglops pingeli, Triglops murrayi, Leptoclinus maculatus, Lycodes seminudis, L. rossi, L. sarsi (+ molluscs), Cyclopterus lumpus, Glyptocephalus cynoglossus (+ molluscs) and Phrynorhombus norvegicus (+ fish)

d) polychaetes, echinoderms, small bottom crustaceans and molluscs: Lumpenus lampretaeformis, Lycodes vahlii, Limanda limanda, Microstomus microcephalus and haddock (+ fish, euphausiids and shrimps)

e) echinoderms, molluscs and large bottom crustaceans: common, spotted and blue catfishes

f) echinoderms: Lycodes esmarki.

3. Fish—eating species.

The fish-eating species feed mainly on capelin, herring, polar cod, as well as on juveniles of redfish, gadoids and of some other species. Based on the secondary food items the following subgroups can be distinguished:

a) species in the diets of which the proportion of large crustaceans (shrimps, crabs, etc.) is fairly high: starry ray, Myoxocephalus scorpius, Greenland halibut (+ cephalopods), cod and saithe (+ euphausiids) and Liparis gibbus

b) species which occasionally feed on large crustaceans and benthic organisms (polychaetes, ophiura, etc.): spiny dogfish, Greenland shark and long rough dab.

The suggested classification is schematic in many aspects but it indicates clearly that almost all commercial species compete for food with both commercial and non-commercial ones. The major food items which occur in the stomachs of almost all the fishes and which induce competition are capelin, shrimp, euphausiids, temisto, and some other species. The toughest food competition is observed during the fattening period when quite a number of fishes change over to feeding on one species (e.g. on capelin or on euphausiids). However, due to gaps in knowledge of feeding of most of the fishes the complicated trophic relationships have not yet been employed in the ecosystem model and predation on species which are commercially important is not taken into account, which results in erroneous assessments of the prey stock size. With this in view the following method of accounting for food competition in the model can be suggested: Due to the lack of data on feeding of mass commercial species, such as redfishes, Greenland halibut, starry ray, saithe, and some others it is feasible to establish fixed values of the proportion in their diet of food items which are commercial

species (capelin, shrimp, young cod and redfish, and some others). Based on the values established the expected predation-caused mortality can be estimated. With further progress in feeding studies these values are supposed to be elucidated.

CONCLUSIONS

1. The suggested classification of the Barents Sea fishes on the basis of feeding habits can not be regarded as ultimate and it should be revised after detailed trophological studies are carried out.
2. Most of commercial fishes compete for food with other species which have similar food spectrum.
3. The classification can be employed in the models intended for multispecies fishery management with due regard to the impact of species with poorly-studied feeding on major forage organisms.

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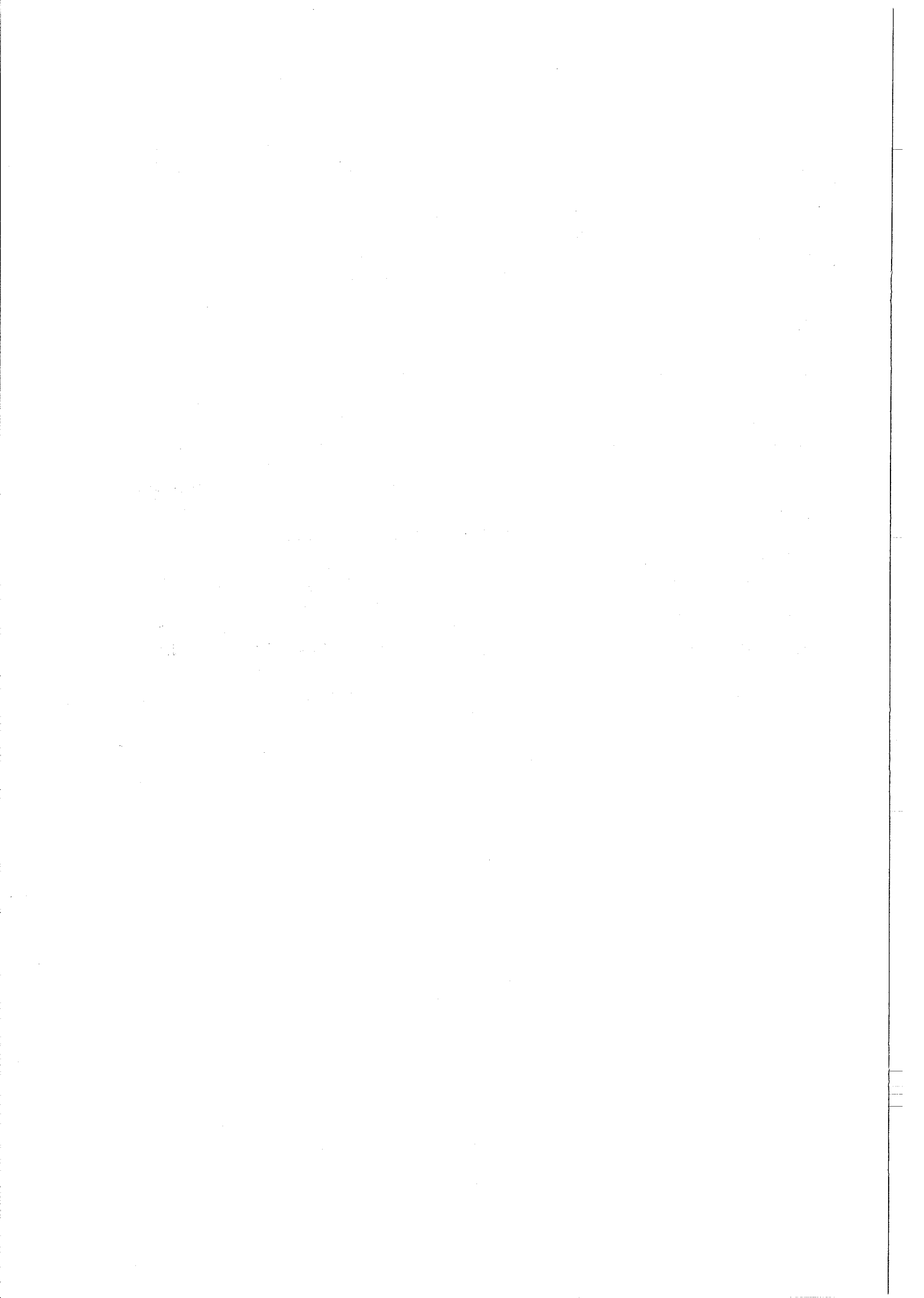
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PREY SIZE PREFERENCE IN COD FEEDING ON CAPELIN AND HERRING IN THE SOUTHERN BARENTS SEA

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ABSTRACT

Against the background of a sharp decrease in commercial fish stock abundance in the Barents Sea, consideration is given to influence of cod on size composition and abundance of its preys (capelin, herring, young redfish and cod). Based on data obtained in 1986-1988 conditions under which predators prefer to feed on particular species or on preys of a definite size are analysed as related to length composition and abundance of predators and preys. Predator-prey size-bound relationships depend in each specific case on their length composition and abundance as well as on trophicity of a given water body. Size preference is most clearly pronounced during predator feeding on one highly available food item. Expansion of prey size range is usually observed in predominant size-groups of predators under deteriorating feeding conditions. From the annual diet of cod of 312 and 446% in 1986 and 1987, respectively, as estimated using Fortunatova's method (1940) the total amount of fish consumed by the cod stock of 1 million tonnes was calculated as 2.8 and 4.4 million tonnes including 0.6-0.9 million tonnes of capelin. With account taken of a drastic reduction in the abundance of both capelin and cod the data obtained can be regarded as comparable to those from the 70s (Ponomarenko et al., 1978). Concurrent calculations of cod daily rations which were carried out using 5 models suggested for cod (Bogstad and Mehl, 1990) and methods suggested by Fortunatova (1940) and Bajkov (1935) yielded similar results, which allows for expecting realistic estimates on the basis of these methods.

INTRODUCTION.

The dramatic decline in catches of a number of commercial Barents Sea fishes observed in late 80s was due both to natural factors and to overfishing (Luka et al. 1989). The latter was particularly strongly pronounced in plankton-eaters (herring, capelin, polar cod and redfish) and it led to disturbances in the trophodynamic structure of communities, insufficient utilization of zooplankton, deterioration of feeding conditions for mass demersal species, and energy loss in the trophic chain (Drobysheva, 1988; Orlova et al., 1988, 1989a). The general direct decrease in fish productivity was also due to fishery-caused reduction in the portion of older age-groups in commercial stocks of cod, haddock and redfish (Nizovtsev et al., 1988, 1990; Sorokin and Shestova, 1988), and, consequently, to low reproduction capacity (Serebryakov, 1988; Mukhina and Yaragina, 1988).

Stock composition and abundance of commercial species is affected both by fishery and by predators. The predation factor acquires special importance since it allows for estimating predation-caused mortality of an individual species, i.e. the natural mortality rate to be employed in stock assessment and catch predictions, which is particularly essential under conditions of energy disbalance in the Barents Sea when new trophic links are likely to appear.

MATERIAL AND METHODS

The analysis of prey-predator relationships is based on the results of all-year-round observations on cod feeding in the southern Barents Sea in 1986-1988. Consideration is given to relations between the predator and its major preys, such as capelin and herring as well as young redfish and young cod during different periods of a feeding season. A total of 1 545 individuals of cod were examined and measurements were made of 1 790 individuals of capelin, 1 060 individuals of herring and 2 170 individuals of redfish taken from cod stomachs. Data on the size composition of capelin and herring are based on the PINRO information.

RESULTS AND DISCUSSION

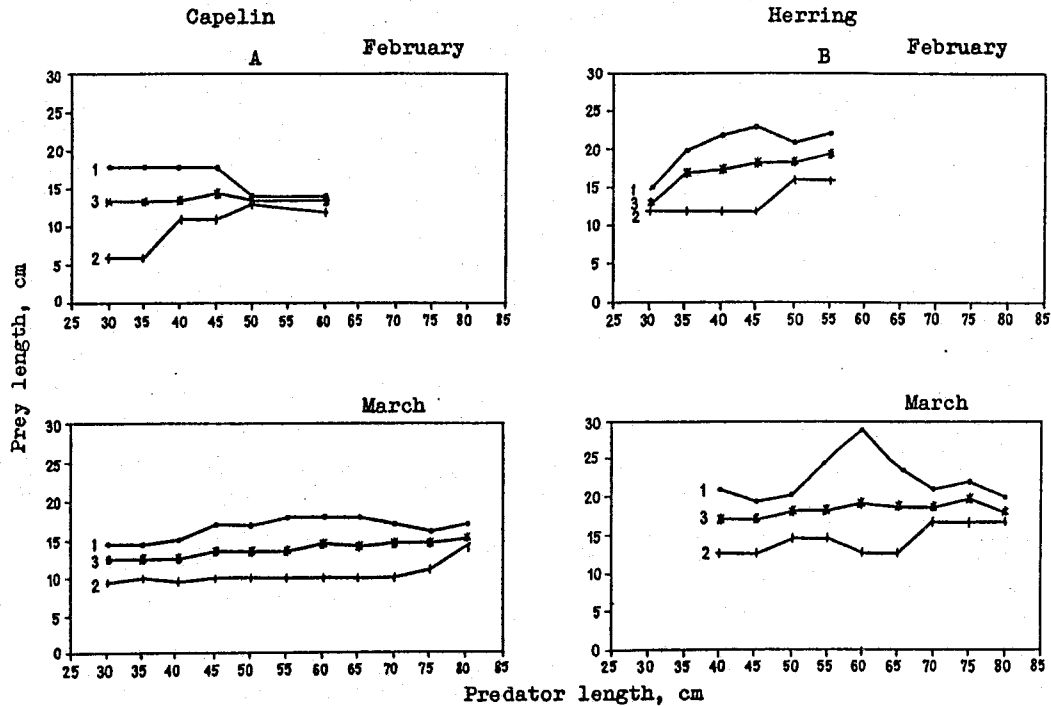
The effect of predation on the structure and abundance of populations is closely connected to abundance and availability of food organisms. Under conditions when one particular food item is consumed (capelin, herring, shrimp or krill) and during "mixed" feeding, when the composition of and ratio between preys and predators is stable or varying, complicated interrelations are established which are governed by a specific sensor system allowing for selecting preys of a definite type and size (Malyukina, 1984 and others), i.e. for feeding at the least energy drain.

The examples considered demonstrate the diversity of forms of size selectivity in the Barents Sea cod during feeding on different types of preys.

In the initial period of spring-winter feeding (the Demidov Bank, the first part of February, 1986) when migrations just started the food spectrum of cod was characterized by a great variety of forage organisms. It comprised up to 10 fish species and more than 20 species of crustaceans, bottom amphipods, worms, coelenterates, ctenophores, echinoderms, and some others. Redfish was recorded most frequently in stomachs of cod of all sizes whereas capelin and herring did not show high abundance (Table 1). In view of low concentrations of food organisms the minimum and maximum sizes of preys were almost similar in all predators except for large-size cod which fed on young immature gadoids and long rough dab. Size preference was demonstrated by cod mainly with reference to redfish.

The increase in the concentrations of capelin and herring in the second part of February was accompanied by a rather strong food competition between predators of different size. Cod below 40 cm in size was predominant in the stock and due to its high food requirements (caused by growth and maturation) it fed mostly (46-80%) on capelin 6-18cm long at the relative (as percentage of the predator length) size as high as 40% in the average and 56-62% at the maximum (Table 2). In predators of larger size the minimal length of capelin consumed was as high as 11 cm and they did not feed on small capelin (of the relative average size of 26-28%). Later the minimum and maximum sizes of capelin from cod stomachs came closer and became almost identical in fish 45-55 cm long (Fig.1), i.e. selective feeding took place. Preys of large size were consumed by the largest predators. As the proportion of capelin in cod diet was decreasing that of herring showed an increase to reach the maximum of 70-100%. Size selectivity with reference to herring was recorded in cod 46-50 cm which fed mainly on individuals 16-22 cm long.

Figure 1 Prey/predator length ratio in February-March 1986
 A — capelin; B — herring
 1 — maximum size, 2 — minimum size, 3 — average size



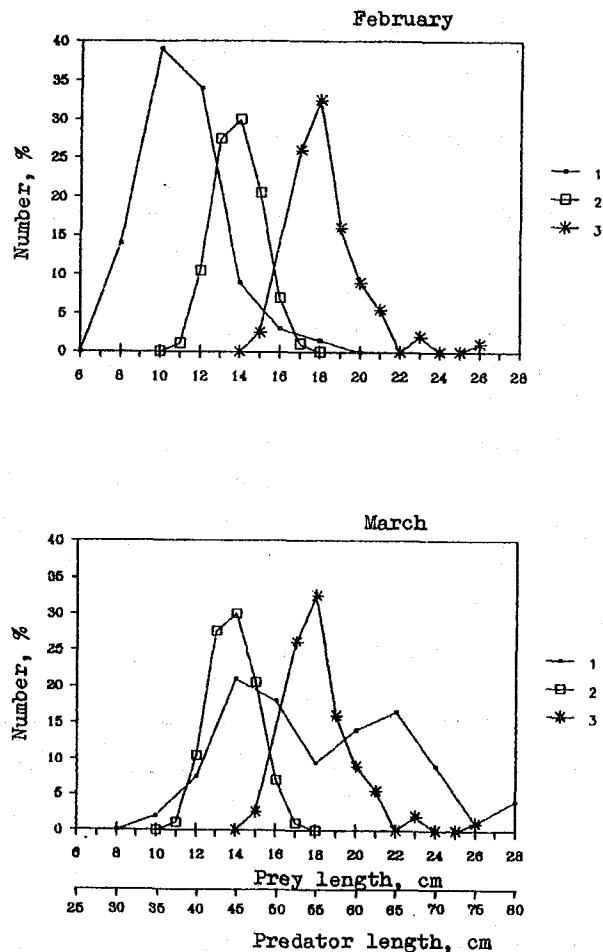
When capelin abundance increased in March predators of all sizes (primarily, the predominant ones 40-70 cm long) started to feed on capelin and differences in the prey size became smoothed. The minimum length increased up to 10 cm (a straight line in Fig.1) whereas the maximum one remained at the February level (17-18 cm). The importance of herring in cod diet was diminished due to a decrease in its concentrations. Since herring is a large-size prey it was consumed by large predators and its maximum length was high in stomachs of cod longer than 50 cm. The relative size of herring constituted 46- 52% and 35-45% of the length of small and large predators respectively. As opposed to February, size preference (consumption of herring 17-22 cm long) was shown by cod 70 cm long (Fig.1). Prey size preference was recorded in small (30-50 cm) cod which fed mostly on 12-16 cm (14 cm at the average) long capelin in the Rybach'ya Bank in March 1987.

Cod feeding on redfish is characterized by certain peculiarities. Redfish is not either a traditional or a chosen food item of cod which is probably due to its high body depth and the presence of a long and hard ray in the dorsal fin. Earlier (Zatsepin and Petrova, 1939) redfish was an occasional food and it was as late as in the 80s that it started to be repeatedly recorded in cod stomachs (Orlova et al., 1988), which is attributed to a general deterioration in feeding conditions for predators. With this in view redfish should be regarded as a forced rather than a free choice for cod in the absence of other food organisms in a water body. The size composition of redfish in cod stomachs (Table 3) was indicative of consumption of immature part of the stock (underyearlings and one-year olds 3-8 cm long and juveniles 12- 18 cm long) and,

(underyearlings and one-year olds 3-8 cm long and juveniles 12- 18 cm long) and, occasionally, of adults 20-25 cm long. When cod fed on redfish a total of 7-12 and 17-22 young small individuals occurred in the stomachs of cod 35-45 and 46-55 cm, respectively, whereas only single large-size individuals were recorded. Cod proved to be selective both in the period when redfish was an additional food (in February-March, 1986 in the Demidov Bank) and when it was major food item (in May 1987 in the Western Trench and in January 1988 in the Demidov Bank) and selectivity was more strongly pronounced in the latter case.

The conclusion can be drawn that size preference which can be an indication of food availability for predators is most distinctly pronounced when they feed on one or almost on one major and easily accessible food organism. Size preference is closely related with abundance of forage organisms. In a number of cases (Fig.2) despite a wide range of prey size (capelin and herring) smaller individuals were selected by predators due to their high abundance. The expansion of prey size range which is indicative of strong food competition was usually observed in the size groups which were characterized by the highest abundance (in February and in March in smaller and larger predators, respectively).

Figure 2 Length composition of preys and predator in February-March 1986
1 — cod, 2 — capelin, 3 — herring



Similar studies made with reference to gadoids in the North Sea and in the Benguela Upwelling area (Feldman, 1989) have also revealed a great variety of forms of prey size preference in predators. In cod, whiting and haddock which feed on sprat and sandeel the prey size preference manifested itself in a change over to feeding on larger individuals (at the expense of an increase in the maximum prey size at the stable minimal ones). The gradual transition to consuming larger preys which was recorded during hake feeding on its own juveniles and on horse mackerel was due to an increase in their minimal size. Ratios between preys and predators doubtlessly reflected food availability level in a given water body as a whole and they were completely dependent on their size composition and abundance.

The analysis of size composition of commercial species (capelin and herring) found in cod stomachs and in catches allows for estimating the summarized effect of both factors on the above populations. Despite insignificant differences, the curves showing size composition of capelin in catches and in stomachs of cod of different size appeared to be basically similar (Fig.3) and so did the average length of capelin (13-14 cm) in stomachs of predators of different size. The spawning stock structure also contributed to this similarity since mature individuals were predominant whereas the abundance of small ones was low. It is worth noting that in the 50-60s the size of capelin in catches was identical to that in predator stomachs and it amounted to 15.5 cm to decrease down to 14.5 cm in 1984-1985 and further down to 13.8 cm (in catches) and 12.9 cm (in cod stomachs) in 1984-1985.

Cod feeding on herring followed a different pattern. Since herring size varied from 12 to 26 cm (the predominant size was 16-20 cm) the fish was not available for small predators and it was rarely recorded in their stomachs. With an increase in cod size the maximum size of herring consumed increased up to 20-23 cm and its role in cod feeding increased accordingly. However, since recruits were mostly of small size the curves showing size composition of herring in catches and in stomachs of small cod differed significantly (Fig.3) but showed close similarity starting from the length of 40 cm.

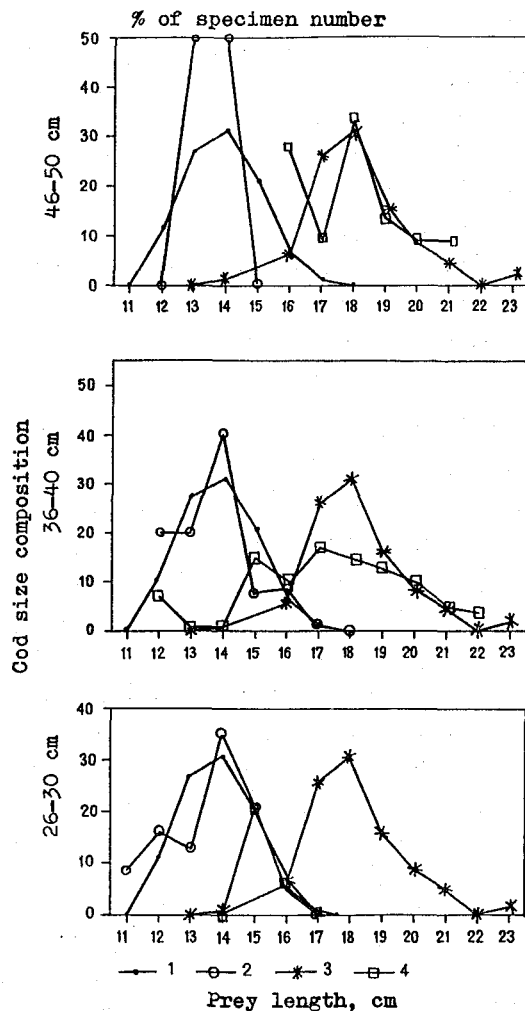
Cannibalism in cod was observed as early as in one-summer olds (Ponomarenko, 1973) and mass feeding on own juveniles was recorded upon the length of 28-30 cm was reached when the maximum relative size of the prey attained 40% of the length of the predator. Cannibalism was closely related to food availability and year-class abundance and it can become a mass phenomenon during the years of high abundance of young fish as a factor contributing to abundance regulation and food competition reduction. It seemed to be the case in the 30s when intense feeding of cod on capelin and herring (Zatsepin and Petrova, 1939) was accompanied by regular and considerable consumption of its own juveniles (Table 4).

Table 4 Average amount of juvenile cod in cod stomachs, per cent of body weight.

| | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec |
|-----------|------|------|------|------|------|------|------|------|------|------|------|------|
| 1934-1938 | 0.23 | 0.31 | 0.22 | 0.18 | 0.11 | 0.07 | 0.10 | 0.15 | 0.40 | 0.31 | 0.21 | 0.15 |
| 1986 | 0.15 | 0.08 | 0.35 | 0.15 | | 0.18 | 0.14 | | 0.12 | | | |
| 1987 | 0.42 | 0.20 | 0.21 | 0.01 | 0.10 | | | | 0.04 | | 0.01 | |

Figure 3 Consumption of capelin and herring by cod of different size in 1986

- 1 — capelin size composition in catches
- 2 — capelin size composition in cod stomachs
- 3 — capelin size composition in catches
- 4 — capelin size composition in cod stomachs



The mass cannibalism can be also due to food scarcity in a water body (1986-1987, original data). The amount of young fish consumed by 1 cod in 1986 was comparable (at least during the first part of the year) to that in the 30s and so were the total annual values which were 20 and 18 %, respectively, whereas they appeared to be as low as 5% in 1987 since cod fed on its own juveniles in the first part of the year only. However, taking into account that a sharp decrease in cod abundance was observed during recent years and that young fish consumed in 1986-1987 were from the weak 1984-1986 year-classes (Anon., 1989) the present rate of cannibalism (Orlova et al., 1989) should be considered as extremely high, which can cause depletion of cod stocks. It must be emphasized that young cod was but rarely recorded in stomachs of adults caught in major feeding grounds (the Demidov and Murman Banks and the Murman Tongue) in winter, spring and summer of 1988- 1989. The young cod concentrations seemed to be so small that they were not attractive for predators due to high energy costs of prey capture. The phenomenon in its turn appears to be highly essential as related to cod stock itself and it is in a good agreement with data which are indicative

of a juvenescent cod stock and a dramatic decrease in parental stock abundance and fecundity rates (Mukhina, Yaragina, 1988; Nizovtsev et al., 1988).

Even in case strong year-classes appear their survival is but problematic due to inadequate food availability for cod which causes young fish grazing by adults.

Repeated attempts were made to estimate predation rates of which the most successful one was that based on the method developed by Novikova (1962). However, the method itself was not widely used and the authors who took it as a basis for calculations of daily rations of cod in 1974-1976 and 1981- 1982 (Ponomarenko et al., 1978, 1990) assumed their value to be either equal to (1st option) or twice as less as (2nd option) that estimated by Novikova in the 60s (as dependent on the frequency of occurrence of capelin in cod stomachs). The data obtained in the early 80s have shown that a total of 4.2 million tonnes of capelin were consumed by cod which exceeded cod biomass (1.6-1.7 million tonnes) by 2.4-2.6 times (2nd option).

The estimates cited demanded certain elucidation from the points of view of both methodology and allowances for varying feeding conditions. It is worth noting that the basic pre- condition of using Novikova's method is that cod feeds preferably on one species (Orlova, 1989) and it can not be applied to estimates of daily rations under conditions of diversified cod diet accompanied by significant fluctuations in capelin consumption in the early and particularly in the late 80-ies (Orlova et al., 1990a). The original estimates of daily, monthly and yearly rations using Fortunatova's method (1940) with account taken of a reconstructed weight of the food consumed and digestion rates (Orlova et al., 1989b) reflected specific feeding conditions of cod in 1986 and 1987. As it might be expected, due to a sharp decrease in capelin abundance during the period of the most intense cod feeding (February-April) the daily diets appeared to be considerably lower than the ones arbitrary assumed by Ponomarenko and Yaragina in the 80s (1-2 % against 2-4%, at the expense of capelin exclusively). The cod stock size in 1986-1987 was also lower (1 million tonnes against 1.6-1.7 million tonnes), which contributed towards reduction in predation on capelin.

The annual rations of cod were estimated as 312.5 and 446.4% in 1986 and 1987, respectively. Based on the proportion of major food items their annual consumption by cod was calculated (Table 5) at 3397 and 4852 thousand tonnes in 1986 and 1987, respectively. Fish constituted 84% or 2885 thousand tonnes and 91.2% or 4415 thousand tonnes, respectively. This included 626-951 thousand tonnes of capelin, 377-2077 thousand tonnes of redfish, 119-247 thousand tonnes of haddock, 252-615 thousand tonnes of cod, up to 710 thousand tonnes of herring and 163-529 thousand tonnes of shrimp. The estimated values should be regarded as tentative since accurate identification of limits in consumption of individual food items presents certain difficulties. Besides, the consumption of capelin is underestimated due to the lack of data on cod feeding on capelin in the central northern areas. On the other hand, the annual food ration in 1987 could have been overestimated since cod feeding followed uneven and local-type pattern of which low growth rates and fat content are indicative (Orlova et al., 1990b). Nevertheless, the data on capelin grazing by cod (600-900 thousand tonnes) appeared to be comparable to those obtained in the 70s (Ponomarenko, Ponomarenko et. al., 1978) with account taken of a sharp decrease in the abundance of both capelin and cod.

Since Fortunatova's method (1940) was applied to estimate daily and annual rations of the Barents Sea cod and use was made of data on the size composition of preys consumed with the subsequent reconstruction of their weight based on reference material (Berestovsky et al., 1989) similar calculations using Bajkov's method (Bajkov, 1935) proved to be feasible which involved index of consumption as estimated on the basis of the reconstructed weight of food bolus. The comparison has revealed similarity in the results obtained by both methods.

To simplify further calculations a relationship was established between indices of stomach fullness and daily rations (dr) which is described by the linear regression equation (Orlova et al., 1990c) : $dr = a+bx$, where a and b are regression coefficients and x is index of fullness (if) or : $dr = - 0.01267 + 0.50047 if$. In a more recent paper (Orlova and Antonov, in press) the a and b coefficients were elucidated as dependent on food spectrum (Table 7), which allows for estimating daily diets using a specific program on the basis of both Fortunatova's (1940) and Bajkov's (1935) methods. Original estimates were performed using 5 models (I, II, IV,V and VI) suggested by Bogstad and Mehl (1990). Results of comparison are presented in Table 6 and they are relatively similar in a number of cases. As it is seen from the table the differences in daily rations as estimated using the methods developed by Fortunatova and Bajkov and the models are not more significant than those within the models themselves. To estimate daily rations of the Barents Sea cod some of the constant coefficients assumed in the models can be specified with account taken of original experimental data.

CONCLUSIONS

1. Prey size preference indicated the level of food availability for predators. At high concentrations of food organisms it manifested itself in selection of dominant preys which contributed to reduction of energy drain due to feeding. Low food availability showed itself in expansion of size range of preys.
2. The period of cod feeding on capelin was highly dynamic. When concentrations of capelin were low it was consumed by predators of all sizes and the length fluctuations of capelin in their stomachs were as wide as 6-18 cm. When capelin concentrations were high (in February) the feeding pattern of small predators remained unchanged whereas larger ones fed on capelin 13-15 cm long. The growth of concentrations in March resulted in consumption of capelin 10-18 cm long by cod 40-70 cm in length.
3. During feeding of cod 30-50 cm long on capelin along the Murman coast the prey size preference manifested itself in the selection of capelin 12-16 cm (14 cm at the average).
4. Curves showing size composition of capelin in catches and in stomachs of predators of different size were similar (at the average capelin length of 13-14 cm).
5. Herring was not easily accessible for small predators and they started to feed on herring after having reached the length of 40 cm. As dependent upon concentration density of herring the prey size preference was recorded in cod at the length of 46-50 cm (high concentration density) or 70 cm (low concentration density) and the average size of herring was 16-22 cm in both cases.
6. Curves showing size composition of herring in catches and in stomachs of small cod differed significantly and they nearly coincided starting from a cod length of 40 cm.

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Table 1 Frequency of occurrence (F), and mean length (L) of major food organisms from stomachs of cod of different size. Length range in brackets.

| Cod size, cm | Redfish | | Cod | | Capelin | | Herring | |
|--------------|---------|-------------|-------|--------------|---------|--------------|---------|--------------|
| | F | L | F | L | F | L | F | L |
| 30-40 | 33-43 | 6.8 (5-7) | | | 0-14 | 15.0 | | |
| 41-50 | 25-33 | 7.6 (5-15) | | | 0-11 | 12.0 | | |
| 51-60 | 41-43 | 7.7 (5.17) | 0-1 | 12.2 (8-17) | 5-8 | 13.0 (12-14) | 1-3 | 19.3 (12-23) |
| 61-70 | 42-51 | 7.8 (5-18) | 2-9 | 30.7 (22-35) | 5-9 | 13.8 (12-17) | 4-9 | 18.5 (18-23) |
| 71-80 | 33-75 | 7.9- (5-18) | 12-13 | 30.3 (28-35) | 0-17 | 15.0 (12-16) | | |
| 81-90 | 20-38 | 8.6 (4-18) | 8-40 | 30.1(25-32) | 0-8 | 14.0 (13-15) | | |
| 91-100 | 12-18 | 9.3 (6-15) | 40-41 | 35.7 (28-40) | | | | |

Table 2 Frequency of occurrence (F), and mean length (L) of major food organisms from stomachs of cod of different size. Length range in brackets.

| Cod size, cm | February | | | | | | March | | | | | |
|--------------|----------|--------------|---------|--------------|---------|-------------|---------|--------------|---------|--------------|---------|-------------|
| | Capelin | | Herring | | Redfish | | Capelin | | Herring | | Redfish | |
| | F | L | F | L | F | L | F | L | F | L | F | L |
| 26-30 | 79.6 | 13.5 (6-18) | 3.7 | 13.0 (12-15) | 38.9 | 7.8 (6-13) | 30.8 | 12.3(10-14) | 7.8 | | 15.5 | 6.0 |
| 31-35 | 59.3 | 13.5 (6-18) | 25.2 | 17.0 (12-20) | 29.2 | 7.8 (6-13) | 24.3 | 12.3 (10-14) | 2.3 | | 28.8 | 8.4 (6-12) |
| 36-40 | 45.8 | 13.6 (11-18) | 49.6 | 17.6 (12-22) | 28.2 | 8.2 (6-13) | 30.2 | 12.3 (10-14) | 12.1 | 17.5 (13-21) | 20.7 | 7.3 (6-14) |
| 41-45 | 22.2 | 14.7 (12-23) | 70.0 | 18.4 (12.23) | 22.2 | 12.7 (6-16) | 37.7 | 13.3 (10-17) | 11.3 | 17.2 (13-19) | 18.8 | 7.9 (6-17) |
| 46-50 | 23.1 | 13.5 (13-14) | 92.3 | 18.4 (16-21) | 7.7 | | 47.7 | 13.4 (10-17) | 22.6 | 18.2 (15-21) | 33.0 | 8.1 (6-16) |
| 51-55 | | 13.7 (12-14) | 100.0 | 19.5 (16-22) | 2.0 | | 58.2 | 13.4 (10-18) | 26.1 | 18.0 (15-25) | 20.4 | 7.7 (6-17) |
| 56-60 | | | | | | | 54.5 | 14.5 (10-18) | 21.3 | 18.7 (13-29) | 23.6 | 9.9 (6-21) |
| 61-65 | | | | | | | 38.5 | 14.0 (10-18) | 18.2 | 18.1 (13-24) | 38.5 | 10.2 (6-22) |
| 66-70 | | | | | | | 57.0 | 14.3 (10-17) | 15.4 | 18.9 (17-21) | 14.3 | 9.9 (7-25) |
| 71-75 | | | | | | | 25.0 | 14.6 (11-16) | 28.5 | 20.0 (17-22) | 25.0 | 16.2 (8-25) |

Table 3 Length composition and abundance of young redfish in stomachs of cod during exclusive feeding on redfish

| Cod size, cm | January 1988 | | May 1987 | |
|--------------|-----------------------------|--------------------------|-----------------------------|--------------------------|
| | Redfish length, (range), cm | Av. no. sp. in 1 stomach | Redfish length, (range), cm | Av. no. sp. in 1 stomach |
| 30-35 | 5.8 (5-7) | 13.0 | | |
| 36-40 | 5.6 (5-6.5) | 7.0 | | |
| 41-45 | 5.4 (4-7) | 11.8 | | |
| 46-50 | 5.7 (5-8) | 22.1 | | |
| 51-55 | 5.6 (4-7.5) | 17.1 | 7.5 (7-8) | 1.0 |
| 56-60 | 5.6 (4-6.5) | 2.5 | 13.4 (7-17) | 0.8 |
| 61-65 | 5.2 (5-6) | 15.0 | 14.3 (10-18) | 2.9 |
| 66-70 | | | 16.9 (11-24) | 2.5 |
| 71-75 | | | 14.5 (10-20) | 2.2 |
| 76-80 | | | 14.6 (12-24) | 5.8 |
| 81-85 | | | 14.9 (12-18) | 8.0 |

Table 5 Consumption of major food items by cod in 1986 and 1987 (at the cod stock biomass of 1087 thousand tonnes).

| Food spectrum | 1986 | | 1987 | |
|---|------|-------------|------|-------------|
| | % | '000 tonnes | % | '000 tonnes |
| Fish | | | | |
| capelin | 28.0 | 951.1 | 12.9 | 625.9 |
| cod | 18.1 | 614.8 | 5.2 | 252.3 |
| redfish | 11.1 | 377.0 | 42.8 | 2076.8 |
| herring | 20.9 | 709.9 | | |
| haddock | 3.5 | 118.9 | 5.1 | 247.5 |
| polar cod | | | 7.3 | 354.2 |
| long rough dab | 1.7 | 57.7 | 2.7 | 131.0 |
| Other | 0.7 | 23.8 | 4.3 | 208.6 |
| Crustaceans | | | | |
| shrimp | 4.8 | 163.0 | 10.9 | 528.9 |
| euphausiids, Themisto, etc. | 0.7 | 23.8 | 7.4 | 359.1 |
| Other (ctenophores, cephalopods, molluscs etc.) | 10.5 | 356.7 | 1.4 | 67.9 |

Table 6 Daily rations of cod (% of body weight) calculated by different methods

| Cod age | 1989 | | | | | | 1990 | | | | | | | | |
|-------------------------|------|------|------|---------|------|------|-------|------|------|------|------|------|------|------|------|
| | July | | | October | | | March | | | | | May | | | |
| | 4 | 5 | 6 | 4 | 5 | 6 | 3 | 4 | 5 | 6 | 7 | 4 | 5 | 6 | 7 |
| Model I | 1.09 | 1.50 | 0.94 | 0.40 | 0.07 | 0.56 | 1.91 | 2.03 | 2.19 | 2.33 | 3.15 | 0.21 | 0.40 | 0.26 | 0.17 |
| Model II | 1.06 | 1.26 | 0.72 | 0.34 | 0.06 | 0.39 | 2.03 | 1.93 | 1.86 | 1.82 | 2.23 | 0.21 | 0.34 | 0.21 | 0.12 |
| Model IV | 0.99 | 1.13 | 0.87 | 0.70 | 0.30 | 0.75 | 1.13 | 1.13 | 1.14 | 1.18 | 1.32 | 0.39 | 0.53 | 0.40 | 0.34 |
| Model V | 0.76 | 0.91 | 0.51 | 0.27 | 0.05 | 0.30 | 1.42 | 1.33 | 1.28 | 1.27 | 1.53 | 0.15 | 0.25 | 0.15 | 0.09 |
| Model VI | 0.89 | 1.23 | 0.77 | 0.35 | 0.06 | 0.48 | 1.91 | 2.03 | 2.76 | 4.34 | 2.61 | 0.05 | 0.13 | 0.32 | 0.14 |
| After Fortunatova | 1.05 | 0.97 | 0.67 | 0.27 | 0.06 | 0.65 | 2.39 | 3.82 | 2.41 | 2.95 | 3.20 | 0.22 | 0.32 | 0.21 | 0.08 |
| After Bajkov | 0.86 | 1.13 | 0.69 | 0.29 | 0.07 | 0.88 | 2.44 | 3.99 | 2.40 | 2.98 | 3.21 | 0.23 | 0.32 | 0.21 | 0.14 |
| Regression equation* | 1.08 | 1.48 | 0.93 | 0.40 | 0.07 | 0.55 | 1.76 | 1.88 | 2.03 | 2.15 | 2.92 | 0.08 | 0.26 | 0.12 | 0.03 |
| Regression equation** | 1.01 | 1.40 | 0.87 | 0.35 | 0.04 | 0.50 | 1.86 | 1.99 | 2.15 | 2.29 | 3.12 | 0.16 | 0.35 | 0.21 | 0.11 |
| Number of fish examined | 25 | 19 | 35 | 9 | 7 | 12 | 14 | 46 | 43 | 10 | 30 | 6 | 27 | 11 | 6 |

* After Fortunatova

** After Bajkov

Table 7 Linear regression coefficients of the relationship between daily ration (calculated by Fortunatova and Bajkov) and stomach fullness index ($Y=a+bX$, where X is stomach fullness index and Y is daily ration).

| Major food items | Fortunatova | | | Bajkov | | | Number of samples |
|------------------------|-------------|--------|-------------------------|----------|--------|-------------------------|-------------------|
| | a | b | correlation coefficient | a | b | correlation coefficient | |
| Total | -0.00758 | 0.5784 | 0.9132 | -0.00251 | 0.5919 | 0.9153 | 64 |
| Fish/crustaceans (1:1) | -0.07852 | 0.4711 | 0.9806 | -0.11378 | 0.4584 | 0.9835 | 11 |
| Fish | -0.04488 | 0.4561 | 0.9593 | -0.00461 | 0.4613 | 0.9711 | 14 |
| Crustaceans | -0.00124 | 0.7142 | 0.9651 | -0.03618 | 0.6911 | 0.9697 | 15 |
| Capelin- | -0.11827 | 0.6697 | 0.9405 | -0.05533 | 0.7256 | 0.9509 | 5 |
| Redfish | -0.06011 | 0.4059 | 0.9294 | -0.02247 | 0.4425 | 0.9356 | 8 |

**SIGNIFICANCE OF THE NORTH—EAST
ARCTIC COD FOR YEAR-CLASS STRENGTH
OF REDFISH IN THE BARENTS SEA**

by

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ABSTRACT

Based on data obtained in different areas of the Barents and Norwegian Seas in 1984-1989 a study was made of the role of the North—East Arctic cod in the formation of the year-class abundance in Sebastes spp. The feeding studies have shown that both fishery and cod predation contribute to the population dynamics in redfish. It is stated that 54-91% of redfish is consumed by cod at the age of 0+ and predation-caused mortality shows a decrease with the redfish age though it remains relatively high till the age of 3-4 years.

INTRODUCTION.

The following 3 species of the genus Sebastes occur in the Barents Sea and the adjacent North Atlantic seas: S. marinus, S. mentella and S. viviparus, the latter being not a commercial species. S. mentella shows the highest abundance in the shelf waters of the Barents Sea (Borodatov and Travin, 1960). In 1979-1984 the commercial stock recruitment of S. mentella was formed of the weak 1973-1979 year-classes whereas the exploitation rate increased in 1984-1988, which was accompanied by deteriorating ecological conditions in the Sea. The sharp decline in the abundance of capelin and deepwater shrimp which are major food items for cod resulted in changes of traditional food spectrum of the latter. The fish started an active search for new food and it fed largely on young Sebastes in the southern and central areas of the Barents Sea throughout 1987 (Norvillo, 1989). The data available (Yaragina, 1988; Orlova et. al., 1988) indicate that redfish, and S. mentella in particular, were not preferable food items for cod and they were recorded in the cod stomachs just incidentally whereas in the 80-ies a regular consumption of redfish by cod was observed, which affected the redfish abundance considerably. In view of the above-said the present paper attempts to assess the impact of cod predation on the redfish year-class strength in the Barents Sea in 1984-1989.

MATERIAL AND METHODS

Use was made of the results of a quantitative-weight analysis of cod stomachs made during the expeditional studies as well as of information on the cod stomach contents from the joint IMR-PINRO stomach content database and of the results of a qualitative analysis of stomachs of cod caught in different areas of the Barents and Norwegian Seas in 1986-1989. The stomachs were analysed and records were made using the methods as described in the Program of stomach sampling in the North Sea (Mehl, 1986). The predation rate of cod on redfish was determined based on the qualitative analysis of feeding of about 30 thousand individuals.

The food organisms which occurred in the cod stomachs were attempted to be identified down to the specific rank and they were weighed and measured in the laboratory. Since the head of the fish is to be used for the species identification and since it was the first (together with the fins) to be disintegrated in the cod stomach the species composition of the redfish was frequently not possible to determine. Besides, it was the genus that was identified for the 1984-1986 data in view of which all the young redfish which were recorded in the cod stomachs (including those which were identified as species) were combined in the genus Sebastes. Since the highest abundance in the Barents Sea is shown by young S. mentella and since their growth rate is close to that of S. marinus (Andriyashev, 1954) the weight and abundance of preys (broken down by age) in the daily diet of the predator as well as the share of the prey in the predator stomach were estimated using size-age keys of S. mentella. The age composition of cod was determined by converting the fish length to age using the respective size-age keys. The initial data for the calculations were borrowed from the joint PINRO-IMR stomach content data base.

The average daily weight of the stomach content of 1 individual at a given age during a quarter serves as a basis of a quantitative analysis of the cod feeding. The consumption

by a predator of preys of different age during a quarter period was estimated using the following formula (Mehl, 1986):

$$D_a = \frac{1}{W_a} \sum_b R_b \sigma_{ab} \beta_b \bar{N}_b n_{ba}$$

where:

D_a is consumption by predatory cod of prey at age a (thousand individuals)

R_b is average weight of stomach content of cod at age b , g

σ_{ab} is share of prey of age a in diet of cod of age b

β_b is daily portion of food bolus evacuated from stomach of cod at age b

\bar{N}_b is average quarterly abundance of cod at age b , thousand individuals

n_{ba} is number of days in a quarter during which cod at age b feeds on prey at age a

W_a is average quarterly weight of prey at age a , g

The annual consumption of redfish by cod was calculated by summing up the quarterly consumption values. The biomass and abundance of the commercial cod stock was taken from the ICES Arctic Fisheries Working Group Reports (Anon., 1988 and Anon., 1989).

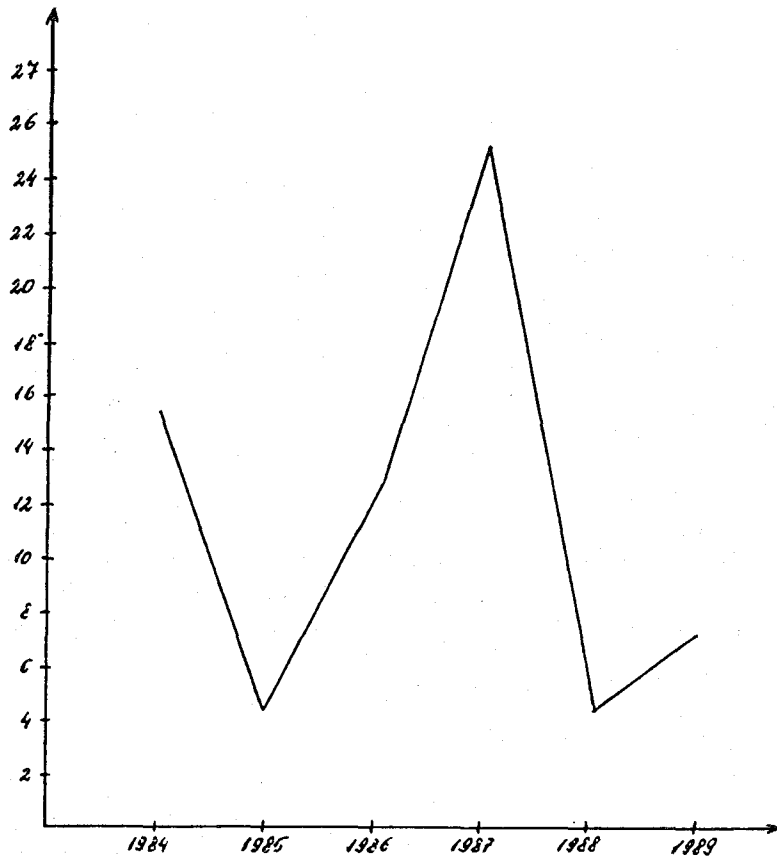
RESULTS AND DISCUSSION

The analysis of food habits of cod in 1984-1989 has shown that young redfish (under the age of 1+) repeatedly occurred in the stomachs of 0-group cod and reached 1.85% of the food bolus in individual years. Young redfish comprised from 0.7% (in 1985) to 32.43% (in 1987) of the diet of cod 0-10 years old (Table 1). As it is shown from Table 2 the annual abundance of redfish consumed by cod amounted to 12-50 billion individuals in 1984-1989 and the highest proportion (54-91%) was constituted by the fish at the age of 0+. Predation - caused mortality proved to decrease with the redfish age though it remained high till the age of 3-4 years. The average amount of 3-year olds of 0.58 billion individuals which were consumed by cod in 1984-1989 was adequate to the strong year-class of S. mentella and that of 4-year-old (0.18 billion individuals) was close to a moderate recruitment. The results of the redfish 0-group survey indicated strong year-classes of 1982 and 1983, however, by the time they were recruited to the fishery the abundance was 2.7 billion individuals lower due to cod predation. Predation-induced mortality of the 1984 year-class appeared to be as high 3.9 billion individuals.

The consumption of redfish by cod was found to be far in excess of the abundance of 6 year-olds of the richest generation of S. mentella (0.8 billion individuals) and higher than the record catch of 0.6 billion individuals in 1976.

The share of fish in the cod diet showed a decrease in 1985- 1986 and an increase in 1987, the latter was due to the forced change over to feeding on young redfish (Fig.1) which constituted about 26% of the cod ration in 1987 and resulted in a predation-caused mortality of 250 thousand tonnes.

Figure 1 Percentage of young redfishes in daily diets of 1 cod in diferent years



The deteriorating feeding conditions and perturbed trophic relationships in the 80s led to an adverse effect of cod on redfish commercial recruitment in the 90s. Taking into account an increase in mortality of redfish at the age of 0+ in the period from 1986 to 1988 these generations of S. mentella are not expected to provide abundant commercial recruitment. It is known (Zatsepin and Petrova, 1939) that the bulk of cod ration is constituted by the food organisms which are predominant in the water layer where cod occur and that fish is always a preferred food item. Consequently, the results of feeding studies of cod can be applied to predictions of the redfish commercial stock recruitment.

CONCLUSIONS

1. Inadequate food availability and perturbed traditional trophic relationships in the 80s led to an increased consumption by the North—East arctic cod of non-traditional food items including redfish. The peak of feeding on S. marinus fell on 1987 when they constituted about 26% of the cod diet, which corresponded to predation-caused mortality of about 250 thousand tonnes of young redfish.
2. The highest amount (54-91%) of redfish were consumed by cod at the age of 0+. Predation-caused mortality decreased rapidly with redfish age though it remained considerable till the age of 3-4 years.

3. The average abundance of 3-year-old redfish (0.58 billion individuals) consumed by cod in 1984-1989 was equal to the high recruitment to the commercial stock of S. mentella and the consumption of 4-year-olds (0.18 billion individuals) corresponded to average recruitment.

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Table 1 Average weight (W, g) and portion (P, g) of young redfish in average annual daily diet of 1 individual of cod at different age in 1984-1989.

| Cod age | 1984 | | 1985 | | 1986 | | 1987 | | 1988 | | 1989 | |
|---------|--------|-------|--------|------|--------|-------|--------|-------|--------|------|--------|-------|
| | W | P | W | P | W | P | W | P | W | P | W | P |
| 0 | 0.005 | 0.88 | 0.003 | 0.70 | 0.005 | 1.85 | | | | | | |
| 1 | 0.12 | 6.10 | 0.04 | 1.50 | 0.13 | 7.93 | | | | | 0.013 | 1.60 |
| 2 | 0.573 | 10.20 | 0.063 | 0.80 | 0.361 | 7.86 | 0.03 | 2.65 | 0.092 | 6.52 | 0.36 | 10.75 |
| 3 | 1.805 | 18.12 | 0.386 | 1.82 | 0.704 | 6.45 | 0.462 | 7.65 | 0.196 | 3.45 | 0.687 | 8.41 |
| 4 | 2.363 | 14.11 | 0.73 | 2.71 | 1.046 | 6.92 | 1.617 | 11.52 | 0.518 | 6.30 | 1.116 | 7.86 |
| 5 | 3.20 | 15.20 | 0.76 | 2.37 | 1.12 | 5.28 | 5.98 | 24.41 | 0.825 | 4.39 | 0.865 | 4.53 |
| 6 | 4.45 | 12.01 | 2.07 | 4.00 | 5.52 | 14.06 | 13.81 | 32.43 | 1.611 | 4.43 | 1.69 | 6.88 |
| 7 | 5.77 | 13.24 | 3.75 | 4.06 | 2.39 | 2.43 | 28.53 | 24.04 | 4.55 | 5.45 | 2.72 | 7.59 |
| 8 | 7.67 | 14.69 | 5.23 | 4.16 | 9.03 | 6.03 | 5.11 | 7.06 | 0.77 | 0.84 | 6.85 | 14.36 |
| 9 | | | 9.12 | 4.47 | 45.91 | 17.72 | | | 1.016 | 1.37 | 7.474 | 10.58 |
| 10 | 12.674 | 14.76 | | | | | | | 7.73 | 4.32 | 5.35 | 2.96 |
| | 38.63 | | 22.152 | | 66.216 | | 55.539 | | 17.308 | | 27.125 | |
| | 3.86 | 15.45 | 2.22 | 4.32 | 6.62 | 12.13 | 7.93 | 25.55 | 1.92 | 4.37 | 2.71 | 7.36 |

Table 2 Young *Sebastes marinus* (billion individuals) consumed by the North-East arctic cod in 1984-1989

| Redfish age | 1984 | | 1985 | | 1986 | |
|-------------|-------|--------|--------|--------|-------|-------|
| 0+ | 14.00 | 8.90 | 28.90 | 32.10 | 45.40 | 13.30 |
| 1 | 9.70 | 1.00 | 5.60 | 7.00 | 3.80 | 0.90 |
| 2 | 1.70 | 0.80 | 2.40 | 0.10 | 0.50 | 0.20 |
| 3 | 0.20 | 0.80 | 1.20 | 1.10 | 0.10 | 0.08 |
| 4 | 0.05 | 0.03 | 0.10 | 0.70 | 0.10 | 0.10 |
| 5 | 0.04 | 0.006 | 0.003 | 0.10 | 0.04 | 0.30 |
| 6 | 0.01 | 0.003 | | 0.01 | 0.01 | |
| 7 | | | | 0.001 | | |
| Total | 25.70 | 11.539 | 38.203 | 41.111 | 49.95 | 14.88 |

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:

$$D_{s,a} = \sum_b \frac{R_b \cdot \delta_{sab} \cdot \beta_b \cdot \bar{N}_b \cdot 91.25}{w_{s,a}}$$

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
- \bar{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

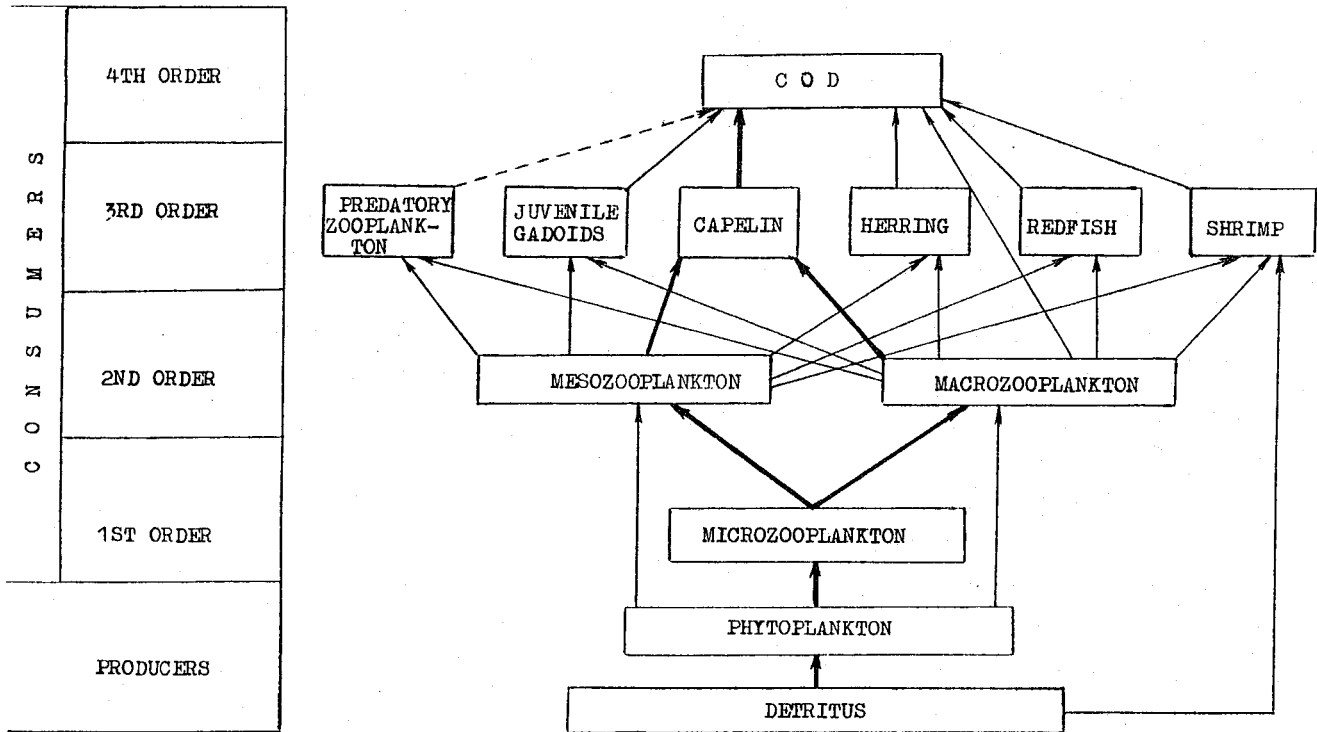
Since the Barents Sea lies in high latitudes the species diversity is not as high as that in the southern seas, which is true for almost all ecological groups of the food web, i.e. phytoplankton, zooplankton, nekton and benthos. A high degree of dominance of individual species is a typical feature of 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 (Astaeva, 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).

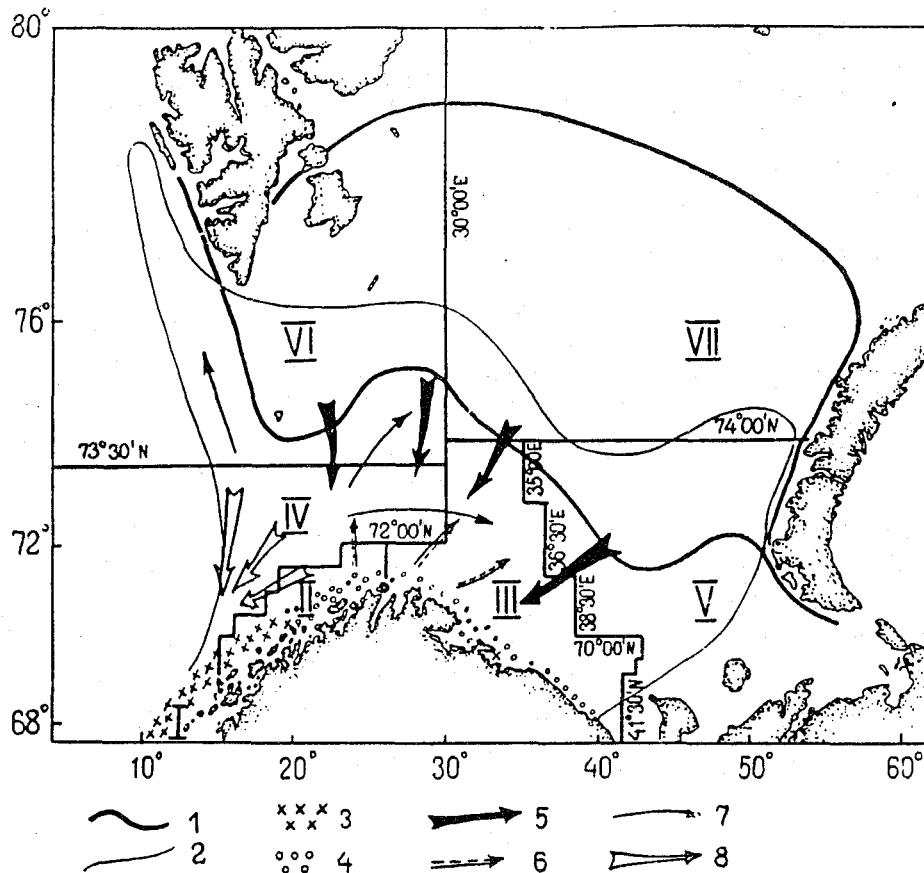
Seasonal dynamics of cod trophic relationships.

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 current-

induced 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 migration, 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 |
| <u>S. mentella</u> | 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 estimating 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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**THE NORTH-EAST ARCTIC COD
STOCK'S CONSUMPTION OF
VARIOUS PREY SPECIES 1984-1989**

by

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ABSTRACT

The North-East Arctic cod stock's consumption of different prey species has earlier been calculated by Mehl (1989) for the period 1984-1986. However, a new model to describe gastric evacuation in cod has now been presented by dos Santos (1990). This model is based on extensive feeding experiments with relevant prey items, done at relevant temperature conditions. This model is combined with the stomach content data to give consumption estimates for each of the years 1984-1989. The results are compared and judged against data on individual cod growth, daily rations and food conversion efficiency.

INTRODUCTION.

One essential requirement for multispecies models is estimates of the food consumption by the main predator stocks over the area of distribution. In addition to data on the number and distribution of the different predator age groups, good estimates of the annual food requirements are needed. The latter can be estimated in two ways:

- from quantitative stomach content data and data on gastric evacuation rates (models)
- from consideration of energy requirements and data on diet composition

The first method has been chosen in several investigations, may be because it consists of more or less straight forward measurements. But these measurements which results in the consumption rates by/of the actual predator/prey stocks are important and sometimes also weak points in the models they are used in.

This is the situation for the MSVPA models both in the North Sea and in the Baltic, and it has the same importance for the multispecies modeling work in the Barents Sea. The first results of this work were presented in Bogstad and Tjelmeland (1990, 1991). In the Barents Sea stomach data were previously combined with temperature-correlated evacuation rates from the North Sea to calculate the cod's consumption rates (Mehl, 1989). Later a preliminary evacuation rate model based on feeding experiments done in Balsfjord, Northern Norway by Jorge dos Santos have been used (Mehl, 1989); (Mehl and Sunnanå, 1991). This evacuation rate model was compared to five other evacuation rate models in Bogstad and Mehl (1990), and the results were then compared with prey stock sizes and data from other investigations on daily ration and food conversion efficiency. The new evacuation rate model given by dos Santos (1990), which is based on experiments done at relevant temperature and with relevant prey, will be used for the consumption calculations made in this paper. The model takes into account both the temperature and the meal size/ body weight ratio in addition to the prey species. As we do not know the meal size from the stomach data, we will need a relationship between the meal size and the stomach content. We will suggest such a relationship, and compare the results with data from other investigations on daily ration and food conversion efficiency as was done in Bogstad and Mehl (1990).

MATERIAL AND METHODS.

The evacuation rate model.

According to dos Santos (1990) the evacuation of a single meal for cod can be described in the following way for prey category i:

$$S_{it} = S_{i0} e^{-\left(\frac{t}{H_i e^{-cT} \left(\frac{S_{i0}}{W}\right)^b}\right)^{K_i} \ln 2}$$

, where S_{it} is the stomach content at time t (hours), S_{i0} is the initial meal size, W the fish body weight and H_i is the evacuation rate constant which is a theoretical value expressing for a given prey i the half-life(hours) of a meal of the same size as the fish body weight at 0° C. T is the temperature in $^\circ$ C, b and c are constants. The shape parameter K_i determines the shape of the evacuation curve. We have here used a notation which differs slightly from the one used by dos Santos (1992).

For consumption calculation purposes, we assume a steady state, i.e that the amount of food eaten is equal to the amount digested. This means that the ration of prey item i eaten per hour, R_i , becomes

$$R_i = \frac{\ln 2 \cdot S_i \cdot K_i}{H_i \cdot e^{-cT} \cdot \left(\frac{S_{i0}}{W}\right)^b} \cdot \left(\frac{t}{H_i \cdot e^{-cT} \cdot \left(\frac{S_{i0}}{W}\right)^b}\right)^{K_i-1}$$

In dos Santos (1990) it is shown that the shape parameter K_i is not a main contributor to the goodness-of-fit of this single-meal model. He has estimated the parameters both when K_i is allowed to vary and when K_i is restricted to 1.0 for all prey. For all prey except shrimp, the 95% confidence interval for K_i was found to contain the value 1.0 (exponential evacuation) when the model was applied in terms of wet matter of prey. Thus, we have chosen to use the parameter values obtained when K_i is restricted to 1.0 for all prey because this is a more convenient formula to work with. Equation (2) can then be simplified to :

$$R_i = \frac{\ln 2 \cdot S_i \cdot e^{cT}}{H_i \cdot \left(\frac{S_{i0}}{W}\right)^b}$$

The parameter values are (wet weight): $b=0.54$, $c=0.11$, $H=205$ (krill), 533 (shrimp), 452 (herring) and 283 (capelin).

For sequential meals, the best fit was found when the term $\frac{S_{i0}}{W}$ was changed following each new meal, assuming that the 'new' total stomach content is the stimulus driving evacuation. Thus, we will relate the initial meal size S_{i0} to the observed stomach content. We will start by assuming that the initial meal size is equal to twice the observed total average stomach content $S=\Sigma S_i$. The final formula for R_i then becomes:

$$R_i = \frac{\ln 2 \cdot S_i \cdot e^{cT}}{H_i \cdot \left(\frac{2S}{W}\right)^b}$$

The cod stock's consumption in tonnes of prey species i , prey size group j in season l ($C_{i,j,l}$) is then given by

$$C_{i,j,l} = \sum_{k,n} R_{i,j,k,l,n} \cdot XN_{n,l} \cdot XP_{k,l,n} \cdot const$$

where $R_{i,j,k,l,n}$ is the ration of prey species i , prey size group j in area k and season l for cod age group n , $XN_{n,l}$ is the number of individuals of predator age group n in season l and $XP_{k,l,n}$ is the proportion of individuals of predator age group n in area k and season l . Const is a scaling factor in order to get the consumption in tonnes per season.

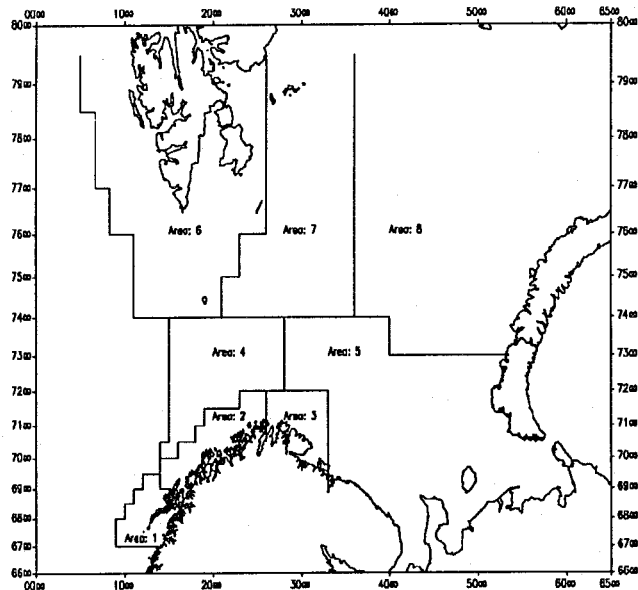
It was decided to apply the evacuation rate for capelin also for amphipods. For cod, haddock and redfish the evacuation rate for herring was applied. For "other" prey species, the evacuation rate for krill was applied for cod age group 1 and 2, because for these age groups "other" consists mainly of smaller crustaceans and other easily digestible food. For the older cod age groups, the evacuation rate for herring was applied, because "other" for these age groups mainly consists of fish prey.

Data used.

The temperatures used are calculated by a temperature model which is also used by the multispecies model for the Barents Sea (MULTSPEC) (Bogstad and Tjelmeland, 1990, 1991). Data from standard hydrographical sections (Fugløya-Bjørnøya, Vardø N, Kola section) are used. At different depths and over different parts of the sections Fourier analysis is used on the temperature data. The temperature is then integrated in time for a representative location in each area to give one temperature for each year, area and month. The procedure is documented in Alvarez and Tjelmeland (1989). A depth of 100m has been used for these calculations. Due to problems with the temperature data base, the temperatures in 1988 have been set equal to the temperatures at the same position/time as in 1987 +0.3 °C, and the temperatures in 1989 have been set equal to the temperatures at the same position/time as in 1987 +0.9 °C. These differences of 0.3 °C and 0.9 °C are equal to the differences in the yearly mean at the Kola section between these years (PINRO, Murmansk, pers.comm.).

Stomach data for the years 1984–1989, collected by IMR and PINRO have been used in the calculations. Details about stomach sampling, analysis and aggregation of data are given in Mehl (1986, 1989) and Mehl and Yaragina (1991). The area distribution used in the multispecies model for the Barents Sea until 1990, which also is the basis for the division of the Barents Sea in areas for consumption calculation purposes, is shown on the map below.

Figure 1 Multispecies area division of the Barents Sea.



The consumption is calculated by 3 areas (II + IV, III + V and VI + VII) for each halfyear and predator age group. Because area VI+VII is sampled only once a year, the data

collected during the second half of the year are also used for the first half of the year. The data collected in 1984 were also used for the first part of 1984. During the second half of 1985 the sampling in the southern part of the Barents Sea (areas II+IV and III+V) was rather poor. Because of the large seasonal changes in the diet in these areas (Mehl, 1986), the data collected for the second part of 1984 in the same areas were used. But the content of shrimp was reduced to the same level (by percentage) as in area VI + VII during the second part of 1985, because of the all-over reduction of the shrimp stock from 1984 to 1985 (Tveranger and Øynes, 1985). In the second half of 1986, data for areas II+IV and III+V combined were used to give the diet for area II + IV due to poor sampling in area II + IV.

Table 5 in the appendix presents the mean weight of cod in 1984–1989 in the first and second half of the year. The weights are calculated using the weight in stock used by the ICES Arctic Fisheries Working group (Anon., 1991a) for ages 3 and older and the average of Norwegian and Russian survey weights for ages 1 and 2 (all at January 1), and assuming that the growth in weight is the same in every quarter during the year. (For the 7–9 group, the weight is calculated as a weighted average of the weights of age groups 7–9). For some of these years, there is a large discrepancy between the Norwegian and Russian survey weights, and this should be kept in mind when evaluating the calculations of daily ration in % of body weight and food conversion efficiency. This discrepancy may to a large extent be due to differences in age reading, and this matter is now under investigation (Anon., 1993). The Working Group makes an arithmetic average of the weight at age from these two surveys.

VPA-data from the Arctic Fisheries Working Group (Anon., 1991a) are used when the total cod stock's consumption is estimated. The number in each age group in the stock in each season is set to be the number in the middle of the season. This is found by reducing the number at the beginning of the year, using one fourth of the yearly natural and fishing mortality for each quarter. For age groups 1 and 2, the number at the beginning of each season is found by back-calculating the number at age 3 (Anon., 1991a) using a yearly natural mortality (M) of 0.2. The numbers are presented in table 6 in the appendix.

The geographical and seasonal distribution of the different cod agegroups are based on survey data, both acoustic and bottom trawl data (Dalen et.al. (1984), Hysten et. al. (1985), Hysten et. al. (1986), Godø et. al. (1987), Hysten et. al. (1988a), Hysten et. al. (1988b), Hysten et. al. (1989), Jakobsen et. al. (1989), Godø et. al. (1989) and unpublished survey data). They are presented in table 7 in the appendix.

DISCUSSION.

The calculated consumption by cod in the period 1984–1989 of the different prey species is shown in table 1.

Table 1 The Northeast Arctic cod stock's consumption in 1000 tonnes of the main prey species in 1984–1989 (% of total consumption in parentheses).

| Year Prey species | 1984 | 1985 | 1986 | 1987 | 1988 | 1989 |
|-------------------------|----------|-----------|-----------|-----------|-----------|-----------|
| Amphi- pods | 16(1) | 113(3) | 721(25) | 742(35) | 1029(44) | 646(27) |
| Shrimp | 417(19) | 156(5) | 125(4) | 177(8) | 128(5) | 137(5) |
| Capelin | 867(40) | 1938(56) | 956(33) | 226(11) | 511(22) | 783(31) |
| Herring | 66(3) | 161(5) | 131(4) | 30(1) | 1(0) | 4(0) |
| Cod | 33(2) | 47(1) | 103(4) | 32(2) | 10(1) | 8(0) |
| Haddock | 45(2) | 40(1) | 79(3) | 3(0) | 5(0) | 36(2) |
| Redfish | 331(15) | 205(6) | 251(8) | 299(14) | 190(8) | 213(9) |
| Others | 371(17) | 813(23) | 565(19) | 631(29) | 482(20) | 670(26) |
| Total | 2146(99) | 3475(100) | 2932(100) | 2141(100) | 2355(100) | 2497(100) |

From the table above, we see that capelin and amphipods were the most important prey species during the period, followed by redfish and shrimp. Young cod (cannibalism), haddock and herring contributed 5% or less each to the total consumption in all years. We see that amphipods, which were almost absent from the diet in 1984 and 1985, were the most important prey in 1987 and 1988. The proportion of capelin in the diet decreased from 1985 to 1987, in accordance with the collapse of the capelin stock, but after that the proportion rose again. The proportion of shrimp in the diet was relatively high in 1984, but stayed at a low level for the rest of the period. Compared to the other prey species, the percentage of redfish and "other" prey in the diet was relatively stable in the period. The cod stock's consumption was highest in 1985, both in tonnes and relative to the biomass of the cod stock at the beginning of the year.

The consumption of redfish, which is relatively stable, is high compared to the biomass of an age group at age 6 (10000–55000 tonnes for *Sebastes mentella* in the period in question, and less for *Sebastes marinus* (Anon., 1991a)). The main part of the redfish consumed is younger than 6 years, and the biomass of an age group of redfish younger than 6 years is less than that at age 6. Thus, the predation by cod on redfish is quite significant.

The decrease in the consumption of shrimp from 1984 to 1985 seem to be consistent with the decrease in the biomass estimate (Tveranger and Øynes, 1985), and the relatively low consumption of shrimp in the following years is also consistent with the biomass estimate time series. The calculated consumption is of the same order as the biomass estimate in the period (Anon., 1991b), which is , however, thought to be an

underestimate. The catch in the period varies between 45 and 120 thousand tonnes, and the predation from cod is thus more important than the catch.

The consumption of mature capelin by cod has been studied by Bogstad and Tjelmeland (1990, 1991). It should be mentioned that for the first half of the year, most of the samples are taken in the first quarter, when there may be intensive predation on mature capelin, and this may lead to an overestimate of the total consumption of capelin.

The high consumption of cod (cannibalism) in the years 1984–1987 may be part of the explanation why the 1984–1986 year classes of cod, which seemed to be very strong at the 0-group stage, turned out to be rather poor. See also Skagen et.al. (1990). To a somewhat lesser extent, this also happened for haddock. The high consumption of haddock in 1989 compared to 1987 and 1988 may be due to an error in the data.

The consumption of herring is highest in the years 1984–1986, coinciding well with the time period when the strong 1983 year class of herring was present in the Barents Sea. For the age groups 1 and 2, krill and small crustaceans dominate the "other" group. For the older age groups, "other" consists of various crustaceans and small fish. The proportion of fish in "other" increases with age.

Table 2 summarizes the annual consumption per cod for the different age groups:

Table 2 Annual consumption per cod (grams) by age group in the Northeast Arctic cod stock in 1984–1989

| Year Age group | 1984 | 1985 | 1986 | 1987 | 1988 | 1989 |
|-------------------|-------|-------|-------|------|-------|-------|
| 1 | 116 | 185 | 72 | 138 | 134 | 143 |
| 2 | 569 | 681 | 387 | 384 | 455 | 619 |
| 3 | 1501 | 1842 | 1094 | 879 | 864 | 1361 |
| 4 | 2716 | 3509 | 2532 | 1574 | 1855 | 2498 |
| 5 | 4823 | 5660 | 4785 | 3120 | 3452 | 4105 |
| 6 | 6829 | 9451 | 7232 | 5959 | 6228 | 6490 |
| 7-9 | 11307 | 15996 | 13583 | 8811 | 13430 | 10641 |

Table 3 gives the daily consumption per cod in percent of the bodyweight in the middle of the year (daily coefficient).

Table 3 Daily coefficient by agegroup for Northeast Arctic cod in 1984–1989.

| Year Age group | 1984 | 1985 | 1986 | 1987 | 1988 | 1989 |
|-------------------|------|------|------|------|------|------|
| 1 | 0.54 | 0.95 | 0.42 | 0.84 | 0.55 | 0.48 |
| 2 | 0.56 | 0.91 | 0.73 | 0.82 | 0.68 | 0.66 |
| 3 | 0.57 | 0.78 | 0.65 | 0.84 | 0.68 | 0.76 |
| 4 | 0.51 | 0.77 | 0.63 | 0.71 | 0.83 | 0.82 |
| 5 | 0.54 | 0.73 | 0.71 | 0.60 | 0.87 | 0.87 |
| 6 | 0.52 | 0.76 | 0.66 | 0.67 | 0.81 | 0.86 |
| 7-9 | 0.59 | 0.85 | 0.75 | 0.53 | 0.82 | 0.74 |

The new evacuation rate model gives a lower consumption estimate than found previously. The introduction of meal size dependence will mostly affect the consumption of capelin, because stomachs with large content usually contains capelin.

We see that the daily coefficient is in the interval 0.4–1.0, which is lower than found in other investigations, see Bogstad and Mehl (1990). Daan (1973) found a drop in the daily coefficient for increasing age for cod in the North Sea. Our calculations do not show such a trend, which leads us to believe that the consumption by the youngest age groups is underestimated. We have relatively few samples of the youngest age groups, and the proportion of empty stomachs is high. Also, in the experiments done by dos Santos cod of sizes corresponding to age 3 and 4 for Barents Sea cod dominated. According to the latest experiments done by dos Santos (pers. comm.) it also seems that the consumption by the youngest fish is somewhat underestimated.

Table 4 presents the annual weight increment in percent of the annual consumption (food conversion efficiency — FCE).

Table 4 Food conversion efficiency (%) by agegroup for Northeast Arctic cod in 1984–1989.

| Year Age group | 1984 | 1985 | 1986 | 1987 | 1988 | 1989 |
|-------------------|------|------|------|------|------|------|
| 1 | 55 | 29 | 53 | 32 | 70 | 98 |
| 2 | 65 | 34 | 34 | 33 | 51 | 46 |
| 3 | 25 | 26 | 16 | 17 | 41 | 28 |
| 4 | 19 | 19 | 13 | 13 | 27 | 26 |
| 5 | 22 | 14 | 11 | 11 | 22 | 21 |
| 6 | 14 | 9 | 13 | 10 | 17 | 18 |

The FCE for the 7–9 age group has not been calculated, because different age groups dominates this group from year to year. Also, the calculations for this group are based on relatively few samples, which leads to a large variation in calculated consumption from year to year.

For the youngest age groups, the FCE is obviously too high. The reason for this is the previously mentioned underestimation of the consumption for these age groups. The consumption estimates seems reasonable compared to the stock estimates of the prey species, while Mehl (1989) found that some prey species were "overconsumed". Still, the predation pressure on some prey year classes is considerable, see e.g. Skagen et. al. (1990).

For cod of medium size, the FCE in 1986/1987 is significantly lower than in the other years. This indicates that the low growth of cod in this period was mostly due to lower energy content in the food (less capelin!), and not so much lower total food consumption. There was, however, low abundance of capelin also in 1988, but a high FCE.

The FCE values above should be compared to values obtained from feeding experiments. Values of FCE obtained for fish in capture can be regarded as an upper limit. It would of course be very interesting to redo these calculations using energy content and not wet weight as done here.

Future improvements: The evacuation rate model could be improved by doing experiments with small and large cod and other prey species (redfish, amphipods, gadoids). Also, more experiments with multiple feeding should be performed. In order to make the best possible use of the new evacuation rate model, new calculations should be done based on individual stomach content and predator size data. It should then also be possible to use the actual temperature at the sampling site. The stomach sampling should be improved in order to get a better coverage in area and time. The differences in predator distribution, stomach content and temperature between bottom and pelagic should also be taken into account by trying to sample more representatively. The stomach content data have so far not been weighted by catch rate, due to data base problems. For the multispecies model in the Barents Sea, it is at the moment most important to get a precise estimate of the consumption of capelin by cod. Given a stock estimate of cod and of capelin, the uncertainty in the consumption estimate should not exceed the uncertainty in the stock size estimates.

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Appendix A Cod stock data used.

Table 5 Cod weight-at-age (kg)

| Cod age Year/ season | 1 | 2 | 3 | 4 | 5 | 6 | 7-9 |
|----------------------------|-------|-------|-------|-------|-------|-------|-------|
| 1984-I | 0.042 | 0.182 | 0.625 | 1.328 | 2.160 | 3.225 | 4.883 |
| 1984-II | 0.074 | 0.367 | 0.815 | 1.583 | 2.680 | 3.855 | 5.468 |
| 1985-I | 0.040 | 0.148 | 0.578 | 1.075 | 1.913 | 3.163 | 4.825 |
| 1985-II | 0.067 | 0.262 | 0.813 | 1.405 | 2.318 | 3.608 | 5.415 |
| 1986-I | 0.036 | 0.113 | 0.365 | 1.010 | 1.708 | 2.755 | 4.613 |
| 1986-II | 0.055 | 0.178 | 0.455 | 1.170 | 1.983 | 3.225 | 5.238 |
| 1987-I | 0.034 | 0.096 | 0.248 | 0.550 | 1.330 | 2.265 | 4.273 |
| 1987-II | 0.056 | 0.159 | 0.323 | 0.650 | 1.498 | 2.555 | 4.718 |
| 1988-I | 0.043 | 0.125 | 0.270 | 0.485 | 0.893 | 1.840 | 3.575 |
| 1988-II | 0.090 | 0.242 | 0.430 | 0.735 | 1.278 | 2.360 | 4.565 |
| 1989-I | 0.047 | 0.186 | 0.395 | 0.673 | 1.075 | 1.768 | 3.490 |
| 1989-II | 0.117 | 0.328 | 0.585 | 0.998 | 1.505 | 2.363 | 4.370 |

Table 6 Number of individuals (million) of each age group by season and year.

| Cod age Year/ season | 1 | 2 | 3 | 4 | 5 | 6 | 7-9 |
|----------------------------|------|-----|-----|-----|-----|-----|-----|
| 1984-I | 1121 | 572 | 363 | 125 | 73 | 42 | 34 |
| 1984-II | 1014 | 517 | 326 | 107 | 57 | 29 | 17 |
| 1985-I | 334 | 917 | 463 | 282 | 85 | 41 | 23 |
| 1985-II | 302 | 830 | 410 | 237 | 64 | 28 | 13 |
| 1986-I | 250 | 273 | 747 | 352 | 184 | 44 | 24 |
| 1986-II | 226 | 247 | 668 | 292 | 131 | 27 | 13 |
| 1987-I | 256 | 205 | 222 | 573 | 222 | 83 | 22 |
| 1987-II | 231 | 185 | 198 | 471 | 155 | 47 | 12 |
| 1988-I | 209 | 209 | 166 | 173 | 362 | 104 | 32 |
| 1988-II | 190 | 190 | 149 | 146 | 260 | 67 | 17 |
| 1989-I | 261 | 171 | 170 | 129 | 120 | 184 | 52 |
| 1989-II | 236 | 155 | 152 | 107 | 96 | 128 | 33 |

Table 7 Proportion of individuals by age group, area, season and year for the Northeast Arctic cod stock in 1984-1989

| Area | Year- Season | Age 1 | Age 2 | Age 3 | Age 4 | Age 5 | Age 6 | Age 7-9 |
|--------|-----------------|-------|-------|-------|-------|-------|-------|---------|
| II+IV | 1984-1 | 0.002 | 0.109 | 0.322 | 0.417 | 0.573 | 0.576 | 0.782 |
| III+V | 1984-1 | 0.980 | 0.827 | 0.653 | 0.544 | 0.398 | 0.409 | 0.208 |
| VI+VII | 1984-1 | 0.018 | 0.064 | 0.025 | 0.039 | 0.029 | 0.015 | 0.010 |
| II+IV | 1984-2 | 0.002 | 0.109 | 0.322 | 0.417 | 0.490 | 0.393 | 0.540 |
| III+V | 1984-2 | 0.980 | 0.827 | 0.653 | 0.544 | 0.453 | 0.577 | 0.439 |
| VI+VII | 1984-2 | 0.018 | 0.064 | 0.025 | 0.039 | 0.057 | 0.030 | 0.021 |
| II+IV | 1985-1 | 0.000 | 0.000 | 0.057 | 0.288 | 0.664 | 0.840 | 0.923 |
| III+V | 1985-1 | 0.654 | 0.917 | 0.854 | 0.479 | 0.302 | 0.058 | 0.000 |
| VI+VII | 1985-1 | 0.346 | 0.083 | 0.087 | 0.233 | 0.033 | 0.102 | 0.077 |
| II+IV | 1985-2 | 0.000 | 0.000 | 0.057 | 0.288 | 0.631 | 0.737 | 0.847 |
| III+V | 1985-2 | 0.654 | 0.917 | 0.854 | 0.479 | 0.302 | 0.058 | 0.000 |
| VI+VII | 1985-2 | 0.346 | 0.083 | 0.087 | 0.233 | 0.066 | 0.204 | 0.153 |
| II+IV | 1986-1 | 0.000 | 0.000 | 0.057 | 0.332 | 0.660 | 0.883 | 0.848 |
| III+V | 1986-1 | 0.991 | 0.868 | 0.846 | 0.550 | 0.295 | 0.066 | 0.000 |
| VI+VII | 1986-1 | 0.009 | 0.132 | 0.096 | 0.119 | 0.045 | 0.050 | 0.152 |
| II+IV | 1986-2 | 0.000 | 0.000 | 0.057 | 0.332 | 0.615 | 0.833 | 0.600 |
| III+V | 1986-2 | 0.991 | 0.868 | 0.846 | 0.550 | 0.295 | 0.066 | 0.000 |

Table 7 (Continued) Proportion of individuals by age group, area, season and year for the Northeast Arctic cod stock in 1984-1989

| | | | | | | | | |
|--------|--------|-------|-------|-------|-------|-------|-------|-------|
| VI+VII | 1986-2 | 0.009 | 0.132 | 0.096 | 0.119 | 0.090 | 0.100 | 0.400 |
| II+IV | 1987-1 | 0.000 | 0.110 | 0.220 | 0.592 | 0.830 | 0.712 | 0.800 |
| III+V | 1987-1 | 0.333 | 0.292 | 0.206 | 0.298 | 0.080 | 0.086 | 0.000 |
| VI+VII | 1987-1 | 0.666 | 0.599 | 0.574 | 0.110 | 0.090 | 0.203 | 0.200 |
| II+IV | 1987-2 | 0.000 | 0.090 | 0.060 | 0.282 | 0.464 | 0.394 | 0.600 |
| III+V | 1987-2 | 0.133 | 0.242 | 0.054 | 0.140 | 0.044 | 0.048 | 0.000 |
| VI+VII | 1987-2 | 0.867 | 0.667 | 0.887 | 0.578 | 0.492 | 0.559 | 0.400 |
| II+IV | 1988-1 | 0.000 | 0.000 | 0.307 | 0.480 | 0.514 | 0.477 | 0.500 |
| III+V | 1988-1 | 1.000 | 0.590 | 0.475 | 0.275 | 0.268 | 0.114 | 0.000 |
| VI+VII | 1988-1 | 0.000 | 0.410 | 0.218 | 0.245 | 0.218 | 0.409 | 0.500 |
| II+IV | 1988-2 | 0.000 | 0.000 | 0.201 | 0.234 | 0.338 | 0.367 | 0.600 |
| III+V | 1988-2 | 1.000 | 0.200 | 0.311 | 0.134 | 0.124 | 0.088 | 0.000 |
| VI+VII | 1988-2 | 0.000 | 0.800 | 0.488 | 0.632 | 0.538 | 0.545 | 0.400 |
| II+IV | 1989-1 | 0.222 | 0.286 | 0.164 | 0.286 | 0.407 | 0.601 | 0.639 |
| III+V | 1989-1 | 0.667 | 0.643 | 0.639 | 0.586 | 0.483 | 0.324 | 0.250 |
| VI+VII | 1989-1 | 0.111 | 0.071 | 0.197 | 0.128 | 0.110 | 0.075 | 0.111 |
| II+IV | 1989-2 | 0.222 | 0.310 | 0.134 | 0.046 | 0.083 | 0.125 | 0.115 |
| III+V | 1989-2 | 0.667 | 0.619 | 0.669 | 0.826 | 0.708 | 0.725 | 0.691 |
| VI+VII | 1989-2 | 0.111 | 0.071 | 0.197 | 0.128 | 0.209 | 0.150 | 0.194 |

AN APPROACH TO ESTIMATE THE DAILY RATION OF COD DURING INTENSIVE FEEDING BASED ON 24 HOUR FISHERY

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ABSTRACT

A model describing gastric evacuation developed by dos Santos (1990) using a modified version of the power exponential model for stomach evacuation is applied to the Northeast Arctic cod stomachs collected during 24 hour fishery. An approach to estimate the individual daily ration that takes into account the effects of initial meal size and fish weight on gastric evacuation rate in the course of 24 hour period is presented. The results indicate that the Northeast Arctic cod (length groups 40–44 cm and 45–49 cm) during intensive feeding on deep sea shrimp Pandalus borealis consumed between 0.50 % and 0.58 % of the body weight.

INTRODUCTION

Trophic supply and demand relationship (Ney, 1990) is one of the central issues in the multispecies management approach. In an ecosystem such as the Barents Sea, it is a well pronounced phenomenon that increased predation pressure from a top predator cause dramatic collapse in a prey stock. The Barents Sea capelin stock collapsed during 1983–1986 and one of the main factors causing the collapse was a rapid increase in consumption of capelin by cod (Bogstad and Tjelmeland, 1990). Mehl (1989) reported that about 675000 tonnes of deep sea shrimp were consumed in 1984 compared to 574000 tonnes of capelin while in 1985 the cod stock's consumption of capelin exceeded 1.8 million tonnes and the consumption of shrimp was reduced to 320000 tonnes.

All published information concerning the cod stock's consumption (Ponomarenko and Ponomarenko, 1975; Yaragina, 1985; Orlova et al., 1988; Mehl, 1989; Orlova et al., 1989; Bogstad and Mehl, 1990) of various prey species in the Barents Sea in general and the consumption of deep sea shrimp by cod in particular, shows that there is an inconsistency between the shrimp stock estimate and the consumption calculations by a factor 2–3. And no comparison of the consumption estimation with requirements based on energetic consideration as a test of validity has been done so far.

In this paper Santos' evacuation model was used to estimate gastric evacuation based on field measurements of the stomach contents and the daily ration of the Northeast Arctic cod during intensive feeding on Pandalus borealis was estimated .

MATERIALS AND METHODS

The data used in the current paper are obtained from the joint PINRO-IMR fish stomachs content data base. Cod stomachs were collected during the 14–15 April, 1987 by bottom trawl on board a Soviet research vessel with one hour tow made every 4 hour at the same position (73° 44' N 30° 30' E). The method of sampling and stomach contents analysis are described in detail in Mehl (1986). Cod of length 40 – 49 cm were selected for further analysis of stomach contents. Table 1 summarizes shrimp distribution by length groups in the cod stomachs.

RESULTS

The power exponential model was modified by Santos(1990) to:

$$W_{it} = W_{i0} 2^{-\left(t / \left(H_i e^{-Tc} \left(\frac{W_0}{BW}\right)^b\right)\right)^{S_i}} \quad (1)$$

This function state that the time (t) dependent trajectory of the gastric remains (W) is a function of initial meal size (W_0), temperature (T), fish size (BW) and a prey—specific evacuation pattern (S_i). The parameters b and c are constant across prey types, and the rate constant (H_i) is a theoretical value expressing (for a given prey i) the half—life (in hours) of a meal of the same size as the fish body weight at 0 °C. We will assume that the evacuation pattern is exponential ($S_i=1$).

Consider a fish whose stomach contents weight of prey (i) are known at t_1 , t_2 , t_n during a 24 h period . The evacuation rate (h^{-1}) of prey (i) at t_1 can be estimated as

$$\frac{\ln 2}{H_i e^{-Tc} \left(\frac{W_{oit1}}{BW_{i1}} \right)^b} \quad (2)$$

where :

$b=0.54$

$c=0.11$

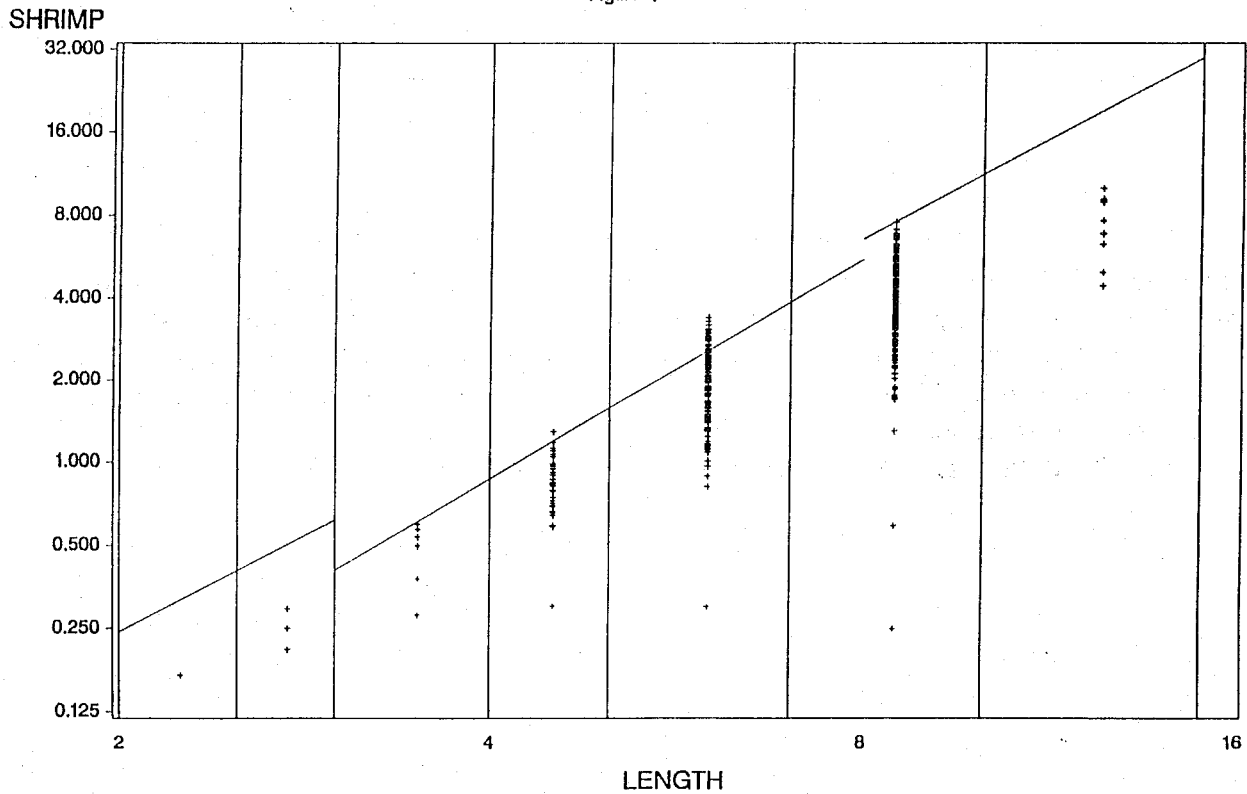
$H=533$ (shrimp)

$T=2.66$ °C (temperature during time of sampling)

W_{oit1} = reconstructed initial meal size of prey (i) at (t_1).

Weight of prey (i) was corrected for digestion by using length —weight relationship (Fig.1) of prey (i) in the Barents Sea (Berestovsky, et al., 1989).

Figure 1



The parameters of the length —weight relationship $W = a \times l^b$ of various length groups of Pandalus borealis is shown in the text table below:

| Pandalus length-cm | a | b |
|--------------------|---------|-------|
| < 3 | 0.0481 | 2.33 |
| 3-8 | 0.0220 | 2.658 |
| >8 | 0.04475 | 2.400 |

The corrected weight of various size groups of the prey (i) can then be summed to provide the initial meal size of prey (i) at time (t_1).

Equation (2) is applied to the stomach content data collected at the various times of the day, and the average daily ration of prey (i) is equal to :

$$C_i = \frac{1}{n} \sum_{t=1}^n \frac{\ln 2 * W_i * 24}{H_i e^{-T_c} \left(\frac{W_{0it}}{B W_i} \right)^b} \quad (3)$$

Application of equation (3) to individual cod stomachs collected at 4 hour intervals provides a daily consumption by cod of shrimp estimate of 0.52 % and 0.58 % of the body weight for cod in length group 40–44 cm and 45–49 cm, respectively, when we assumed that the initial meal size equal to individual total stomach content weight (method 1). The overall mean of the daily ration calculated using the length-weight relationship to find the initial meal size (method 2) amounted to 0.53 % and 0.62 % for the same length groups. The data and results are shown in Table 2 and Figures 2a, 2b and 3.

Figure 2b

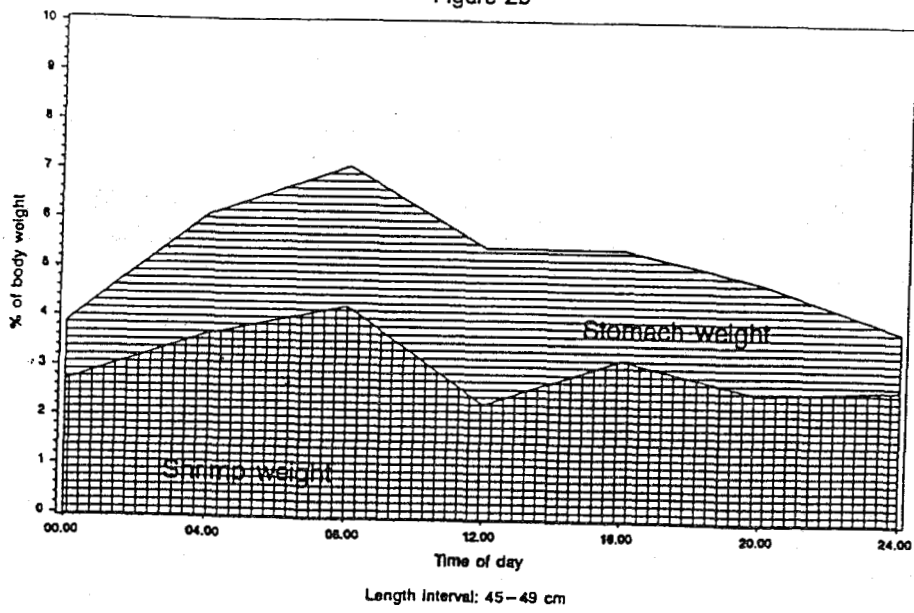


Figure 2a

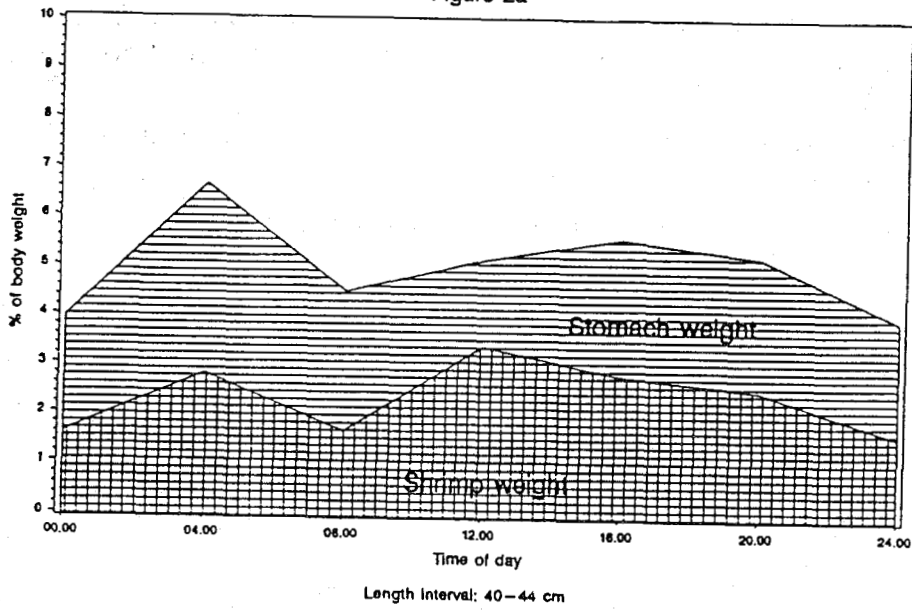
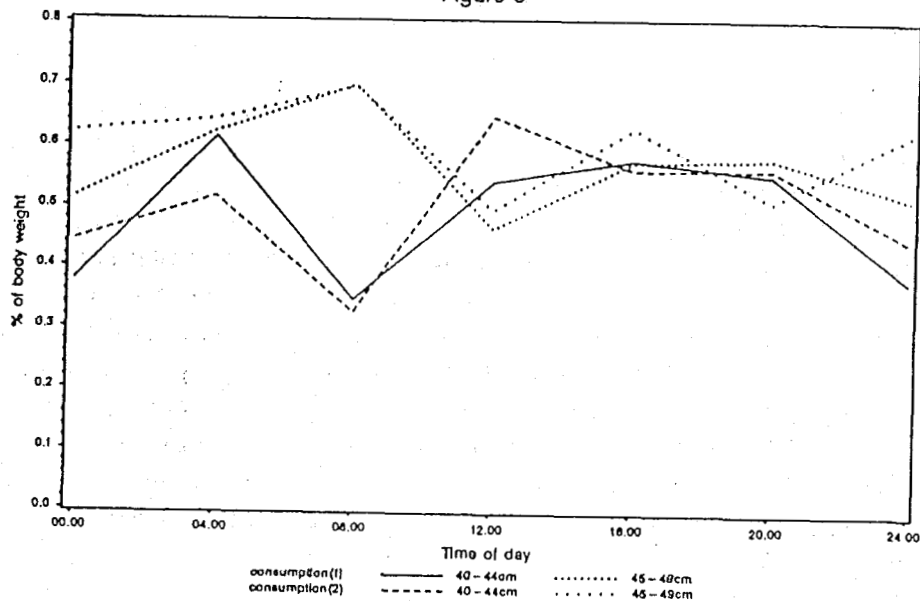


Figure 3



Converting consumption in weight to consumption in numbers

If the consumption of a prey is calculated it is possible to calculate the numbers consumed if one has the following information. The length distribution of preys in the stomachs and the length-weight relationship. This is best illustrated through an example:

Let C denote the total consumption for one day of this prey for a given area/population. The weighted length distribution of the prey is calculated:

$$F_j = \frac{\sum_{i=1}^s w_i n_{ij}}{\sum_{j=1}^k \sum_{i=1}^s w_i n_{ij}} \quad (4)$$

where F_j is the fraction of preys in length interval j . ($j=1..k$), n_{ij} is the number of preys in length interval j in haul number i ($i=1..s$) and w_i is the weight given to haul number i . The weight could be calculated as: total catch weight/sample weight and would very often be equal 1.

Using the length-weight relationship, we can calculate the mean prey weight (in grams) for each length interval $W_1..W_k$.

Total numbers consumed can then be calculated as:

$$N = \frac{C}{\sum_{j=1}^k F_j W_j} \quad (5)$$

or for each length interval:

$$N_j = N * F_j \quad (6)$$

DISCUSSION

The basic assumption of Santos' model is that every prey item evacuated independently of other food items which has already been consumed but not completely evacuated. This was the assumption of several food consumption models, such as Elliot and Persson (1978), Eggers (1979), Pennington (1985), Olsen and Mullen (1986) and Sainsbury (1986). However, the "dependent" form of the same model above predicted increased clearance of the first prey and a low evacuation rate of the second prey while the "independent" form model tended to overestimate the contents of the first prey remaining in the stomach and faster evacuation of the second prey than observed (dos Santos, 1990). Tyler (1970) reported that single meal evacuation model led to underestimate of the total food remaining in the stomach after consumption of multiple meal and suggested that this was caused by a starvation period. Ruggerone (1989) show that single meal evacuation rate models can accurately describe the evacuation of multiple meals and may therefore be used to estimate the daily ration.

The accuracy of any method of estimating daily ration in wild fish rests ultimately upon an assumption that laboratory results are representative of field conditions (Swensen and Smith, 1973). The estimated values of the equation parameters appear to be satisfactory for use in field study since Northeast Arctic cod are very seldom found outside the experimental temperature and stomach contents higher than 9% of body weight, which is the highest value used in the experiments (dos Santos, 1990), do not normally occur.

The model proposed in this paper for estimating the consumption of various prey items based on 24 h fishery, removes the possible bias associated with:

- 1) Violation of the assumption that feeding occurs only during a discrete feeding period (Sainsbury, 1986; Krasnoper, 1988) during feeding cycle.

- 2) The assumption that the rate of food consumption is constant over an interval between samples (Elliot and Persson, 1978).

- 3) "guesstimate" this was the approach followed by Bogstad and Mehl (1990) by changing initial meal size in dos Santos' evacuation model to set equal to double stomach contents weight for yearly average and to average stomach content during intensive feeding.

Several authors have been estimating the daily ration of Northeast Arctic cod based on field observation (Yaragina, 1985; Tarverdieva and Yaragina, 1989; Dolgov and Yaragina, 1990). Their model assumed a constant gastric evacuation rate, basically cod stomach was collected during many days station every 4 hour and the hourly evacuation rate is estimated as (maximum stomach content weight - minimum stomach contents weight)/4. However, it has been shown that the exponential model explains reasonably well the trends observed in gastric emptying in cod (dos Santos, 1990) and the linear model is appropriate for determining the daily ration for larvae and stomachless fish species (Krasnoper, 1988). Using the linear model is impossible in conditions of food resource instability as observed recently in the Barents Sea (Orlova, 1989).

The curve fitting to the diel changes in stomach fullness of the Barents Sea cod reported by Tarverdieva and Yaragina (1989), explains only 26% of the variability in the stomach fullness during three days of observation. This results led the mentioned authors to conclude that the feeding rhythm was poorly expressed. The daily ration during intensive feeding on shrimp reported by the same authors amounted from 6.2% to 6.5% of the body weight.

One of the advantages of this approach is that the effect of the initial meal size and fish weight on gastric evacuation rate in the course of 24 hour period have been taken into account. In addition, equation (3) can be used to calculate the daily ration regardless of whether the stomach samples were taken between time interval or at the end of each interval.

Table 1 Shrimp size distribution in cod stomachs by time.

| time/ shrimp size cm | 04:00 | 08:00 | 12:00 | 16:00 | 20:00 | 24:00 | Total |
|----------------------------|-------|-------|-------|-------|-------|-------|-------|
| 2.0-2.4 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| 2.5-2.9 | 0 | 1 | 0 | 2 | 1 | 4 | 4 |
| 3.0-3.9 | 6 | 1 | 0 | 2 | 1 | 0 | 10 |
| 4.0-4.9 | 10 | 14 | 10 | 10 | 2 | 7 | 53 |
| 5.0-6.9 | 124 | 90 | 81 | 203 | 39 | 91 | 628 |
| 7.0-9.9 | 93 | 109 | 106 | 144 | 81 | 98 | 631 |
| 10.0-14.9 | 6 | 1 | 1 | 1 | 3 | 0 | 12 |
| Total | 239 | 216 | 198 | 362 | 128 | 196 | 1337 |

Table 2 Consumption, mean stomach weight and shrimp weight as a percent of the cod body weight during 24 hour.

| time of day | Consumption method (1) | | Consumption method (2) | | Stomach weight | | Weight of shrimp | |
|----------------|---------------------------|-------|---------------------------|-------|----------------|-------|------------------|-------|
| | 40-44 | 45-49 | 40-44 | 45-49 | 40-44 | 45-49 | 40-44 | 45-49 |
| 00.00 | 0.38 | 0.52 | 0.44 | 0.62 | 3.96 | 3.86 | 1.60 | 2.68 |
| 04.00 | 0.61 | 0.62 | 0.52 | 0.64 | 6.67 | 6.08 | 2.81 | 3.64 |
| 08.00 | 0.35 | 0.70 | 0.32 | 0.70 | 4.50 | 7.09 | 1.66 | 4.23 |
| 12.00 | 0.54 | 0.47 | 0.65 | 0.50 | 5.17 | 5.47 | 3.39 | 2.29 |
| 16.00 | 0.58 | 0.57 | 0.56 | 0.63 | 5.60 | 5.47 | 2.81 | 3.23 |
| 20.00 | 0.55 | 0.58 | 0.56 | 0.51 | 5.24 | 4.81 | 2.52 | 2.56 |

ACKNOWLEDGMENT

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DAILY RATIONS OF COD FROM THE BARENTS SEA

by

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ABSTRACT

Diurnal feeding rhythms and daily diets of the North—East Arctic cod were investigated based on data obtained at several stations made in the summer of 1988-1989. A well- pronounced feeding rhythmicity was recorded under conditions of a stable occurrence of food organisms and in case cod fed on a single prey species. The daily rations of cod which fed on Euphausiacea, Themisto, fish and shrimps varied from 2.10 to 3.7 % and from 0.28 to 0.99 % of the body weight in 1988 and 1989, respectively.

INTRODUCTION.

24-hour stations have been traditionally carried out during the PINRO research cruises to study feeding patterns and food habits of the Barents Sea commercial species. Studies of daily rations were initiated in 1959 (Novikova, 1962) to be continued in the 60-80-ies (Ponomarenko, 1973; Antipova and Yaragina, 1984; Yaragina, 1985, 1988; Tarverdieva and Yaragina, 1989 and Dolgov, 1990).

The studies have acquired special importance at the present time in view of the multispecies modelling which require reliable estimates of the cod predation on other commercial species. Such estimates may be obtained from experiments conducted in controlled conditions and with the aid of bioenergetic models. Since both methods are subject to errors, estimates of daily diets under natural conditions are needed as independent information.

MATERIAL AND METHODS

Use was made of data obtained at two 24-hour stations made in the summer of 1988 and three 24-hour stations carried out in the summer of 1989 (Table 1).

Bottom trawl hauls, each of one hour duration, were made using 125 mm mesh size and a fine (16 mm) cod-end insertion in the areas of stable concentrations of cod. The hauls were made every 4 hours where possible and mostly along the same tracks and at the same depths. Out of each catch a total of 30 individuals of cod were measured, weighed and their sex and maturity stage were determined. Stomach contents were analysed using the quantitative-weight method (Anon, 1974). Daily rations were estimated employing the Santos model (Bogstad and Mehl, 1991) and the linear regression equations derived by Fortunatova and Bajkov (Orlova, 1991) since the recent findings (Orlova, 1991; Tseitlin, 1991) have revealed the deficiency of the method which implied a drop in the indices of stomach fullness to calculate daily rations. The methods developed by Krasnoper (1988) and Novikova (1949, 1951) were also applied to compare the results obtained.

RESULTS

The stations were divided into the following 3 groups:

1) Stations where Themisto comprised the bulk of the cod diet:

a) The Goose Bank southern slope where cod fed mainly (64.5% in terms of weight) on Parathemisto libellula 2-4.5 cm long and on P. abyssorum 0.8-1.5 cm long (Table 2). Fish (31.0% of the food bolus) was represented by Leptoclinus maculatus and Lumpenus spp. (12.5%), long rough dab (9.1%) and by several species of the family Cottidae (3.0%). Various species of Decapoda and Euphausiacea constituted 2.1 and 1.6%, respectively. Other food items occurred incidentally and in minor quantities.

Themisto-fish quantitative relationship varied inversely within one and the same station (Fig.3B). The proportion of Themisto was high during the 1st day of the station and it decreased down to 20.1% between 8 and 12 a.m. on the 2nd day (July, 30) and then increased again. The above variations were the most considerable on record, though an insignificant reduction in the Themisto portion in the diet was recorded at 4 p.m. on

July 31 and at 8.45 p.m. on August 1. Fluctuations in the frequency of occurrence of Themisto in the food bolus corresponded to those in their weight. The proportion of fish in the diet increased gradually by the end of the station and it had two peaks (at 8 p.m. on July 30 and at 8 a.m. on July 31). The cod feeding rate was of an irregular pattern and no clearly pronounced rhythmicity was revealed. Cod fed usually 1- 2 times a day mostly during the periods from 4 to 12 a.m. and from 8 to 12 p.m. The daily diets as calculated using Fortunatova's, Bajkov's and Santos' method made up 0.91, 0.85 and 0.99% of the body weight, respectively;

b) The Demidov Bank where cod catches varied from 63 kg to 4 tonnes to be stable during the 1st day and to decrease sharply at 8 a.m. and between 4 and 8 p.m. on the 2nd day (Fig.1B).

Themisto, predominantly Parathemisto libellula 1.5-4 cm long and P. abyssorum constituted the bulk of the cod food (74.1% in terms of weight) (Table 2). The important food items were also Decapoda, mainly Pandalus borealis 4-12 cm long and fish (mainly Sebastes marinus 4-11 cm long and capelin 7-14 cm long). No variations in the food spectrum were observed within the station, however some reduction in the share of Themisto was noted because the share of fish increased (Fig.4B). The frequency of occurrence of different food items in the cod diet showed the following dynamics (Fig.4B) : a reduction in the feeding rate was accompanied by an increase in the proportion of fish and decapods in the diet whereas the share of Themisto remained unchanged. A well-pronounced feeding rhythmicity was established (Fig.4A) with peaks between 9 and 12 a.m. on the 2nd day and in the period from 0 to 8 a.m. and from 4 to 8 p.m. on the 3rd day. During the maximum feeding activity the proportion of Themisto in the diet showed an increase in terms of weight. The daily rations calculated using the 3 methods constituted 3.76, 3.61 and 0.74% of the body weight, respectively.

2) Stations where Euphausiacea were predominant in the cod diet:

a) The Murman shallow where catches varied from 108 to 1,034 kg (Fig.2B) and the proportion of cod varied from 44 to 73%. The maximum and minimum yields were taken at 4 and 12 a.m. and at 8 a.m., respectively. Thysanoessa inermis and Th. raschii 2.0-2.5 cm long as well as Meganyctiphaenes norvegica 3.0-3.5 cm long made the bulk (48.4%) of the food bolus (Table 2). Fish comprised 31.3% in terms of weight and it was represented by long rough dab (13.3%) and by species of the family Lumpenidae (8.2%) and Cottidae (4.6%). Decapoda constituted 16% of the food bolus out of which 13.6% fell on Pandalus borealis. Significant variations in the food spectrum of cod were recorded (Fig.5B). Euphausiacea and fish were major food items in the beginning of the station whereas on the 3rd day (August 7) after 4 a.m. the proportion of Decapoda increased rapidly (both in terms of weight and the frequency of occurrence). The maximum feeding rates were recorded at 8 a.m. and 8 p.m. on August 6 and 7, respectively. The hydrographic observations conducted at the station indicated interaction between two different water masses (from the Kanin Bank shallow and from the Murman Current branch) characterized by inhomogeneous salinity and temperature, which induced formation of euphausiid concentrations to be recorded by the acoustic devices in the feeding ground. Cod were registered as large individual schools and their behaviour was determined by migrations of euphausiids. The euphausiid aggregations migrated to 0-40 m layer during 24 hours which was accompanied by the cod migration to the layer 10-15 m from the bottom to result in the catch reduction. The 2nd drop in the

yield was observed at 8 a.m. when euphausiids moved to the layer 20-30 m above the bottom. However, the vertical migrations of cod did not necessarily follow the euphausiid distribution since fish also constituted a large portion in the cod diet. The daily ration as calculated by the 3 methods constituted 0.33, 0.28 and 0.48% of the body weight, respectively;

b) The Rybachy'a Bank where cod catches varied from 65 to 238 kg (Fig.1A) with no pronounced dynamics observed. A gradual reduction was noted in the beginning of the station to be followed by a sharp drop and steady but small catches in the end. Euphausiids formed the bulk (84.1% in terms of weight) of the cod diet (Table 2). Important food items were also fish (12.0% in terms of weight), mainly capelin 6-14 cm long (5.9% in terms of weight), young haddock (3.9%) and redfish 4-8 cm long (1.2%). Other food organisms occurred in minor quantities. The food spectrum remained unchanged throughout the station (Fig.6B). An insignificant reduction in the share of euphausiids (in terms of weight) in the food bolus was recorded during the period from 8 p.m. to 4 a.m., which was accompanied by an increase in the proportion of fish (in terms of weight). The frequency of occurrence of euphausiids did not show actual variations whereas that of fish and decapods increased between 8 p.m. and 4 a.m. The maximum feeding activity was observed in the period from 8 p.m. to 4 a.m. The daily rations as calculated using the 3 methods constituted 2.20, 2.10 and 0.64% of the body weight, respectively.

3. Station at which mixed feeding of cod was observed:

a) A 5-day station in the Kanin-Kalguev shallow where fish was the major food item of cod (40.9% in terms of weight) and it was represented by species of the family Lumpenidae (24.1%), Cottidae (4.0%) and long rough dab (10.7%) (Table 2). Essential food organisms were also Euphausiacea (18.2%), Decapoda (17.5%) and Mollusca (13.0%). Molluscs were mainly represented by Serripes groenlandicus 3.5 cm long. Themisto and Gammaridea comprised 5.5 and 1.0% of the food bolus, respectively. The food spectrum showed significant variations during the station (Fig.7B). In the beginning of the station (August 13) the proportion of euphausiids showed a reduction in the cod diet and fish became a major food item. On the second day (August 14) the share of shrimp increased. On August 15 the proportions of both fish and shrimp decreased sharply and cod fed mainly on euphausiids, which was followed by an increase in the proportion of Serripes groenlandicus (51.3% of the food bolus). The variations in the frequency of occurrence of different food organisms was accompanied by the respective weight dynamics (Fig.7B). No distinctly pronounced feeding rhythmicity was revealed (Fig.7A). The daily rations as calculated by the 3 methods constituted 0.71, 0.65 and 0.54% of the body weight, respectively.

DISCUSSION

The investigations carried out during the summer feeding period of cod in 1988-1989 have revealed new food items along with the traditional ones. A small crustacean of the genus Parathemisto has become an important food item for cod since 1986 and in some areas it was the major food organism (Orlova et al., 1989). In the eastern parts of the Barents Sea cod fed largely on young long rough dab, non-commercial species of the families Lumpenidae and Cottidae, as well as on the bevalve mollusc

Serripes groenlandicus which were not known earlier to be within food spectrum of cod. According to data obtained by Zatsepin and Petrova (1939) the proportion of non-commercial species constituted 4-8, 9-34 and 5-9 % of the food bolus of cod from the Murman shallow, the Goose Bank slope and the Kanin-Kolguev shallow, respectively, in 1934-1938 (against 26.3, 24.7 and 38.7%, respectively, in 1989).

A clearly-pronounced feeding rhythmicity was noted when cod fed on one food organism, which was the case in the Rybach'ya Bank area when the share of euphausiids was as high as 84.1%. The feeding rhythmicity was not clearly pronounced in cod from the Murman shallow since euphausiids and fish comprised 48.4% and 31.1% of the food bolus, respectively. Feeding rhythmicity was not recorded in cod from the Kanin- Kolguev shallow where the fish fed on 4 species. It can be concluded that the results obtained are in full agreement with the concept that the diurnal feeding rhythms can be observed only under conditions of a stable food availability (Novikova and Mikhalkovich, 1963; Dolgov, 1990).

No significant differences were recorded in the diurnal feeding rhythms when cod fed on several preys. The maximum feeding activity was observed from 0 to 4 a.m. and from 4 to 8 p.m. (Yaragina, 1985) when cod fed on euphausiids, from 4 to 8 a.m. and from 8 p.m. to 0 a.m. when they fed on shrimp (Yaragina, 1988; Tarverdieva and Yaragina, 1989) and from 4 to 8 p.m. when feeding on shrimps, euphausiids and fish took place (Antipova and Yaragina, 1984). However, as it was noted by Zadul'skaya and Smirnov (1939), the maximum feeding activity for the entire summer fell on the period between 8 and 12 a.m., which was the case when cod fed on fish (Tarverdieva and Yaragina, 1989). The peak of feeding took place between 4 and 8 a.m. or between 4 and 8 p.m. in cod from the Murman shallow and the Demidov and Rybach'ya Banks, which agrees well with literature data.

The original calculated cod daily rations for 1988 proved to be significantly higher than the average values for the summer period of 1984-1986 (Orlova et al., 1989) and the respective values for the previous years (Novikova, 1962; Antipova and Yaragina, 1984; Yaragina, 1985, 1988; Tarverdieva and Yaragina, 1989).

The cod daily rations in 1989 did not exceed the average values for the summer (Yaragina, 1985) and they were in line with the literature data available (Novikova, 1962; Antipova and Yaragina, 1984 and Yaragina, 1985, 1988). The cod rations in the summer of 1986 differed from the above data significantly (Tarverdieva and Yaragina, 1989).

The high values of cod daily rations in the summer of 1988 can be caused by inadequate feeding on capelin due to a reduction in the capelin stock, which resulted in cod feeding on other preys. The reduction in daily rations in 1989 apparently indicated a certain improvement of food availability for cod and a more steady feeding pattern.

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Table 1 Characteristic features of 24-hour stations

| Area | Latitude, N | Longitude, E | Date | Water temp. °C | Depth, m | Number of hauls | Number of cod stomachs analysed |
|------------------------------------|-------------------|--------------------|-------------------------------|----------------------|----------|--------------------|--|
| Rybach'ya Bank | 70°20'- 70°25' | 32°13'- 32°17' | 27-28 June 1988 | 1.4-1.6 | 175-240 | 12 | 192 |
| Demidov Bank | 73°00'- 73°05' | 32°18'- 32°22' | 5-8 July 1988 | 1.2-1.4 | 210-250 | 12 | 390 |
| Goose Bank southern slope | 70°55'- 71°40' | 44°32'- 46° 11' | 29 July- 2 August, 1989 | 1.2-2.3 | 135-150 | 23 | 634 |
| Murman shallow | 69°26'- 69°29' | 40°54'- 40°55' | 5-7 August 1989 | 2.3-2.6 | 125-150 | 14 | 420 |
| Kanin- Kolguev shallow | 69°21'- 69°30' | 44°27'- 44°31' | 13-16 August 1989 | 2.17-2.38 | 70-75 | 19 | 569 |

Table 2

Upper part: Frequency of occurrence (F, %) and proportion by weight (W, %) of different food items in cod stomachs. (Subgroups in brackets).

Lower part: Biological characteristics of cod

| Prey species | Rybach'ya Bank | | Demidov Bank | | Goose Bank southern slope | | Murman shallow | | Kanin-Kolguev shallow | |
|-----------------------------------|----------------|-------|--------------|--------|---------------------------|--------|----------------|--------|-----------------------|--------|
| | W, % | F, % | W, % | F, % | W, % | F, % | W, % | F, % | W, % | F, % |
| Ctenophora | - | - | 0.1 | 3.8 | 0.1 | 1.4 | - | - | + | 0.2 |
| Euphausiidae | 84.1 | 99.0 | 1.1 | 44.5 | 1.6 | 53.7 | 48.4 | 79.0 | 18.2 | 58.1 |
| Parathemisto | 2.0 | 82.2 | 74.1 | 97.4 | 64.5 | 93.3 | 0.5 | 25.2 | 5.5 | 35.8 |
| Gammaridea | 0.1 | 6.3 | + | 3.1 | 0.4 | 24.7 | 0.4 | 12.6 | 1.0 | 31.6 |
| Decapoda | 0.5 | 9.4 | 13.2 | 53.7 | 2.1 | 31.8 | 16.0 | 23.6 | 17.5 | 63.7 |
| Pandalus borealis | (0.4) | (6.8) | (13.2) | (52.4) | (0.9) | (17.4) | (13.6) | (17.2) | (0.3) | (1.1) |
| Polychaeta | 0.1 | 15.7 | + | 5.4 | 0.2 | 7.9 | 1.9 | 29.1 | 3.1 | 41.7 |
| Echino-dermata | + | 0.5 | - | - | - | - | 0.3 | 1.7 | 0.1 | 0.2 |
| Mollusca | + | 1.6 | + | 0.5 | + | 0.1 | 0.2 | 1.5 | 13.0 | 30.4 |
| Pisces | 12.0 | 22.0 | 11.5 | 52.9 | 31.3 | 75.1 | 31.3 | 39.8 | 40.9 | 72.8 |
| Mallotus villosus | (5.9) | (9.9) | (3.1) | (16.7) | (0.5) | (6.3) | (2.0) | (4.2) | (0.4) | (2.9) |
| Sebastes spp | (1.2) | (4.2) | (6.1) | (36.2) | (1.3) | (20.4) | (0.2) | (1.0) | (0.1) | (1.4) |
| Lumpenidae | (0.4) | (2.1) | + | (1.3) | (12.5) | (42.4) | (84) | (19.7) | (24.0) | (57.9) |
| Cottidae | - + | (0.5) | (0.1) | (1.3) | (3.0) | (19.6) | (4.6) | (3.5) | (4.0) | (17.4) |
| Hippo-glossoides platessoides | - + | (0.5) | - | - | (9.1) | (21.5) | (13.3) | (9.1) | (10.7) | (12.4) |
| Mean fish length, cm | 53.9 | | 51.3 | | 62.0 | | 54.1 | | 54.1 | |
| Mean weight, g | 1124 | | 1042 | | 2067 | | 1431 | | 1165 | |
| Mean fatness, % of body weight | no data | | no data | | 6.5 | | 7.0 | | 7.5 | |
| Mean index of stomach fullness, % | 30.86 | | 53.68 | | 20.95 | | 8.62 | | 16.64 | |
| Mean degree of stomach fullness | 3.41 | | 3.66 | | 2.84 | | 2.19 | | 2.85 | |
| % of cod consuming fish | 99.5 | | 99.5 | | 99.5 | | 96.7 | | 97.7 | |

Figure 1 Cod catches at 24-hour stations in 1988 A — The Rybachya Bank. B — The Demidov Bank.

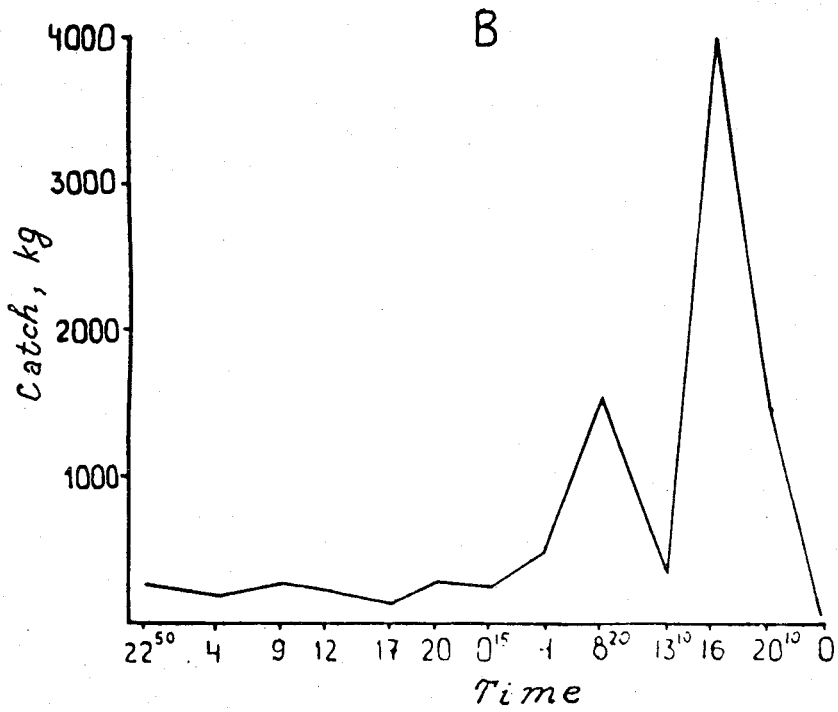
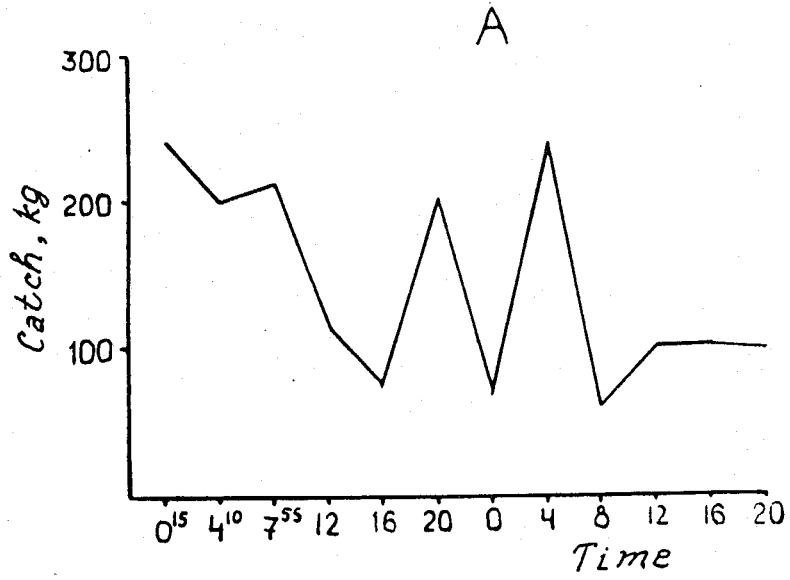


Figure 2 Cod catches at 24-hour stations in 1989 A — The Karin-Kolguev shallow. B — The Goose Bank southern slope. C — The Murman shallow

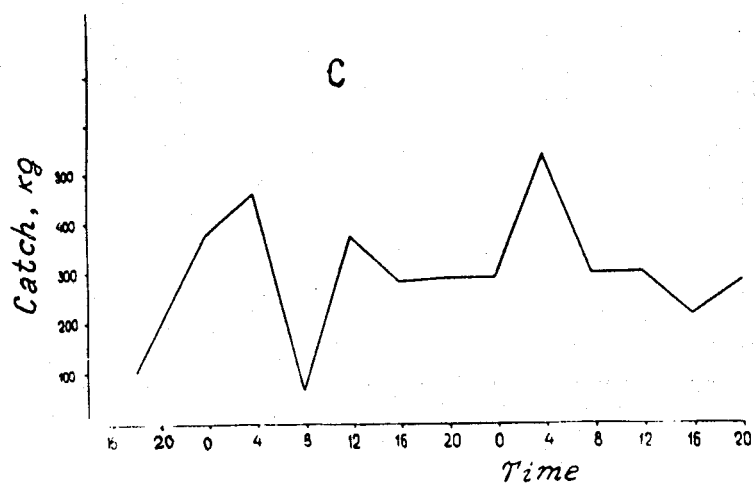
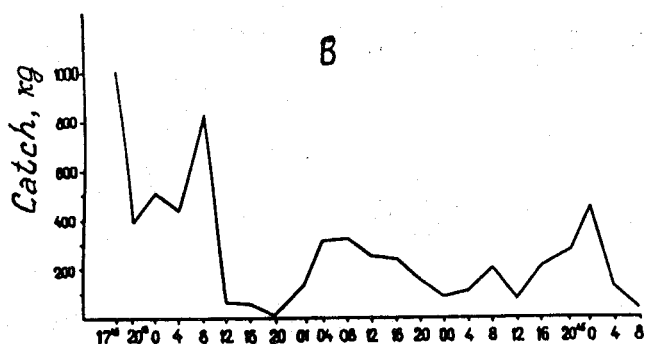
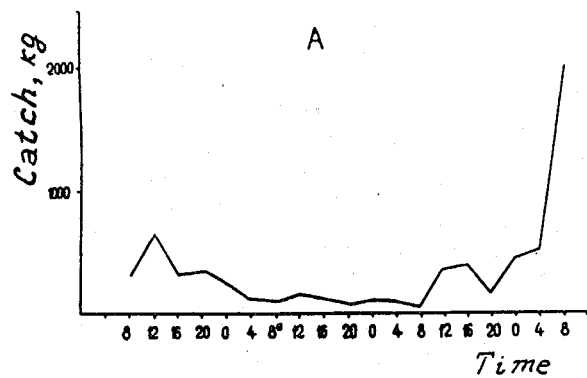


Figure 3 Diurnal feeding of cod on the Goose Bank southern slope
 A — mean index (1) and mean degree (2) of stomach fullness:
 B — food spectrum, % of weight
 C — frequency of food items occurrence, % of number of fish fed on
 (1: euphausiids; 2: Themisto; 3: Decapoda; 4: molluscs;
 5: polychaetes; 6: Echinodermata; 7: fish; 8: others).

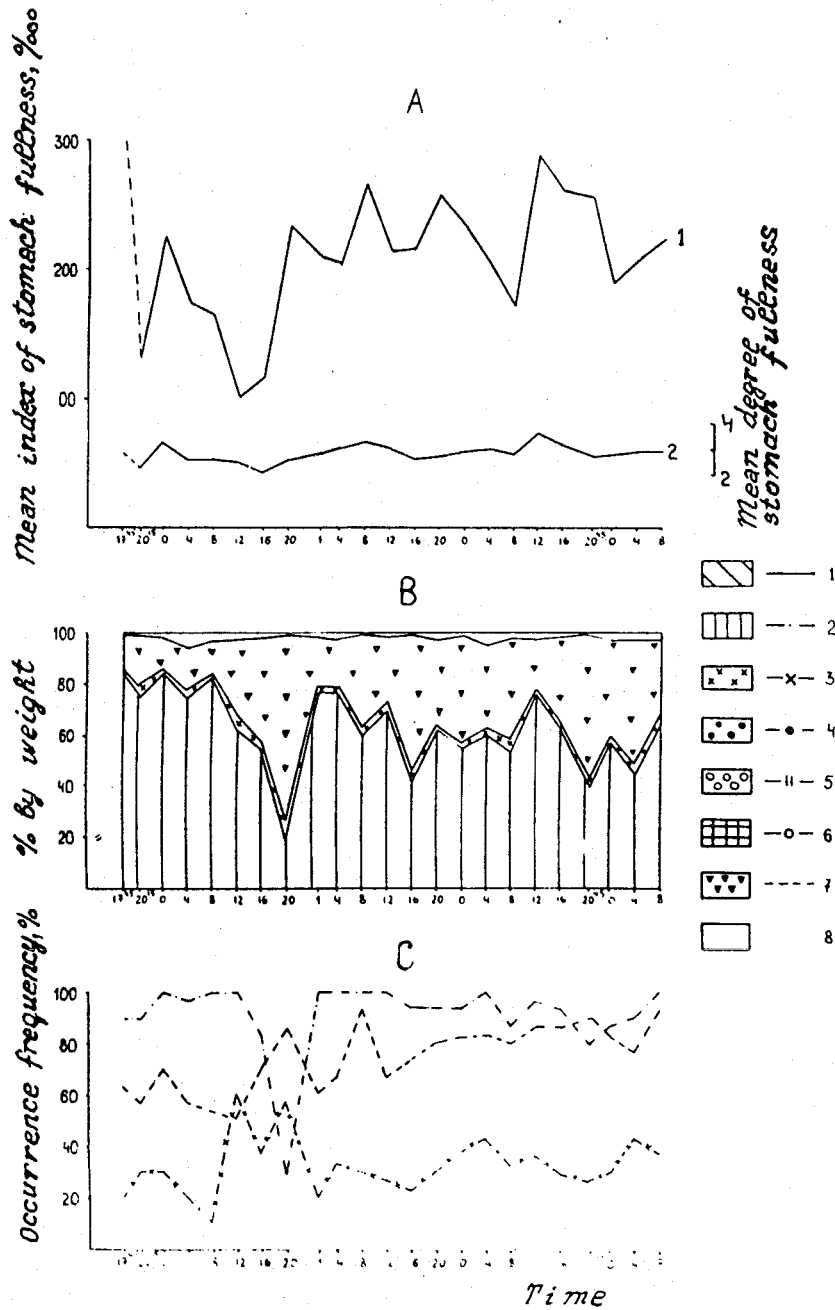


Figure 4 Diurnal feeding of cod on the Demidov Bank

A — mean index (1) and mean degree (2) of stomach fullness:

B — food spectrum, % of weight

C — frequency of food items occurrence, % of number of fish fed on

For symbols see Fig. 3.

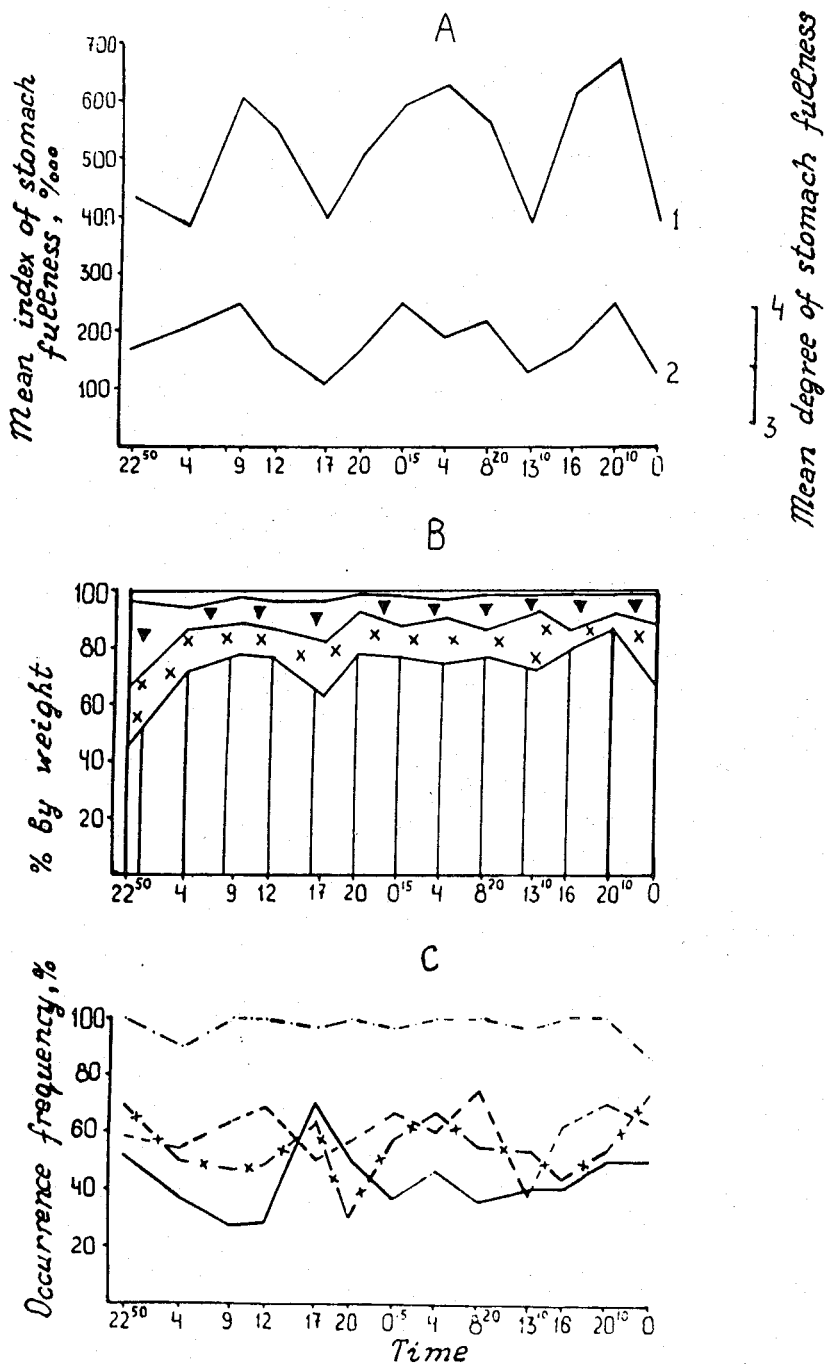


Figure 5 Diurnal feeding of cod in the Murman shallow

A — mean index (1) and mean degree (2) of stomach fullness:

B — food spectrum, % of weight

C — frequency of food items occurrence, % of number of fish fed on

For symbols see Fig. 3.

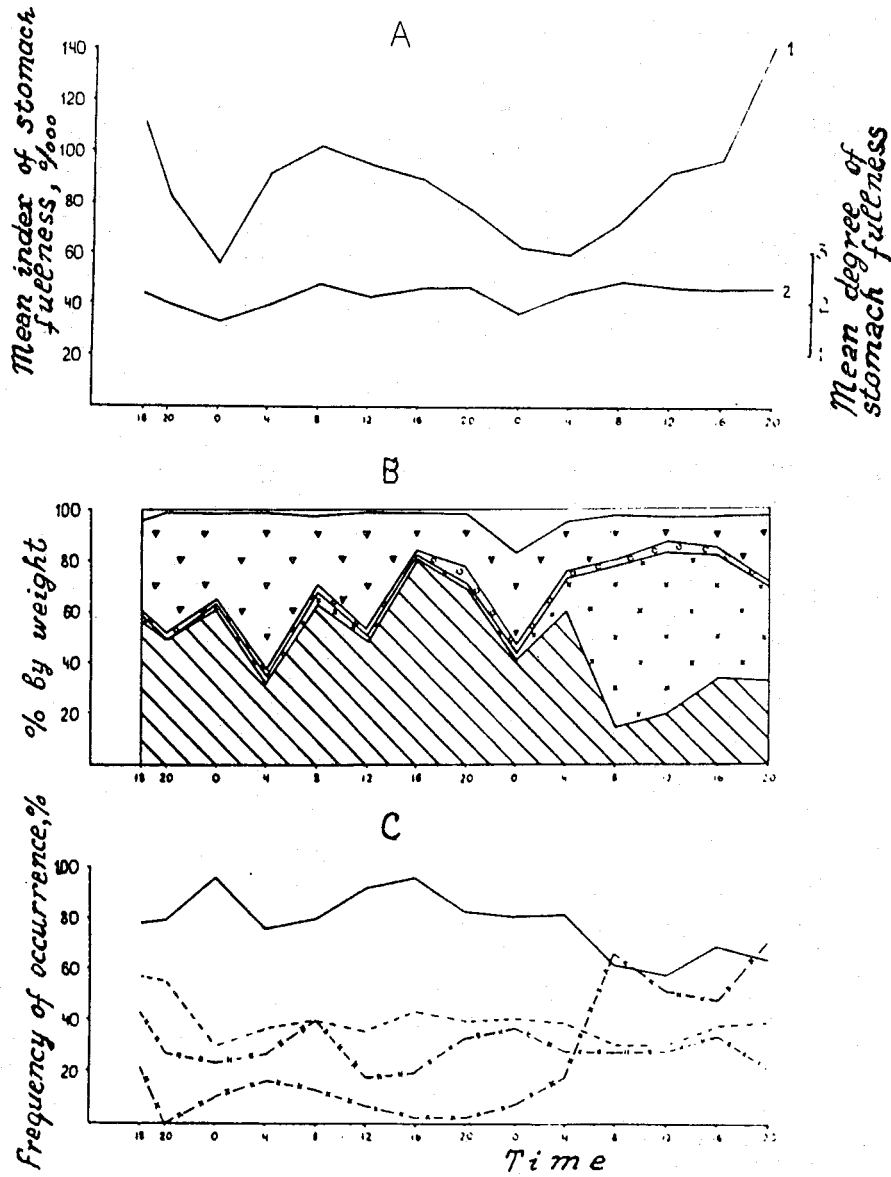


Figure 6 Diurnal feeding of cod on the Rybachya Bank

A — mean index (1) and mean degree (2) of stomach fullness:

B — food spectrum, % of weight

C — frequency of food items occurrence, % of number of fish fed on

For symbols see Fig. 3.

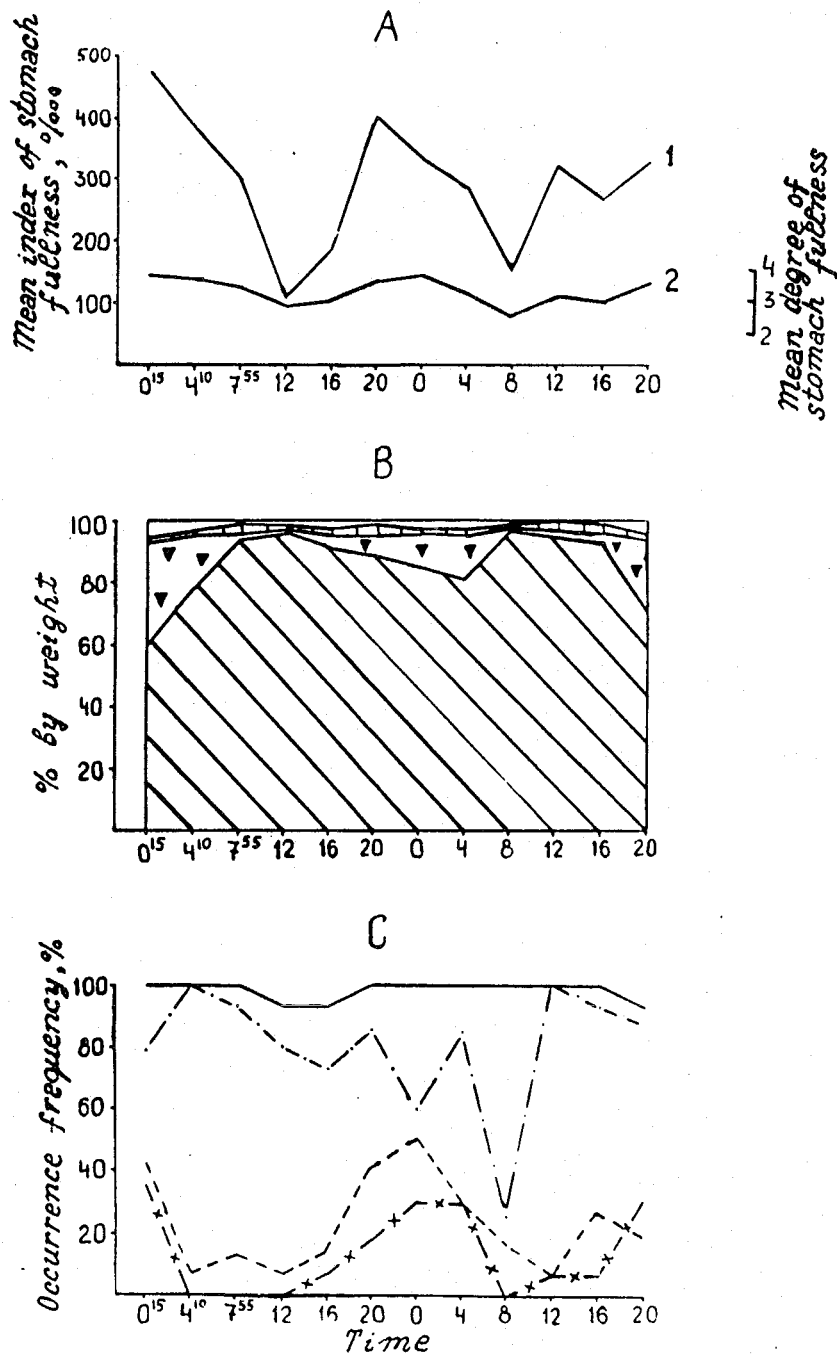
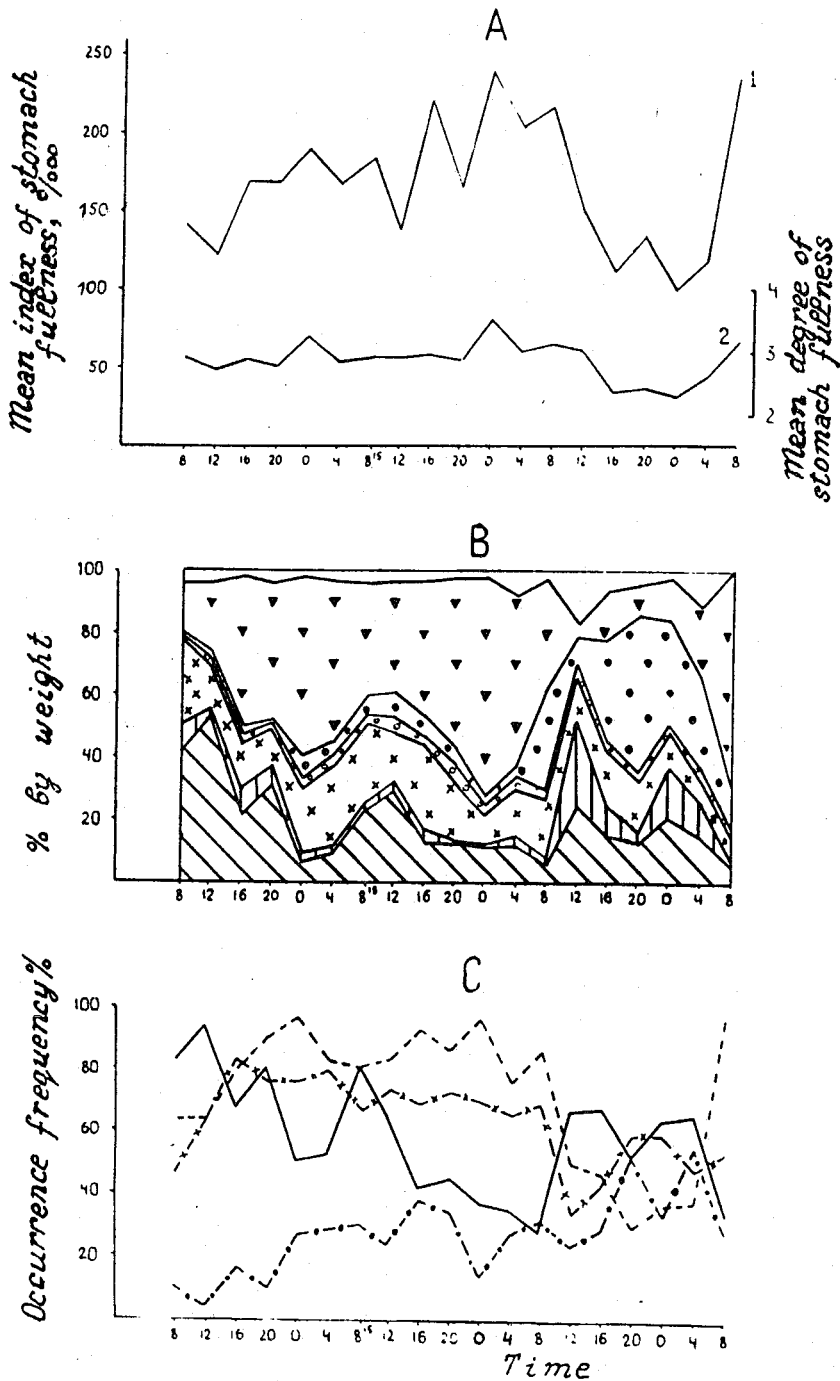


Figure 7 Diurnal feeding of cod in the Kanin-Kolguev shallow
 A — mean index (1) and mean degree (2) of stomach fullness:
 B — food spectrum, % of weight
 C — frequency of food items occurrence, % of number of fish fed on
 For symbols see Fig. 3.





NORTH—EAST ARCTIC COD IMPORTANCE IN CAPELIN STOCK DYNAMICS

by

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ABSTRACT

Average quarterly food consumption of 1 individual of the North—East Arctic cod and the portion of capelin in it was estimated and distributed by age using the joint IMR-PINRO stomach content data base. The abundance and biomass of age groups, natural mortality rates and capelin mortality due to cod predation were obtained by the Multispecies VPA. A model for capelin exploitation with account taken of the trophic relations with cod is suggested. A rate of exploitation at which the annual biomass of mature capelin would be close to 2.5 million tonnes is recommended.

INTRODUCTION

A large-scale international capelin fishery was initiated in the 70's and the total catch was increasing almost steadily to reach 2.9 million tonnes in 1977. During the subsequent years, despite a somewhat decrease, it still remained considerable. From 1978 to 1985 the average catch was equal to 1.6 million tonnes. In 1972-1985 3-4 year old capelin made up over 65 % of catch. The results of trawl-acoustic surveys indicated an upward trend in the total mortality rate of capelin from these age groups. The average total mortality rate 3-4 year-olds from the 1971-1975 year-classes was as high as 1.07 and it increased almost by 2 times to constitute 2.10 in the next 5 year-classes, and to reach 3.52 in the 1981-1985 year-classes. Extremely high exploitation rate and an increase in the total mortality was accompanied by a reduction both in the total biomass of capelin commercial stock and of its mature portion. The total biomass of commercial stock and that of mature fish have decreased since 1982 and in 1986 they constituted 0.12 and 0.06 million tonnes, respectively. In our opinion, one of the reasons for a heavy depression of the stock was the fishery management without due regard for consumption of capelin by other marine organisms, such as fish, marine mammals and birds. Capelin plays an important role in the nutritive balance of the Barents Sea animal world. The North—East Arctic cod prey on capelin during a considerable part of the year, mainly from February to May, during capelin spawning migration and in open areas. The present paper attempts at demonstrating cod impact on the abundance and biomass of capelin of different age and at making recommendations for capelin fishery management with account taken of cod predation.

MATERIAL AND METHODS

The abundance of age groups from commercial stocks of the North—East Arctic cod and the Barents Sea capelin and parameters indicating their trophic relationships were determined by Multispecies VPA (MSVPA) described by Sparre (1984). The method involves a generalized single-species VPA with reference to several species with account taken of predator-prey relationships. The application of the MSVPA requires the following data to be broken down by age and quarters of the year: annual catch of the species, average weight of 1 individual, average food consumption rate of the predator and a portion of the prey in the predator diet as well as natural mortality rate due to causes other than predation, and starting rates of fishing mortality. Data on catches and average weights of cod and capelin were obtained during numerous research cruises conducted by PINRO and from material of the ICES Working Groups. Cod quarterly diet and a portion of capelin in it were estimated using the joint IMR-PINRO stomach content data base containing information on nutrition of more than 42 thousand individuals of cod for a period from 1984 to 1990.

Bajkov's formula (1935) has been used in the calculations:

$$R = D \frac{24}{t} \quad (1)$$

where:

R is daily consumption of a given prey by a fish

t is digestion time for a given food

D is food consumption index.

The time required for digestion of capelin by cod was calculated from the formula suggested by Jones (1974) on the basis of experimentally-determined evacuation rates of different types of food consumed by cod 40 cm long at the temperature of 6°C:

$$T = 175 \frac{W^{0.54} L^{-1.4}}{Q \times 10^{0.035(T_0-6)}} \quad (2)$$

where:

W is reconstructed weight of food, g

L is predator length, cm

Q is evacuation rate for a given type of food

T_0 is ambient temperature, °C

Mortality of commercial fishes due to natural causes results from interaction between individuals from commercial stock and a great number of interdependent and independent ecological factors. The paper deals with 2 components of capelin natural mortality, namely mortality due to causes other than predation (M1) and mortality due to cod predation (M2). M1 of 0.40 was assumed to be constant for all years and age groups considered. The M2 values were estimated using Pope's model (Sparre, 1984). The reliability of starting coefficients for fishing mortality was checked by comparing the MSVPA-derived average (for 2-4 years) abundance of capelin year-classes with the respective values obtained during acoustic surveys. Parameters of capelin fishery management with account taken of cod predation were derived based on the following relationship:

$$P(Y) = \sum_t \sum_a \bar{N}_{capelin}(t, a) W_{capelin}(t, a) \delta(a) \quad (3)$$

where:

Y is number of years of fishery during which average biomass of mature fish is P_i

$W_{capelin}(t, a)$ is weight of capelin at age a_i , g

$\delta(a)$ is portion of mature capelin at age a_i

$\bar{N}_{capelin}(t, a)$ is average capelin abundance during the time period t , thousand individuals

Predation was taken into account in calculations of M2 using Pope's model:

$$M2(t, a) = \frac{\sum_b \bar{N}_{cod}(b, t) V(b, t) S(a, b)}{\sum_a \bar{N}_{capelin}(t, a) W_{capelin}(t, a) S(a, b)} \quad (4)$$

where:

$V(b, t)$ is total consumption of food by 1 indiv. of cod at age b , kg

$\bar{N}_{cod}(b, t)$ is average cod abundance during period t , 1000 individuals

$S(a, b)$ is coefficient of suitability of capelin at age a as food for cod at age b

Simulation of the capelin fishery management was done in 2 steps. The 1st stage involved single-species optimization of the cod fishery at the biomass of mature portion

(P1) equal to 200, 350, 500, 650, 800 and 1500 thousand tonnes. Abundance of cod by age groups in 1977-1990 was obtained for each of these P1 values. Capelin catch with account taken of estimated cod abundance was calculated during the 2nd stage. Abundance, biomass and catch of capelin with mature fish biomass equal to 1,2,3,4 and 5 million tonnes were calculated for each of the above values of P1. All options were estimated at the actual values of recruitment to cod and capelin commercial stocks.

RESULTS AND DISCUSSION

The quarterly cod rations, calculated from formulae (1) and (2), as well as weight and portion of capelin in them (Tables 1,2), indicate that the period from 1984 to 1989 can be divided into 2 parts (1984-1986 and 1987-1989) of different temporal pattern of cod predation on capelin. The weight and portion of capelin in cod stomachs was much lower during the 2nd interval than during the 1st one. MSVPA envisages the known values of average quarterly cod diet and portion of the prey in it. No quantitative data on consumption of capelin by cod are available for 1971-1983. As indicated by data on the occurrence of capelin in cod stomachs, the consumption of capelin by cod in 1971-1983 can be assumed to be at the level of 1984-1986. Therefore, to estimate the abundance and biomass of capelin by MSVPA the whole 1971-1989 period was divided into 2 intervals (1971-1986 and 1987- 1989).

As a result of calculations the abundance and biomass of cod and capelin, the amount of capelin consumed by cod and rates of fishing and natural (M2) mortalities of capelin (Table 3) have been obtained. From 1971 to 1976 capelin biomass was at a stable and fairly high level of about 10 million tonnes. Capelin catches were also stable and did not exceed 1.5 million tonnes per year. Cod biomass increased in the period from 1971 to 1975 to reach 2.33 million tonnes in 1974. Biomass of capelin consumed by cod also grew accordingly to constitute 1.7 million tonnes in 1974, i.e. cod can consume over 1.5 million tonnes of capelin under relatively stable conditions. A gradual and stable reduction in the capelin stock started in 1977 and at the same time the catch increased significantly. By 1980 the capelin biomass was reduced from 10 down to 5.3 million tonnes and the annual catch was around 1.8 million tonnes. The decrease in cod abundance did not prevent capelin stock reduction down to 2.8 million tonnes whereas the catch remained as high as 1.6-1.9 million tonnes. In 1984-1985 mortality due to fishery and predation constituted more than a half of the total stock size. Bearing in mind that mainly commercial and mature part of population are affected by both fishery and predation, a depressive stock status led to cessation of capelin fishery. The stock restoration could take place only in case of favourable environmental conditions which were observed in 1988 and 1989 when a moderate and a rich yearclass appeared, respectively. The total capelin biomass in 1990 was estimated at 4.0 million tonnes and over 5 million tonnes based on data from MSVPA and a trawl-acoustic survey, respectively. Insignificant differences were revealed between the 1990 abundance of age groups obtained by MSVPA and from a trawl-acoustic survey. The discrepancies in the total capelin biomass based on MSVPA and on trawl-acoustic survey were due to high weight increments in 2- and 3-year olds. The weight of 1 individual at the age of (2+) averaged 12.3 g in 1984-1989, and in 1990 it reached 15.3 g. The average weight of 1 individual at the age of (3+) was 16.2 g in 1984-1989 and it was as high as 27.2 g in

1990. The high rate of growth in 1990 was due to extremely favourable environmental conditions, which provided a high survival rate of capelin eggs and juveniles, adequate food availability and stable feeding pattern. Results of simulation of capelin fishery management with account taken of cod predation indicate that fishery for capelin should have been stopped in 1985. The highest total catch for the period from 1977 to 1984 would have been over 15 million tonnes at mature cod biomass (P1) equal to 200 thousand tonnes (Fig.1, Table 4). At an increase in the mature cod biomass (P1) up to 500 thousand tonnes the total catch would have to be reduced down to about 9 million tonnes. As it can be seen in Fig.1 the catch curve has a well-pronounced maximum at all the P1 values which corresponds to 2.5 million tonnes of mature capelin.

CONCLUSIONS

The role of cod in formation of capelin year-class abundance is extremely important. Young cod (mainly at the age 1-3) influence the abundance of recruitment to the commercial stock of capelin. In spite of the fact that the portion of capelin in the young cod stomachs is not considerable, predation-caused mortality rate of capelin is high due to a high abundance of cod. However, the highest impact on capelin stock is produced by 3-5 years old cod on which 75- 80% of the total amount of consumed capelin fall. The annual consumption of capelin by the cod stock reaches 2 million tonnes and mostly large mature individuals are preferred. The intensive capelin fishery started in the 70s and it was continued until 1985 with no account taken of trophic relationships between cod and capelin. The total biomass of capelin and its mature part reached critical values by the early 80s, which was accompanied by unfavourable environmental conditions to result in a depressive state of capelin stock. Capelin fishery should be regulated with allowance for cod predation. The exploitation rate of capelin should be kept at the level allowing for the annual biomass of the mature part of the stock to be kept at the level of 2.5 million tonnes.

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Table 1 Mean weight (W, g) and portion (P) of capelin in cod daily ration for 1984-1986

| Cod age, years | Capelin age, years | Quarter | | | | | | | |
|----------------|--------------------|---------|--------|-------|--------|-------|--------|-------|-------|
| | | I | | II | | III | | IV | |
| | | W | P | W | P | W | P | W | P |
| 3 | 1 | 0.020 | 0.002 | 0.003 | 0.000 | 0.053 | 0.005 | 0.023 | 0.003 |
| | 2 | 0.355 | 0.018 | 0.772 | 0.055 | 0.087 | 0.003 | 0.037 | 0.005 |
| | 3 | 2.750 | 0.153 | 2.839 | 0.197 | 0.195 | 0.020 | 0.020 | 0.003 |
| | 4 | 6.804 | 0.348 | 1.735 | 0.131 | 0.098 | 0.003 | 0.000 | 0.001 |
| | 5 | 1.209 | 0.055 | 0.217 | 0.017 | 0.007 | 0.000 | 0.000 | 0.000 |
| | 6 | 0.105 | 0.0044 | 0.007 | 0.001 | 0.000 | 0.000 | 0.000 | 0.000 |
| 4 | 1 | 0.063 | 0.002 | 0.000 | 0.000 | 0.416 | 0.022 | 0.211 | 0.012 |
| | 2 | 0.644 | 0.022 | 1.079 | 0.064 | 1.112 | 0.057 | 0.585 | 0.032 |
| | 3 | 4.442 | 0.195 | 3.086 | 0.113 | 1.244 | 0.063 | 0.351 | 0.019 |
| | 4 | 10.105 | 0.385 | 2.677 | 0.104 | 0.149 | 0.008 | 0.023 | 0.001 |
| | 5 | 1.1857 | 0.058 | 0.314 | 0.013 | 0.006 | 0.0003 | 0.000 | 0.000 |
| | 6 | 0.161 | 0.004 | 0.008 | 0.0004 | 0.000 | 0.000 | 0.000 | 0.000 |
| 5 | 1 | 0.013 | 0.001 | 0.000 | 0.000 | 0.722 | 0.024 | 0.244 | 0.007 |
| | 2 | 1.041 | 0.032 | 0.240 | 0.047 | 1.706 | 0.054 | 0.678 | 0.019 |
| | 3 | 4.558 | 0.147 | 9.193 | 0.194 | 2.198 | 0.070 | 0.407 | 0.011 |
| | 4 | 2.042 | 0.341 | 5.275 | 0.119 | 0.351 | 0.012 | 0.027 | 0.001 |
| | 5 | 1.632 | 0.042 | 0.493 | 0.014 | 0.010 | 0.0005 | 0.000 | 0.000 |
| | 6 | 0.161 | 0.004 | 0.017 | 0.001 | 0.000 | 0.000 | 0.000 | 0.000 |
| 6 | 1 | 0.090 | 0.002 | 0.000 | 0.000 | 0.000 | 0.017 | 0.587 | 0.010 |
| | 2 | 1.704 | 0.046 | 3.629 | 0.060 | 0.060 | 0.046 | 1.140 | 0.019 |
| | 3 | 5.749 | 0.129 | 6.091 | 0.101 | 0.101 | 0.052 | 0.687 | 0.011 |
| | 4 | 13.626 | 0.302 | 2.978 | 0.049 | 0.049 | 0.008 | 0.047 | 0.001 |
| | 5 | 2.514 | 0.047 | 0.149 | 0.003 | 0.003 | 0.0003 | 0.000 | 0.000 |
| | 6 | 0.314 | 0.007 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| 7 | 1 | 0.000 | 0.000 | 1.410 | 0.073 | 0.060 | 0.001 | 0.857 | 0.012 |
| | 2 | 1.111 | 0.038 | 0.643 | 0.033 | 0.498 | 0.006 | 0.173 | 0.002 |
| | 3 | 15.942 | 0.175 | 3.037 | 0.156 | 0.536 | 0.006 | 0.103 | 0.001 |
| | 4 | 36.459 | 0.398 | 1.317 | 0.068 | 0.069 | 0.001 | 0.001 | 0.000 |
| | 5 | 5.786 | 0.060 | 0.050 | 0.003 | 0.003 | 0.0001 | 0.000 | 0.000 |
| | 6 | 0.445 | 0.004 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| 8 | 1 | 0.000 | 0.000 | | | 0.500 | 0.005 | 0.500 | 0.005 |
| | 2 | 0.449 | 0.004 | | | 4.497 | 0.043 | 4.497 | 0.043 |
| | 3 | 14.484 | 0.121 | | | 4.697 | 0.045 | 4.697 | 0.045 |
| | 4 | 32.299 | 0.263 | | | 0.300 | 0.003 | 0.300 | 0.003 |
| | 5 | 3.108 | 0.022 | | | 0.000 | 0.000 | 0.000 | 0.000 |
| | 6 | 0.316 | 0.002 | | | 0.000 | 0.000 | 0.000 | 0.000 |

Table 2 Mean weight (W, g) and portion (P) of capelin in cod daily ration for 1987-1989.

| Cod age, years | Capelin age, years | Quarter | | | | | | | |
|----------------|--------------------|---------|--------|-------|-------|-------|--------|-------|--------|
| | | I | | II | | III | | IV | |
| | | W | P | W | P | W | P | W | P |
| 3 | 1 | 0.037 | 0.008 | 0.120 | 0.032 | 0.093 | 0.030 | 0.010 | 0.001 |
| | 2 | 0.593 | 0.093 | 0.277 | 0.065 | 0.150 | 0.028 | 0.023 | 0.003 |
| | 3 | 1.200 | 0.186 | 0.403 | 0.055 | 0.023 | 0.005 | 0.000 | 0.000 |
| | 4 | 0.590 | 0.110 | 0.177 | 0.015 | 0.003 | 0.001 | 0.000 | 0.000 |
| | 5 | 0.277 | 0.044 | 0.007 | 0.001 | 0.000 | 0.000 | 0.000 | 0.000 |
| | 6 | 0.013 | 0.003 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| 4 | 1 | 0.293 | 0.041 | 0.025 | 0.024 | 0.477 | 0.026 | 0.020 | 0.015 |
| | 2 | 0.587 | 0.047 | 0.727 | 0.068 | 0.233 | 0.028 | 0.043 | 0.003 |
| | 3 | 1.593 | 0.133 | 1.577 | 0.133 | 0.017 | 0.002 | 0.000 | 0.000 |
| | 4 | 0.740 | 0.059 | 0.430 | 0.027 | 0.003 | 0.001 | 0.000 | 0.000 |
| | 5 | 0.073 | 0.008 | 0.013 | 0.001 | 0.000 | 0.000 | 0.000 | 0.000 |
| | 6 | 0.003 | 0.0003 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| 5 | 1 | 0.337 | 0.016 | 0.473 | 0.072 | 0.943 | 0.025 | 0.033 | 0.001 |
| | 2 | 0.703 | 0.037 | 1.713 | 0.125 | 0.930 | 0.023 | 0.133 | 0.005 |
| | 3 | 1.820 | 0.097 | 2.280 | 0.144 | 0.120 | 0.003 | 0.317 | 0.012 |
| | 4 | 1.290 | 0.085 | 1.613 | 0.028 | 0.013 | 0.0003 | 0.013 | 0.0003 |
| | 5 | 0.043 | 0.003 | 0.677 | 0.021 | 0.000 | 0.000 | 0.000 | 0.000 |
| | 6 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |

Table 2 (Continued) Mean weight (W, g) and portion (P) of capelin in cod daily ration for 1987-1989.

| | | | | | | | | | |
|---|---|-------|-------|-------|--------|-------|--------|-------|--------|
| 6 | 1 | 0.350 | 0.019 | 0.570 | 0.021 | 0.433 | 0.008 | 0.097 | 0.003 |
| | 2 | 0.613 | 0.030 | 3.210 | 0.125 | 2.043 | 0.032 | 0.217 | 0.007 |
| | 3 | 2.517 | 0.120 | 3.300 | 0.123 | 0.293 | 0.005 | 0.007 | 0.0003 |
| | 4 | 0.880 | 0.039 | 0.490 | 0.015 | 0.023 | 0.0003 | 0.000 | 0.000 |
| | 5 | 0.063 | 0.003 | 0.007 | 0.0003 | 0.000 | 0.000 | 0.000 | 0.000 |
| | 6 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| 7 | 1 | 0.067 | 0.003 | 0.330 | 0.016 | 0.167 | 0.003 | | |
| | 2 | 0.200 | 0.008 | 1.713 | 0.082 | 0.583 | 0.012 | | |
| | 3 | 0.777 | 0.030 | 2.333 | 0.111 | 0.030 | 0.001 | | |
| | 4 | 0.353 | 0.013 | 1.000 | 0.048 | 0.007 | 0.0001 | | |
| | 5 | 0.020 | 0.001 | 0.000 | 0.000 | 0.000 | 0.000 | | |
| | 6 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | | |
| 8 | 1 | 0.000 | 0.000 | | | | | | |
| | 2 | 1.267 | 0.026 | | | | | | |
| | 3 | 4.267 | 0.086 | | | | | | |
| | 4 | 0.470 | 0.009 | | | | | | |
| | 5 | 0.067 | 0.001 | | | | | | |
| | 6 | 0.000 | 0.000 | | | | | | |

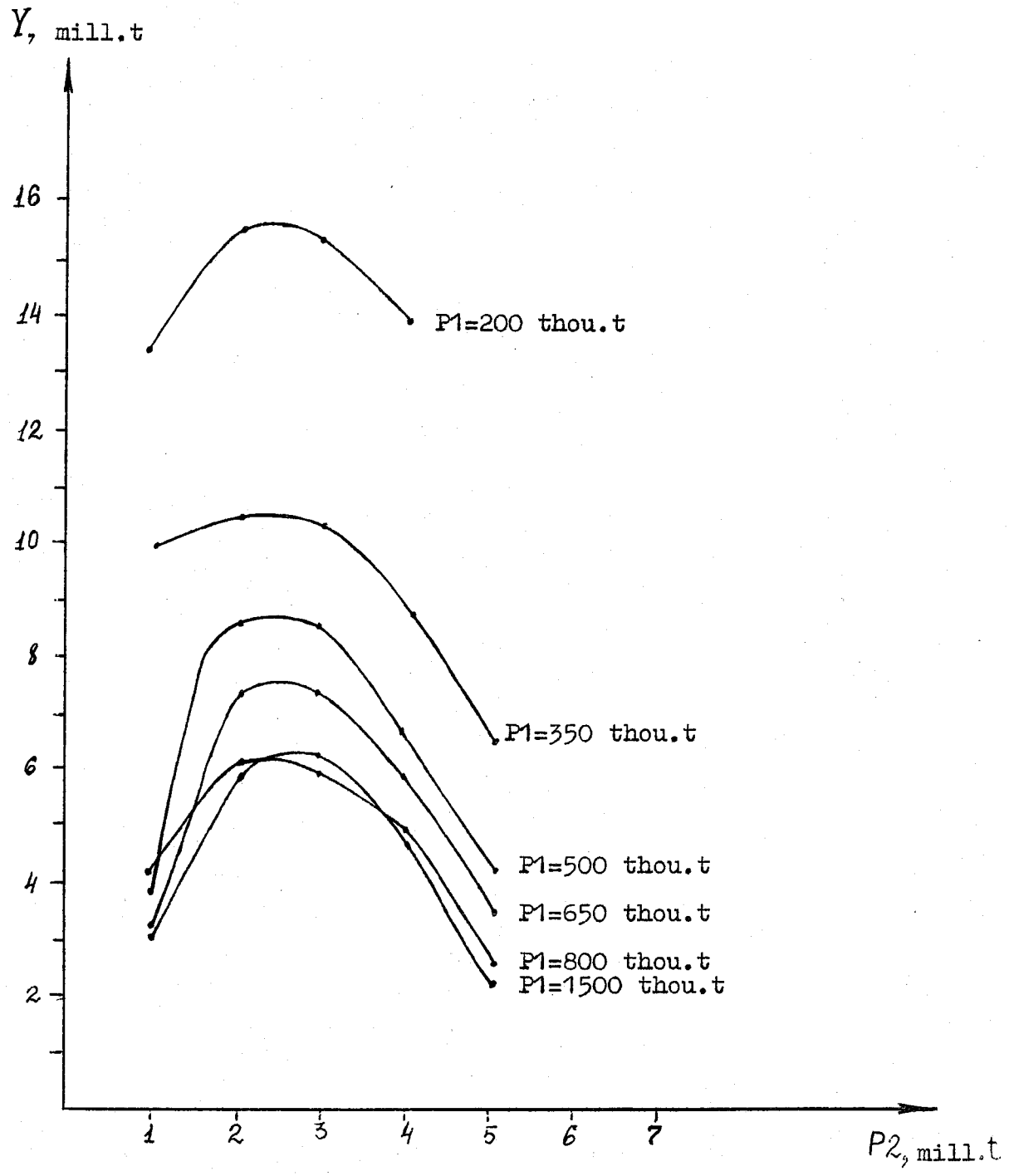
Table 3 Fishing mortality (F1), biomass (B1) and catch (C1) of North-East Arctic cod and Barents Sea capelin (F2, B2, C2), biomass of capelin consumed by cod (D) natural mortality (M2) and biomass of mature capelin (P2), estimated by MSVPA. Biomasses in million tonnes.

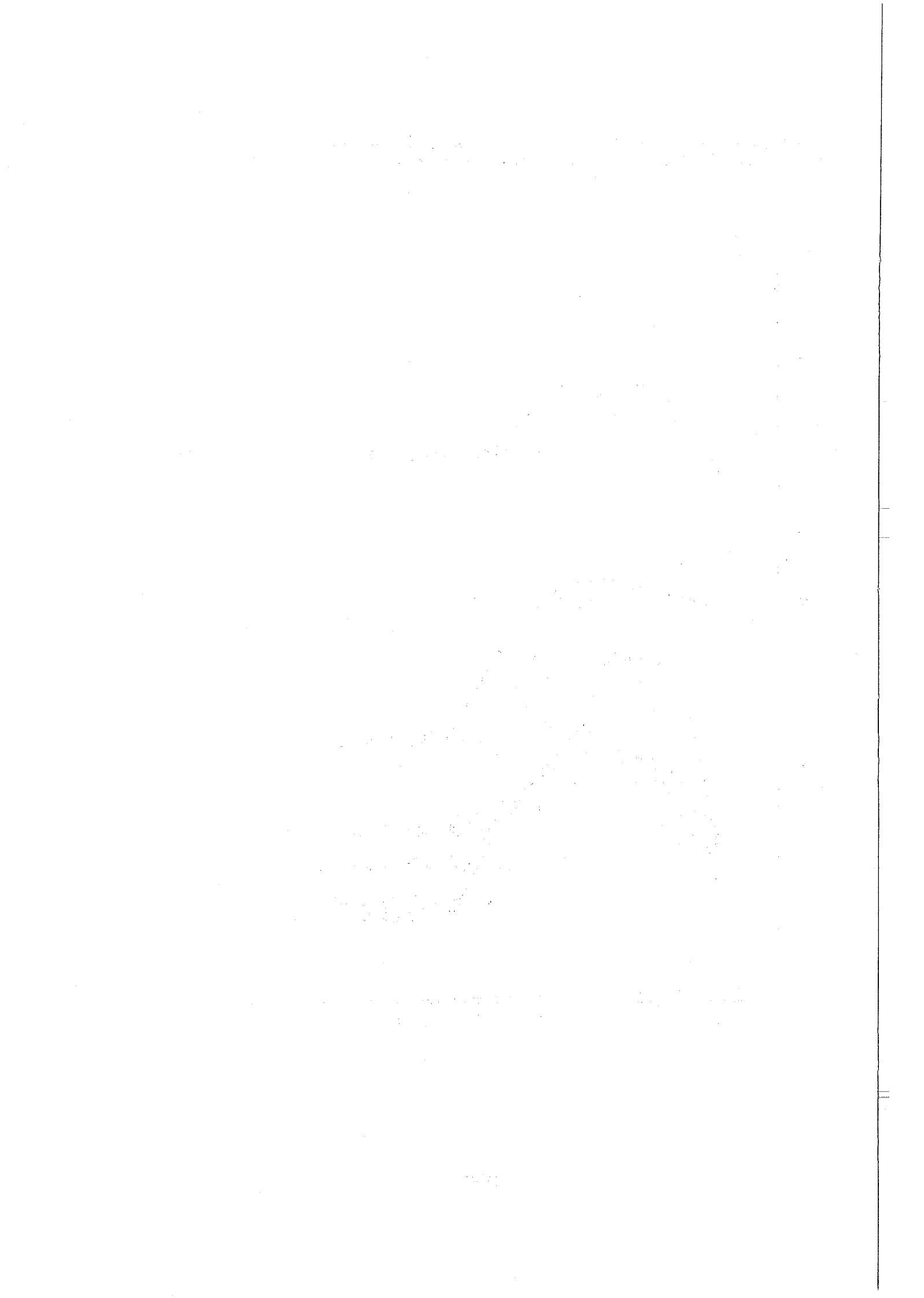
| Year of fishery | Cod | | | Capelin | | | | | |
|-----------------|------|------|------|---------|-------|------|------|------|------|
| | F1 | B1 | C1 | F2 | B2 | C2 | D | M2 | P2 |
| 1971 | 0.52 | 1.37 | 0.73 | 1.16 | 7.10 | 1.26 | 0.76 | 0.11 | 3.36 |
| 1972 | 0.69 | 1.50 | 0.60 | 1.58 | 9.62 | 1.35 | 0.87 | 0.12 | 4.29 |
| 1973 | 0.53 | 2.20 | 0.87 | 1.78 | 9.61 | 1.35 | 1.59 | 0.29 | 4.01 |
| 1974 | 0.64 | 2.33 | 1.20 | 1.69 | 10.07 | 1.11 | 1.72 | 0.23 | 4.83 |
| 1975 | 0.63 | 2.07 | 0.91 | 1.02 | 9.62 | 1.38 | 1.53 | 0.16 | 5.36 |
| 1976 | 0.58 | 1.91 | 0.93 | 0.64 | 10.26 | 2.60 | 1.33 | 0.13 | 6.84 |
| 1977 | 0.70 | 1.65 | 0.93 | 1.83 | 8.35 | 2.90 | 1.08 | 0.15 | 5.25 |
| 1978 | 1.05 | 1.35 | 0.73 | 2.06 | 6.64 | 2.08 | 0.83 | 0.18 | 3.47 |
| 1979 | 0.75 | 1.03 | 0.47 | 1.74 | 5.80 | 2.03 | 0.69 | 0.12 | 3.43 |
| 1980 | 0.68 | 0.92 | 0.41 | 1.26 | 5.25 | 1.39 | 0.63 | 0.11 | 3.50 |
| 1981 | 0.58 | 0.81 | 0.42 | 2.45 | 5.04 | 1.92 | 0.53 | 0.12 | 3.15 |
| 1982 | 0.56 | 0.69 | 0.39 | 1.18 | 4.97 | 1.59 | 0.45 | 0.11 | 2.48 |
| 1983 | 0.49 | 0.61 | 0.31 | 2.49 | 4.36 | 1.90 | 0.37 | 0.11 | 2.37 |
| 1984 | 0.59 | 0.79 | 0.22 | 1.10 | 3.50 | 1.05 | 0.44 | 0.12 | 2.26 |
| 1985 | 0.73 | 1.17 | 0.25 | 1.88 | 2.77 | 1.00 | 0.60 | 0.28 | 1.75 |
| 1986 | 0.62 | 1.29 | 0.36 | 0.47 | 1.92 | 0.12 | 0.92 | 1.08 | 0.66 |
| 1987 | | 1.13 | 0.50 | | 0.35 | - | 0.17 | 1.25 | 0.12 |
| 1988 | | 1.15 | 0.48 | | 0.35 | - | 0.26 | 1.01 | 0.07 |
| 1989 | | 0.95 | | | 1.32 | . | 1.01 | 0.96 | 0.14 |

Table 4 Capelin catch for 1977–1985 at different values of capelin spawning biomass P2 and mature cod P1.

| P1, thousand tonnes | P2, thousand tonnes | Y, million tonnes |
|---------------------|---------------------|-------------------|
| 200 | 1000 | 13.31 |
| | 2000 | 15.41 |
| | 3000 | 15.18 |
| | 4000 | 13.81 |
| 350 | 1000 | 9.89 |
| | 2000 | 10.38 |
| | 3000 | 10.25 |
| | 4000 | 8.84 |
| | 5000 | 6.43 |
| 500 | 1000 | 3.82 |
| | 1500 | 7.82 |
| | 2000 | 8.57 |
| | 3000 | 8.52 |
| | 4000 | 6.48 |
| | 5000 | 4.12 |
| 650 | 1000 | 3.26 |
| | 2000 | 7.39 |
| | 3000 | 7.34 |
| | 4000 | 5.75 |
| | 5000 | 3.38 |
| 800 | 1000 | 4.19 |
| | 2000 | 6.17 |
| | 3000 | 5.85 |
| | 4000 | 4.72 |
| | 5000 | 2.39 |
| 1500 | 1000 | 3.07 |
| | 2000 | 5.86 |
| | 3000 | 6.21 |
| | 4000 | 4.54 |
| | 5000 | 2.16 |

Figure 1 Variation in total for 1977-1986 Barents Sea capelin catch (Y) depending on impact of mature capelin biomass (P_2) and biomass of mature cod (P_1)





**A METHOD FOR ESTIMATION OF PREDATION
MORTALITIES ON CAPELIN USING A
COD—CAPELIN MODEL FOR THE BARENTS SEA**

by

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ABSTRACT

The Barents Sea capelin stock collapsed during the period 1983–1986. One of the main factors causing the collapse was a rapid increase in consumption of capelin by cod, caused by the strong 1983 cod year class. Based on measurements of stomach evacuation rates in the appropriate temperature interval and data from a combined Russian-Norwegian stomach sampling programme, predation mortalities are estimated by the IMR multispecies model for the Barents Sea — MULTSPEC. In order to estimate these predation mortalities, cod-capelin interaction parameters and yearly migration parameters for capelin are also estimated.

INTRODUCTION

Prior to 1990, all fish species in the Barents Sea have been managed without taking species interactions into account. This has caused problems both in the management of capelin (increased mortality due to predation from cod), and of cod (decreased food abundance due to the collapse of the capelin stock, leading to low growth).

The capelin stock started to decline in 1983, as a consequence of an abrupt shift in oceanographic conditions the winter 1982–1983. The exact processes mediating the decline are not fully known, but there is good reason to believe that good recruitment conditions in 1983 and 1984 for herring and cod have had a substantial effect through species interactions, see (Hamre, 1989).

The change of physical conditions leading to altered natural mortality and recruitment conditions through species interactions was pointed out by the ICES Working Group on Atlanto-Scandian Herring and Capelin (hereafter: the Capelin Working Group) in 1985 (Anon, 1986) which concluded with a ban on fishery (this advice was not followed). However, this management action was taken in a rather late stage in the decline process. The working group was not able to give warning signals in 1983 and in 1984. It could only point to unexpectedly low population numbers, especially for the 1-group (Anon, 1985) without any possibilities of taking appropriate action in terms of revising the model assumptions.

The work presented in this paper may serve as a basis for improvement of future management of capelin, taking the predation from cod into account.

The need for taking multispecies effects into account when managing the fish stocks is recognized worldwide and several gatherings of scientists have addressed this question. So far, there have been little outcome that has been used in the ICES fish assessment working groups. Many different approaches are feasible. The present paper demonstrates an approach that might be applicable to boreal systems, where the effect of climatic changes (believed to influence the geographical distribution and migration of fish) is incorporated into a simulation model for the fish stocks. Much of the work in this paper relies on research that is still in progress (i.e. application of evacuation rate models, measurement of fish stocks in absolute terms) and on data that will be improved when the IMR data base is improved. The management-relevant outcomes must be re-evaluated at a later stage. However, the paper addresses most of the practical problems that arises when working with an area-distributed multispecies model based on stomach content data. Although the purpose of the paper is to explore the possibilities of improving the scientific basis for the management of capelin, it could also serve as a useful case study for discussions of alternative multispecies approaches for boreal systems in the scientific community.

The work in this paper is based on an ongoing multispecies modeling project called MULTSPEC at IMR.

Aside from the spawning mortality, the predation from cod is the largest component of the natural mortality on mature capelin. In this paper we will not take into account predation from other predators. During the spawning migration the capelin has to cross the area inhabited by cod, and is subject to predation. Also the immature capelin will be eaten by cod in the months April-July, where it may be found far south in the Barents

Sea. However, both the measurements of capelin distribution and the stomach content data for cod from this period are sparse.

BIOLOGY.

Capelin

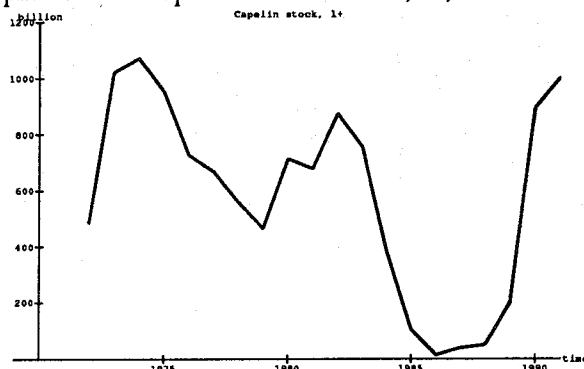
Distribution and migration.

The capelin spends all its life in the Barents Sea. It spawns at the coasts of Norway and Russia along the southern borders of the Barents Sea, and the larvae drift north- and eastwards. The capelin is one of the most important plankton feeders in the Barents Sea. From a management point of view, the capelin is a transporter of the secondary production to higher trophical levels. The capelin is one of the most important food items for cod (Mehl, 1989), (Bogstad and Mehl, 1992). The geographical distribution and migration is described in an accompanying paper to this symposium (Tjelmeland, 1992).

Stock development

The development of the capelin stock in the period 1972–1991 is dramatic indeed:

Figure 1 The development of the capelin stock 1972–1991, 2+, billion. Acoustic estimates in September.



The period 1972–1991 may be divided into three when it comes to management and our understanding of the biological processes in the sea:

1. 1972–1983. The stock peaked in 1975 because of no predation pressure from herring and because slow growth led each individual to spawn late. Since the capelin dies after spawning, this led to delayed maturation mortality and a build-up of the stock. The most important factor behind the decrease from 1975 came to a large extent because most of the population matured. The development of the stock can in this period be understood in a single-species context where the maturation process is length-dependent.
2. 1983–1987. The capelin stock collapsed after the strong 1983 year class of herring occurred in the Barents Sea and because the cod stock recovered due to the strong 1983 and 1984 year classes. The driving forces are here stock interactions and the development can only be understood in a multispecies context. The fishery was closed in April 1986.
3. 1988–1991. In this period the stock has rebuilt quickly. The recruitment has been good in relation to the small spawning stock, and the individual growth in 1990 was

much higher than expected. Therefore, the capelin fishery was resumed in winter 1991.

Management.

In 1990, the consumption of capelin by cod was, for the first time, taken explicitly into account when setting the capelin quota for the coming year. One then assumed that the consumption per cod biomass would be the same as in 1985, which is the year in the time series with the highest consumption. This assumption was made because the capelin biomass available for cod in 1991 would be larger than the biomass in any of the years 1984–1989. A similar approach was taken in 1991, see (Bogstad and Gjørseter, 1991).

Cod

Distribution and migration.

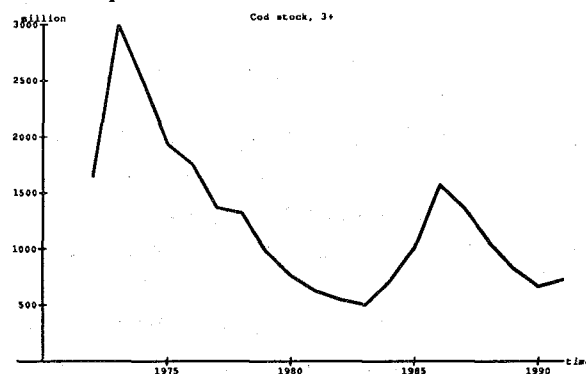
The North-East Arctic cod stock has two components: The Barents Sea component is distributed mainly to the south of the capelin distribution as measured in September. The main spawning area is Vesterålen/Lofoten, but spawning may also occur further south. The Spitsbergen component is distributed in the area west of Spitsbergen and on the Spitsbergen-Bear Island shelf. Most of the spawning occurs south of Lofoten, as far south as to Møre. There is no clear biological distinction between the two components, and larvae originating from one component may drift into the area of the other component, thus providing for an exchange between the two components.

The juveniles grow up in the eastern Barents Sea. A seasonal westwards migration takes part in the first part of the year, followed by a return migration. As the cod grows older, the return migration will not end as far east as where it started. Thus the distribution is shifted to the west as the fish grows older.

Stock development.

The development of the cod stock is no less dramatic than that of the capelin stock:

Figure 2 The development of the cod stock 1972–1990, 3+, million, VPA data (1990).



The decline until 1983 was due to high fishing pressure and weak recruitment (Bergstad *et al.*, 1987). The subsequent increase is due to improved recruitment. However, the stock soon started to decrease again. This may partly have been due to cannibalism, unreported fishery or discards. Also, the individual growth of the cod declined from 1985 to 1988 (Mehl and Sunnanå, 1991). This growth decline was not anticipated by

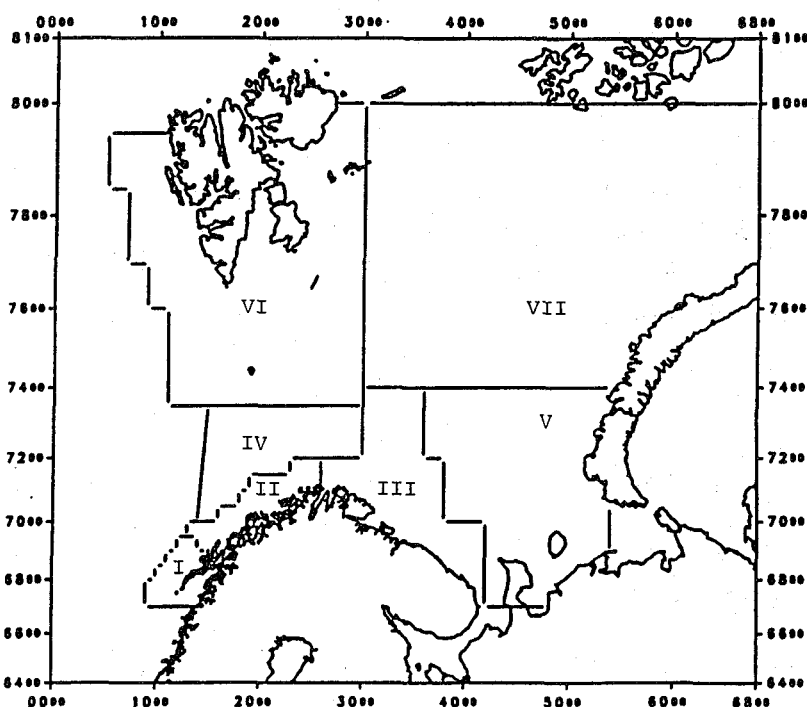
the Arctic Fisheries Working Group and the quotas amounted to a higher number of individuals than expected (Anon, 1989a). The main reason for this growth decline was probably the collapse of the capelin stock (Mehl and Sunnanå, 1991). The fishing mortality was in 1990 brought down to the F_{low} level, which should give hope for a recovery of the stock. Both the recruitment and the individual growth have improved markedly in the last two years, but the stock will still be at a low level for some years.

MODEL.

Geographical distribution and migration.

The standard time step in the model is one month. The area division used in the present paper is shown on the map below:

Figure 3 Model area distribution of the Barents Sea.



A division into these 7 areas is a compromise between the desire to have a fine resolution in order to describe the distributions properly and the ability to handle a complex box model.

Denote the time (month number) by t , the stock (immature or mature) by m and the age by a . The migration between the areas is then implemented in the following way:

$$N_{m,a,t+1} = V_{m,a,t} \times N_{m,a,t} \quad (1)$$

where the 7-dimensional column vector N is the population number in each area for given time, stock and age. The 7×7 migration matrix $V_{m,a,t}(i,j)$ is the relative proportion of fish in stock m and age a in area i that in the course of the time step from t to $t+1$ migrates to area j .

Capelin.

Stock data.

The input data for the capelin stock are acoustic estimates obtained in September—October each year, where 5–6 Russian and Norwegian vessels participate in a coordinated survey. The method is described in (Dommasnes and Røttingen, 1985). The data are presented each year in the working group. For the present analysis, the data are split on area, length and sex using the method described in (Gjøsæter, 1985).

Maturation.

In September the capelin stock is divided into a mature and an immature part by the following function:

$$m(l) = \frac{1}{1 + e^{4 \times P_1 \times (P_2 - l)}} \quad (2)$$

Here:

$m(l)$: Proportion of mature fish at length l .

P_1 : Change in maturation proportion when $l = P_2$

P_2 : Fish length at 50% maturity, referred to as "length at maturity".

These two parameters have one component for each sex.

In the present use of the model, we will use the simplifying assumption that:

All age groups have same maturation parameters.

Migration.

We assume that all predation from cod on capelin in the period January to March is on mature capelin. In order to avoid predation on immature capelin in February/March, the migration parameters for immature capelin in the autumn are set so that all the immature capelin is found in areas 5, 6 and 7 by the end of the year. It is assumed that the immature capelin in areas 2 and 4 migrate to area 6, and that the immature capelin in area 3 migrates to area 7. In the period January to March, the migration of immature capelin is set to zero.

Catch data

The model needs catch in numbers for each length group, area and month. The following data sources are used to obtain this:

1. The number caught per age group and month and average weight in the catch for each age group as reported to the capelin working group.
2. The Norwegian catch statistics for the part of the Norwegian catch that has been used for reduction to meal and oil. This gives the number caught in each length group for each area.
3. Russian catch information (tonnes fished for each area and month) exchanged at the April 1990 meeting in Murmansk between IMR and PINRO.

These data are combined in the following way:

For the Norwegian data, it is assumed that the area distribution of the number caught for a given month is the same as the area distribution of the numbers caught according to the catch statistics for Norwegian reduction catch. The numbers caught by Norway of each length group in each area for a given month is then found by scaling the total number caught in Norwegian reduction catch in this month to the number caught by Norway as reported to the working group.

The number caught by Russia according to the official statistics (1) is then scaled by the total Russian catch (biomass) in this month from (3) divided by the "official" catch (biomass) from (1). It is then distributed on area and length group assuming that the area distribution of numbers caught is equal to the area distribution of the biomass caught and applying the length distributions from the Norwegian reduction catch for each area. However, we do not have length distributions for all month/area combinations. This is handled in the following way: All Norwegian autumn catch that is not reported by area, is allocated to area 6. September catches in area 6 are neglected, because this area is covered in the end of the cruise. For area/month combinations where no length distributions are available, the length distribution is assumed to be equal to the average length distribution for this half-year. For autumn 1983, the length distribution for autumn 1984 has been used because length distribution data for autumn 1983 are lacking.

In the model, the capelin stock is divided into 0.5 cm length groups, while the catch length distribution is given on 1 cm length groups. If the catch exceeds the stock for one length group, the excess catch is redistributed on other length groups, if possible. It will be attempted to set the migration parameters in such a way that there is no excess catch for any month/area combinations. If such excess catch still occurs, however, it is not distributed on other areas or months, but subtracted from the calculated spawning biomass if the catch is assumed to be mature capelin. The catch in September-March for 1983-1984, 1984-1985 and 1985-1986 in numbers for each area is given in the appendix.

Cod.

We consider the cod stock stationary, i.e. the geographical distribution does not change with time during the period of capelin spawning migration (January-March). This might be a good approximation, since the measurement of the distribution is obtained in the middle of the period of the capelin spawning migration.

Stock data

The data used by the model are primarily the number of cod per age group and mean weight per age group. Also, mean length per age group is needed in the model to determine the size-dependent part of the suitability. However, the suitability curve used in this paper is based on rather coarse, although data-substantiated, assumptions, see page 120.

The number per age and weight per age data used are VPA data from the 1990 Arctic Fisheries working group (Anon, 1991). The weight at age is calculated as an arithmetic average of the weight at age in the Russian survey in October-November and the Norwegian survey in January-March. However, it is evident from the Working Group

report that there is a larger discrepancy in weight at age between these two surveys than can be accounted for by growth in the intermediate time. This discrepancy may to a large extent be due to differences in age reading, and this matter is now under investigation (Anon, 1993). The number of 1- and 2-year old fish is found by back-calculating the number at age 3 with $M=0.2$. The length is assumed normally distributed, and when higher order terms are neglected, the mean length l can be calculated from the mean weight W by the formula

$$W = c(l^3 + 3l\sigma^2)$$

where c is the condition factor (unit: $\frac{g}{cm^3}$) and σ is the standard deviation. The condition factors used are $c=0.008$ for age 4 and younger and $c=0.009$ for older fish (Anon, 1988). The standard deviation used is 3 cm for age 1, 4 cm for age 2 and 5 cm for age 3 and older. Details of the derivation of the mean length-mean weight relationship can be found in (Magnusson and Palsson, 1991). The area distribution is based on data from the annual winter surveys (Dalen *et al.*, 1984), (Hysten *et al.*, 1985), (Hysten *et al.*, 1986), (Godø *et al.*, 1987), (Hysten *et al.*, 1988), (Jakobsen *et al.*, 1989). It is assumed that the mature part of the cod stock, calculated using the maturity ogives from the working group report (Anon, 1991), is found in Area 1 (Lofoten/Vesterålen) during the time of the capelin spawning migration and thus does not prey on capelin in that period. Only fish of age 3 and older are considered potential predators on mature capelin.

We will have to redo these estimations each year when the VPA data are updated. Still, we think it is better to use VPA data than survey data for the cod stock in numbers. This is due to the problems of assessing the cod stock with acoustic methods and trawling. The model variables for each age group are: Number of fish, mean length and mean weight.

Stomach data.

31698 stomachs of cod have been sampled in the Barents Sea in the years 1984–1989 by Norwegian and Russian vessels. The methods used for sampling, analysis and data recording are described in (Mehl, 1989). The number of stomachs sampled and the calculated average daily consumption of capelin by cod in model areas 2–5 for January, February and March 1984–1989 are given in the appendix.

Since we restrict the study to predation on mature capelin, all capelin below 10 cm is deleted from the stomach data set before any likelihood calculations are carried out. When the stomach samples are worked up, the prey size group is recorded. The relevant prey size groups used in the stomach data base are: 5–6.9 cm, 7–9.9 cm, 10.0–14.9 cm, 15.0–19.9 cm, indeterminate size. For our purposes, a finer grouping would be desirable.

Temperature.

A temperature model is needed because of the strong variation of stomach evacuation rates with temperature, also the maximal consumption is temperature dependent. Temperature is included in the MULTSPEC growth model, and might also prove to be important in a future development of migration models. We use data from standard hydrographic sections. At different depths and over different parts of the sections Fourier

analysis is used on temperature data. The coefficients of the Fourier series are then written to a file and read into MULTSPEC during the initialization of the program.

The temperature is then integrated in time for a representative location in each area, to give one temperature T ($^{\circ}\text{C}$) for each year, area and month. The procedure is documented in (Alvarez and Tjelmeland, 1989). Due to problems with the temperature data base, the temperatures in 1988 have been set equal to the temperatures at the same position/time as in 1987 + 0.3°C , and the temperatures in 1989 have been set equal to the temperatures in 1987 + 0.9°C . These differences of 0.3°C and 0.9°C are equal to the differences in the yearly mean at the Kola section between these years (PINRO, pers. comm.).

Interactions.

General equations.

We will here give the general interaction equations used for all prey species, even though capelin is the only prey species in the model runs presented in this paper.

The prey length is denoted by l and the predator (cod) length by L . The feeding level (Andersen and Ursin, 1977) for a cod of length L is given by:

$$f(\phi(L)) = \frac{\phi(L)}{P_3 + \phi(L)} \quad (4)$$

where

$$\phi(l, L, \text{species}) = G(l, L, \text{species}) \times N_{\text{species}}(l) \times W_{\text{species}}(l) \quad (5)$$

and

$$\phi(L) = \sum_{l, \text{species}} \phi(l, L, \text{species}) + \text{other food}$$

$G(l, L, \text{species})$ is a piecewise linear suitability function. In the present study, $G(l, L, \text{capelin})$ is zero for cod lengths below 20 cm, unity for cod lengths above 30 cm and linearly interpolated for intermediate cod lengths. Capelin below 10 cm is neglected.

$N_{\text{species}}(l)$ is the number of fish (millions) per square nautical mile, and $W_{\text{species}}(l)$ is the individual fish weight (kg). The unit of P_3 and of other food thus becomes 1000 tonnes / square nautical mile.

P_3 is the value of ϕ when a cod eats half its maximal consumption.

The amount of prey of species species of length l eaten per time unit (month) by a cod of length L is given by:

$$R_{\text{cod}}(l, L, \text{species}) = H \times f(\phi(L)) \times \frac{\phi(l, L, \text{species})}{\phi(L)} \quad (6)$$

where the maximal consumption H (kg/ month), which is taken from (Jobling, 1988), is made size-dependent:

$$H = P_4 \times e^{0.104 \times T - 0.000112 \times T^3 - 1.5} \times W_{\text{cod}}^{0.802} \quad (7)$$

where W_{cod} is the individual cod weight in kg. P_4 will be estimated from the data.

It is important to note that the amount of food eaten by one cod is independent of the size of the cod stock. Thus, "outpredating" is possible, but during the estimations, we restrict the parameters so that this is not allowed to happen.

In this study, we have decided to turn off the predation in September-December. The reason for this is that we have insufficient data on the geographical distribution of cod in this period.

Suitability. Based on the work of (Mehl, 1989) we assume that the cod does not start to feed on capelin before it becomes 20–30 cm long. This is implemented by a function that increases linearly from 0 to 1 when the cod length increases from 20 to 30 cm. For the sake of computer time savings, all cod in each age group are supposed to have the same length. The MULTSPEC software, however, allows for full age by length predator distributions, but the calculations are then so costly that this option is not used here.

Evacuation rate model used when comparing the modeled predation to the stomach content data.

An exponential evacuation rate model taken from dos Santos' thesis (dos Santos, 1990) is used:

$$\frac{dS(i)}{dt} = -E_i\left(T, \frac{M}{W}\right) \times S(i) + C(i) \quad (8)$$

In the above equations:

$S(i)$: Stomach content of prey species i in cod (grams).

$C(i)$: Consumption rate by cod of prey species i (grams per hour).

The variables above are averaged over the time step

$E_i(T, M/W)$: Exponential stomach evacuation rate in cod for prey species i , unit h^{-1} .

M : Meal size (grams)

W : Body weight of cod (grams)

Using the parameter values for wet weight, and assuming exponential evacuation (the shape parameter in Santos' paper equal to 1), we get:

$$E_i\left(T, \frac{M}{W}\right) = \frac{\log(2)}{H e^{-cT} \left(\frac{M}{W}\right)^b}$$

where $c=0.11$, $b=0.54$ and $H=205$ (krill), 533 (shrimp), 452 (herring) and 283 (capelin, used also for polar cod and cod). For other food, H has been set to the unweighted mean of these four prey species, i.e 368.

This evacuation rate model gives a much lower consumption than the evacuation rate model used in (Bogstad and Tjelmeland, 1990).

We have in this paper chosen twice the stomach content as the initial meal size for the "key run", and then studied the effects of changing this assumption. The calculations are based on individual cod stomach content data. If the cod weight was not recorded, it has been calculated from the length using a condition factor of 0.009. The relevant depth and date/year has been used for calculating the temperature from the temperature model. When increasing the temperature with 1 °C, the consumption increases by 12%.

PARAMETER ESTIMATION.

The following parameters will be estimated:

1. Migration pattern, equation 1. The migration parameters have been reduced, see page 124.
 - a. x_1 . East-west migration in January, February and March.
 - b. x_2 . North-south migration in February.
 - c. x_3 . North-south migration in March.
2. Predation, equations 4 and 7.
 - a. P_3 . Feeding level half value.
 - b. P_4 . Maximum consumption.

Estimation of predation parameters, with some reference to migration parameters — mature capelin/cod January-March.

Theory

It is much more convenient to compare the consumption calculated directly from the stomach content data with the modeled consumption, than to compare the observed stomach content with the stomach content calculated from the modeled consumption. The reason for this is that in order to calculate the stomach content from the modeled consumption, a non-linear set of equations has to be solved when it is assumed that the initial meal size is a function of the measured stomach content.

When equation 8 is used to estimate model predation parameters, a stationary state is assumed. This assumption is motivated by the fact that the model time step (one month) is long compared to a typical evacuation time constant.

If we assume that the mean consumption is normally distributed with expectation value C when viewed fish by fish, the following variable will be t-distributed:

$$t = \frac{\sqrt{N_{sample}} \times (\bar{X} - C)}{s} \quad \text{where :} \quad (10)$$

$$s^2 = \frac{1}{N_{sample} - 1} \times \sum_{i=1}^{N_{sample}} (X_i - \bar{X})^2$$

Here:

X_i : Calculated consumption of fish i in the sample.

\bar{X} : Mean calculated consumption of cod averaged over cod length and the area and time period under consideration.

s^2 : an unbiased estimator of variance.

N_{sample} : Number of stomachs in the area and time period under consideration.

Because we record the stomach content of each individual fish, we have the opportunity to calculate the variance, and may then calculate s . Therefore, the maximum likelihood method is applicable. The probability of obtaining \bar{X} given that the model represents the truth, is given by the t-distribution:

$$f(t) = \frac{\Gamma\left(\frac{N+1}{2}\right)}{\sqrt{N\pi} \times \Gamma\left(\frac{N}{2}\right)} \times \frac{1}{\left(1 + \frac{t^2}{N}\right)^{\frac{(N+1)}{2}}} \quad (11)$$

The analysis has to be performed over predator (cod) length, because cod is not sampled in proportion to the distribution in the sea.

There might also be methodical problems of a more fundamental biological origin. During the most interesting period, the mature part of the cod population will be on spawning migration. Above some length other feeding habits might be expected.

The procedure above relies on the assumption that the calculated consumption is normally distributed. However, the calculated consumption for an individual fish can not be approximated by the normal distribution in situations of low food abundance, since there never can be any negative consumption. Therefore, the mean calculated consumption measured over several fish can not be approximated by the normal distribution at very low food levels if not the number of sampled fish is high, making the procedure above inapplicable. This problem becomes severe in cases of no capelin in the stomachs. We then need the probability of obtaining no capelin in a situation where there is capelin present (i.e. in the model), which is undefined with the above procedure. In this case we will utilize the properties of the Poisson distribution.

We might then treat the problem as follows:

Suppose the probability of a cod catching a prey within a given time interval is constant. That is, the catching of one prey is independent of the catching of other preys. This holds true only for low food levels, since we might believe that a cod with a full stomach pursues the prey less actively than a hungry cod (however, occasional samples of big cod having very full stomachs may make such an assumption dubious). Then the number of prey eaten during one time interval is distributed as the Poisson distribution. We now reason as follows:

The probability of obtaining one meal in one day is γ . The distribution of the number of meals in one month is Poisson, that is, the probability of eating r meals in one month is given by:

$$P(X = r) = \frac{(30\gamma)^r e^{-30\gamma}}{r!}$$

with expectation value:

$$E(r) = 30\gamma$$

This will correspond to an average stomach content of:

$$m\tau r = m\tau 30\gamma$$

where m is the weight of a prey (assumed constant) and τ is the time constant for stomach evacuation, measured in months.

We now assume that the "true" average stomach content is S , giving

$$S = 30\gamma m\tau$$

$$30\gamma = \frac{S}{m\tau}$$

This gives a probability of having zero meals of

$$P(X = 0) = \frac{\left(\frac{S}{m\tau}\right)^0 e^{-\frac{S}{m\tau}}}{0!} \\ = e^{-\frac{S}{m\tau}}$$

We now set the evacuation constant to 85 hours which is the time needed for 95% evacuation of a 20 g capelin meal given to a 1 kg cod at 5° C. This gives a probability of having zero stomach content of

$$e^{-\frac{S}{(85/36)}}$$

if one fish with an empty stomach was sampled. If N fish with empty stomachs were sampled, the probability becomes

$$e^{-\frac{SN}{(85/36)}}$$

This analysis is a crude one indeed, and may be improved in the future, when more work on the statistical properties of the distributions of stomach content is done.

The model results should not be very sensitive to a change in the evacuation constant, as the number of stomachs sampled in areas with no capelin in the stomachs, is relatively small.

Other food and maximum consumption rate.

The amount of other food is important, not for constructing the likelihood function, but because it determines the development of the capelin stock and hence the spawning stock biomass and amount of capelin in later time steps, which in turn affects the likelihood function.

In the model, we use the same ratio of other food to capelin food that we find in the stomachs for each age group. When there are no stomach data at hand, an overall other food concentration pattern is used, calculated as follows:

For all year/month/area combinations where we have stomach data:

1. The maximum consumption per cod is calculated using the model predation parameter P_4 , equation 7.
2. The feeding level is calculated by dividing consumption calculated from stomach data by maximum consumption.
3. The total food abundance is calculated by using the feeding level function equation 4 (inversely).
4. The abundance of other food is calculated by distributing the total food abundance on capelin and other food using the observations.

The results are averaged over month and year for each area.

The other food calculations are dependent on the value of the parameter P_4 . If a lower limit on this parameter is estimated from the consumption calculated from the stomach data directly, the calculations of other food should be done after the final estimate of P_4 .

Using results from (Jobling, 1988), we get a value for P_4 of 0.993 (kg/month) when the food is capelin with an energy content of 7.7 kJ/g. For a 1-kg cod at 5° C this gives a consumption of approximately 12 g/day (1.2% of body weight), which seems reasonable as a yearly average. It should be possible for cod to have a significantly higher consumption during intensive feeding on capelin.

It should be possible to find a lower bound on P_4 as a by-product of the calculation of the other food pattern. The essence is that there should be consistence between the stomach content data, the evacuation rate model and the predation parameters. In the calculation of the other food pattern the feeding level is calculated by dividing the actual consumption by the maximum consumption. The former is calculated from the stomach content and the evacuation rate model, both entities are independent of the multispecies model. The latter is calculated using the model parameter P_4 . If the feeding level calculated in this way exceeds unity, the feeding level and an error message are reported. A practical way to obtain a lower bound on P_4 is to increase the parameter until the error messages just disappears, thus reaching the asymptotic range of formula 4. If there is reason to believe that in at least one of the area-month boxes used the cod has had excess of food, this procedure also yields a reasonable good value of the parameter. This value, which depends on the choice of initial meal size, was found to be 1.94 when the meal size is set to twice the measured stomach content. Remark: This value is obtained when one assumes that there should be no error messages for any age groups in any area/month boxes. If one only assumes that the average feeding level in an area/month box should be < 1.0 , a lower value will be obtained.

Baseline parameters for migration. Reduction of migration parameters.

In January to March the migration matrix V (equation 1, page 115) of mature capelin is set to:

Table 1 Migration in January.

| From To | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|------------|---|---|---|---|-----|--------------------|-------------------|
| 1 | | | | | | | |
| 2 | | | | | | | |
| 3 | | | | | 1.0 | $\max(0,-x_1)$ | |
| 4 | | | | | | $1.0-\max(0,-x_1)$ | $\max(0,x_1)$ |
| 5 | | | | | | | $1.0-\max(0,x_1)$ |
| 6 | | | | | | | |
| 7 | | | | | | | |

Table 2 Migration in February

| From To | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|------------|---|---|---|----------------------|---|---|---|
| 1 | | | | | | | |
| 2 | | | | $0.25(1+x_1)(1+x_2)$ | | | |

Table 2 (Continued) Migration in February

| | | | | | | | |
|---|--|--|--|----------------------|-----|--|--|
| 3 | | | | $0.25(1-x_1)(1+x_2)$ | 1.0 | | |
| 4 | | | | | | | |
| 5 | | | | | | | |
| 6 | | | | | | | |
| 7 | | | | | | | |

Table 3 Migration in March

| From To | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|------------|---|---|---|----------------------|---|---|---|
| 1 | | | | | | | |
| 2 | | | | $0.25(1+x_1)(1+x_3)$ | | | |
| 3 | | | | $0.25(1-x_1)(1+x_3)$ | | | |
| 4 | | | | | | | |
| 5 | | | | | | | |
| 6 | | | | | | | |
| 7 | | | | | | | |

When the adjustments x_1 , x_2 and x_3 are equal to zero, we have the basic migration pattern. x_1 represents the east/west part of the migration in all three months, while x_2 and x_3 represents the north/south part of the migration in February and March, respectively. x_1 is positive for increased westwards migration compared to the basic pattern, while x_2 and x_3 are positive for increased southwards migration compared to the basic pattern. As the migration matrix elements have to be in the interval $[0.0,1.0]$, thus all three parameters can vary between -1.0 and 1.0 . With this choice of basic pattern and parameters to be estimated, it is possible to get both easterly and westerly migration, and both early and late migration to the coast. All mature fish migrate out of areas 6 and 7 in January. The fish found in area 5 in autumn will always migrate into area 3.

Estimation of half value and migration.

We are then left with the estimation of 4 parameters, the 3 migration parameters and the feeding level half value parameter. However, it may not be a good idea to treat the migration as an overall migration pattern, because the possibility of large year-to-year fluctuations. We thus adopt the following scheme:

1. Estimate the 3 migration parameters on a year-to-year basis keeping the half-value parameter fixed.
2. Estimate the half-value parameter on the whole time range keeping the annual migration parameters fixed.
3. Go to step 1 until convergence.

The parameters should be constrained so that there is no outfishing or outpredating in any area in any of the months January-March in any year.

Reference estimation, using the length at maturity used by the working group and the initial meal size equal to 2.0 times the measured stomach content.

The initial meal size was set equal to 2.0 times the measured stomach content, and the following maturation parameters, corresponding to the length at maturity used by the working group (Anon, 1989b).

Table 4 Maturation parameters, working group.

| Maturation intensity P_1 , all ages | Length at maturity P_2 , all ages: |
|--|---|
| Females: 10.00 Males: 10.00 | Females: 13.94 Males: 13.94 |

It was decided to allow outfishing in area 2 in January 1984 because in order to avoid this one would have to allow migration from area 5, 6 or 7 to area 2 in January, which would be difficult to incorporate in a migration pattern reduced to 3 parameters. The excess catch in January 1984, area 2 is 47000 tonnes, and it is impossible to avoid this no matter what value x_1 and x_2 have. There is also 5000 tonnes excess catch in December 1985, area 3. There are also minor (< 1000 tonnes each) excess catches in September 1983, area 2, September 1984, area 3, December 1984, area 3, October 1985, area 3 and November 1985, area 3.

We estimated the feeding level half value P_3 to be 0.0123. Using a value of P_4 of 1.94 the other food pattern becomes (with $P_3 = 0.0123$):

Table 5 Other food pattern.

| Area | 2 | 3 | 4 | 5 |
|--|--------|--------|--------|--------|
| Other food concentration (1000 t pr sq. n. mi.) | 0.0003 | 0.0011 | 0.0019 | 0.0000 |

The migration parameters found are shown in table 6 and the spawning biomasses and mortalities in table 7.

Table 6 Migration parameters, calculated using the length at maturity used by the working group and initial meal size equal to twice the measured stomach content.

| Param. | 1983-1984 | 1984-1985 | 1985-1986 | 1986-1987 | 1987-1988 | 1988-1989 |
|--------|-----------|-----------|-----------|-----------|-----------|-----------|
| x_1 | -0.00 | 0.49 | 0.34 | 0.45 | -0.18 | -0.85 |
| x_2 | -0.75 | 0.24 | -0.97 | -0.90 | -0.50 | -1.00 |
| x_3 | 0.35 | -0.21 | 1.00 | -1.00 | -1.00 | 1.00 |

Table 7 Spawning biomasses and mortalities, calculated using the length at maturity used by the working group and initial meal size equal to twice the measured stomach content.

| | 1983-1984 | 1984-1985 | 1985-1986 | 1986-1987 | 1987-1988 | 1988-1989 |
|--------------------------------|-----------|-----------|-----------|-----------|-----------|-----------|
| Spawning biomass (1000 tonnes) | 245 | 212 | 56 | 19 | 8 | 129 |
| Total mortality | 0.98 | 0.96 | 1.12 | 0.64 | 0.48 | 0.32 |
| Natural mortality | 0.23 | 0.24 | 0.76 | 0.64 | 0.48 | 0.32 |

The mortalities calculated are mortalities for the period September-March.

The simulated consumption is given in appendix B together with the consumption calculated directly from the stomach content data. We get a bad fit (likelihood value < -10.0) for the following month/area combinations: February 1984, area 3 and 4. March 1984, area 2, March 1985, area 2 and 4, February 1988, area 3, January 1989, area 3. Best fit: 1987, Worst: 1984. It may be possible to reduce the migration parameters in a better way, ref. problems with catch in area 2, but a significantly better fit can probably only be achieved by increasing the number of predation parameters to be estimated. The estimation of predation parameters does, however, already require much computing time, and will require much more if more migration parameters are to be estimated. It will also be more difficult to interpret a larger number of migration parameters in terms of classifying the migration as early/late or easterly/westerly.

SENSITIVITY TESTS.

Choice of initial meal size.

Estimation using initial meal size equal to 1.5 times the measured stomach content and "working group" maturation parameters.

The assumption that the initial meal size is equal to twice the observed stomach content is not very well substantiated. It was decided to perform a sensitivity analysis with initial meal size = 1.5 times the measured stomach content.

Because the consumption calculated directly from the stomach content data changes when the meal size is changed, a new value had to be found for P_4 . This value was found to be 2.26. The other food pattern was found to be:

Table 8 Other food pattern.

| Area | 2 | 3 | 4 | 5 |
|---|--------|--------|--------|--------|
| Other food concentration (1000 t pr sq. n. mi.) | 0.0004 | 0.0013 | 0.0022 | 0.0000 |

We found the feeding level half value P_3 to be 0.0140. The migration parameters found are shown in table 9 and the spawning biomasses and mortalities in table 10. The overall fit is in this case slightly worse than for the baseline estimation.

Table 9 Migration parameters, calculated using initial meal size equal to 1.5 times the measured stomach content and "working group" maturation parameters.

| Param. | 1983-1984 | 1984-1985 | 1985-1986 | 1986-1987 | 1987-1988 | 1988-1989 |
|--------|-----------|-----------|-----------|-----------|-----------|-----------|
| x1 | -0.00 | 0.47 | 0.24 | 0.49 | -0.23 | -0.83 |
| x2 | -0.74 | 0.22 | -0.96 | -1.00 | -0.61 | -1.00 |
| x3 | 0.30 | -0.45 | 1.00 | -1.00 | -1.00 | -1.00 |

Table 10 Spawning biomasses and mortalities, calculated using initial meal size equal to 1.5 times the measured stomach content and "working group" maturation parameters.

| | 1983-1984 | 1984-1985 | 1985-1986 | 1986-1987 | 1987-1988 | 1988-1989 |
|--------------------------------|-----------|-----------|-----------|-----------|-----------|-----------|
| Spawning biomass (1000 tonnes) | 226 | 193 | 53 | 17 | 8 | 124 |
| Total mortality | 1.07 | 1.04 | 1.17 | 0.68 | 0.50 | 0.35 |
| Natural mortality | 0.32 | 0.32 | 0.81 | 0.68 | 0.50 | 0.35 |

As expected, we see that the resulting spawning biomasses become somewhat smaller when the meal size is decreased, because the consumption then increases. The changes in the migration parameters are relatively small. It is, however, surprising that the half value increases when the consumption increases. This may be due to the restrictions on no outfishing.

Maturation parameters.

Maturation parameters estimated by CAPSEX.

In an accompanying paper to this symposium (Tjelmeland, 1992), the following maturation parameters are calculated by CAPSEX.

Table 11 Maturation parameters estimated by CAPSEX.

| Maturation intensity P_1 , all ages | Length at maturity P_2 , all ages: |
|--|---|
| Females: 0.60 Males: 0.60 | Females: 13.64 Males: 13.93 |

We found the feeding level half value P_3 to be 0.0123. We get a better fit than for the baseline estimation because it is easier to avoid outfishing when the mature stock is larger. The other food parameters are equal to those in the key run, because P_3 is the same.

Table 12 Migration parameters, calculated using initial meal size equal to twice the measured stomach content and "CAPSEX" maturation parameters.

| Param. | 1983-1984 | 1984-1985 | 1985-1986 | 1986-1987 | 1987-1988 | 1988-1989 |
|--------|-----------|-----------|-----------|-----------|-----------|-----------|
| x1 | 0.62 | 0.55 | 0.41 | 0.47 | -0.15 | -0.85 |
| x2 | -0.87 | 0.31 | -0.98 | -0.90 | -0.50 | -1.00 |
| x3 | 0.30 | -1.00 | 1.00 | -1.00 | -1.00 | 1.00 |

Table 13 Spawning biomasses and mortalities, calculated using initial meal size equal to twice the measured stomach content and "CAPSEX" maturation parameters.

| | 1983-1984 | 1984-1985 | 1985-1986 | 1986-1987 | 1987-1988 | 1988-1989 |
|--------------------------------|-----------|-----------|-----------|-----------|-----------|-----------|
| Spawning biomass (1000 tonnes) | 370 | 274 | 66 | 19 | 8 | 143 |
| Total mortality | 0.74 | 0.80 | 1.04 | 0.64 | 0.48 | 0.31 |
| Natural mortality | 0.19 | 0.24 | 0.77 | 0.64 | 0.48 | 0.31 |

The resulting spawning biomasses increases substantially, as could be expected from the change in mature stock. The migration parameters for the years with fishing quite different from the parameters in the baseline estimation, as the "no outfishing" restriction is easier to comply with when the mature stock is increased. There are only small changes in the migration parameters for the years without fishing.

DISCUSSION.

The estimates of the total mortality differ somewhat. However, the variation in mortality from year to year is now established, and it is linked to the changes of the cod stock, as well as to changes in the environment. Obtaining "true" mortalities and hence "true" spawning stock biomasses for capelin is only possible when the cod stock and the capelin stock can be estimated in absolute terms. Also, one should keep in mind that in the calculations made in this paper only predation in January-March is considered.

Also, the migration pattern is remarkably consistent between the three sets of meal size/maturation parameters used for the years without catch. For the years with catch, the restrictions of no outfishing gives a large variation in some of the migration parameters when changing the maturation parameters. However, on several occasions the migration parameters have been estimated at their limits, which suggests that a more elaborate migration model or another transformation of parameters could be used.

Further work

Weighting of stomach samples by catch rate will be introduced. So far, this has been difficult to do due to IMR data base problems and the unavailability of Russian data on catch rate. As most stomach data from the period January-March are sampled by Norwegian vessels, the number of samples will not be reduced much when we exclude the Russian data in order to weight the data by catch rate. As the variation in stomach

content between hauls is much larger than the variation within hauls, the number of stations with stomach samples in each area should also be taken into account in the estimations in addition to the number of stomachs. The distribution of stomach content within a station and data from 24-hour stations should be utilized to get better knowledge about the meal size. The model will be updated yearly with new VPA data for cod and capelin stock data and stomach content data for more years. Also, the temperature should be calculated directly from the CTD stations taken at the cruises where stomachs are sampled. More sensitivity analyses (e.g. using Norwegian data for weight at age in the cod stock) should also be performed, and the maximum consumption should be estimated together with the half value. Also, the effect of scaling the capelin stock by a constant factor should be investigated. The estimation package MINUIT from CERN will be linked to the model in order to speed up the estimations.

Conclusion.

The present work is a first attempt to quantify stock interactions in the Barents Sea using a multispecies model. The main goal has been to explore the methodological problems, but it is shown that the approach of combining area-structured stomach content data, experimental data on stomach evacuation rate, catch data and stock data may lead to a quantification of the impact of the cod stock's predation on the mature capelin. However, considerable work is still to be done in order to utilize the results in practical management. The first steps towards such an utilization are taken in (Tjelmeland, 1992). The main uncertainty factors are the geographical distribution and timing of the capelin spawning migration, together with the maturation parameters and the stomach evacuation rate (especially the choice of initial meal size).

Appendix A Capelin stock data.

In the tables below, the mature stock in numbers for each area in September 1983–1988 is given for the different sets of maturation parameters used in the paper.

Table 14 Calculated mature capelin stock in numbers (million) for the years 1983–1988 using "working group" maturation parameters.

| Area Year | 3 | 4 | 5 | 6 | 7 |
|-----------|------|-----|------|-------|-------|
| 1983 | 1658 | 560 | 7065 | 54113 | 6292 |
| 1984 | | | 941 | 27285 | 26135 |
| 1985 | | | 3541 | 2923 | 11288 |
| 1986 | 210 | | 378 | 1693 | 1910 |
| 1987 | 81 | | 40 | 736 | 333 |
| 1988 | 69 | | 2889 | 2919 | 6046 |

Table 15 Calculated mature capelin stock in numbers (million) for the years 1983–1988 using maturation parameters estimated by CAPSEX.

| Area Year | 3 | 4 | 5 | 6 | 7 |
|-----------|------|-----|------|-------|-------|
| 1983 | 3097 | 529 | 7888 | 59735 | 8971 |
| 1984 | | | 1001 | 30414 | 30940 |
| 1985 | | | 3670 | 3677 | 13963 |
| 1986 | 285 | | 393 | 1761 | 1976 |
| 1987 | 90 | | 65 | 728 | 349 |
| 1988 | 12 | | 3490 | 3188 | 7380 |

Appendix B Stomach data.

Number of cod stomachs sampled and the calculated and simulated (reference estimation) average daily consumption of capelin by cod (grams) in model areas 2-5 in January, February and March 1984-1989:

Table 16 Calculated (simulated) daily consumption of capelin — January 1984

| | |
|--------|--------------------------------|
| Area 4 | Area 5 |
| Area 2 | Area 3 0.13 (0.00) 20 |

Table 20 Calculated (simulated) daily consumption of capelin — February 1985

| | |
|----------------------------------|---------------------------------|
| Area 4 3.00 (3.44) 251 | Area 5 0.00 (0.00) 49 |
| Area 2 10.72 (10.92) 60 | Area 3 5.25 (4.49) 885 |

Table 17 Calculated (simulated) daily consumption of capelin — February 1984

| | |
|---------------------------------|---------------------------------|
| Area 4 3.88 (8.24) 124 | Area 5 |
| Area 2 0.58 (0.34) 50 | Area 3 0.30 (0.68) 550 |

Table 21 Calculated (simulated) daily consumption of capelin — March 1985

| | |
|-----------------------------------|--------|
| Area 4 5.04 (1.63) 132 | Area 5 |
| Area 2 18.01 (28.01) 147 | Area 3 |

Table 18 Calculated (simulated) daily consumption of capelin — March 1984

| | |
|----------------------------------|--------|
| Area 4 7.73 (6.53) 68 | Area 5 |
| Area 2 15.42 (10.20) 94 | Area 3 |

Table 22 Calculated (simulated) daily consumption of capelin — January 1986

| | |
|--------|---------------------------------|
| Area 4 | Area 5 0.00 (0.02) 17 |
| Area 2 | Area 3 0.72 (0.96) 240 |

Table 19 Calculated (simulated) daily consumption of capelin — January 1985

| | |
|--------|---------------------------------|
| Area 4 | Area 5 0.20 (0.17) 147 |
| Area 2 | Area 3 |

Table 23 Calculated (simulated) daily consumption of capelin — February 1986

| | |
|---------------------------------|---------------------------------|
| Area 4 4.73 (2.43) 222 | Area 5 |
| Area 2 0.07 (0.06) 148 | Area 3 1.72 (2.61) 827 |

Table 24 Calculated (simulated) daily consumption of capelin — March 1986

| | |
|--------|---------------------------------|
| Area 4 | Area 5 |
| Area 2 | Area 3 2.43 (1.79) 237 |

Table 25 Calculated (simulated) daily consumption of capelin — January 1987

| | |
|--------|--------------------------------|
| Area 4 | Area 5 |
| Area 2 | Area 3 0.36 (0.03) 51 |

Table 26 Calculated (simulated) daily consumption of capelin — February 1987

| | |
|---------------------------------|---------------------------------|
| Area 4 0.15 (0.26) 461 | Area 5 |
| Area 2 0.07 (0.03) 110 | Area 3 0.22 (0.35) 555 |

Table 27 Calculated (simulated) daily consumption of capelin — March 1987

| | |
|--------------------------------|--------------------------------|
| Area 4 0.46 (0.22) 48 | Area 5 |
| Area 2 0.00 (0.00) 90 | Area 3 5.02 (0.32) 45 |

Table 28 Calculated (simulated) daily consumption of capelin — January 1988

| | |
|--------|---------------------------------|
| Area 4 | Area 5 |
| Area 2 | Area 3 0.05 (0.04) 545 |

Table 29 Calculated (simulated) daily consumption of capelin — February 1988

| | |
|---------------------------------|---------------------------------|
| Area 4 0.37 (0.14) 382 | Area 5 |
| Area 2 0.14 (0.05) 167 | Area 3 0.60 (0.19) 900 |

Table 30 Calculated (simulated) daily consumption of capelin — March 1988

| | |
|---------------------------------|--------------------------------|
| Area 4 0.30 (0.14) 102 | Area 5 |
| Area 2 | Area 3 5.31 (0.09) 20 |

Table 31 Calculated (simulated) daily consumption of capelin — January 1989

| | |
|--------------------------------|---------------------------------|
| Area 4 0.00 (0.23) 26 | Area 5 |
| Area 2 | Area 3 8.44 (2.38) 124 |

Table 32 Calculated (simulated) daily consumption of capelin — February 1989

| | |
|---------------------------------|---------------------------------|
| Area 4 0.37 (0.27) 872 | Area 5 |
| Area 2 0.00 (0.00) 148 | Area 3 2.65 (2.39) 956 |

Table 33 Calculated (simulated) daily consumption of capelin — March 1989

| | |
|--------------------------------|--------------------------------|
| Area 4 2.18 (0.00) 50 | Area 5 |
| Area 2 6.65 (0.02) 25 | Area 3 7.37 (4.81) 25 |

Appendix C Catch data.

In the tables below, the catch in numbers by month and area for 1983–1984, 1984–1985 and 1985–1986 is given.

Table 34 Capelin catch in numbers (million) by month and area, 1983–1984

| Area Month | 2 | 3 | 4 | 5 | 6 | 7 |
|---------------|------|------|-----|-----|-------|------|
| Sep | 8 | 6 | | 17 | 22004 | 1394 |
| Oct | | | 1 | | 14537 | 2 |
| Nov | | 1 | | | 3855 | 1 |
| Dec | | 856 | | 137 | 844 | 1396 |
| Jan | 2073 | 7951 | 634 | 120 | 6 | 4 |
| Feb | 1856 | 2217 | 27 | 49 | 4 | + |
| Mar | 2533 | 6693 | 96 | 1 | + | 14 |

Table 35 Capelin catch in numbers (million) by month and area, 1984–1985

| Area Month | 2 | 3 | 4 | 5 | 6 | 7 |
|---------------|-----|------|------|------|-------|------|
| Sep | | 55 | | | 21236 | 53 |
| Oct | | | | | 8026 | 570 |
| Nov | | | | | 1627 | 1291 |
| Dec | | 23 | | 6 | 5915 | 68 |
| Jan | | 425 | 25 | 6694 | 524 | 447 |
| Feb | 347 | 54 | 2962 | 426 | 129 | 6 |
| Mar | 463 | 7228 | 189 | 5 | | + |

Table 36 Capelin catch in numbers (million) by month and area, 1985-1986

| Area Month | 2 | 3 | 4 | 5 | 6 | 7 |
|---------------|---|------|----|-----|------|------|
| Sep | | | | + | 9856 | 139 |
| Oct | | | | 129 | 1380 | 269 |
| Nov | | + | | 660 | 7 | 1967 |
| Dec | | 347 | | 43 | 1 | 1597 |
| Jan | | 184 | 15 | 110 | + | 92 |
| Feb | | 142 | | 16 | | |
| Mar | | 1365 | | 40 | | 2 |

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**A STOCHASTIC MODEL FOR THE BARENTS
SEA CAPELIN STOCK WITH PREDATION
FROM AN EXOGENOUS COD STOCK**

by

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ABSTRACT

Based on the model CAPELIN used with management of the Barents Sea capelin stock until 1986, a model that is structured on age and sex is constructed. The predation on the mature part of the stock is connected to the size of the cod stock, and predation parameters calculated by the area-structured multispecies model MULTSPEC are used. The effect of the geographical overlap of cod and capelin is modeled using a scalar overlap index variable. The uncertainty connected to the modeled biological processes are displayed and the future use of the model for management of capelin briefly discussed.

INTRODUCTION

The Barents Sea capelin stock declined severely during the period 1983 to 1986, and did not start recovering until 1990. It is believed that the decline was initiated by an abrupt change of oceanographic conditions during the winter 1982–1983. An increase in the inflow of Atlantic water caused very good recruitment conditions for the Norwegian spring spawning herring and the Northeast Arctic cod stock. During the fall of 1983 it is likely that the 0-group herring caused a decline in capelin recruitment by predation (Moxness and Øiestad, 1979). As the 1983 year class of cod grew older, the natural mortality of adult capelin increased rapidly. Most likely as a consequence of the vanishing of the capelin as source of food, the individual growth of the cod decreased dramatically. The model used for management — CAPELIN — (Tjelmeland, 1985, Hamre and Tjelmeland, 1982) did not take into account these effects.

As the capelin stock now is at a level that it again can sustain fishery, the following issues must be dealt with:

1. What management measures should be taken in periods of much herring in the Barents Sea?
2. The predation from cod should be taken into account when the capelin quotas are set.
3. The importance of capelin as source of food for cod should be taken into account when the capelin quotas are set.

This paper addresses the above questions. A new model in which the predation from cod on mature capelin is evaluated using the actual size of the cod stock is presented. Also, a recruitment relation incorporating the significance of herring is implemented. An important goal of the paper is to reflect the uncertainty of management due to uncertain data and crude models.

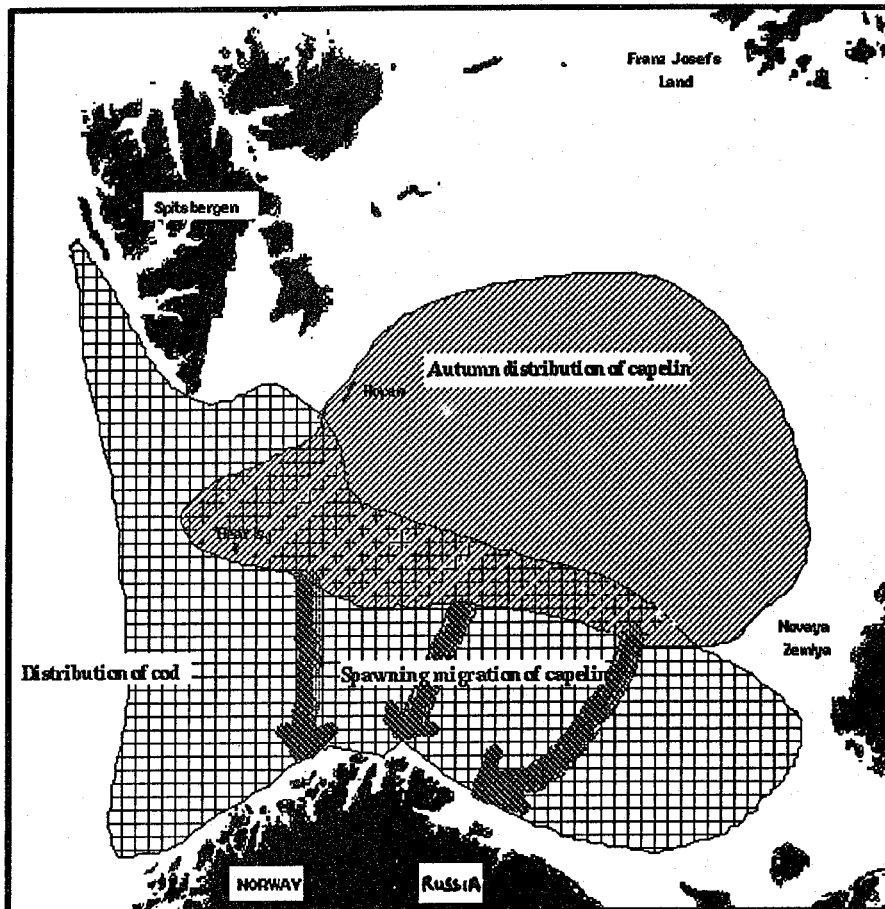
In the paper the predation from cod on mature capelin is evaluated, using results from the model MULTSPEC presented in an accompanying paper to this symposium (Bogstad and Tjelmeland, 1992). Since the actual level of the cod stock is used in evaluating predation, the calculated size of the capelin spawning stock can not be compared to previously published figures, since the latter were based on a rather unsubstantiated and yearly constant M-value.

Only two biological processes are modeled in the sense that they are connected to other model variables: maturation of capelin and predation on mature capelin. The present version of CAPSEX is, so to speak, a multispecies minimum variant. The other processes important for management relevant modeling, i.e. growth, natural mortality on immature capelin and recruitment, are dealt with without any attempt of explaining these processes from other variables.

It is assumed that the reader has some familiarity with the Barents Sea ecosystem and its past management, especially for capelin.

BIOLOGY.

Figure 1 Distribution of cod and capelin, spawning migration of capelin.



Life history of capelin.

The capelin was in focus at the second PINRO—IMR symposium, where the assessment and biology of the stock was described (Gjøsæter, 1985). Here, the main points relevant for the modeling work presented in this paper are mentioned.

In the autumn the capelin stock feeds in the northern parts of the Barents Sea, mainly north of 74°N in the western regions. In the eastern regions the capelin may be found far south also in the autumn but not in great abundance and consisting of mostly young fish. The capelin stock has been surveyed each year during September since 1972 in a joint Russian-Norwegian cruise using acoustic information combined with trawl data. These survey data are the foundation of the capelin modeling and management.

The geographical distribution in the autumn may vary strongly from year to year, in some periods being more southern and western and in other periods being more northern and eastern, see distribution maps in (Dommasnes and Røttingen, 1985).

At the end of the year and the following winter the mature part of the population moves southwards and will eventually spawn at the coast of Norway and Russia in April. In some years the capelin will have a westerly spawning migration, in other years an easterly spawning migration. The mechanisms governing the geographical variation of the spawning migration are poorly understood, although there have been some attempts to make conceptual models (Tjelmeland, 1987a), (Ozhigin and Luka, 1987).

It is believed that most of the mature capelin die after spawning.

The larvae will drift with the coastal and Atlantic currents into the central and southern Barents Sea. When the spawning is westerly, a significant portion of the larvae will drift to the west of Spitsbergen and may then be lost from the Barents Sea capelin stock.

The immature capelin may also migrate far southwards, but later than the mature component. The data for assessing the migration of the immature capelin are poor, but an overall impression is that the extent of the southwards migration may vary from year to year and that the most southern distribution may be in the months May and/or June. The northwards migration will take place in July and August.

Predation from cod.

During the spawning migration the capelin will overlap fully with the cod stock, and be subject to heavy predation. The magnitude of the predation will depend on the migration route, because there is an east-west gradient in both the abundance and age distribution of cod.

It is likely that the cod stock's predation on immature capelin is more variable than the predation on mature capelin, since the migration, and thereby the overlap, may be more variable. But there is no doubt that in some years the predation from cod also on immature capelin may be highly significant.

Predation from herring.

The pattern of herring abundance in the Barents Sea is that in some years of good recruitment herring juveniles may be entered in great quantities. The herring will grow up in the southeastern part and gradually move westwards as it grows older. It will leave the Barents Sea at age 3 or 4.

During the 0-group stage there may be considerable overlap between herring and capelin. Due to the size difference, the herring may prey on capelin, thus having an influence on capelin recruitment (Moxness and Øiestad, 1979). As the herring grows older, the predation on capelin larvae will depend on the overlap and in most cases probably will be of little significance, if not the geographical distribution of capelin larvae is extremely south— and easterly.

The fishery.

The capelin fishery is conducted in two seasons.

In the autumn season from August to December both immature and maturing capelin are caught. It is suspected that a considerable quantity of 1-group capelin may be killed

in the autumn fishery without being reported as catch. Thus, in periods where the 1-group capelin overlaps the older capelin in the autumn, there may be reason to suspect a somewhat reduced recruitment measured as 2 year old capelin the following year.

In the winter season from January to April mainly the migrating mature capelin is caught, although some immature capelin may be found in the catches.

Development of the capelin and cod stocks.

Figure 2 shows the recent development of the capelin stock:

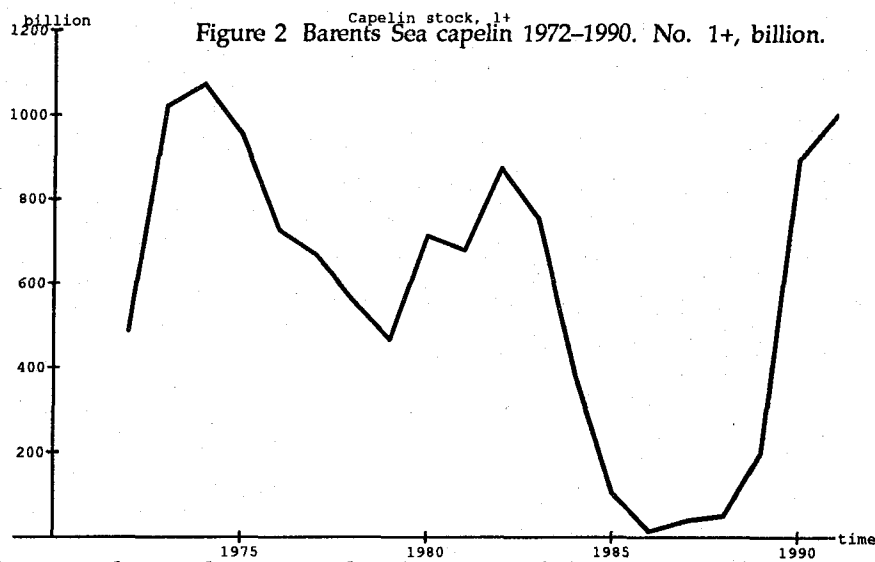
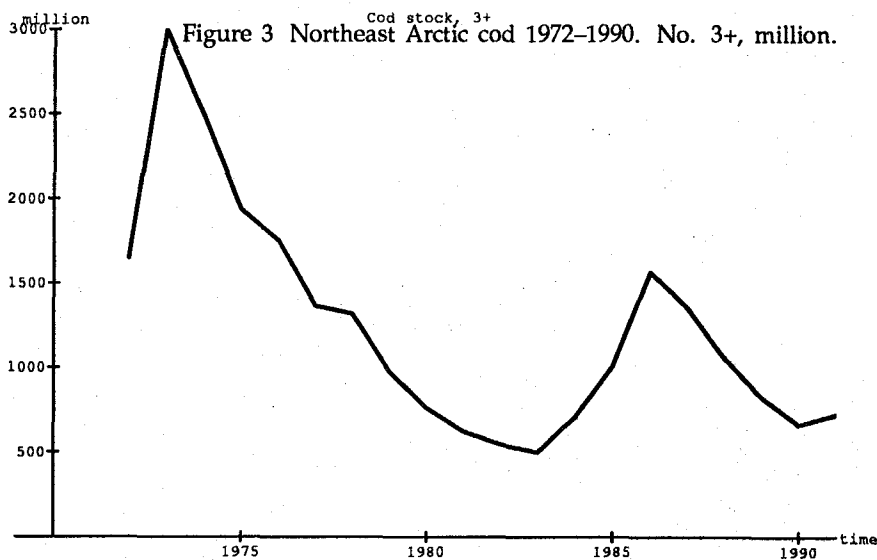


Figure 3 shows the recent development of the cod stock:



MANAGEMENT.

The management of the Barents Sea capelin up to 1984 is described by (Hamre, 1985). Prior to 1982 the stock was managed by using a spawning stock of 0.5 million tonnes as a lower safeguarding limit. This number was based on a comparison of historical calculations of the spawning stock and observed recruitment. In the autumn 1982 results from (Hamre and Tjelmeland, 1982) (CAPELIN model) was used to introduce MSY management. The optimal spawning stock calculated by the CAPELIN model did not differ much from the previous used safeguarding limit. It is worth noting that already in 1982 multispecies considerations were taken in the regulation of the capelin stock, since the value of the stock as source of food for predating organisms was explicitly considered (Anon, 1983).

In 1984 the first signs of capelin recruitment failure were manifest (Anon, 1985) as the number of one year old capelin was extremely low. The implications of this observation was not fully understood, to a large extent because the acoustic abundance estimate of the one-group had proven not to be reliable on earlier occasions.

In its 1985 meeting the Atlanto-Scandian Herring and Capelin Working Group (Anon, 1986) noted that the capelin stock had decreased far more that could be accounted for by the fishery. The conclusion was that environmental changes had taken place that invalidated the model. The working group did not recommend any fishing in 1986.

The stock was at a low level in 1986-1989, and retained its earlier strength in 1990, if measured in biomass units.

MODEL FORMULATION AND PARAMETER ESTIMATION.

Maturation and natural mortality on immature capelin.

In the following, a revised model will be described and the parameters will be estimated process by process. The natural starting point is the maturation, because in the present version of the model the estimated values of the maturation parameters will not be dependent on the values of other parameters. This follows from the conceptual model of the life history of capelin presented earlier and from the fact that the stock data are from September, prior to the separation of the stock into a mature and an immature component. The converse is not true. The estimated values of the parameters governing growth and natural mortality will be strongly dependent on the estimated values of the maturation parameters.

The maturation of capelin is believed to be above all a length-dependent process, although for a given length there might be a higher probability for maturation with higher age (Forberg and Tjelmeland, 1985).

Formulation

The maturation, applied on the September cruise data, is given by:

$$m(l) = \frac{1}{1 + e^{4 \times P_1^{sex} \times (P_2^{sex, age} - l)}}$$

where l is the fish length in cm.

The estimation of maturation parameters poses severe difficulties. A study of gonads reveal that maturation also may depend on age. With some support from (Forberg and Tjelmeland, 1985) we fix P_1^{sex} to 0.6 for both sexes. In (Tjelmeland, 1987b) a relation between maturation parameters between sex and age was assessed from gonadal data and an overall scaling was estimated by using the model. In (Tjelmeland, 1987a) the maturation was taken from gonadal data alone. Maturation studies should later be done using all collected gonadal data to lessen the burden on model estimations.

The natural mortality on immature capelin is supposed to be the same for all age groups and both sexes.

Estimation method.

The data inputs to the model are the acoustic estimate obtained during September each year, the catch in number and the weight in the catches by age and month, assuming all catch in the period January-April to be on mature capelin. The analysis will for the time being be restricted to utilizing only these data, although several other sources of data exist that may improve the basis for parameter estimation and that may be a foundation for refined models. For the moment disregarding recruitment, the biological processes affecting the population from one year to the next are the maturation and mortality. The parameters in the maturation and mortality models will be estimated by comparing the number of fish at age 3, 4 and 5 years simulated by starting the model in the previous autumn, to corresponding measured values.

In choosing the estimation method, assumptions on the stability of the parameters have been made:

1. The probability of a fish of given age, sex and length to mature is constant from year to year.
2. The mortality of immature capelin is regarded as stochastic, i.e. no pre-estimation assumptions on the mortality is made.

Thus, the following estimation scheme is adopted:

1. The maturation parameters are fixed throughout the whole time period of estimation.
2. The mortality is estimated year by year.
3. The estimation is performed by varying the maturation parameters until the least-squares goal function attains its minimum value.

The estimation is thus performed in a double iteration.

Uncertainty estimates.

There is not enough knowledge of the uncertainties connected to the acoustic estimate to construct a goal function that gives the probability of obtaining the actual measurements given that the model is true, i.e. a maximum likelihood method for constructing the parameter confidence intervals cannot be used. Therefore, resampling is used. From the period of available data, 18 one-year periods are picked at random and the estimation of maturation and mortality parameters is performed. 85 estimations are performed and the parameter confidence intervals and correlation are calculated from these estimates (table 2).

Goal functions.

Two different goal functions have been tried, both using unweighted least squares:

1. Comparing absolute simulated number of fish in each age group and for each sex to absolute measured number of fish in each age group and for each sex.
2. Comparing the ratio of simulated number of fish to measured number of fish to 1.0 in each age group and for each sex.

Given that the maturation and mortality models both are correct, the two goal functions should give the same estimated values for the parameters. However, both the maturation model and the mortality model are highly idealized. Thus, differences in the estimated values tell us something about how the model assumptions deviate from the realities. For instance, goal function 1 put more weight on the more numerous 3 year old fish than on older fish. If there is something wrong with the assumptions on age dependence, we will get different estimates.

It is not straightforward to determine how simple the models of maturation, spawning survival and mortality can be. We have made 24 series of estimations using the two different goal functions, ages 3 and 4 or ages 3, 4 and 5, increased length at maturity for 2 year old fish for females, males and both sexes, and no spawning survival or some spawning survival of females.

None of the 24 estimations performed significantly better than one of the simplest: Using goal function 2, ages 3 and 4, no spawning survival and no age dependence of maturation parameters.

In later versions of the model, it might prove possible to utilize a relation between observed energy content of the fish and spawning survival being worked upon at PINRO (Lebskaya, pers. comm.).

Consistency with weight at age in the catches of mature capelin.

Once the maturation parameters are determined, the mean weight at age of the maturing population is determined. During the estimation of the maturation parameters, the simulated individual weight of the maturing capelin from October 1. to spawning at April 1. is not changed. The mean weight at age is compared to the mean weight at age in the catches of mature capelin in the period January-April. If the simulated weight is higher than the measured weight there is an inconsistency if no real weight decrease has taken place. In this case, the goal function has been increased with a (somewhat arbitrary) penalty function, which is the quadratic deviation of the ratio between simulated and measured weight from unity.

The weight at age data from the catches in the mature population may be difficult to interpret. Some of the catch may have been taken on immature capelin. Also, it is difficult to construct reliable weight at age because the geographical distribution of the catch may differ from the geographical distribution of the mature stock. Hence, a weight at age gradient may cause errors in the estimate. The data used are weighted averages between Russian and Norwegian catches.

We consider the use of weight at age data from the catch statistics to be the weakest part of the analysis presented in this paper.

Estimation results.

The parameter estimate obtained fixing the maturation over the whole time period is shown in table 1:

Table 1 Basic maturation parameter estimate.

| | |
|----------------------------|-------|
| Length at maturity females | 13.68 |
| Length at maturity males | 14.00 |

To investigate the uncertainty associated with the maturation parameter estimates, a series of 85 estimations each using 18 one-year periods drawn at random (with replacement) from the available data were run. The result is shown in table 2:

Table 2 Bootstrap parameter estimates and covariance matrix.

| | Length at maturity, females | Length at maturity, males |
|-------------------|-----------------------------|---------------------------|
| Means | 13.65 | 14.04 |
| Covariance matrix | | |
| | 0.078 | 0.438 |
| | | 0.125 |

The estimates in table 1 are reasonably close to the estimates in table 2, in view of the bootstrap-estimated variances.

Natural mortality and growth of immature capelin.

As for the natural mortality, a model relating growth to model variables has not been used, although such a model is implemented into the CAPSEX software. Instead, the growth per year has been estimated year by year for males and females separately. An ordinary least squares goal function has been used, without measurement error. There is no need for estimating growth with a confidence interval because the statistical uncertainty the variation in growth imposes on the overall model results will be found by drawing estimated growth at random from the estimated growth by year. Table 3 shows the results.

Table 3 Estimated growth of immature capelin.

| | Natural mortality, month ⁻¹ | Females length, cm year ⁻¹ | Males length, cm year ⁻¹ | Females weight, g year ⁻¹ | Males weight, g year ⁻¹ |
|-------------|--|---------------------------------------|-------------------------------------|--------------------------------------|------------------------------------|
| 1972 - 1973 | 0.108 | 2.18 | 3.04 | 7.88 | 14.89 |
| 1973 - 1974 | 0.044 | 1.43 | 3.51 | 2.51 | 14.34 |
| 1974 - 1975 | 0.040 | 2.72 | 2.41 | 7.64 | 8.07 |
| 1975 - 1976 | 0.058 | 2.27 | 2.70 | 6.08 | 8.61 |
| 1976 - 1977 | 0.035 | 2.31 | 3.00 | 8.37 | 12.08 |
| 1977 - 1978 | 0.050 | 2.08 | 2.96 | 6.12 | 10.19 |
| 1978 - 1979 | 0.090 | 2.47 | 2.67 | - | 7.25 |
| 1979 - 1980 | 0.037 | 2.77 | 3.70 | 8.59 | 16.02 |
| 1980 - 1981 | 0.066 | 2.48 | 3.12 | 7.54 | 12.32 |
| 1981 - 1982 | 0.064 | 2.77 | 3.66 | 7.99 | 14.39 |
| 1982 - 1983 | 0.202 | 2.41 | 3.95 | 8.37 | - |
| 1983 - 1984 | 0.066 | 2.73 | 3.55 | 7.53 | 14.37 |
| 1984 - 1985 | 0.173 | 2.18 | 2.64 | 5.54 | 8.34 |
| 1985 - 1986 | 0.215 | 1.83 | 3.12 | 2.71 | 8.61 |
| 1986 - 1987 | 0.249 | 2.38 | 3.38 | - | - |
| 1987 - 1988 | 0.079 | - | - | - | - |
| 1988 - 1989 | 0.209 | 3.15 | 3.82 | - | 2.71 |
| 1989 - 1990 | -0.046 | 2.59 | - | 10.52 | - |

With one exception (1974-1975) the growth in length has been estimated at a higher value for males than for females. Without exception the growth in weight has been estimated at a higher value for males than for females.

There are some problems with the present version of the data base used, leading to the growth in some years not being estimated or estimated at an unreasonably low value. In these cases the estimate is not given in table 3 and the growth has been set to a lower limit of 2.0 for growth in length for females, and 2.5 cm for males. This probably gives a biased growth when the model is used, but the effect should be small.

Growth of mature capelin.

No model relating the weight of mature capelin at time of spawning to model variables have been applied. A constant rate of growth in the period October 1 to April 1 has been assumed. Once the maturation parameters have been estimated the growth of mature capelin is determined. The relative weight increase from October 1 to April 1 is shown in table 4.

Table 4 Weight increase factors from October to April for mature capelin, using weight at age in the catch.

| | 2-3 years | 3-4 years | 4-5 years |
|-----------|-----------|-----------|-----------|
| 1973-1974 | 1.75 | 1.18 | 1.18 |
| 1974-1975 | 2.00 | 1.61 | 0.99 |
| 1975-1976 | 2.00 | 1.62 | 1.35 |
| 1976-1977 | 2.00 | 0.74 | 1.34 |
| 1977-1978 | 1.13 | 1.14 | 0.53 |
| 1978-1979 | 0.88 | 1.30 | 1.39 |
| 1979-1980 | 1.42 | 1.39 | 1.17 |
| 1980-1981 | 2.00 | 1.30 | 1.15 |
| 1981-1982 | 2.00 | 0.72 | 1.31 |
| 1982-1983 | 1.27 | 1.09 | 1.15 |
| 1983-1984 | 1.07 | 0.93 | 1.15 |
| 1984-1985 | 1.60 | 1.21 | 1.10 |
| 1985-1986 | 1.91 | 1.26 | 1.76 |

During the estimation an upper limit of 2.00 has been set, and it is seen from table 4 that the weight increase has been determined to the upper limit in several cases for capelin 2-3 years. Such high growth seems unlikely and may be connected either to a bias in data or to the maturation model being wrong. A greater length at maturity for 2 year old fish, as suggested in (Forberg and Tjelmeland, 1985) would lower the estimated weight increase. This problem might be dealt with either by introducing a new parameter to be estimated for each sex or by estimating relations between maturation parameters, as was attempted in (Tjelmeland, 1987b).

If the data for weight at age in the mature population consists of more males than females the we would also obtain a too large growth in weight.

In some cases there is a decrease in weight in spite of the penalty used in estimating the maturation parameters, see page —146—. How much this penalty should be weighted is a trade-off between belief in the model for immature capelin and the model for the mature capelin, as well as the trust in the autumn acoustic data and the weight at age data for the mature stock. It appears from table 4 that the penalty might have been weighted more, giving a lower length at maturity (and hence a greater spawning stock and a lower natural mortality for immature capelin). However, this would also have increased the estimated growth of mature 2-3 year old capelin which already is unlikely high.

In future versions of the model, weight at age data split on sex should be used.

Predation from cod on mature capelin.

Formulation.

The effect of predation on mature capelin is evaluated by using parameters estimated by the area-distributed model MULTSPEC. The results using data from 1984 to 1989 are given in an accompanying paper to this symposium (Bogstad and Tjelmeland, 1992). The MULTSPEC predation equations are formulated in an area-integrated form as follows (details concerning different units in MULTSPEC and CAPSEX are omitted):

The capelin abundance is transformed to capelin density:

$$\text{Capelin concentration} = \frac{\text{Capelin abundance}}{\text{Area size}}$$

Total food concentration is given by:

$$\text{Total food} = \text{Capelin concentration} + \text{Other food concentration}$$

The capelin length part of the suitability is neglected.

The individual cod's predation ability is made dependent on the age. The mature cod at this time of the year migrating towards the spawning grounds is supposed not to prey on capelin. The maximum consumption of cod on capelin then becomes:

$$\text{Cod} = P_4 \times \text{Temp} \times \sum_{\text{age}=3}^{10} N_{\text{Year}}^{\text{Cod}}(\text{age}) \times (1 - \text{Ogive}_{\text{Year}}^{\text{Cod}}(\text{age})) \times W_{\text{Year}}^{\text{Cod}}(\text{age})^{0.802}$$

where the cod length part of the suitability has been implemented by starting the summation at age 3.

The temperature effect is given by:

$$\text{Temp} = e^{0.104 \times T_{\text{Year}} - 0.000112 \times T_{\text{Year}}^3 - 1.5}$$

where the temperature T_{year} is the April temperature from the Kola section, integrated in depth and along the section (PINRO, pers. comm.)

The feeding level is given by:

$$f = \frac{\text{Total food}}{\text{Total food} + P_3}$$

The consumption on capelin then becomes:

$$\text{Cons} = \text{Overlap} \times \text{Cod} \times f \times \frac{\text{Capelin concentration}}{\text{Total food concentration}}$$

The variable *Overlap* is a measure of the difference between CAPSEX and MULTSPEC given the same data and parameters. This difference stems from MULTSPEC having a geographical dimension, thus taking into account the overlap between the species and how the temperature is distributed geographically.

The natural mortality becomes:

$$M = \frac{\text{Cons}}{\text{Capelin concentration}}$$

The cod stock abundance and cod maturity ogives are taken from the work of the Arctic Fisheries Working Group, and the data files are the same as used by MULTSPEC. The parameters P_3 , P_4 and the other food concentration are taken from estimation work with MULTSPEC (Bogstad and Tjelmeland, 1992). The area size used in converting abundance to concentration is set to the sum of the sizes of MULTSPEC areas 2, 3, 4 and 5, in which the capelin occurs during the spawning migration.

Cod model.

For the historic runs used to estimate the parameters of the CAPSEX model, the VPA-estimates made by the Arctic Fisheries Working Group are used (Anon, 1991). The area distribution is based on the Norwegian young cod survey in February. It is assumed that only immature cod eats capelin during January-March, and the immature part of the cod stock is calculated using the maturity ogive given by the Working Group. The weight at age data for cod are those used by the Working Group, which makes an arithmetic average of the weight at age from these two surveys. However, it is evident from the working group report that there is a larger discrepancy in weight at age between the Russian late autumn cod survey and the Norwegian young cod survey the following winter than can be accounted for by growth. This discrepancy may to a large extent be due to differences in age reading, and this matter is now under investigation (Anon, 1993)

For the runs into the future, a cod model dynamic in number at age has been used, with the following assumptions:

1. The natural mortality equals 0.2 for all age groups.
2. The fishing mortality equals 0.3 times the fishing pattern for 1990 given by the Working Group.
3. A constant maturity ogive and weight at age given by the Working Group for 1990 is used.
4. The recruitment is made stochastic with a uniform probability between 200 and 600 million individuals.

These assumptions bring the biomass of the immature cod stock up to about 1 million tonnes in about 10 years of simulation time.

Estimation of the overlap variable.

The overlap variable has been estimated by demanding that the capelin spawning biomass should be the same using MULTSPEC and CAPSEX for the years 1984-1989, provided the predation parameters, growth of mature capelin and capelin maturation parameters are the same. The result is:

Table 5 Overlap variable, CAPSEX adjustment to MULTSPEC.

| | |
|------|------|
| 1984 | 2.04 |
| 1985 | 1.82 |
| 1986 | 2.12 |
| 1987 | 2.56 |
| 1988 | 2.71 |
| 1989 | 1.55 |

In using the immature capelin to estimate the maturation parameters and the MULTSPEC parameters to evaluate predation on mature capelin it is assumed that the amount of late maturing capelin (i.e. capelin spawning in June-July) is negligible.

Recruitment.

A recruitment model incorporating the influence from herring was used:

$$R = P_5 \frac{B}{B_{\frac{1}{2}} + P_6 \times H_0 + P_7 \times H_{1+} + B}$$

where :

B = Spawning stock biomass (million tonnes)

R = Number of recruits (2 year old, billion)

$B_{\frac{1}{2}}$ = Spawning stock biomass half value neglecting influence from herring

H_0 = Index of 0 - group herring

H_{1+} = index of older herring

The index used for older herring is the acoustic estimate for the 1983 year class in the Barents Sea herring and shown in table 6.

Table 6 Index for herring (billion).

| | | | |
|------|------|------|------|
| 1984 | 1985 | 1986 | 1987 |
| 40 | 23 | 8 | 4 |

The index used for 0-group herring is the exponential of the logarithmic 0-group index. The data used are shown in table 7.

Table 7 Index for 0-group herring.

| | | | | | | | | | | | | | | | | | | |
|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| 1972 | 1973 | 1974 | 1975 | 1976 | 1977 | 1978 | 1979 | 1980 | 1981 | 1982 | 1983 | 1984 | 1985 | 1986 | 1987 | 1988 | 1989 | 1990 |
| 0.0 | 0.05 | 0.01 | 0.00 | 0.00 | 0.01 | 0.02 | 0.09 | 0.00 | 0.00 | 0.00 | 4.87 | 0.40 | 0.26 | 0.00 | 0.00 | 0.38 | 0.80 | 0.38 |

The model will not account for more of the variance in the data if 0-group of cod is included.

The parameter estimates are:

Table 8 Recruitment parameter estimates.

| | |
|------------------|---------------------------|
| P ₅ | 274 billion |
| P ₆ | 0.55 |
| P ₇ | 0.80 - estimated at limit |
| B _{1/2} | 0.0033 million tonnes |

The influence from a 1983-type herring event will dominate the dynamics of the capelin totally. The spawning biomass half value is extremely small, giving very good recruitment in absence of herring.

This model accounts for 2/3 of the variance in the data.

The above recruitment model has the property that even if there may be great variation in recruitment due to fluctuation in the amount of herring, an additional amount of spawning capelin will always give an additional amount of recruits.

When this model is being used stochastically:

1. The index of 0-group herring is drawn at random from the 0-group indices calculated from the yearly 0-group survey.
2. The index of older herring is calculated by drawing a 1983-type herring event with a probability of two instances in an 18-year period.
3. The recruitment is calculated by using the above model and adding a stochastic term drawn from a uniform probability density function with a range given by the standard deviation of the residuals.

Some important processes have been neglected:

1. Influence from 0-group cod on recruitment.
2. Influence of larval drift on capelin recruitment.
3. Influence on recruitment of killing of 1-group capelin during the autumn fishery.
4. Cheating on the reports on catch of mature capelin. Some capelin may have been discarded in connection with roe production and fishing for roe capelin for the consumption market.

Also, the stock-recruitment results are strongly dependent on the stock data for cod being correct. Several tuned VPAs for cod with different values of M should be run to check the sensitivity towards M.

With improved area coverage of the Barents Sea the later years, to a great extent due to an increased effort both from the Norwegian and Russian side, it might be possible to use the estimate of the 1 group as recruitment. However, we feel that at present the time series of reliable data is somewhat short.

Fishing.

The catch data used are numbers caught by age and month. The same data files as in the older model CAPELIN are used. The catch is converted to fishing mortality, assumed to be the same for females and males.

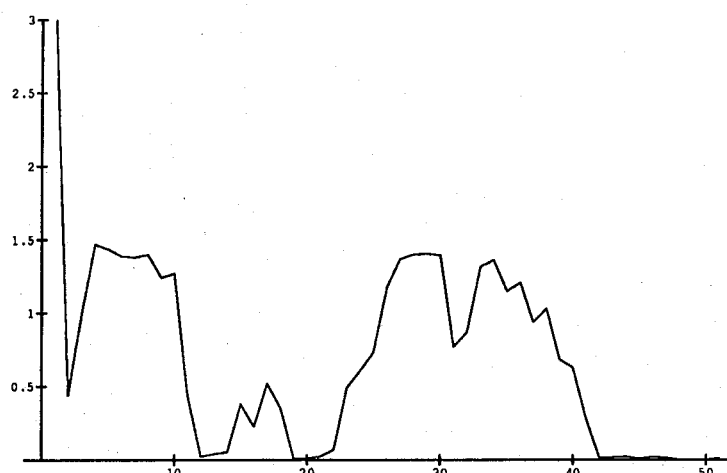
In the period January to April all catch is assumed to occur on mature capelin.

Running the model into the future, it is supposed that the same F-value apply in all catching months, and that the F-value is the same for all age groups. The catching months for runs into the future are October-December (autumn fishery) and January-March (winter fishery, mature capelin only).

RANKING SOURCES OF UNCERTAINTY — LONG TIME SIMULATIONS.

In order to get a feeling of how much the uncertainty in each of the modeled processes contributes to the overall uncertainty 30 runs from 1990 to 2040 have been made, drawing only one process at random each time. For the other processes mean values have been used. It turned out that if the influence from herring were averaged, the capelin stock would vanish in the course of 10–15 years due to the increased predation pressure from the growing cod stock. If the influence from herring is random the capelin stock turns out to be sustainable because in years of low herring influence the recruitment will be good even if the spawning biomass is poor due to the low $B_{1/2}$ value, see table 8. In order to compare the uncertainties of the other processes, in all runs the same sequence of herring events have been used. In all runs the spawning stock biomass (million tonnes) only is plotted. The baseline run is shown in figure 4.

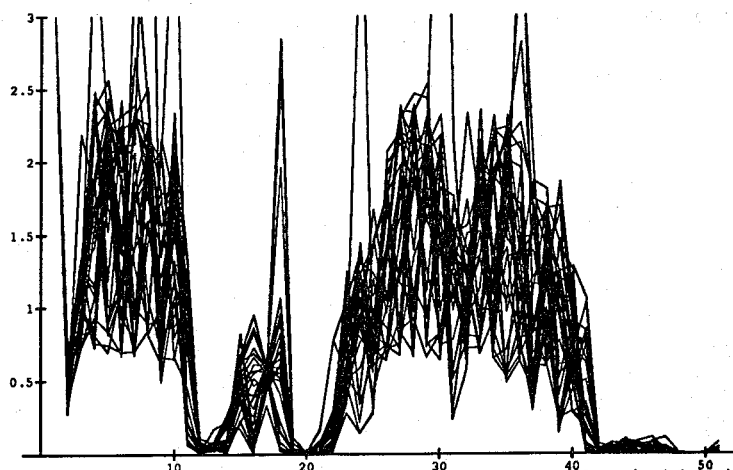
Figure 4 Stochastic runs — baseline.



During the baseline run, herring events occurred in years 6, 13, 36 and 42. This leads to two long periods of capelin and two shorter periods where the capelin stock is very poor or almost absent from the Barents Sea.

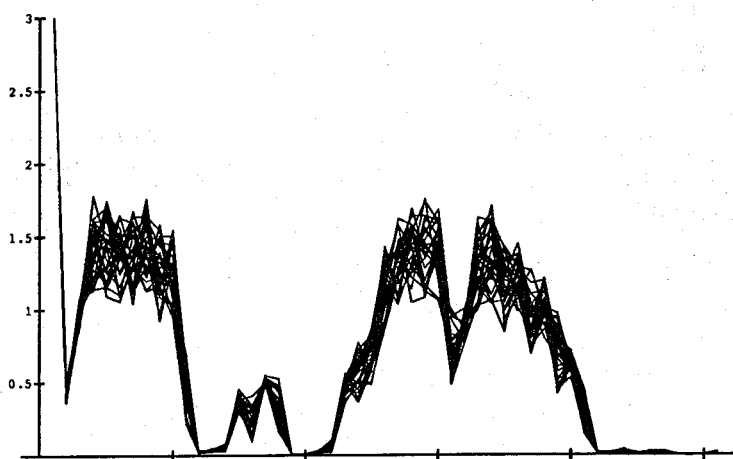
The influence of variation in natural mortality (table 3) on the development of the spawning stock biomass is shown in figure 5.

Figure 5 Stochastic runs — natural mortality.



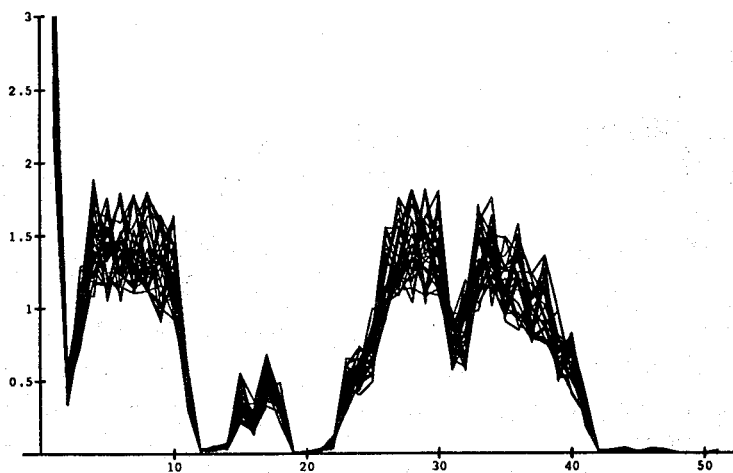
The influence of variation in growth of immature capelin (table 3) on the development of the spawning stock biomass is shown in figure 6.

Figure 6 Stochastic runs — growth of immature capelin.



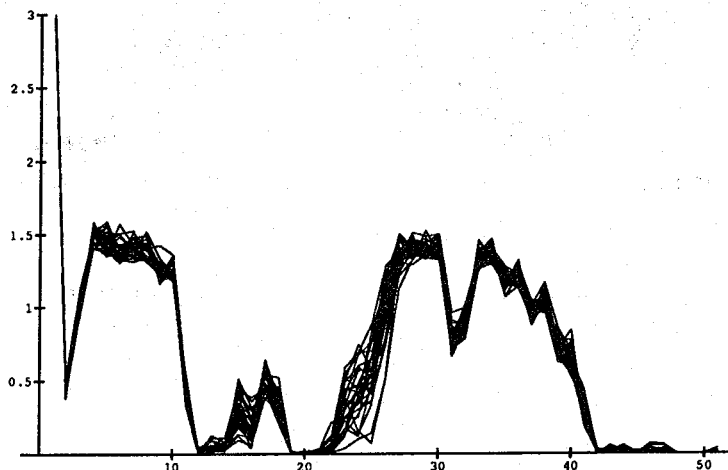
The influence of variation in growth of mature capelin (table 4) on the development of the spawning stock biomass is shown in figure 7.

Figure 7 Stochastic runs — growth of mature capelin.



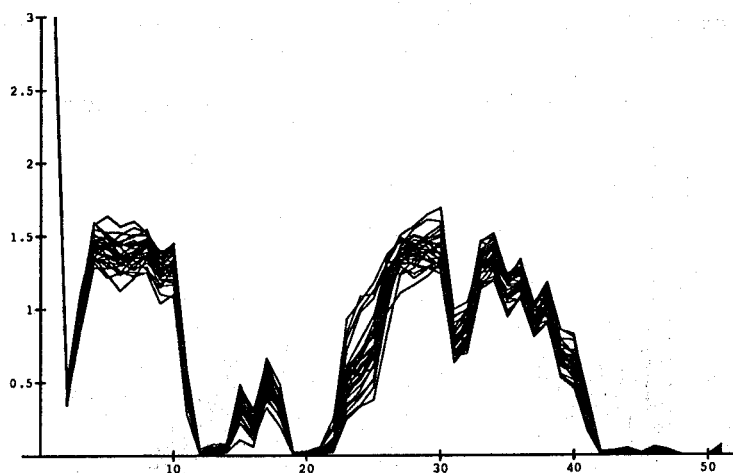
The influence of variation in the index for overlap between capelin and cod (table 5) on the development of the spawning stock biomass is shown in figure 8.

Figure 8 Stochastic runs — overlap index.



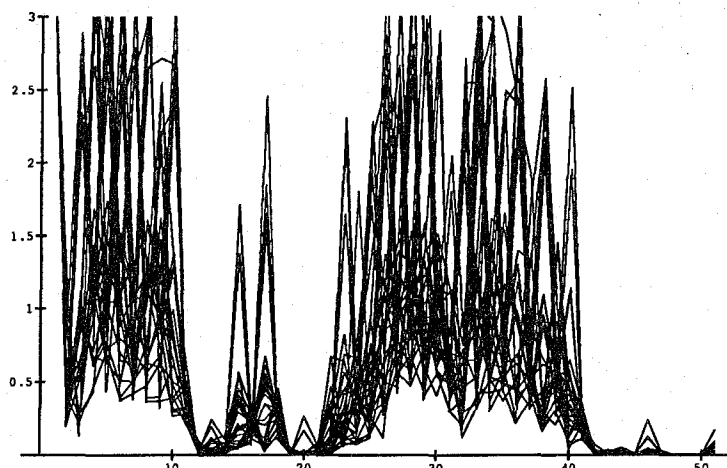
The influence of variation in the recruitment of cod on the development of the spawning stock biomass is shown in figure 9.

Figure 9 Stochastic runs — overlap index.



The influence of variation in the recruitment of capelin other than the variation due to random fluctuation of predating herring on the development of the spawning stock biomass is shown in figure 10.

Figure 10 Stochastic runs — recruitment index.



The variation in recruitment and natural mortality of immature capelin are by far the most dominating sources of uncertainty. Thus, the future work of constructing models for the CAPSEX processes which are not modeled should focus on these two processes. An obvious starting point would be to look for environmental variables that could explain some of the variation in recruitment and connect natural mortality also on immature capelin to the cod stock.

FUTURE WORK:

1: —IMPLEMENTING THE MODEL INTO MANAGEMENT OF CAPELIN.

In order to utilize the CAPSEX model for management of capelin, one should use long time simulations to find operational management decision rules, for instance if there is some value of the spawning stock that in the long runs yields the largest catch. Even if there is rather large uncertainty in the model such rules may be found. The line of work might be:

1. Find an optimal management criterion for a fixed series of random events.
2. Repeat for a large number of distinct series of events to find the precision of the management criterion.

Also, one might try to make the management decision rule adaptive. For instance, it may well prove more effective to allow a different quantity to spawn in cases of a rich year class of herring coming up than when the sea is more or less empty of herring.

2: —IMPROVEMENTS OF THE MODEL.

The present paper presents a minimum model. Future improvements might be:

1. Working out a better stock-recruitment relationship. (See page —153—).
2. The natural mortality on immature capelin should be modeled, with one component due to the cod stock and one residual component.
3. The growth should, if possible, be modeled by seeking relations between growth, temperature and capelin abundance. In the CAPSEX software there is built in a possibility for relating growth to observed plankton abundance.

4. It should be explored whether the overlap variable could be related to temperature or trends in temperature.
5. Before the results from the model are taken into use for management, extensive sensitivity analysis should be done, including:
 - a. Temperature.
 - b. Development of the cod stock (M and F values, individual growth).
 - c. Maturation parameters.

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EFFECT OF CANNIBALISM ON RECRUITMENT TO THE NORTH—EAST ARCTIC COD STOCK

by

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ABSTRACT

Consumption by 1-9 year old cod of their own young at age 0+-3 was estimated from observations on feeding under natural conditions in 1984-1989. Cod first demonstrates cannibalism at the age of 1 year but the oldest age at which mortality due to cannibalism takes place is only 3 years. With this in view the natural mortality caused by factors other than cannibalism was estimated for ages 4-15 and it was extrapolated to younger ages down to 0+. The natural mortality due to cannibalism was estimated for ages 0+ - 3 using a singlespecies VPA accounting for cannibalism. The number of young cod consumed by adults is equivalent to the average in abundance year class at age 3 and exceeds the number of cod caught during the year by 1.4 - 3.3 times. The paper attempts at optimizing cod fishery with due regard for cannibalism. A biological criterion, namely the spawning stock biomass, which can provide a successful reproduction was used to contribute to optimization of the fishery.

INTRODUCTION

The ecological conditions in early 1980s were favourable for survival of the North—East Arctic cod at early stages of development. The 1982 and 1984 year-classes were characterized by medium abundance and the 1983 generation was strong (Anon.,1989). After a continuous and an unprecedented decline in the commercial stock biomass observed during nine years a possibility appeared for its recovery in the second half of the 1980s. The improvement of the stock which was observed since 1984 was expected to continue till 1990. However, it proved to be insignificant and lasted for three years only. During the mid-1980s a deterioration of trophic conditions in the Barents and Norwegian Seas was observed. The abundance of capelin which is the major food item of cod dropped dramatically to cause an increase in the proportion of crustaceans in cod diet in 1985 - 1986, and to extremely low growth rates of cod of the age 3-7 years as well as to low fat content and condition factor, and, finally, to aggravated cannibalism. Fishery for a depleted stock is usually limited by reducing catch and fishing effort but under conditions of growing cannibalism such regulatory measures would be of no efficiency. The reduction of exploitation rate results in an increase in the cod stock abundance, i.e.the number of cannibals increases accordingly to cause a decrease in recruitment, which prevents stabilization and growth of the commercial North—East Arctic cod stock abundance.

The paper attempts at estimating the number of the young fish consumed by adults in 1984-1989 and at optimizing the exploitation rate with cannibalism taken into account.

MATERIAL AND METHODS

The problem was resolved in two steps. First the main parameters of cod population such as natural, cannibalism-caused and fishing mortalities, abundance and biomass were estimated and age-distributed.

At this stage all the calculations were based on the 1984-1989 data on average weight of 1 fish and the total number of cod caught at the age of 0+ —15 years as well as on young cod (0+ — 3+) consumed during the year by 1 individual of different age. The data were collected during numerous cruises conducted by PINRO and IMR and borrowed from material of the ICES Working Groups.

The rate of predation of adult cod on their own youngs' is estimated from the quantitative feeding analyses of 30 thousand individuals of different age. Data from processing of samples obtained during the PINRO research cruises in 1986-1989 were lumped together with the IMR data for 1984-1989.

The paper considers two components of cod natural mortality and their variations with age. One of them (M2) is assumed to be caused by cannibalism and the other (M1) by a combined effect of all other intra- and interspecific relationships and abiotic factors.

Observations on feeding of 0+-9 year olds under natural conditions show that cod becomes a cannibal at the age of 1 but the oldest age at which mortality due to cannibalism was recorded appeared to be 3 years. In view of this the second component (M1) only was estimated for ages 4-15 and extrapolated to younger ages down to 0+.

Variations in M1 with age is shown in a convex down function

$$M1(t) = A(-t - (\tau_e - \tau_s)\ln(\tau_e - t)) + B \quad (1)$$

where the minimum is attained at the average age of mature fish ($\tau_s = 7$). The maximal longevity (τ_e) which is theoretically possible under the existing ecological conditions is assumed to be equal to 30 years.

The relationship (1) was derived from the following differential equation :

$$\frac{d(M1)}{dt} = -A \frac{(\tau_s - t)}{(\tau_e - t)} \quad (2)$$

which is adopted *a priori* and shows that the variation rate of the natural mortality M1 is directly proportional to the $\frac{(\tau_s - t)}{(\tau_e - t)}$ ratio. It decreases after the age of 4 years to become zero at τ_s and increases thereafter.

The parameters A and B in (1) were estimated by the method developed by Tretyak (1984). Mortality of fish at age τ due to fishing and cannibalism was described by the following function:

$$C_\tau + D_\tau = N_\tau \frac{F_\tau + M2_\tau}{Z_\tau} (1 - e^{-Z_\tau})$$

where :

$$Z_\tau = M1_\tau + M2_\tau + F_\tau \quad (3)$$

C_τ is catch

D_τ is number of young fish consumed by adults

F_τ and $M2_\tau$ were estimated from the following relationship:

$$\frac{C_{\tau+1} + D_{\tau+1}}{C_\tau + D_\tau} = e^{-Z_\tau} \times \frac{F_{\tau+1} + M2_{\tau+1}}{F_\tau + M2_\tau} \times \frac{Z_\tau}{Z_{\tau+1}} \times \frac{1 - e^{-Z_{\tau+1}}}{1 - e^{-Z_\tau}} \quad (4)$$

where $Z_\tau = M1_\tau + M2_\tau + F_\tau$

which in the absence of cannibalism, i.e. at $D_\tau = D_{\tau+1}$ and $M2_\tau = M2_{\tau+1} = 0$ represents the main relationship in a single-species VPA (Cushing, 1979).

The initial (N_τ) and mean (\bar{N}_τ) abundance of 4, 5, . . . 15 year old fish were estimated on the basis of a single-species VPA because for these age groups D_τ and $M2_\tau$ are zero. The number of 3-year old fish dying from cannibalism was estimated from the formula:

$$D_a = \frac{1}{1000W_a} \sum_{b=a+1}^{\tau_a} R_b \sigma_{ab} \beta_b \bar{N}_b M_{ba} \quad (5)$$

where:

D_a is consumption by predatory cod of prey at age a (thousand individuals)

R_b is average weight of stomach content of cod at age b , g

σ_{ab} is share of a prey of age a in cod diet

β_b is daily portion of food evacuated from stomach of cod at age b

\bar{N}_b is average quarterly abundance of cod at age b , 1000 individuals

n_{ba} is number of days in a quarter during which a cod at age b feeds on a prey at age a

W_a is average quarterly weight of a prey at age kg

The equation (4) was solved to determine $F_3 + M2_3$. Using these coefficients and D_a from equation 3 the initial and average abundance of fish at this age was determined. The coefficients F_τ and $M2_\tau$ were calculated as $F_\tau = \frac{C_\tau}{N_\tau}$ and $M2_\tau = \frac{D_\tau}{N_\tau}$. The abundance of younger age groups and their mortality due to cannibalism were estimated applying the same procedure for the age of $\tau = a-1, a-2, \dots (0+)$. Estimates of digestion rate in cod at age b were borrowed from Mehl (1986).

During the second stage the optimum exploitation pattern of commercial stock was established and optimum abundance, biomass and catch levels were determined. The biomass of mature fish was used as a biological criterion for fishery optimization.

The exploitation level in the year considered was assumed to be optimal if during T subsequent years ($T=4$) the average biomass of mature fish corresponded to the annual optimal spawning stock biomass which is required to provide successful reproduction. This value was assumed to be constant and equal to 300 thousand tonnes in 1984-1989, which is lower than the one required to guarantee abundant year class under moderate conditions of cod survival at early stages of ontogeny and higher than the critical level, a decrease of which results in a long-term decline in abundance (Serebryakov et al., 1984). The optimum exploitation rate for each year considered was obtained as a solution of the following equation at F_G^{opt} :

$$\sum_{j=G}^{G+T-1} \sum_{\tau=\tau} \frac{N_{\tau j} W_\tau S_\tau}{M1_\tau + M2_\tau + F_G^{opt} \frac{F_\tau}{F_\Phi}} \left(1 - e^{\left(-M1_\tau - M2_\tau - F_G^{opt} \frac{F_\tau}{F_\Phi} \right)} \right) - T P_S^{opt} = 0$$

where :

$N_{\tau j}$ is number of cod of age τ in year j

W_τ is weight at age τ

S_τ is maturity ogive

$\frac{F_\tau}{F_\Phi}$ is fishing pattern

P_S^{opt} is optimal spawning biomass

(6)

It forms the age composition of cod cannibals which along with other factors determines the abundance of generations at ages (0+)-3 years. Cannibalism—caused mortality in each age group was estimated from (5). Natural mortality due to cannibalism was obtained from:

$$D_\tau = N_\tau \frac{M2_\tau}{Z_\tau} \left(1 - e^{(-Z_\tau)} \right) \quad (7)$$

Age composition of a population ($N_{\tau j}$) during the first year of fishery optimization ($j=1$) and recruitment during the subsequent years was determined from the modified VPA. Efficiency of optimization was determined by comparing actual and optimal catches during the period considered.

RESULTS AND DISCUSSION

The cannibalism-caused natural mortality is age- and fishery-dependent (Table 2). As a rule it decreases by one order of magnitude during the three first years of the fish

life. As compared to M1 which shows a 2-time decrease approximately in the period from (0+) to 6-7 years M2 is always higher at the age of (0+). However, different ratio between the coefficients has been recorded since the age of 2 years, namely $M2 < M1$. Fishing mortality in cod at the age of 3 years is below M1 but higher than M2 in most cases and it exceeds M1 by many times in 4-year old and older cod.

The number of young cod consumed by adults in 1985-1988 is equivalent to the average in abundance year-class at the age of 3 years and it exceeds the total number of cod caught by 1.4- 3.3 times. The major cause of mortality in young (0+) fish was cannibalism and it diminished with age though remained high in one-year olds (Table 3). Cod mortality at the age of 1-3 years had an upward trend in 1984-1988. The increase in the rate of cannibalism was apparently caused by a sharp decrease of capelin and shrimp portion in cod diet on the one hand and an increase in the adult fish abundance on the other.

The actual exploitation of the cod stock was not optimum in 1984-1989 against the biological criterion considered, namely the mature fish biomass. It was characterized by a high exploitation rate which was far beyond the optimal one (Table 4). The total catch exceeded the optimum level by more than 300 thousand tonnes during this period, which resulted in a decrease in the average annual biomass of cod stock in 1987 and a decline in the total catch in 1988. At the optimum exploitation rate the stock would have continued to grow up to 1988 and the biomass would have reached its maximum of 2,110 thousand tonnes, which is by 2.4 times higher than the actual maximum recorded in 1986. The catch would have been increasing till 1989 inclusive to exceed 700 thousand tonnes in 1989-1990.

Under conditions of optimum exploitation rate the stock biomass varies due to increase in the abundance of 4-15 year-olds, which leads to higher rates of cannibalism-caused mortality in 1-3 year olds (Table 5) whereas a decrease in the abundance of cannibals of these age groups results in an increase in the average abundance of cod at the age of (0+).

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Table 1 Average weight (W, g) and proportion (P) of young cod at the age of 0+, 1, 2 and 3 years in the daily diet of adult cod of different age in 1984-1990

| Age of cannibals, years | Average annual daily diet of cod, g | Age of preys | | | | | | | |
|-------------------------|-------------------------------------|--------------|--------|--------|--------|--------|--------|--------|--------|
| | | 0+ | | 1 | | 2 | | 3 | |
| | | W | P | W | P | W | P | W | P |
| 0+ | 0.37 | | | | | | | | |
| 1 | 1.64 | 0.0013 | 0.0008 | | | | | | |
| 2 | 4.39 | 0.0369 | 0.0084 | | | | | | |
| 3 | 10.73 | 0.0429 | 0.0040 | 0.0215 | 0.0020 | | | | |
| 4 | 18.64 | 0.0485 | 0.0026 | 0.0298 | 0.0016 | 0.0056 | 0.0003 | | |
| 5 | 26.18 | 0.0367 | 0.0014 | 0.2513 | 0.0096 | 0.0471 | 0.0018 | | |
| 6 | 41.01 | 0.0328 | 0.0008 | 0.4470 | 0.0109 | 0.5823 | 0.0142 | 0.3035 | 0.0074 |
| 7 | 52.00 | 0.0312 | 0.0006 | 1.8564 | 0.0357 | 1.2168 | 0.0234 | 0.7124 | 0.0137 |
| 8 | 94.84 | | | 0.3794 | 0.0040 | 4.7230 | 0.0498 | 4.6851 | 0.0494 |
| 9 | 138.57 | | | | | 5.7784 | 0.0417 | | |

Table 2 Fishing mortality (F) and natural mortality due to cannibalism (M2) and other causes (M1) in cod of different age in 1984-1989

| Age, years | 1984 | | 1985 | | 1986 | | 1987 | | 1988 | | 1989 | |
|---------------|-------|-------------|-------------|-------------|-------------|-------------|-------|------|------|------|------|--|
| | M1 | M2 F | M2 F | M2 F | M2 F | M2 F | M2 F | M2 F | M2 F | M2 F | | |
| 0+ | 0.119 | 0.275 | 0.476 | 0.511 | 0.309 | 0.300 | 0.110 | | | | | |
| 1 | 0.104 | 0.046 | 0.112 | 0.254 | 0.384 | 0.350 | 0.360 | | | | | |
| 2 | 0.092 | 0.037 | 0.014 | 0.040 | 0.069 | 0.100 | | | | | | |
| 3 | 0.081 | 0.017 0.028 | 0.012 0.062 | 0.008 0.027 | 0.028 0.016 | 0.044 0.036 | 0.033 | | | | | |
| 4 | 0.072 | 0.156 | 0.183 | 0.223 | 0.158 | 0.154 | 0.139 | | | | | |
| 5 | 0.066 | 0.350 | 0.426 | 0.548 | 0.647 | 0.419 | 0.391 | | | | | |
| 6 | 0.063 | 0.651 | 0.657 | 0.861 | 1.126 | 0.769 | 0.728 | | | | | |
| 7 | 0.063 | 1.150 | 1.054 | 1.042 | 1.324 | 1.196 | 1.123 | | | | | |
| 8 | 0.066 | 1.298 | 1.064 | 1.117 | 1.235 | 1.322 | 1.245 | | | | | |
| 9 | 0.073 | 1.290 | 1.054 | 0.697 | 0.932 | 1.137 | 1.058 | | | | | |
| 10 | 0.083 | 0.940 | 0.694 | 0.901 | 0.790 | 0.998 | 0.953 | | | | | |
| 11 | 0.098 | 0.636 | 0.455 | 0.634 | 0.594 | 0.732 | 0.690 | | | | | |
| 12 | 0.118 | 0.521 | 0.307 | 0.666 | 0.572 | 0.698 | 0.635 | | | | | |
| 13 | 0.142 | 0.712 | 0.301 | 0.224 | 0.376 | 0.486 | 0.454 | | | | | |
| 14 | 0.173 | 0.101 | 2.958 | 0.299 | 0.239 | 0.640 | 0.631 | | | | | |
| 15 | 0.210 | 0.670 | 0.520 | 0.700 | 0.500 | 0.653 | 0.585 | | | | | |

Table 3 Cannibalism-caused mortality in cod at the age of 0+-3 years in 1984-1989 (million individuals).

| Age years | Year of fishery | | | | | |
|--------------|-----------------|------|------|------|------|------|
| | 1984 | 1985 | 1986 | 1987 | 1988 | 1989 |
| 0+ | 184 | 339 | 344 | 255 | 233 | 73 |
| 1 | 43 | 56 | 111 | 147 | 186 | 192 |
| 2 | 13 | 12 | 17 | 23 | 27 | |
| 3 | 4 | 4 | 6 | 10 | 13 | |
| Total | 244 | 441 | 478 | 435 | 459 | 265 |

Table 4 Actual and optimal average biomass of cod commercial stock, exploitation rate and catch

| Year of fishery | Biomass (thousand tonnes) | | Exploitation rate | | Catch, (thousand tonnes) | |
|-----------------|---------------------------|---------|-------------------|---------|--------------------------|---------|
| | actual | optimal | actual | optimal | actual | optimal |
| 1984 | 564 | 581 | 0.654 | 0.087 | 278 | 49 |
| 1985 | 644 | 908 | 0.749 | 0.241 | 308 | 184 |
| 1986 | 865 | 1441 | 0.611 | 0.276 | 430 | 268 |
| 1987 | 786 | 1876 | 0.655 | 0.377 | 523 | 479 |
| 1988 | 664 | 2110 | 0.711 | 0.414 | 435 | 677 |
| 1989 | 680 | 2000 | 0.641 | 0.408 | 333 | 759 |

Table 5 Natural mortality (M2) and abundance of young cod consumed (D, million individuals) by adults at the optimal exploitation rate.

| Age, years | Year of fishery | | | | | | | | | |
|------------|-----------------|-------|------|-------|------|-------|------|-------|------|-------|
| | 1984 | | 1985 | | 1986 | | 1987 | | 1988 | |
| | D | M2 | D | M2 | D | M2 | D | M2 | D | M2 |
| 0+ | 175 | 0.255 | 312 | 0.429 | 298 | 0.427 | 273 | 0.335 | 230 | 0.295 |
| 1 | 63 | 0.068 | 83 | 0.168 | 121 | 0.267 | 148 | 0.350 | 224 | 0.452 |
| 2 | 24 | 0.068 | 31 | 0.039 | 35 | 0.089 | 45 | 0.135 | 57 | 0.197 |
| 3 | 7 | 0.028 | 9 | 0.030 | 10 | 0.014 | 11 | 0.034 | 13 | 0.047 |
| Total | 269 | | 435 | | 464 | | 477 | | 524 | |

IMPACT OF COD ON DYNAMICS OF BIOMASS OF Pandalus borealis IN THE BARENTS SEA

by

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ABSTRACT

Changes in biomass of deep-water shrimp Pandalus borealis have mainly been caused by varying predation from cod and lack of proper fishery management. Since 1984-1985 when the fishing mortality rate (F) reached 0.4 and the predation-caused natural mortality rate (M2) was 0.76-0.86, the total biomass of shrimp decreased by more than 50% during 3-4 years. The fishing mortality dropped by 4-5 times in the older age group of the commercial stock and increased in the younger age one. The juveniscent stock can be regarded as a consequence of overfishing in view of which measures are to be taken to reduce the exploitation rate of the deep-water shrimp in the Barents Sea. Because M2 is high the total allowable catch (TAC) of shrimp should be established using the multispecies virtual population analysis (MSVPA) as modified by Pope with account taken of cod-shrimp trophic relationships.

INTRODUCTION.

The deep-water shrimp Pandalus borealis is the only species in the Barents Sea that is subject to high exploitation which has no international regulation measures in force. The total catches of the shrimp in the Barents Sea and adjacent waters (ICES Area I, Subareas IIa and IIb) have been rather high. During the period from 1976 to 1984 the annual yield increased from 8 to 128 thousand tonnes which were taken mainly by Russia and Norway (Table 1). Since the shrimp is an important food item for cod (Ponomarenko and Yaragina, 1984) the shrimp fishery should be regulated with account taken of cod predation.

MATERIAL AND METHODS.

Data on the catches of Pandalus borealis in the ICES Area I, Subareas IIa and IIb were derived from the ICES Statistical Bulletin for 1976-1990.

The average catch per effort was estimated based on data from the annual and monthly 1983-1990 reports from the Russian stern trawlers with the main engine 1000 h.p. in capacity. Data on the frequency of occurrence of the shrimp in cod stomachs were obtained by the PINRO scientists on the basis of analysis of stomach contents of more than 430 thousand individuals in 1977-1990.

The quarterly consumption of the shrimp by cod was calculated using data on the stomach contents of cod caught in 1984-1990 from the joint PINRO—IMR stomach content data base. To estimate the VPA-derived population parameters data on the age composition are required, which presents a problem due to the absence of age-registering structures in shrimps. Additional difficulties are created due to the fact that the populations of P. borealis occurring in the open parts of the Barents Sea consists of individuals recruited from both inside and outside this area and it is not actually possible to distinguish between age classes nor is it feasible with the help of the methods used for the fjord populations (Skuladottir, 1979). Considering the points mentioned above, the entire set of data was divided into 4 age groups on the basis of the analysis of size-sex composition of the shrimp population occurring off the Kola Peninsula coast (Fig.1).

This assumption seems valid since the Barents Sea shrimp comprises a single stock which consists of several populations (Berenbojm, 1982; Berenbojm and Lysy, 1987). Taking into account the known differences in the growth rates of the shrimps from the northern and southern parts of the range (Allen, 1959) the suggested parameters of size-age groups appeared to be comparable to the size at age data on the deepwater shrimp from the Skagerrak (Anon., 1990). With this in mind an assumption was made that the carapace length (Rasmussen, 1953) of below 17, 17-21, 21-23 and exceeding 23 mm corresponded to the age of 2 (and under), 3, 4 and 5 (and over) years, respectively.

The terminal fishing mortality rates were determined so that the residual variance for the regression equation between the estimated shrimp biomass and the stock size as derived from the results of trawl surveys was minimized. The accuracy of the trawl survey data is of special importance in the VPA-applied studies. The trawl survey-based estimates of the shrimp biomass in the Barents Sea are regarded as reliable since they are in good agreement with the average catches per unit effort of the similar Russian trawlers as well as with the frequency of occurrence of the shrimp

in cod stomachs which is a clear indicator of the shrimp abundance (Berenbojm et al., 1986). The MSVPA-derived estimates imply that the terminal rates of fishing and natural mortalities are known. The rate of the total natural mortality consisted of two components one of which (M2) was predation-related and the other (M1) was caused by factors other than predation. The total natural mortality rate was determined using the method developed by Tretyak (1984). Pope's model was applied to the M2 estimates. The food evacuation rates were borrowed from Mehl (1986) with allowance made for the temperature regime in the Barents Sea.

RESULTS AND DISCUSSION

The analysis of catch statistics has shown that the total shrimp yield in the Barents Sea showed significant fluctuations in 1976-1990 (Table 1). A rapid increase in catches of P.borealis was observed in the early 80s which was followed by a just as rapid drop in 1985-1987 and a rise during the latest years. The comparison of the catch dynamics in the ICES Area I, Subareas IIa and IIb with that in the other two areas where the international fishery is conducted in the Atlantic part of the shrimp range has revealed significant differences. In contrast to the fishery for P.borealis in the Barents Sea the fishery in the NAFO Areas 0 and 1 and in the Danish Strait was characterized by insignificant fluctuations and a stable upward trend in the annual catches. Worth noting is that TAC has been established for the shrimp fishery in the Davis and Danish Straits. In the Barents Sea and the Spitsbergen Archipelago area the total biomass of the shrimp as estimated on the basis of the results of the trawl surveys correlated well ($r=0.80$) with the total catch and evidences were revealed of a direct biomass-cpue relationship ($R = 0.77$; $n = 10$). Changes in the average cpue throughout the year were confirmed by the fluctuations in the average catches for the respective months of 1980-1990.

The above-described allows for supposing that the Barents Sea shrimp stock was overexploited in mid-80s and an adverse effect of the fishery was indicated by the fishing mortality rates in the 80s. The F rates in 1984-1985, and in 1986-1987 in particular (when the stock size declined dramatically) were significantly higher than the respective values during the other years (Table 2).

It is important to mention that the maximum total catch of the shrimp in 1984 was retained in 1985 when a rapid decline in the stock size was already observed (Fig. 2). Besides, the changes observed in the exploitation rate pattern of different age groups were typical of overfishing. This was the case during the 2 years following the high exploitation rate in 1984-1985 when F rate decreased by 4-5 times in the old age group and increased by more than an order in the young one (Table 2), which can be identified as fishery-caused juveniscent trend in the population structure.

The second reason for fluctuations in biomass and catches of P.borealis in the Barents Sea lied in changes in the cod predation rate due to significant variations in cod abundance. Based on the analysis of data from a period of more than 30 years a close ($r = -0.76$) inverse relationship was found between the commercial cod stock size and the frequency of occurrence of shrimp in the cod stomachs (Ponomarenko and Yaragina, 1984). In the 30-50s the shrimp abundance in the cod stomachs was low (5-7% in terms of frequency of occurrence and 1% in terms of weight). The role in the cod diet of the shrimp increased considerably (Fig.3) in the late 70s when the latter was recorded in

the stomachs of one third of the fish. The highest (44-51%) frequency of the shrimp occurrence in the cod stomachs was recorded in 1981-1984 when the shrimp biomass was at its maximum. During these years the shrimp constituted about 20% (in terms of weight) of the cod diet. The intimate inverse relationship between the shrimp biomass and the commercial cod stock size was confirmed by the results of the analysis of data from shrimp biomass measurements and the cod abundance in 1981-1991 (Fig. 4).

Meanwhile, it was due to the overexploitation of the shrimp stock that the close inverse relationship between the cod stock size and the frequency of occurrence of the shrimp in the cod stomachs was disturbed in 1985-1988 (Fig. 3).

Proceeding from the revealed impact of cod on the shrimp stock size the natural mortality (M2) of shrimp was estimated. Despite a comparatively low cod abundance in 1984-1987 the M2 rate of the shrimp varied from 0.74 to 1.04 (Table 3), which is somewhat higher than the total mortality rate (M) of 0.75 which is used by the Pandalus Working Group of ICES to estimate TAC of the shrimp from the Skagerrak area (Anon., 1990).

Considering all the above-described the TAC for P.borealis was established using the MSVPA as modified by Pope with allowance made for cod predation on the shrimp.

CONCLUSIONS.

The significant fluctuations in the biomass and catches of P.borealis in the Barents Sea in the 80s were found to be due to both the varying cod predation rate and the unregulated shrimp fishery.

Evidences of overexploitation of the deepwater shrimp stock were observed in the Barents Sea in 1985-1987.

Regulatory measures for the shrimp fishery are to be implemented by means of establishing the TAC and national quotas.

Due to the high predation-induced natural mortality rate of the shrimp the TAC is recommended to be established using the MSVPA as modified by Pope with account taken of prey-predator relationships between cod and shrimp.

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Table 1 Deepwater shrimp catches in the Barents Sea and adjacent waters (ICES Areas I,IIa,IIb) in 1976-1990.

| Year | Country | I | IIa | IIb | Total |
|------|---------|-------|-------|------|-------|
| 1976 | Norway | 2700 | 4450 | 350 | 7500 |
| | USSR | 2 | 166 | 380 | 548 |
| 1977 | Norway | 10500 | 3250 | 3743 | 17493 |
| 1978 | Norway | 17490 | 106 | 2687 | 20283 |
| | USSR | 18002 | 74 | 194 | 18270 |
| 1979 | Norway | 17590 | 3630 | 4215 | 25435 |
| | USSR | 8843 | 1569 | 62 | 10474 |
| | | 368 | | 22 | 390 |
| 1980 | Norway | 23824 | 5205 | 6032 | 35061 |
| | USSR | 7665 | 3554 | | 11219 |
| 1981 | Norway | 22636 | 4785 | 5221 | 32642 |
| | USSR | 6649 | 3237 | | 9886 |
| | Faroe | | 652 | | 652 |
| 1982 | Norway | 29009 | 10578 | 3926 | 43513 |
| | USSR | 12217 | 3335 | | 15552 |
| 1983 | Norway | 39726 | 23104 | 5265 | 68095 |
| | USSR | 23703 | 5351 | 51 | 29105 |
| | Denmark | | 221 | | 221 |
| 1984 | Norway | 35258 | 32268 | 9175 | 76701 |
| | USSR | 24939 | 18241 | | 43180 |
| | Faroe | | 8132 | | 8132 |
| | Denmark | | 114 | | 114 |
| 1985 | Norway | 29102 | 44919 | 8102 | 82123 |
| | USSR | 11814 | 20290 | | 32104 |
| | Faroe | | 10262 | | 10262 |
| 1986 | Norway | 12691 | 27863 | 7780 | 48334 |
| | USSR | 3131 | 7085 | | 10216 |
| | Denmark | 370 | 352 | | 722 |
| 1987 | Norway | 8850 | 17640 | 4863 | 31353 |
| | USSR | 5702 | 988 | | 6690 |
| 1988 | Norway | 14473 | 13913 | 3139 | 31525 |
| | USSR | 8118 | 4202 | | 12320 |
| 1989 | Norway | 25015 | 18853 | 3356 | 47244 |
| | USSR | 10438 | 1814 | | 12252 |
| | Faroe | 13 | 3414 | 5 | 3432 |
| 1990 | Norway | 29018 | 22165 | 1800 | 54034 |
| | USSR | 10616 | 39679 | | 20295 |
| | Faroe | 833 | 5665 | | 6498 |

Table 2 Fishing mortality rates of Pandalus borealis in the Barents Sea

| Year of fishery | Length, mm. | | | | Mean |
|-----------------|-------------|-------|-------|------|------|
| | < 17 | 17-21 | 21-23 | > 23 | |
| 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 | 0.11 | 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 |

* Preliminary data

Table 3 Natural mortality rates of Pandalus borealis due to cod predation in the Barents Sea

| Year of fishery | Length, mm. | | | | Mean |
|-----------------|-------------|-------|-------|------|------|
| | < 17 | 17-21 | 21-23 | > 23 | |
| 1980 | 0.09 | 0.33 | 0.44 | 0.95 | 0.45 |
| 1981 | 0.06 | 0.24 | 0.31 | 0.68 | 0.32 |
| 1982 | 0.10 | 0.37 | 0.49 | 1.08 | 0.51 |
| 1983 | 0.11 | 0.42 | 0.56 | 1.23 | 0.58 |
| 1984 | 0.14 | 0.55 | 0.73 | 1.62 | 0.76 |
| 1985 | 0.16 | 0.62 | 0.83 | 1.85 | 0.86 |
| 1986 | 0.20 | 0.75 | 0.99 | 2.23 | 1.04 |
| 1987 | 0.14 | 0.53 | 0.70 | 1.58 | 0.74 |
| 1988 | 0.10 | 0.40 | 0.53 | 1.16 | 0.55 |
| 1989 | 0.08 | 0.47 | 0.49 | 0.81 | 0.46 |
| 1990* | 0.06 | 0.33 | 0.41 | 0.78 | 0.39 |

* Preliminary data

Figure 1 Length-sex composition of shrimp *Pandalus borealis* population distributed off the Kola Peninsula in April — May.
 Males — not shaded,
 shrimp at transition stage — sparse shading,
 females — dense shading.

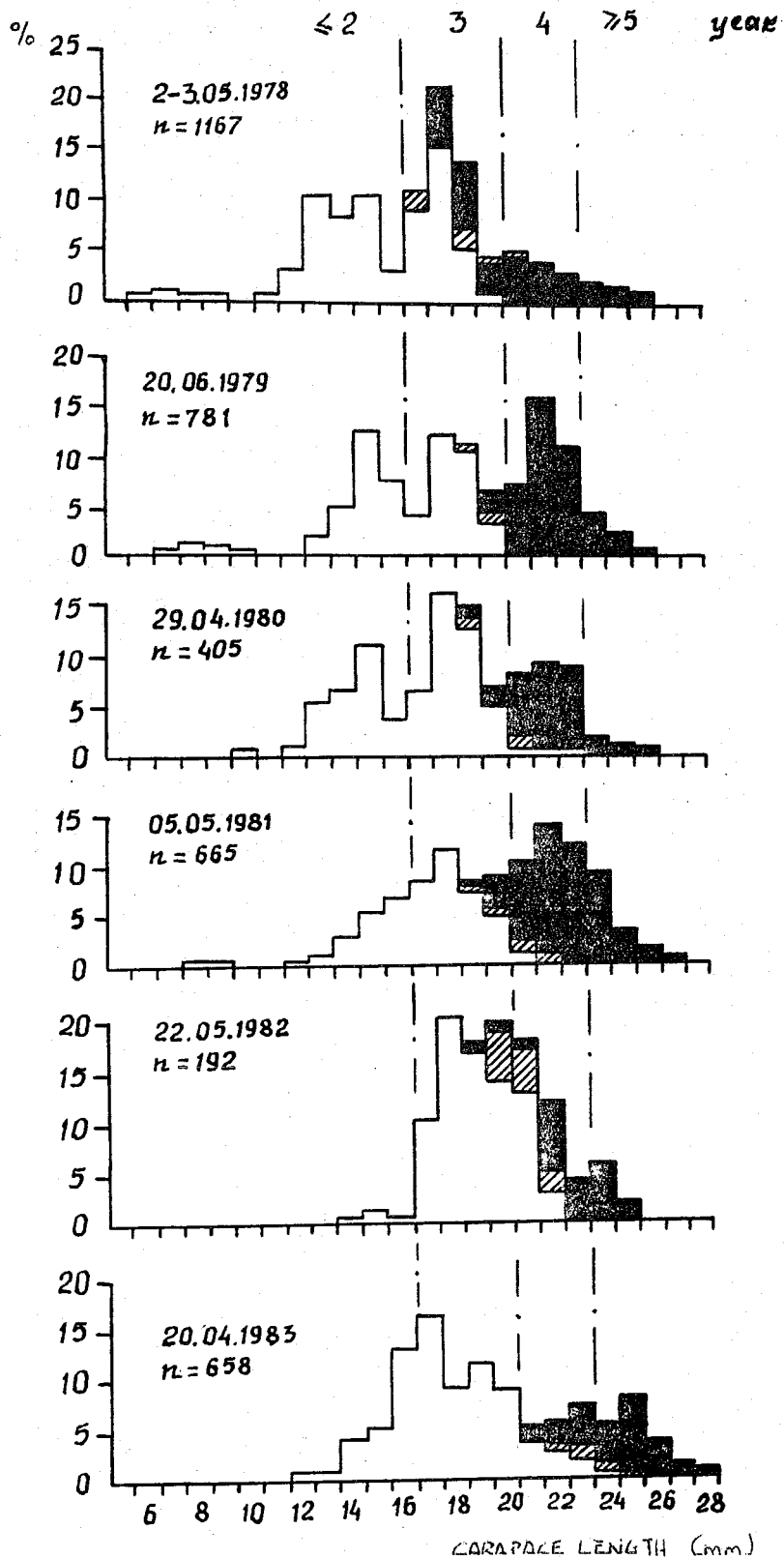


Figure 2 Deepwater shrimp biomass in the Barents Sea and Spitsbergen area (solid line), abundance of North-East Arctic cod stock from the ICES data (dash line) and total shrimp catch in subarea I, Divs. IIa, IIb (dash-dotted line)

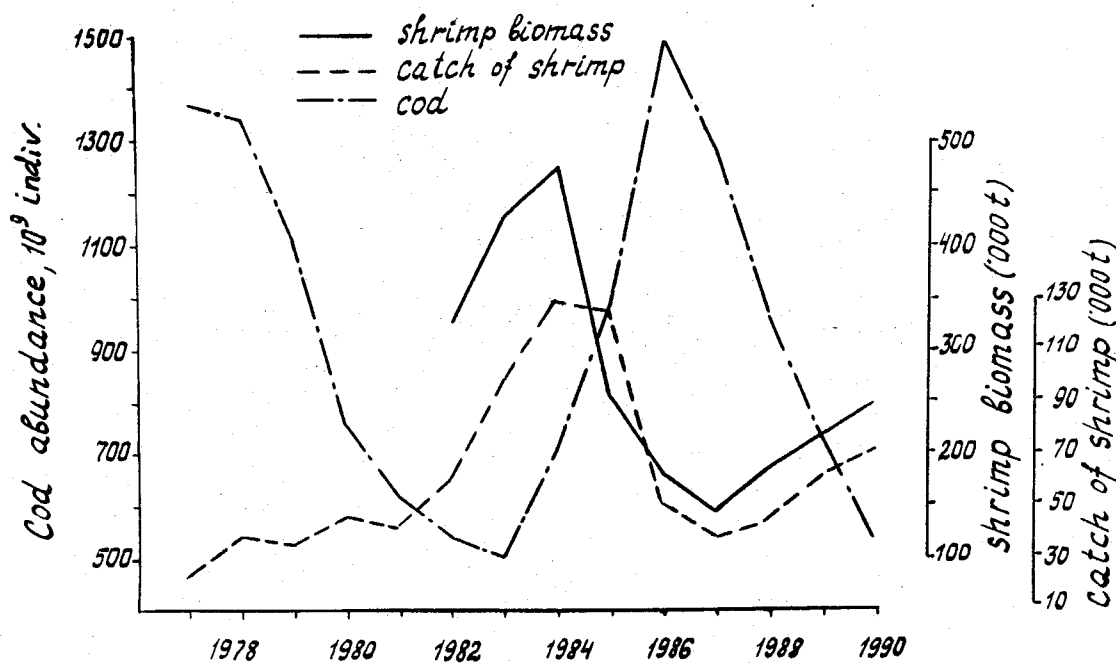


Figure 3 Dynamics of the North-East Arctic cod stock (solid line) and frequency of deepwater shrimp occurrence in cod stomachs.

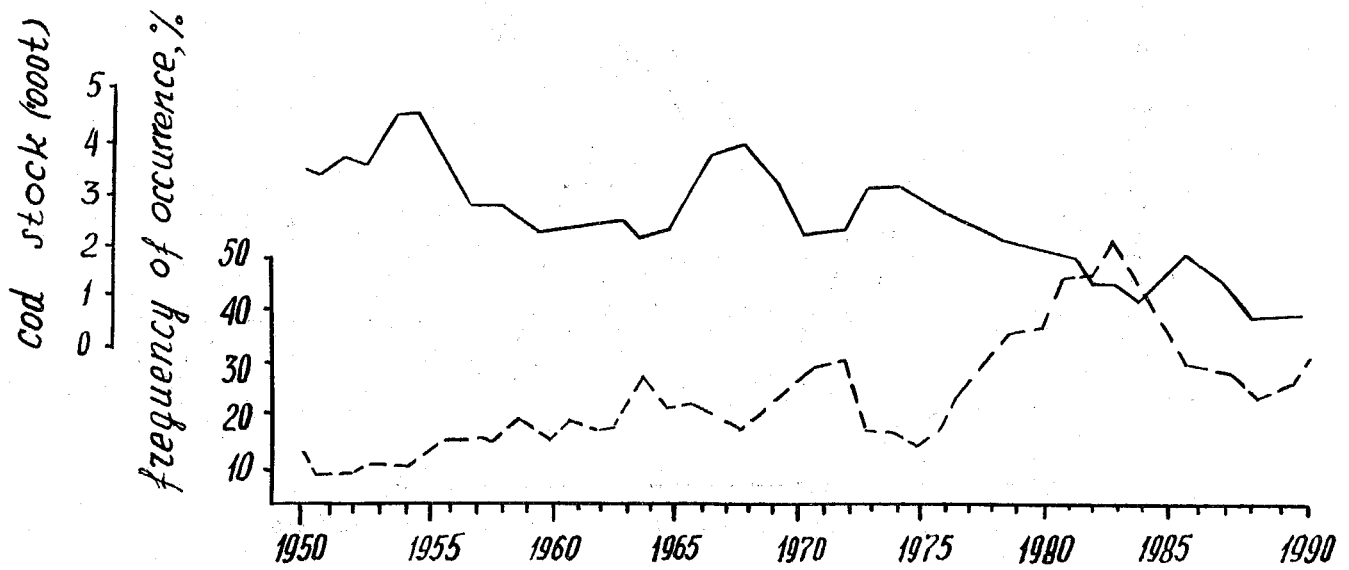
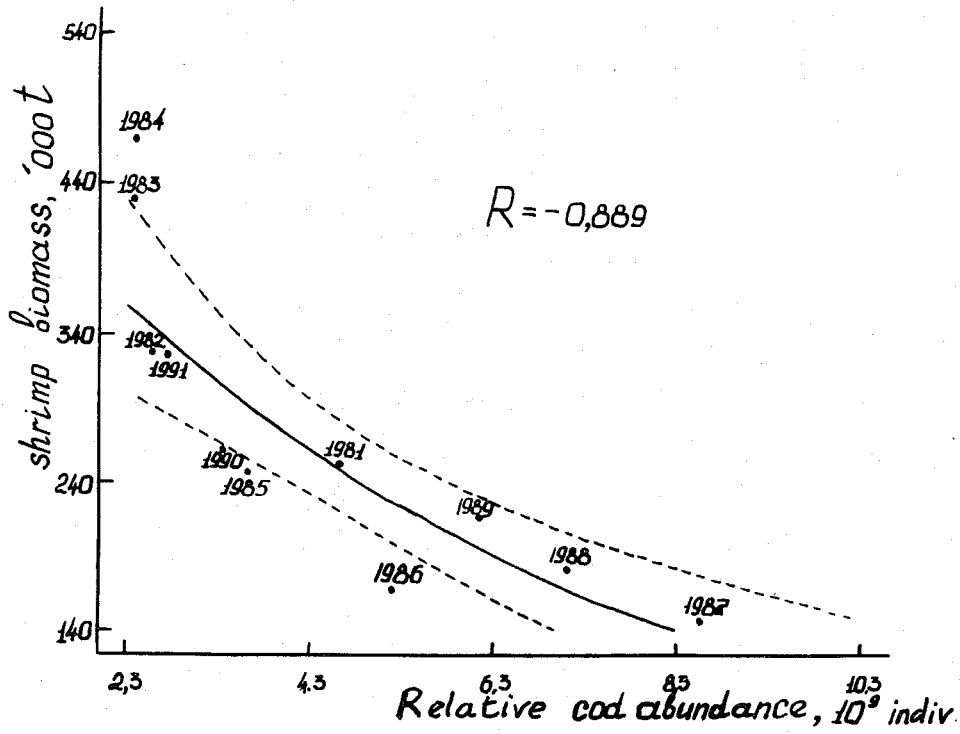


Figure 4 Trawl survey — derived biomass of the Barents Sea Pandalus borealis as the function of the relative abundance of cod at the age of 3 — 5 years (with the shift of 1 year back)





THE DAILY FEEDING DYNAMICS IN VARIOUS LENGTH GROUPS OF THE BARENTS SEA CAPELIN

by

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ABSTRACT

A total of 692 capelin stomachs collected in the Goose Bank area in August 1989 by 24 hour fishery were analyzed by 3 cm capelin length groups. The number of prey categories consumed by the Barents Sea capelin showed a tendency to increase with increasing fish length up to 12 cm. Calanus finmarchicus was the major contributor in the diet (66.4 % of total stomach weight) of length group 6–8.9 cm. Capelin in length group 9–11.9 cm had mainly fed on Calanus finmarchicus (33.5 %), Parathemisto abyssorum (14.5 %) and Thysanoessa raschii (28.0 %) while the two species Thysanoessa inermis and Thysanoessa raschii occupied 95.2% of the stomach content weight in length group 12–14.9 cm. The feeding seemed to have a peak in the evening and a minimum during the midday for all length groups. The daily ration during this period is estimated to between 1.3 and 2.2 % of fish body weight. Accordingly, these data gives between 3640 and 6160 tonnes as the daily consumption of zooplankton by the capelin stock in the Goose Bank area.

INTRODUCTION.

Capelin Mallotus villosus is one of the most important predators on zooplankton organisms in the Barents Sea and it has been shown to play a major role in the ecosystem during their feeding migration to the northern part of the Barents Sea (Panasenko and Soboleva, 1980; Panasenko and Nesterova, 1983, Hassel, 1984, 1986; Panasenko, 1989; Skjoldal and Rey, 1989). Furthermore, Hassel et al. (1991) reported that if capelin consumes 10% of its body weight per day, the zooplankton will be depleted in only 3–4 days where the capelin is heavily concentrated.

The heat content of the water masses exerts a significant influence on the feeding migration routes. During the warm years the immature part of the population is distributed in the northeastern area while in cold years the capelin stock mainly found at the western and the northwestern parts of the Barents Sea (Panasenko and Soboleva, 1980).

The development of the capelin stock during 1972–1989 was dramatic and the driving forces were stock interactions (Bogstad and Tjelmeland, 1990), operating under strong influence of physical environmental variability, particularly on the climatic scale (Skjoldal and Rey, 1989). The capelin stock development can only be understood in a multispecies context (Bogstad and Tjelmeland, 1990), and hence the consumption rate have to be estimated for a larger number of species in the ecosystem.

The objective of the present study is to determine the diel feeding pattern of various length groups, to estimate gastric evacuation rate based on field data from the observed decline in stomach fullness during part of the diel cycle and to estimate the consumption by the capelin stock in the area during the first half of August.

MATERIAL AND METHODS

The data on capelin stomach contents was obtained from the joint PINRO — IMR fish stomach content data base. Capelin stomachs were collected during the 9–11 August 1989 by bottom trawl on board a Russian vessel with one hour tows made every 4 hour at the same geographical position (70° 51' N and 44°56' E) at a depth of 106–110 m. Capelin of length 6–15 cm were selected for further analysis. Table 1 summarizes the number of stomachs by 3 cm length groups collected during the 24h fishery. Figure 1 shows the geographical position of the 24h station from which the capelin stomachs were collected.

Table 1 Number of the stomachs in each length group by time from 9/8–11/8 1989.

| Time Date length group | 9 Aug 7:00 | 12:20 | 16:00 | 20:00 | 23:20 | 10 Aug 4:00 | 8:00 | 11:45 | 16:40 | 20:00 | 24:00 | 11 Aug 4:00 | 7:20 | total |
|------------------------------|------------------|-------|-------|-------|-------|-------------------|------|-------|-------|-------|-------|-------------------|------|-------|
| 6-8.9cm | 15 | 15 | 16 | 15 | 1 | 6 | 12 | 15 | 13 | 17 | 3 | 8 | 9 | 145 |
| 9-11.9cm | 19 | 22 | 24 | 23 | 12 | 5 | 22 | 32 | 41 | 37 | 18 | 21 | 11 | 287 |
| 12-14.9cm | 1 | 22 | 21 | 24 | 17 | 22 | 6 | 15 | 28 | 22 | 22 | 19 | - | 219 |
| 15-17.9cm | - | 1 | 1 | - | 3 | 2 | - | - | 3 | 11 | 7 | 3 | - | 31 |
| total | 35 | 60 | 62 | 62 | 33 | 35 | 40 | 62 | 85 | 87 | 50 | 51 | 20 | 682 |

RESULTS AND DISCUSSION

Species composition of prey

The number of prey categories varied between the different capelin size groups. 18 different prey categories have been recorded in length group 6–8.9 cm and 22 in 9–11.9 cm while only 13 prey categories are found in the larger size group 12–14.9 cm. Three preys were considered as important component of the capelin diet, Calanus spp., Parathemisto and Thysanoessa. Calanus finmarchicus was the major contributor in the diet (66.4 % of total stomach content weight) of length group 6–8.9 cm. Capelin in size group 9–11.9 cm had mainly fed on Calanus finmarchicus (33.5 %), Parathemisto abyssorum (14.5 %) and Thysanoessa raschii (28.0 %) while the two species Thysanoessa inermis and Thysannoessa raschii occupied 95.2 % of the stomach weight in length group 12–14.9 cm. (Tables 5, 6 and 7 in Appendix).

Prey size

Prey size distribution based on stomach contents analysis of three length groups seems to change with length of the fish. Prey in size less than one cm consist of 100% of prey size distribution in the stomachs of fish less than 9 cm, while in length groups 9–11.9 cm and 12–14.9 cm, the same prey size contributed 82% and 58%, respectively. The possible explanation of consuming smaller prey items in length groups 6–8.9 cm: 1) fish in this size group are unable to capture the larger size of the same prey due to their swimming speed. 2) the larger size of the same prey are scarce. 3) prey size is a function of the predator mouth size. When capelin in total length reached 9–11.9 cm, food preference shifted only slightly to the larger preys (Table 6). This shift did not appear to be a response to changes in prey availability since the abundance of the same prey taxa and size in stomachs increases in the larger size group (12–14.9 cm). Other studies on diet compositions of the Barents Sea capelin have indicated that selection of prey species and prey size seems to change with the length of the fish (Lund, 1981; Hassel, 1984; Panasenko, 1984).

Diet analysis shows a critical length group between 12–14.9 cm within which a slight reduction in the number of preys consumed was recorded while prey size increased. The switch in feeding strategy of capelin in this length group was most likely related to the transition stage between mature and immature fish since maturation of individual fish is known to be length dependent, rather than age dependent in the Barents Sea capelin (Forberg and Tjelmeland, 1984) and maturity starts when capelin reaches 12 cm, especially for females (Gjøsæter pers. comm.).

Diet overlap between capelin and polar cod

Polar cod and capelin have a similar annual rhythm of feeding and in the period of maximum feeding (July, August) they are feeding in the same area (Panasenko and Soboleva, 1980). There was a high similarity of the diet (much Euphausiids) and possibly intensive competition between polar cod and capelin in this area (Goose Bank) (Panasenko and Soboleva, 1980). Our data on diet compositions of polar cod sampled from the same area (Ajjad and Gjøsæter, 1990) revealed that in the length group 8–10.9

cm, Copepoda and Euphausiidae were the major dietary components (36.7 % and 47.8 % of the total stomach content weight). This data clearly demonstrated that the polar cod in this length interval are sharing the same prey taxa (Copepoda) with capelin 6–8.9 cm, while with capelin in length 9–11.9 cm and 12–14.9 cm (Tables 5, 6 and 7 in Appendix), the two species are preying upon Copepoda and Euphausiidae. Another possible interaction between capelin and polar cod is predation on polar cod larvae by capelin, especially the young year classes (Skjoldal and Rey, 1989). No single incidence confirms this interaction during the present investigation. The only fish species recorded in capelin stomachs (length group 12–14.9 cm) was from the genus Lumpenus. A key question in trophic interrelation between capelin and polar cod is to what extent the food competition is more important between the two species than a competition between different length groups of the same species.

Length-weight relationship

Log-transformation of length —weight relationship of the Barents Sea capelin showed increase in the slope of the regression line for fish below 12 cm (Fig. 2). This relationship has the following form for fish between 6–11.9 cm and 12–17.9 cm, respectively:

$$W = 0.00092L^{3.6928}$$

F_{1,277} = 4650, P > F = .0001; S.E slope = .0541

$$W = 0.00371L^{3.1604}$$

F_{1,250}=853.61, P > F= .0001: S.E.slope = .1081

Commonly the growth stanzas in fish are separated by a change in a body form which shows up in the length-weight relationship (Ricker,1975). The two growth stanzas may reflect an increase in a gross conversion efficiency in a capelin smaller size compared to the larger fish and indicate that the proportion of the total food energy available for growth is slightly higher in smaller fish. Niimi (1981) found that the gross conversion efficiency decrease with increasing fish weight because the body surface area of the fish increases as the body weight raised to 0.6–0.7.

Biphasic growth patterns can also arise, if the sample were biased towards the number of females within the length interval since the capelin growth is higher in males than in females (Gjøsæter, 1984). The length —weight relationship was analyzed for each sex for capelin above and below 12 cm. Table 2 summarizes the relationship for females which indicate that the slope of the relationship in the smaller fish is substantially higher than in the larger fish (Fig. 3):

Table 2 Length — weight relationship for female capelin.

| length groups | n | slope | S.E slope | intercept | P>F |
|---------------|-----|---------|-----------|-----------|-------|
| 6-11.9 cm | 232 | 3.6708 | 0.05869 | 0.000963 | .0001 |
| 12-17.9 cm | 188 | 3.15867 | 0.12429 | 0.00370 | .0001 |

Diel feeding pattern

Maximum stomach filling occurred between 16:00 and 23:20 approximately for all length groups (Table 4, Fig. 5A and 5B). The daily level of the food intake during that period was higher than that observed during the first half of the day, and the feeding was at minimum during the midday (12:00). The evening peak in feeding during August has also been reported by Panasenko (1984, 1989), and the reason is thought to be due to the prey behavior. According to Panasenko (1984), Copepoda, Euphausiacea and Hyperiididae in that period of the year formed dense concentration at the deeper layer and their vertical migration were poorly pronounced. Two daily peaks of feeding activity from May to August was reported for capelin in the estuary and Western Gulf of St. Lawrence (Vesin et. al., 1981). In the southern part of the Bering Sea capelin has a single peak of feeding activity during the afternoon hours during winter (Naumenko, 1986).

Gastric evacuation rate

The amount of food in the stomach at any time (t) of a nonfeeding period follows an exponential decay function (Elliot and Persson, 1978):

$$S_t = S_0 e^{-rt}$$

The equation for S_t can be used to estimate r if it assumed that capelin has a nonfeeding period. The period chosen was from 9 August 23:20 to 10 August 11:45. The best exponential curve was fitted with a non linear regression (Fig. 4), all regression lines were forced through $t=0$, $S_t = S_0$. Estimated regression parameters were run by SAS using non linear least square regression of the type $y = B_0 e^{-B_1 x}$. Table 3 summarizes the regression for capelin length group 6–17.9 cm.

Table 3 Gastric evacuation rate parameters for capelin

| Source | DF | Sum of Squares | Mean Square |
|-------------------|----------|----------------|-------------------|
| Regression | 2 | 2.4930 | 1.2465 |
| Residual | 2 | .0072 | .0036 |
| Uncorrected total | 4 | 2.5002 | |
| Parameter | Estimate | Std.error | 95% Conf.interval |
| Bo | 1.2395 | .05749 | .9921-1.4869 |
| B1 | 0.1037 | .01037 | .05907-.1483 |

Daily food consumption

Two methods were applied to the capelin stomach content data to estimate the daily ration:

1. The calculation of daily consumption follows the formula (Elliot and Persson, 1978):

$$C_t = \frac{(S_t - S_0 e^{-rt})rt}{1 - e^{-rt}}$$

where C_t = the consumption of food by fish over the time interval T_0 to T_t , S_t and S_0 = the amount of food in the stomach at time T_t and T_0 , r = exponential gastric evacuation

rate. C_t is calculated for each time interval and then summed to give the total daily ration (Durbin et. al., 1983). For the time periods used in estimating the evacuation rate, the consumption is set to 0.0. This is also done for other periods where this model gives a negative consumption.

2. The total daily ration calculated as:

$$C_t = 24rS$$

where S equals the mean stomach contents weight over 24h (Elliot and Persson, 1978). This model assumes that during a 24h period the food ingested is equal to the amount of food passed through the stomach (Doble and Eggers, 1978). In our calculations, the average is taken over all individual fish sampled during the 24 hour period.

Table 4 Stomach fullness and estimates of daily food consumption for capelin. All length groups combined.

| n | day, time | mean length-cm | mean weight gram | mean stomach fullness % of BW | consumption method 1 %BW | consumption method 2 %BW |
|----|-------------|----------------|------------------|-------------------------------|--|--------------------------|
| | 9 Aug 1989 | | | | | |
| 35 | 07:00 | 9.19 | 3.72 | 0.553 | | |
| 60 | 12:20 | 10.95 | 7.97 | 0.556 | 0.303 | |
| 62 | 16:00 | 11.09 | 7.89 | 1.052 | 0.808 | |
| 62 | 20:00 | 10.97 | 8.10 | 0.985 | 0.355 | |
| 33 | 23:20 | 12.68 | 12.60 | 1.262 | 0.667 | |
| | 10 Aug 1989 | | | | total 07:00-23:20 : 2.232 | 2.009 |
| 35 | 04:00 | 12.51 | 11.88 | 0.711 | set to 0.0 | |
| 40 | 08:00 | 10.31 | 6.28 | 0.491 | set to 0.0 | |
| 62 | 11:45 | 10.36 | 5.92 | 0.402 | set to 0.0 | |
| 85 | 16:40 | 11.04 | 7.28 | 1.062 | 1.048 | |
| 87 | 20:00 | 11.47 | 9.22 | 0.589 | set to 0.0 | |
| 50 | 24:00 | 12.75 | 12.47 | 0.581 | 0.234 | |
| | 11 Aug 1989 | | | | total 23:20 Aug 9 -24:00 Aug 10: 1.282 | 1.699 |
| 51 | 04:00 | 11.62 | 9.12 | 0.318 | set to 0.0 | |
| 20 | 07:20 | 9.47 | 4.32 | 0.278 | 0.083 | |

The capelin daily ration based on the present investigation provided an evidence of low predation pressure on the zooplankton community at the Goose Bank area. The above data questions whether the Goose Bank is an ideal feeding ground compared to the northern area. Hassel (1986) reported that the index of stomach fullness increased markedly towards the northern limit of capelin distribution. However, a high index of stomach fullness reflects the feeding activity of the fish population (Lilly, 1991) and do not necessarily indicate a high consumption rate, since gastric evacuation rate is a function of temperature. Digestion, being a physiological process, accelerates with

rising temperature (Ney, 1990). One would assume a low daily ration in fish distributed in the area dominated by Arctic water.

The estimated total capelin biomass based on the acoustic survey during September — October in the same area (Gjørseter, pers. comm.) was about 280 000 tonnes of capelin of length 8–16.9 cm. When combining these data with our estimates of capelin daily ration (1.3 — 2.2 % of body weight), the daily consumption by capelin becomes between 3640 tonnes and 6160 tonnes.

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Appendix A Capelin stomach content data

Table 5 Diet compositions of length group 6-8.9 cm of capelin during 9/8-11/8-1989.

| TAXA | SIZE-CM | MGRAMS/ PREDATOR | WEIGHT % |
|---------------------------|----------|---------------------|-------------|
| Gastropoda | .02-.029 | .00 | .00 |
| | .03-.039 | .00 | .00 |
| | .04-.049 | .00 | .00 |
| | .1-.14 | .00 | .00 |
| Bivalvia | .02-.029 | .02 | 1.86 |
| | .03-.039 | .04 | .35 |
| Calanus glacialis | .06-.069 | .04 | .35 |
| | .4-.49 | .09 | .81 |
| | .5-.69 | .06 | .58 |
| Calanus finmarchicus | .15-.19 | .06 | .58 |
| | .2-.24 | 1.71 | 15.58 |
| | .25-.29 | 1.78 | 16.28 |
| | .3-.39 | 3.68 | 33.60 |
| | .4-.49 | .37 | 3.37 |
| | indet | .04 | .35 |
| Microcalanus pygmaeus | .06-.069 | .09 | .81 |
| | .07-.079 | .01 | .12 |
| | .08-.089 | .00 | .00 |
| Pseudocalanus elongatus | .08-.089 | .09 | .81 |
| | .1-.14 | .08 | .70 |
| | .15-.19 | .27 | 2.44 |
| | .2-.24 | .01 | .12 |
| Metridia longa | .1-.14 | .00 | .00 |
| | .15-.19 | .00 | .00 |
| | .2-.24 | .51 | 4.65 |
| | .25-.29 | .00 | .00 |
| | .3-.39 | .01 | .12 |
| Acartia | .1-.14 | .00 | .00 |
| Microsetella norvegicus | .06-.069 | .00 | .00 |
| Oncaea borealis | .05-.059 | .00 | .00 |
| Oithona similis | .06-.069 | .03 | .23 |
| | .07-.079 | .01 | .12 |
| | .08-.089 | .00 | .00 |
| Oithona atlantica | .06-.069 | .00 | .00 |
| | .07-.079 | .00 | .00 |
| | .1-.14 | .01 | .12 |
| Parathemisto abyssorum | .25-.29 | .01 | .12 |
| | .5-.69 | .09 | .81 |
| | .7-.99 | .09 | .81 |
| Euphausiidae | .06-.069 | .00 | .00 |
| | .08-.089 | .00 | .00 |
| | .09-.099 | .00 | .00 |
| | .1-.14 | .18 | 1.63 |
| | .15-.19 | .00 | .00 |
| Decapoda | .3-.39 | .03 | .23 |
| Oikopleura | .3-.39 | .02 | .14 |
| Oikopleura labradoriensis | .1-.14 | .00 | .00 |
| | .2-.24 | 1.34 | 12.18 |
| Indeterminatus | egg | .01 | .13 |

Table 6 Diet compositions of length group 9-11.9 cm of capelin during 9/8-11/8-1989.

| TAXA | SIZE - CM | MGRAMS/ PREDATOR | WEIGHT % |
|--------------------------------|-----------|---------------------|----------|
| Gastropoda | .03-.039 | .04 | .15 |
| | .06-.069 | .00 | .00 |
| | .1-.14 | .00 | .00 |
| <i>Clione limacina</i> | indet | 1.47 | 5.25 |
| Bivalvia | .02-.029 | .03 | .11 |
| | .03-.039 | .03 | .11 |
| | .06-.069 | .00 | .00 |
| Copepoda | .03-.039 | .00 | .00 |
| <i>Calanus glacialis</i> | 4-.49 | .48 | 1.70 |
| | 5-.69 | .34 | 1.20 |
| <i>Calanus finmarchicus</i> | .02-.029 | .04 | .13 |
| | .1-.14 | .00 | .00 |
| | .15-.19 | .01 | .02 |
| | 2-.24 | 1.62 | 5.78 |
| | 2.5-.29 | 2.20 | 7.85 |
| | 3-.39 | 4.63 | 16.55 |
| | 4-.49 | .79 | 2.81 |
| | 5-.69 | .10 | .37 |
| | indet | .01 | .02 |
| <i>Microcalanus pygmaeus</i> | .06-.069 | .00 | .00 |
| | .07-.079 | .01 | .02 |
| <i>Pseudocalanus elongatus</i> | .08-.089 | .00 | .00 |
| | .1-.14 | .06 | .22 |
| | .15-.19 | .14 | .50 |
| <i>Metridia longa</i> | .15-.19 | .01 | .02 |
| | 2-.24 | .62 | 2.22 |
| | 2.5-.29 | .07 | .24 |
| | 3-.39 | .04 | .15 |
| <i>Microsetella norvegica</i> | .03-.039 | .00 | .00 |
| <i>Oncaea borealis</i> | .1-.14 | .00 | .00 |
| <i>Oithona similis</i> | .06-.069 | .01 | .02 |
| | .07-.079 | .00 | .00 |
| <i>Oithona atlantica</i> | .07-.079 | .00 | .00 |
| | .1-.14 | .01 | .02 |
| <i>Parathemisto abyssorum</i> | .06-.069 | .06 | .23 |
| | 2-.24 | .01 | .03 |
| | 2.5-.29 | .01 | .05 |
| | 3-.39 | .07 | .25 |
| | 5-.69 | .44 | 1.59 |
| | 7-.99 | .85 | 3.05 |
| | 1-.14 | 2.01 | 7.17 |
| 1.5-1.9 | .78 | 2.17 | |
| Euphausiidae | .02-.029 | .00 | .00 |
| | .06-.069 | .01 | .04 |
| | .08-.089 | .00 | .00 |
| | .1-.14 | .00 | .00 |
| | .15-.19 | .00 | .00 |
| Thysanoessa inermis | indet | 1.04 | 3.71 |
| | indet | 1.04 | 3.71 |
| <i>Thysanoessa raschii</i> | 3-.39 | 1.46 | 5.21 |
| | 1-.14 | .53 | 1.90 |
| | 1.5-1.9 | 1.39 | 4.96 |
| | 2-.24 | .62 | 2.20 |
| | 2.5-2.9 | 2.08 | 7.43 |
| | 3-.39 | 1.77 | 6.32 |
| Echinodermata | .03-.039 | .00 | .00 |

Table 6 (Continued) Diet compositions of length group 9–11.9 cm of capelin during 9/8–11/8–1989.

| | | | |
|---------------------------|----------|------|------|
| Asteriidae | .04-.049 | .00 | .00 |
| Oikopleura | 2-.24 | .34 | 1.21 |
| | 3-.39 | .46 | 1.65 |
| | 5-.69 | .12 | .43 |
| Oikopleura labradoriensis | .05-.059 | .02 | .07 |
| | 4-.49 | 1.15 | 4.12 |
| Indeterminatus | - | .04 | .15 |

Table 7 Diet compositions of length group 12–14.9 cm during 9/8–11/8–1989.

| TAXA | SIZE-CM | MGRAMS/ PREDATOR | WEIGHT % |
|---------------------------|----------|---------------------|-------------|
| Calanus glacialis | 4-.49 | .07 | .04 |
| Calanus finmarchicus | 2-.24 | .11 | .07 |
| | 25-.29 | .32 | .19 |
| | 3-.39 | 1.11 | .68 |
| | 4-.49 | .08 | .05 |
| | 5-.69 | .03 | .02 |
| | indet | .03 | .02 |
| Microcalanus pygmaeus | .06-.069 | .00 | .00 |
| Pseudocalanus elongatus | .1-.14 | .00 | .00 |
| Metridia longa | 2-.24 | .03 | .02 |
| | 3-.39 | .01 | .00 |
| Oithona similis | .06-.069 | .00 | .00 |
| | .07-.079 | .00 | .00 |
| Parathemisto abyssorum | 4-.49 | .08 | .05 |
| | 5-.69 | .54 | .33 |
| | 7-.99 | 1.01 | .62 |
| | 1-.14 | .25 | .15 |
| | 1.5-1.9 | 1.91 | 1.16 |
| | 2.5-2.9 | .49 | .30 |
| Thysanoessa inermis | 25-.29 | .55 | .33 |
| | 5-.69 | 3.87 | 2.36 |
| | 1.5-1.9 | 1.18 | .72 |
| | 2-.24 | 8.44 | 5.14 |
| | 2.5-2.9 | 63.43 | 38.64 |
| | 3-.39 | 37.15 | 22.63 |
| Thysanoessa raschii | 2-.24 | .37 | .22 |
| | 1-.14 | .14 | .08 |
| | 1.5-1.9 | .81 | .50 |
| | 2-.24 | 5.51 | 3.35 |
| | 2.5-2.9 | 24.34 | 14.82 |
| | 3-.39 | 10.58 | 6.44 |
| Ophiurida | .01-.019 | .00 | .00 |
| Oikopleura | 2-.24 | .03 | .02 |
| | 4-.49 | .35 | .22 |
| Oikopleura labradoriensis | .15-.19 | .03 | .02 |
| Lumpenus | 3-.39 | 1.31 | .80 |

**FOOD REQUIREMENTS OF THE
BARENTS SEA Sebastes mentella**

by

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ABSTRACT

Based on data on the average weight of S. mentella from the Barents Sea the method developed by Vinberg was used to estimate daily and annual rations of all the age-groups and the amount of food consumed by the commercial part of the population at the age exceeding 6 years in 1971-1988.

INTRODUCTION.

One of the major trends in the development of a multispecies model of the Barents Sea is the simulation of trophodynamic processes with particular emphasis on estimation of the amount of food consumed annually by a population. The estimates are performed on the basis of data on the stomach content weights and evacuation rates. However, temporal and spatial inhomogeneity in sampling of the quantitative data on feeding results in certain errors. With this in view the model should envisage another method of estimating the annual diets to assist in drawing comparison between the results obtained. The method developed by G.G. Vinberg is considered to be convenient since it is based on the weight increments and metabolism values and it does not employ data on the stomach contents. The present paper provides an example of the above-mentioned calculations with reference to S. mentella from the Barents Sea.

MATERIAL AND METHODS

The daily rations were calculated using Vinberg's method (1956) with the subsequent modifications (Vinberg, 1983):

$$R = 1.3(I + G + T)$$

where

R is daily ration, % of body weight

I is average growth increment, % of body weight

G is energy drain due to generative metabolism, % of body weight

T is energy drain due to total metabolism, % of body weight

The factor of 1.3 was taken rather than of 1.25 since the most recent data (Anon., 1983) indicate that a total of 70% of food are assimilated by fish. The values of the energy drain due to total metabolism were remained unchanged in view of the fact that they show a 1.7 increase only at the water temperature exceeding 7°C (Umnov et al., 1986). The average daily weight increments (I) were estimated as follows:

$$I = \frac{2(W_i - W_{i-1})}{n(W_i + W_{i-1})} 100, \%$$

where

W_i is average weight of the i - th age group in a given year, g

W_{i-1} is average weight of the i - th age group during the previous year, g

n is duration of weight increment, days

The average daily energy drain due to generative metabolism (G) was calculated from the following formula:

$$G = 100 \frac{H_i X}{N W_i}$$

where

H_i is fecundity of the i - th age group, thousand individuals

X is the weight per egg, g

N is egg producing time, days

The average daily energy drain due to total metabolism (T) was estimated as:

$$T = \frac{24 * 4.8 * A * W_i^k * 100}{W_i * 1000} * Q_{10}^{\frac{T-20}{10}}$$

where :

4.8 is oxycaloricity factor (1 ml of O₂ consumed by fish is equivalent to 4.8 cal.), mg O₂/g

24 is coefficient to reduce metabolism value to that per 1 day

A is O₂ intake by 1 fish 1 g in weight

k is an exponent determining change of metabolism with weight

Q₁₀ is Vant Hoff's temperature coefficient (equal to 2.25)

1000 is caloric content of 1 g of S. mentella (raw weight)

The average weights of S. mentella at the age of under 6-7 years were obtained based on the results of the annual young fish trawl surveys made in October-December. Data on the average weights of adult individuals and on the proportion of mature fish in each age-group were borrowed from age samples collected by the PINRO vessels. Due to the lack of material the average weights were estimated based on samples taken throughout the year and they were averaged for each age-group despite the existing differences between the growth rates in males and females. Data on the abundance of the fish of each age at the beginning of the year were taken from the ICES material (Anon. 1990). The biomass of each age-group was estimated as the abundance multiplied by the average weight of 1 individual at a given age. The increment time was assumed as 365 days. The values of fecundity of females from each age-group were borrowed from Lukmanov (1988). The weight of 1 egg of 1.17 mg was calculated based on data on fecundity of the Irminger Sea S. mentella at Stage IV in 1987- 1988. The egg production time was taken as equal to 150 days, i.e. from the time when Stage III was first recorded in August and up to the time when Stage IV was no longer observed in December (Sorokin and Shestova, 1988). Since no literature material was available the k and A coefficients of 0.321 and 0.79, respectively, were assumed as equal to the average ones for marine fishes (Vinberg, 1956). The average ambient temperature of S. mentella was taken as 4°C, which was the average annual temperature in the Kopytov Bank area where the species mainly occurred (Adrov, 1957). The average caloricity of S. mentella was assumed to be 1000 cal per 1g of raw weight (Anon., 1974). A correction factor (z) was introduced to estimate the annual rations with account taken of the fish maturity:

$$R_{an} = 1.3 (I + z \times G + T), \% \text{ or Cal,}$$

where z is fraction of mature fish in a given age group.

Due to the lack of data on the abundance of young age groups the amount of food consumed (C) was estimated for the commercial part of the population (fish over the age of 6 years) using the following formula:

$$C_i = B_i R_{an}$$

where:

C_i is food consumed by the i-th age-group, tonnes

B_i is biomass of the i-th age group, tonnes

R_{an} is ration of the i-th age-group (%of body weight)

The correction factor for calorificity was not taken account of since the data on the feeding of S. mentella were not adequate to provide a reliable quantitative assessment (Konchina, 1970; Antonov et al., 1989). To compare the results obtained the rations of the redfish in 1934 were calculated using data obtained by Veshchezerov (1944). The paper by Veshchezerov deals with S. marinus, however, in view of the fact that S. marinus was not distinguished from S. mentella before 1952 and the areas of sampling were within the range of S. mentella the data could refer to the latter. Using the same material the fecundity - weight linear relationship was established as $Y = 118.11 + 0.35X$ ($r=0.84$) to be used in fecundity estimates in 1934 and in determination of age at maturity (14 years). In view of the lack of data on the proportion of mature individuals an assumption was made of a 100% maturity in fish older than 14 years.

RESULTS AND DISCUSSION

The daily and annual rations in S. mentella proved to be relatively low as compared to those in other fish species. The maximal (in underyearlings) and minimal (in old fish) daily diets constituted 1.6 - 2.0 and 0.3 - 0.4 % of the body weight respectively. In immature individuals the respective values appeared to be by 0.02-0.09 % of body weight lower than in the mature ones of the same age and the difference was found to grow with the fish age. The annual diets varied from 470-599 to 125-142 % of the body weight in underyearlings and 19 year- olds, respectively, and did not exceed twice the body weight in individuals older than 6 years. In terms of energy the annual rations varied from between 6.5-25.1 to between 1247-1676 Cal. The literature data are indicative of much higher values of annual and daily rations in other species. In the North Sea whiting the daily and annual rations constituted 3.72-4.80 and 490-659 % of the body weight, respectively, or 202.1-5304.4 Cal (Malyshev, 1980). In cod from different populations the annual rations vary from 215 to 770% of body weight or from 1000 to 14500 Cal (Daan, 1975; Popova, 1988 and Shatunovsky, 1988). The above values are by several times higher than the ones in S. mentella. However, the low rations are realistic with account taken of higher longevity and low growth rates in S. mentella as compared to gadoids and they are confirmed by data on the species feeding under natural conditions. The paper by Antonov et al. (1989) indicates that the daily diet of S. mentella from the Bear Island Bank was as low as 0.38 % of the body weight in September 1982.

The year to year dynamics of annual and daily rations (Fig. 1- 4) is characterized by distinctly expressed periods of high feeding rate which do not coincide in young and mature fish due to different food spectra. Based on food habits Boldovsky (1944) distinguished the following groups within the genus Sebastes: 1) individuals below 30-35 cm in length which fed on Calanoida, Sagitta and euphausiids and 2) individuals longer than 30-35 cm which fed on fish and euphausiids. These groups corresponded to the age of under 10- 11 years and older than 10-22 years, i.e. to immature and mature individuals (Veshchezerov, 1944). The divergence between the periods of active feeding in young and adult fish can be explained by different food habits and different patterns of development of the respective food organisms. Besides it is not food availability that governs the stock size of S. mentella. The intensive predation of cod on young S. mentella (11 and 42 % of the food bolus in 1986 and 1987 respectively) (Orlova

et al., 1988) contributed to an increase in the food availability and, consequently, in food rations.

The biomass of food consumed by the commercial part of the population (at the age of more than 6 years) (Fig.5) showed variations from 245.9 thousand to 1.5 million tonnes. Changes in the amount of food consumed were found to be synchronous to those in commercial stock biomass. The maximum amount of food was consumed in 1973-1975 which was followed by a gradual reduction during the period of up to 1986 and an increase since 1987 due to a rise in the commercial stock biomass. In view of the lack of quantitative data on the feeding of S. mentella the effect of the latter on different food organisms was not possible to assess. Comparison was drawn between the rations of S. mentella in 1971-1988 and 1934 (Table 1.). On the whole, the annual and daily rations in the 30s appeared to be lower if taken as % of the body weight and much higher in terms of calories, which can be explained by differences in the food spectra. Herring (40.6 % in terms of weight) and capelin (13.2 %) formed the bulk of food in the 30s (Boldovsky, 1944). According to the results of the PINRO expeditional studies S. mentella started to feed on euphausiids (17.2-50% of occurrence), hyperiids (3.4-66.2 %) and shrimps (3.6-31.4 %) in 1968-1988. Since Daan (1975) states that the caloric content of crustaceans is lower than that of herring (1.06 against 1.36 cal/mg) the decrease in the food caloricity was responsible for an increase in the amount of food consumed.

CONCLUSIONS

The daily and annual rations of S. mentella from the Norwegian -Barents Sea stock constituted 0.3-2.0 and 125-599 % of the body weight, respectively, or 6.5-1676 Cal. The present-day daily and annual diets were higher if taken as % of the body weight and significantly lower in terms of caloricity than those in 1934. The amount of food consumed by the commercial part of the population varied from 1.5 million tonnes in 1973 to 245 thousand tonnes in 1986. The method developed by Vinberg can be recommended as an additional aid to estimate the annual food diet of the Barents Sea commercial fishes and to draw comparison with the results of analogous calculations based on data on the food bolus weight. The implementation of the method demands determination of the species specific coefficients (A and k).

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Table 1 Rations of Sebastes mentella in 1934 and 1971-1988.

| Age | Daily diets, % of body weight | | | | Annual diets | | | |
|-----|-------------------------------|-----------|-------------|-----------|------------------|-----------|--------|-----------|
| | immature fish | | mature fish | | % of body weight | | kcal | |
| | 1934* | 1971-1988 | 1934* | 1971-1988 | 1934* | 1971-1988 | 1934* | 1971-1988 |
| 10 | 0.48 | 0.46 | | | 170.9 | 167.5 | 676.9 | 512.2 |
| 11 | 0.46 | 0.43 | | | 161.4 | 157.8 | 865.9 | 567.9 |
| 12 | 0.36 | 0.43 | | | 131.3 | 157.6 | 727.9 | 691.0 |
| 13 | 0.43 | 0.41 | | | 152.5 | 151.2 | 1149.1 | 770.1 |
| 14 | 0.39 | 0.40 | 0.41 | 0.45 | 142.1 | 150.9 | 1351.7 | 935.7 |
| 15 | 0.40 | 0.38 | 0.40 | 0.44 | 140.0 | 147.2 | 1802.2 | 1088.5 |
| 16 | 0.31 | 0.38 | 0.36 | 0.46 | 120.5 | 139.8 | 1651.5 | 1264.3 |
| 17 | 0.31 | 0.36 | 0.37 | 0.42 | 122.7 | 144.2 | 1841.3 | 1403.9 |
| 18 | 0.36 | 0.35 | 0.44 | 0.41 | 138.7 | 136.4 | 2715.9 | 1412.6 |
| 19 | 0.31 | 0.33 | 0.39 | 0.41 | 126.0 | 137.4 | 2476.8 | 1474.6 |

* Estimated based on data obtained by Veshchezorov (1944)

Figure 1 Daily rations of immature *S. mentella* (0-8 years).

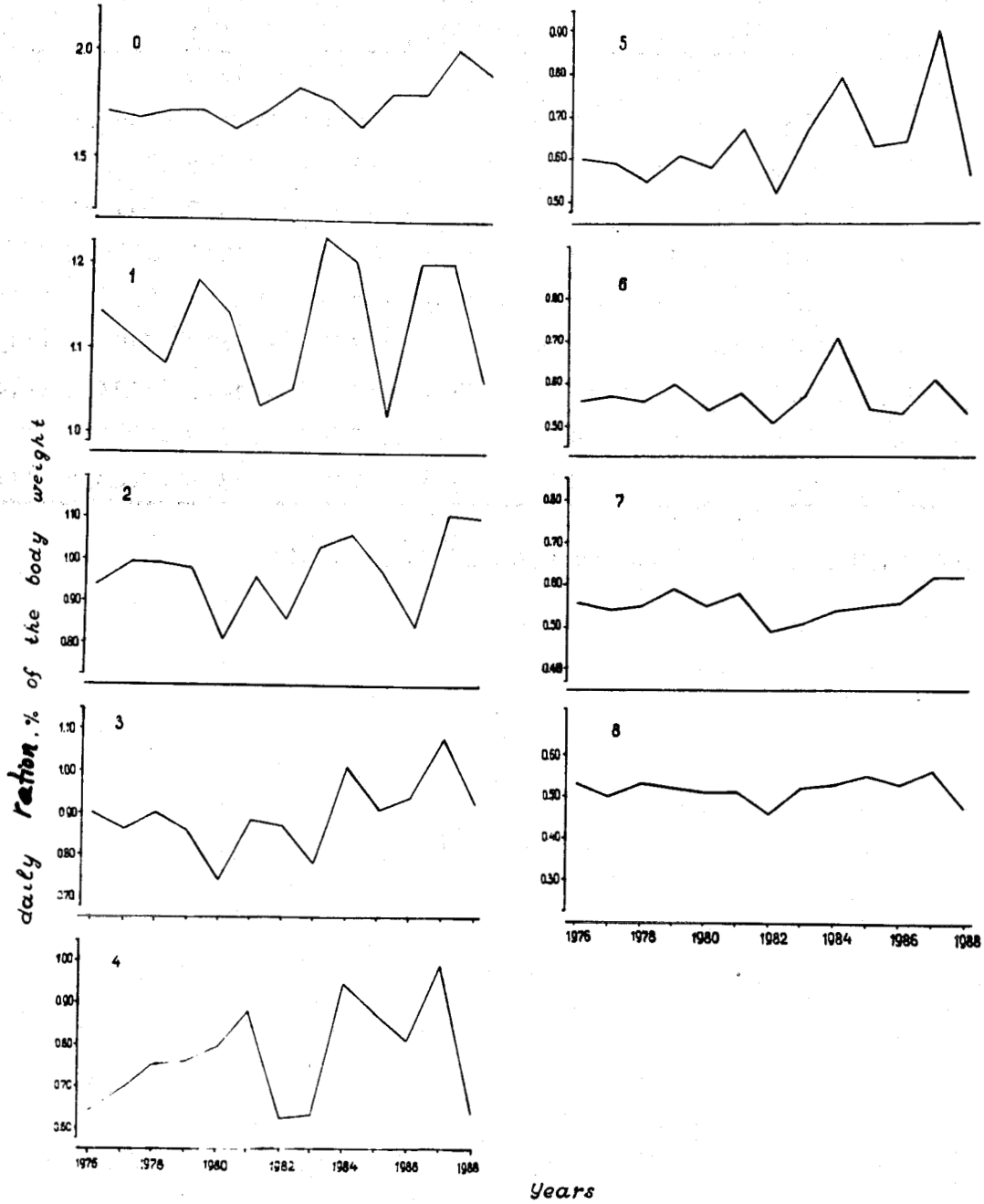


Figure 2 Daily rations of mature (solid line) and immature (dotted line) *S. mentella* at age 9-19 years.

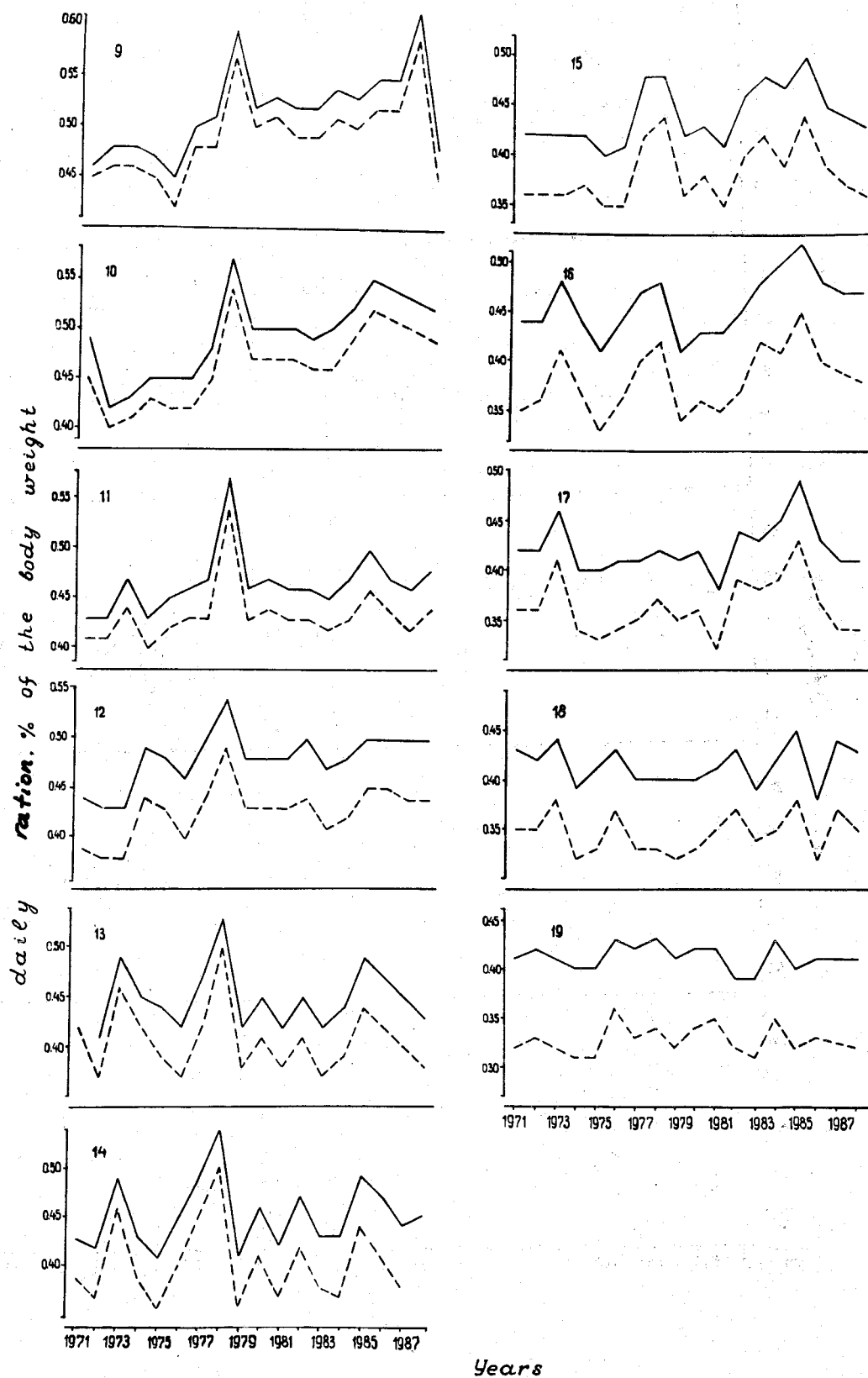


Figure 3 Annual rations of *S. mentella* at age 0-9 years in Cal. (solid line) and as % of the body weight (dotted line).

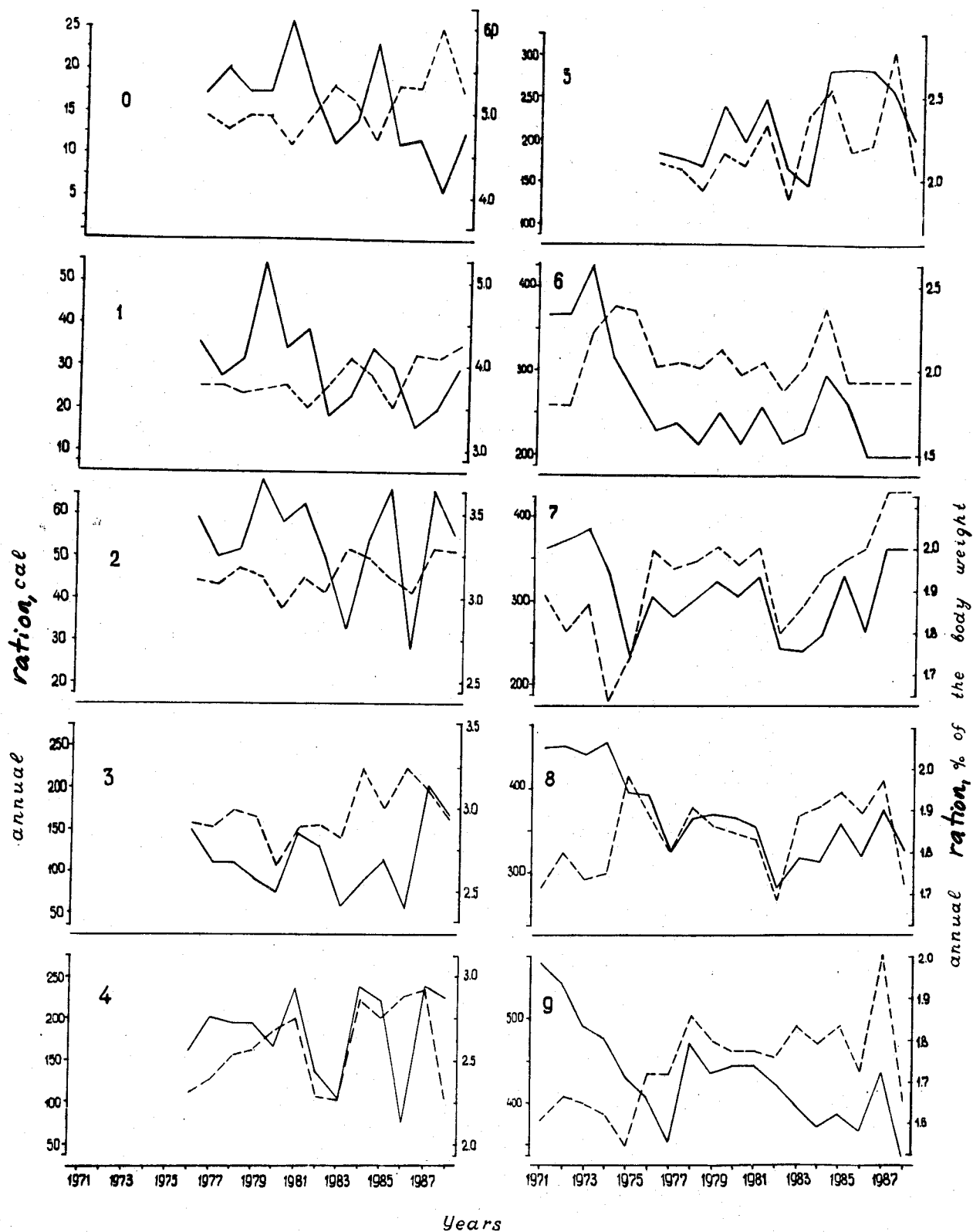


Figure 4 Annual rations of *S. mentella* at age 10–19 years in Cal. (solid line) and as % of the body weight (dotted line).

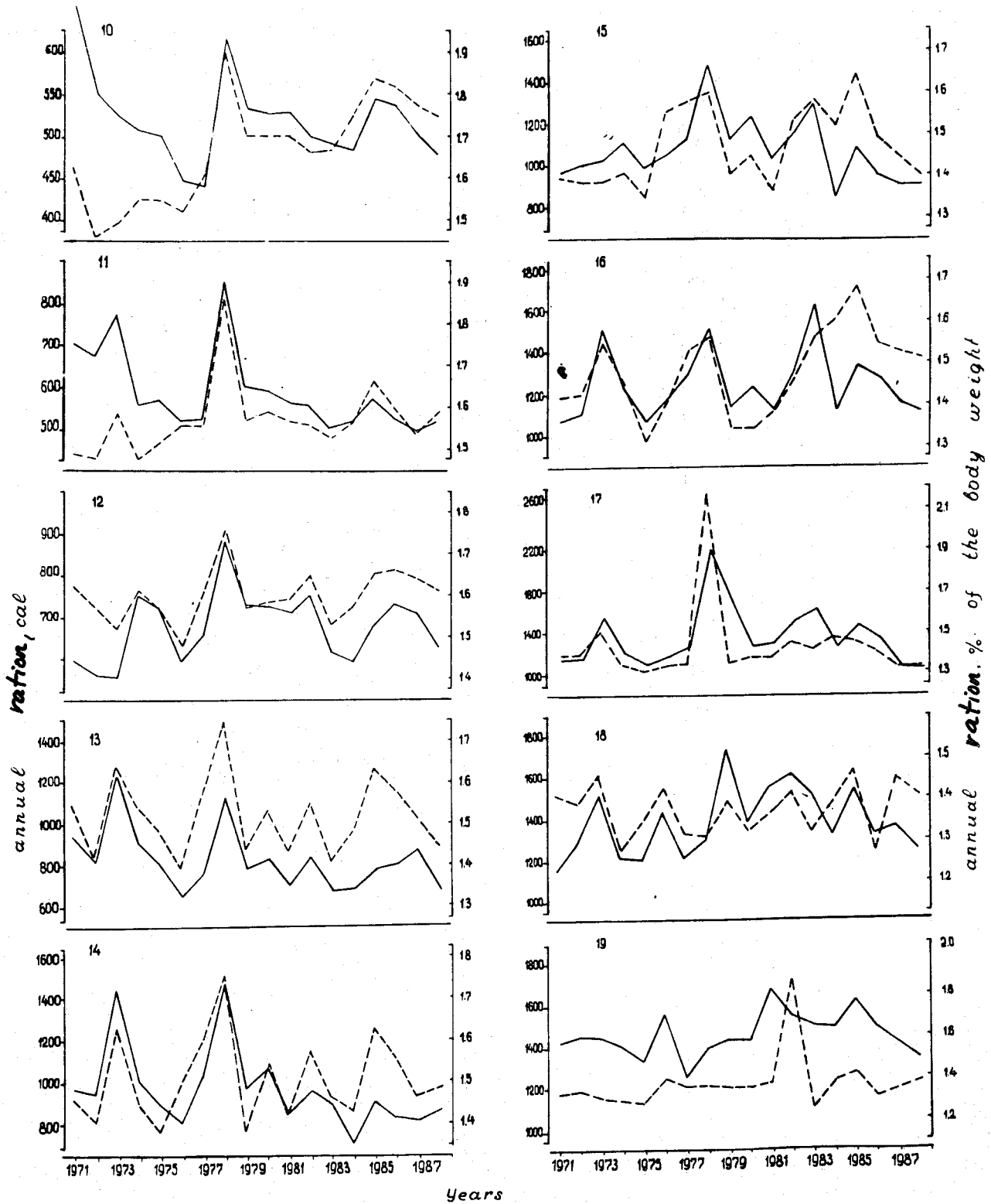
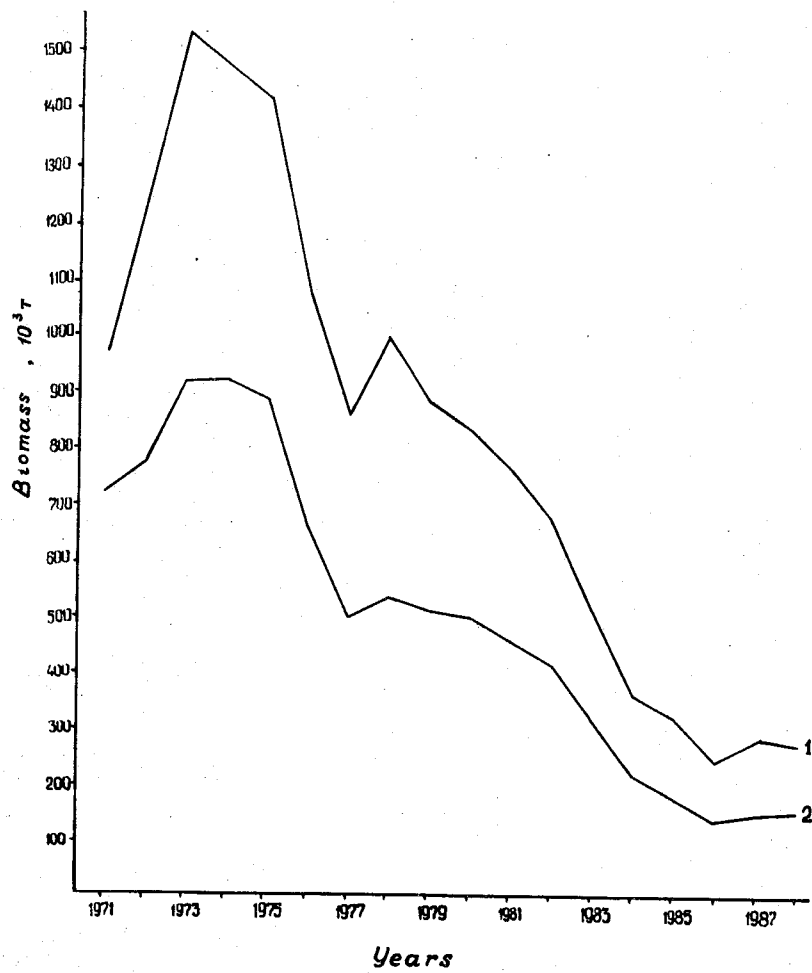


Figure 5 Biomass of the exploited stock of S. mentella (2) and the amount of food consumed by it (1)..



RESULTS OF AERIAL SURVEYS OF SEA BIRDS IN THE BARENTS SEA

by

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ABSTRACT

The paper gives the results of an aerial survey of sea birds carried out by the PINRO scientists from board the IL-18 DORR aircraft. The survey aimed at determining the abundance of the Barents Sea birds which feed on fish and the results were supposed to be employed in the joint IMR-PINRO program on "Studies of commercial stock interactions in the Barents Sea". Consideration was also given to the possibility of using the results of the survey for detection of capelin concentrations, which can be applied to short-term catch predictions and to identification of optimum areas of trawl-acoustic surveys of pelagic species in September and October.

INTRODUCTION

The high exploitation rates of biological resources in the Arctic seas have contributed towards creating stressful situations and disturbances in the trophic chains of the Barents Sea ecosystem (Borkin and Bezdenezhnykh, 1988; Borkin, 1990; Luka et al., 1989; Drobysheva, 1990; Belikov et al., 1991, Erikstad et al., 1990; Erikstad, 1990 and Vadar et al., 1990). With this in view detailed and differentiated studies of individual links of marine communities are required to provide a proper scientific background of utilization of potential natural resources. Up to now little attention has been paid to the ecological studies of the higher trophic levels including sea birds which are not only predators as related to other aquatic animals but also a component of the organic matter cycle in the trophic links and they directly participate in the energy flux and substance redistribution (Gerasimova, 1965; Jarris, 1978,1989; Belopolsky and Shuntov, 1980; Golovkin et al., 1965; Anon., 1991; Farness and Barret, 1985 and Gabrielsen et al., 1989).

MATERIAL AND METHODS

The sea bird survey was a part of the complex Barents Sea aerial survey performed from board the IL-18 DORR aircraft during the period from August 24 to September 10, 1991. The aircraft specifications are as follows:

| | |
|-------------------------|---------|
| Flight range, km | 6500 |
| Speed range, km/hr | 350-650 |
| Maximum flight time, hr | 11 |

The aircraft was supplied with measuring devices allowing for automatic record of such environmental parameters as air and water temperature and transparency, chlorophyll concentration in water, and etc. Visual observations on sea birds, marine mammals as well as on sea surface pollution were carried out through convex illuminators (blisters) located on both sides of the plane. The observations were made by 1 or 2 zoologists who reported the results to the computer operator for them to be entered in the flight protocol together with data which were supplied automatically from the measuring devices (time, coordinates, altitude, careen, temperature and salinity of air and water, and etc.). The flight parameters during the observations were as follows:

| | |
|-----------------------------|---------------|
| Flight speed, km/hr | 360 |
| Operational altitude, m | 200 |
| Observation time, hr | 12.00 - 19.00 |
| Average flight duration, hr | 10-11 |
| Observation period, hr | 6 |

During the survey all the birds encountered were recorded including non-identified species which were registered as "others". The abundance of birds in concentrations was rounded off as "hundreds" and "thousands". It should be noted that only well-distinguishable non-diving birds, primarily, sea gulls and fulmars can be recorded

from board the heavy and speedy IL-18 aircraft. Rest of the species were obviously underestimated. Data on the observed number of birds together with the "legend" signs of the species were entered in the "item" column of the flight protocol and recorded on a diskette to be further processed on land. A total of 8 flights 77 hours long were made. A general scheme of the flight routes is given in Fig. 1. The major requirement to the routes was an even coverage of the area with tracks some of which were supposed to overlap the ones of the vessels which were performing a 0-group survey (Anon.,1991). The accuracy of determination of the area surveyed is an important factor contributing to precise estimates of the total number of birds above the sea surface surveyed. With this in mind data on the distance from the sea and the number of observers (on one or on both sides of the plane) were filed. The sighting angle was assumed to be 45 degrees. The area surveyed was determined from the following formula:

$$S_{obs} = \sum_i K_i L_i H_i \tan(45)$$

where :

S_{obs} – Total observed area, sq. km (1)

K_i – Number of observers (1 or 2)

L_i – Distance between i – th and $(i - 1)$ th observation, km

H_i – Flight altitude, km

Under unfavorable weather conditions (rain or fog) observations were conducted from lower altitude which was automatically taken into account during data processing. The total abundance of the sea birds counted is given in Table 1.

Table 1 Total number of birds observed

| Species | Number observed | % |
|-----------------|-----------------|-------|
| Fulmar | 23958 | 58.9 |
| Kittiwake | 14881 | 36.6 |
| Glaucous gull | 353 | 0.9 |
| Tern | 68 | 0.2 |
| Skua | 40 | 0.2 |
| Guillemot | 33 | 0.2 |
| Little auk | 12 | 0.03 |
| Black guillemot | 1 | 0.002 |
| Duck | 422 | 1 |
| Gull | 112 | 0.3 |
| Other | 793 | 1.9 |
| Total | 40673 | 100 |

Table 1 (Continued) Total number of birds observed

The most reliable data were obtained on kittiwakes and fulmars since the birds were more or less evenly distributed throughout the entire area surveyed. The number of other species recorded was too low to draw reliable statistical conclusions. The average distribution density of a given species can be taken as:

$$Density = \frac{\sum_i N_i}{\sum_i S_i}$$

The total surveyed area $\sum_i S_i$ equals 3,607 sq.km. The total number of birds above the polygon can then be estimated using the following formula:

$$T = Density \times S_p \quad (3)$$

where S_p is the total area of the polygon which equaled 1,262,000 km². The polygon area was assumed to be the area covered with tracks except for the region north of 80° N since the aim of the survey was to record birds above the sea surface excluding islands (Franz Josef Land and Novaya Zemlya). Under these conditions the biotypic uniformity of the area was ensured. The area in which the bird abundance was estimated is shown by the broken line in Fig.1. The results of estimates are given in Table 2.

Table 2 Total estimated number of birds.

| Species | Number, 1000 individuals | Density, spec/ km ² | % |
|---------------|--------------------------|--------------------------------|------|
| Fulmar | 8300 | 6.5 | 59.0 |
| Kittiwake | 5200 | 4.1 | 37.0 |
| Glaucous gull | 123 | 0.1 | 0.9 |
| Skua | 14 | 0.01 | 0.1 |
| Duck | 147 | 0.12 | 1.1 |
| Other | 277 | 0.22 | 2.0 |
| Total | 14061 | 11.5 | 100 |

RESULTS AND DISCUSSION

Out of all the species observed the most abundant were kittiwake (Charadriiformes) and fulmar (Procellariiformes) which constituted 96-99% of the total abundance (Table 2). Fulmar occurred practically throughout the entire area surveyed (Fig.2), however, the distribution density was as low as 1-2 individuals per 100 sq.km in the southern and northeastern parts of the Sea. The birds were frequently recorded as small (5-20 individuals) flocks in the area west of Novaya Zemlya and above the central parts of the Sea north of 75° N. Dense concentrations in the form of small and large patches of

irregular configuration were observed in the area north and northeast of Bear Island. The flock length reached incidentally several kilometers and the abundance was as high as 5-15 thousand individuals. The general pattern of distribution of kittiwake was found to be similar to that of fulmar (Fig. 3), however a northernmore and denser location of areas of high abundance was noted. The maximum abundance of kittiwake was recorded in mixed flocks with fulmar in the area northeast of Hopen Island and along the eastern slopes of the Bear Island Bank. Out of other birds observed a total of 353 glaucous gulls, 68 terns and 40 skuas were identified (see Table 2). The detection of species of the family Alcidae (guillemots, little auk and black guillemot) presented a problem due to their dark protective color and the instinct of diving as soon as the plane was approaching.

Numerous observations made by fishermen as well as recent biological studies have indicated that concentrations of birds stick to areas where food organisms showed high abundance. Fish comprise a considerable portion in the diet of fulmar and of kittiwake in particular (Luka et al., 1989). With this in mind a comparative analysis was made of maps of distribution of capelin and polar cod obtained as a result of International Trawl and Acoustic Survey (TAS) in September (Fig.4) and those of the most abundant birds, such as fulmar and kittiwake obtained during the aerial survey. The results have revealed the closest spatial relationship between the distribution of kittiwake flocks and capelin shoals. The overlap of concentrations of the birds and the fish was close to its maximum in the northern parts of the range which were reached by capelin in the late summer and where the fish formed stable concentrations for a certain period of time and they did not make notable migrations. A shift in the concentrations of capelin and kittiwake was observed in the area east of Bear Island, which can be attributed to a certain difference in time between the aerial survey and the ship observations. The spatial relationship was less intimate between concentrations of fulmar and capelin, however in more than 50% of cases the abundant flocks were distributed in the areas of prey concentrations (east of the Bear Island Bank and the northeastern part of the Sea). The difference in the spatial distribution can be due to the fact that fulmar feed mainly on invertebrates and fish has a secondary importance in the diet. A close correlation between the distribution of the preys and predators was established as a result of combining the abundance of fulmar and kittiwake. The lack of spatial relationship between concentrations of polar cod and sea birds can be explained by the non- availability of the prey which stuck mostly to depths exceeding 100 m during the major part of the polar summer whereas both fulmar and kittiwake fed in the subsurface layer down to 0.5-1 m since they are non-diving species (Shuntov, 1982 and Yudin and Firsova, 1988). The results of studies of Norwegian and Russian ornithologists have shown that young fish formed the bulk of food in a number of the Barents Sea birds (Belopolsky and Shuntov, 1980; Belopolsky, 1957; Uspenskij, 1959; Erikstad et al., 1990; Giertz et al., 1985 and Mehlum and Giertz, 1984). With this in view an analysis was made of the distribution patterns of young food fishes based on data obtained from the 0-group surveys conducted during the same period. No satisfactory relationship was established between the distribution of fulmar and kittiwake and of the potential preys despite the fact that one-year olds usually occurred in the surface 0-20m layer where they are easily accessible. Exception was made of young polar cod and capelin the distribution of which notably coincided with those of birds in the

northwestern parts of the Sea (Anon., 1991).

CONCLUSIONS

The results of the survey have shown that the bulk of the ornithofauna above the off-shore areas of the Barents Sea was formed by fulmar and kittiwake which showed the total abundance of 14 million individuals. The lack of retrospective data does not allow for performing a thorough comparative analysis and making a reliable assessment of the data obtained. However, the literature material available on the abundance of these species during the nesting period (Belopolsky, 1957; Shuntov, 1982; Yudin and Firsova, 1988; Barrett and Vadler, 1984 and Barrett and Mehlum, 1989) allows for considering these values to be realistic ones. Birds are regarded to be predators in relation to many animals and similar to other predators their searching behavior aims at detecting the highest number of preys at the lowest energy expenditure due to which birds and their preys appear to be closely interrelated. The intimate spatial relationship between distribution of birds and capelin in the Barents Sea can be applied to fish scouting since bird flocks are indicative of the occurrence of fish concentrations in the same area. The data obtained are of significance with regard to the development of a Barents Sea ecosystem model at the trophic level. The employment of data on the abundance of sea birds related to the amount of fish consumed permits an estimation of the abundance of fish stock which is required to provide normal ecosystem functioning. The tentative estimates of the amount of fish consumed by the sea birds were made on the basis of the widely known literature data (Belopolsky, 1957; Uspensky, 1959; Golovkin, 1963,1972; Gerasimova, 1965; Erikstad, 1990 and Farness and Barrett, 1985). The daily diet of 1 bird was taken as a basis of the calculations. It constituted 200 and 120 g in fulmar and kittiwake respectively and the share of fish in their diet was known to be 20 and 70 % respectively during the period considered. Consequently, the amount of fish consumed during the 4 month long feeding period (from September to December) by 8,300 000 fulmars and 5,200 000 kittiwakes was 39 and 49 thousand tonnes, respectively, most of which was capelin (according to the original observations). The aerial surveys can, apparently assist in elucidation of areas intended for annual trawl and acoustic surveys of pelagic fish stocks. It is recommended that aerial surveys be conducted annually to contribute to the knowledge of dynamics of biological and climatic processes in the Barents Sea.

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Figure 1 General scheme of flight routes of IL-18 DORR over the barents Sea in August-September 1991.

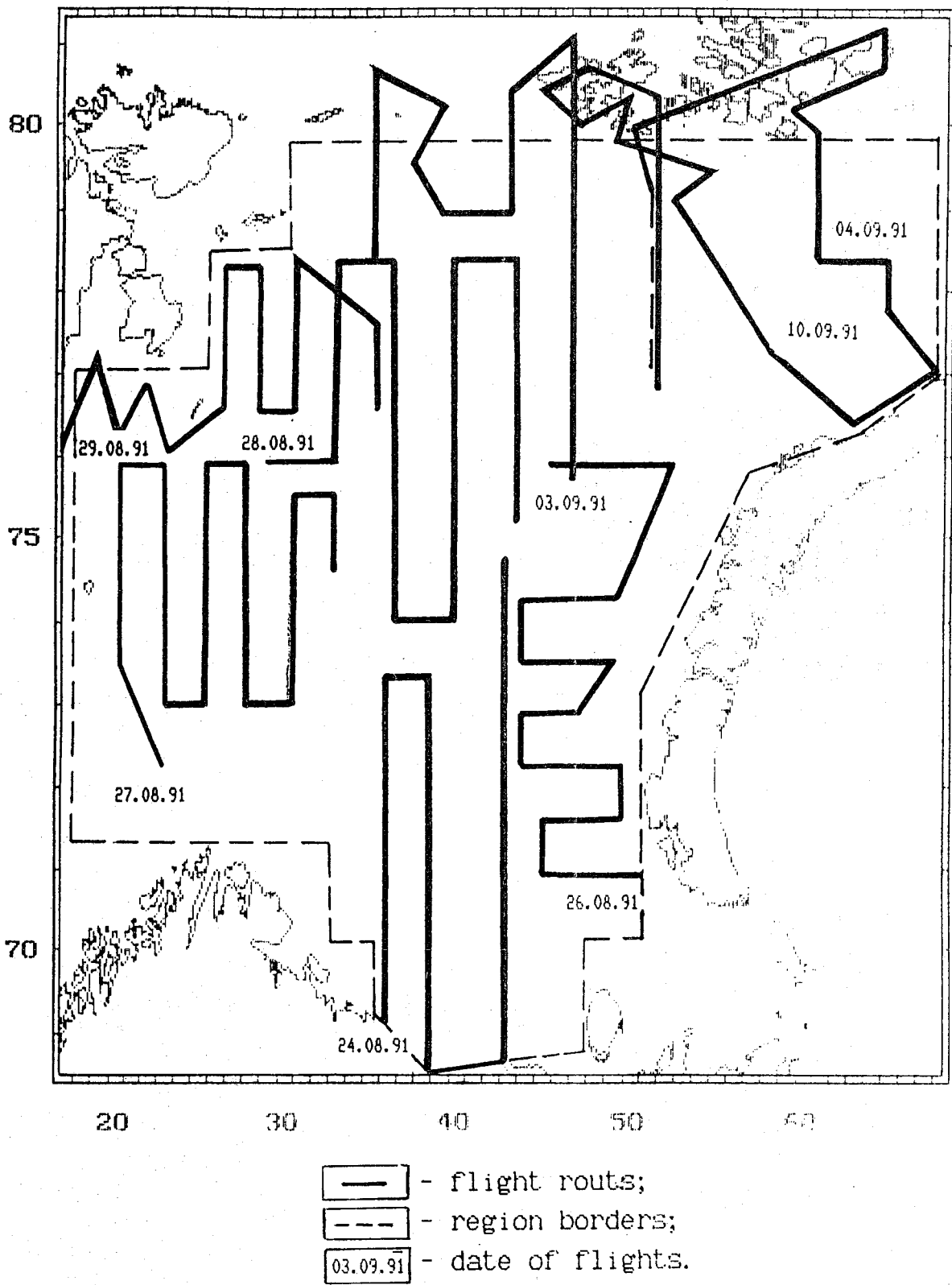


Figure 2 Distribution of fulmars, individual/km².

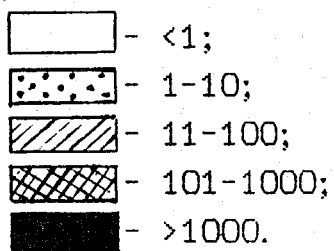
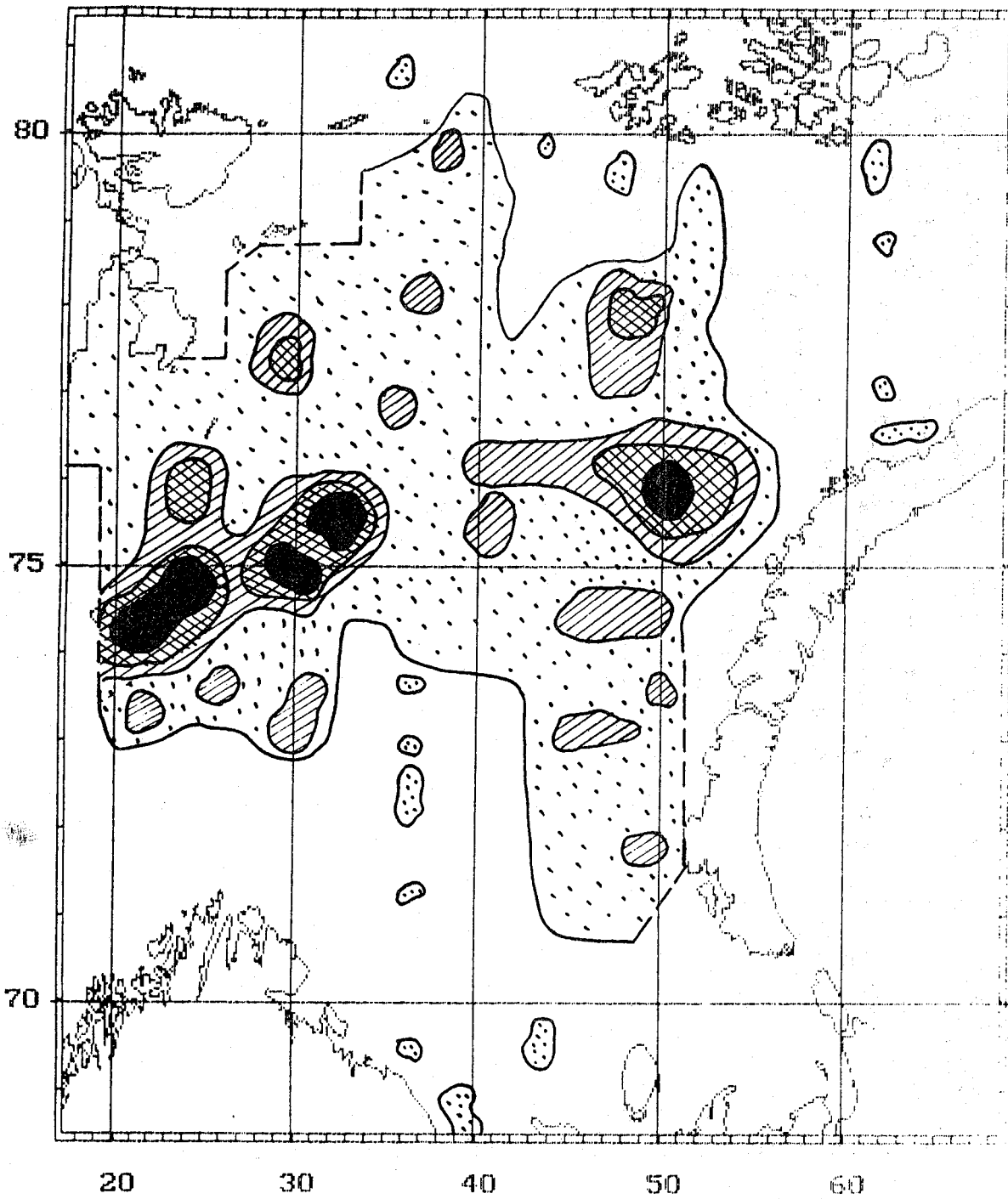


Figure 3 Distribution of kittiwakes, individual/km².

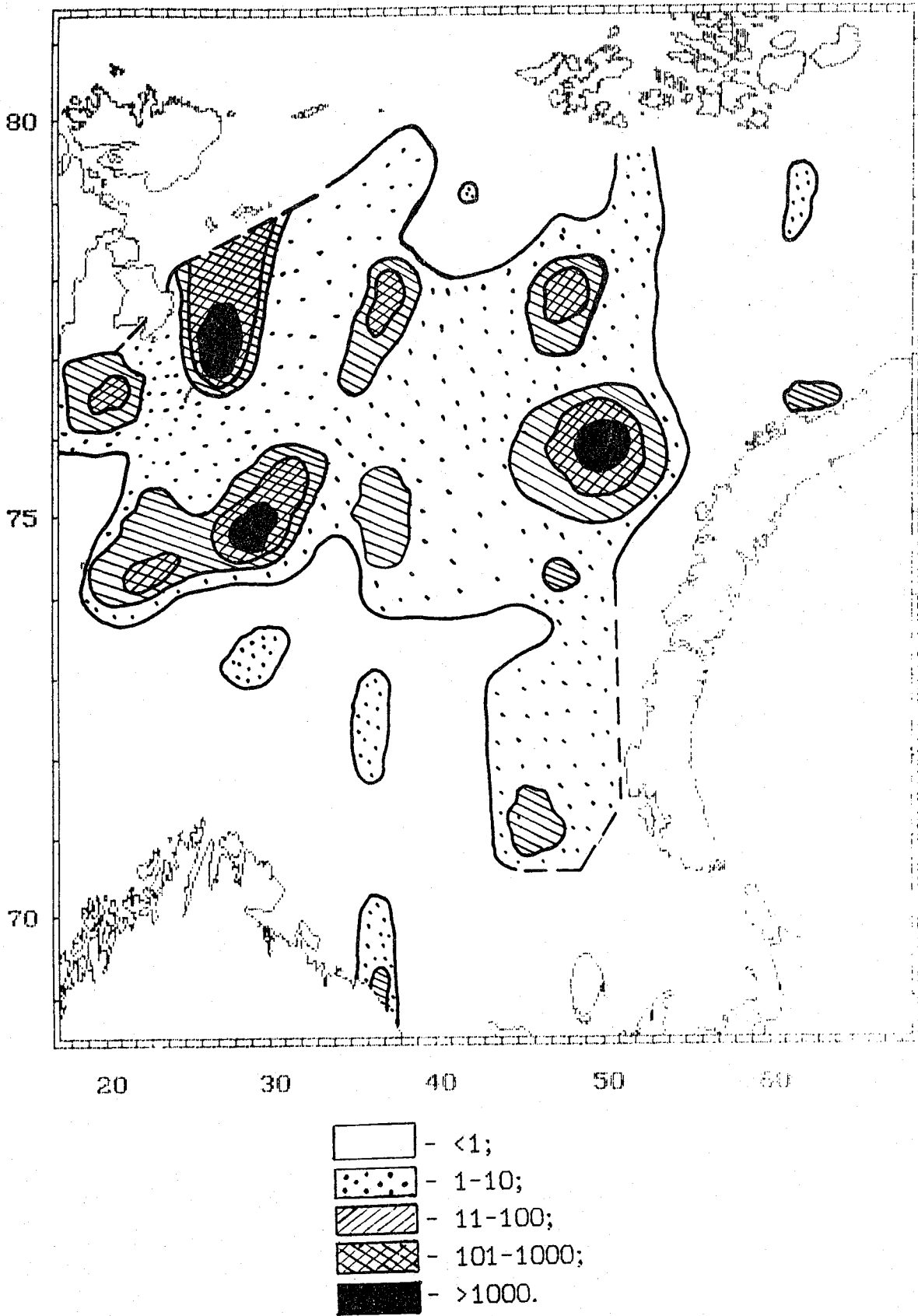
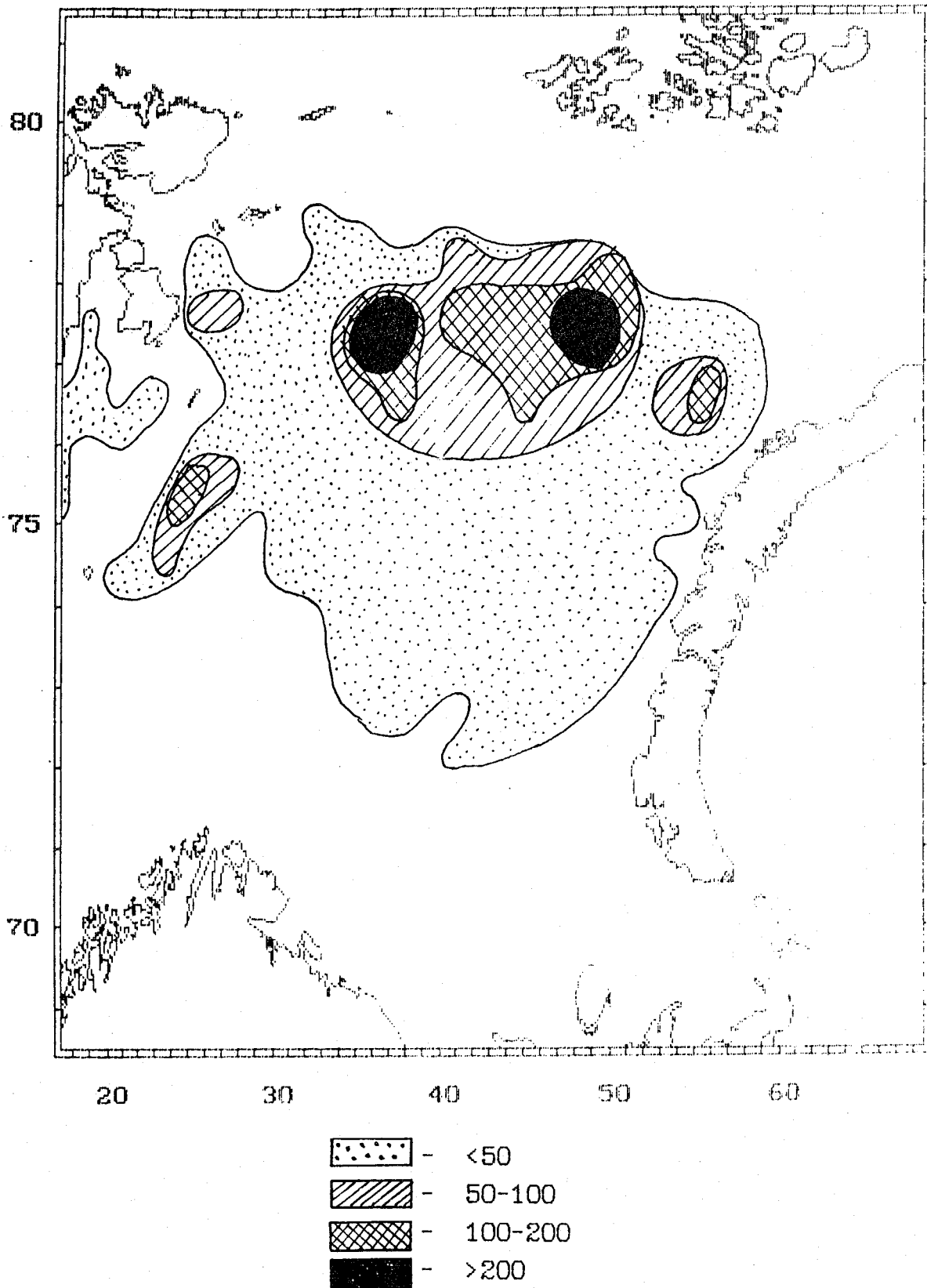


Figure 4 Distribution of capelin, tonnes/n.mi.² from trawl-acoustic survey data in September 1991.



THE BARENTS SEA ECOSYSTEM IN THE 1980s: OCEAN CLIMATE, PLANKTON AND CAPELIN GROWTH

by

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ABSTRACT

The 1980s were characterized by large ecological fluctuations in the Barents Sea ecosystem. A long period of cold ocean climate from 1977 to 1981 ended with a major inflow event of Atlantic water during 1982 and early 1983. A second major inflow event occurred in 1989 and 1990. The first major inflow event ended in late winter and left the southwestern Barents Sea filled with water containing low abundance of the dominant copepod Calanus finmarchicus. This reflects the large scale seasonal vertical migration whereby C. finmarchicus overwinters in the adjoining Norwegian Sea deeper than the depth at the entrance to the Barents Sea. This mechanism caused a minimum in zooplankton biomass in the central Barents Sea in 1984, which again resulted in poor individual growth rate of capelin and contributed to the sharp decline of the capelin stock from 1984 to 1986. Coinciding with the decline of the capelin stock, there was an increase in zooplankton biomass up to a maximum around 1987. Released predation pressure from capelin was probably a major reason for this increase. High abundance of zooplankton, particularly of larger forms such as krill and amphipods, is considered to be a major factor which caused very high growth rate and rapid recovery of the capelin stock up to 1990. The 1980s have provided us with examples of the dynamics of the Barents Sea ecosystem and the complex and intricate relationships which exist between ocean climate variability as a primary driving force, zooplankton stocks, and growth rate and population dynamics of capelin. Only through insight into the basic mechanisms can such relationships be properly described and used for future predictive purposes.

Editors note: This paper was presented at the symposium, but published elsewhere (Skjoldal, H. R., Gjøsæter, H., and Loeng, H. 1992. The Barents Sea ecosystem in the 1980s: ocean climate, plankton and capelin growth. - ICES mar. Sci. Symp.). However, due to its significance in explaining underlying factors behind changes in the fish-fish interactions, it is also included in the present proceedings.

INTRODUCTION.

The 1980s was a period of dramatic fluctuations in the Barents Sea ecosystem. The most notable event was the collapse of the capelin stock to a very low level in 1986 and its subsequent rapid recovery back to a high level by 1990 (Hamre, 1988, 1991, 1992; Skjoldal and Rey, 1989). The low abundance of capelin, which is a key intermediate link in the food web, had a drastic effect on higher trophic levels. Among the effects were massive invasions of harp seals along the Norwegian coast, high mortality of seabirds, and poor individual growth of cod (Mehl, 1989, 1991; Hamre, 1991, 1992; Skjoldal 1990; Blindheim and Skjoldal, 1992). The 1980s was also a period of intensified research in the Barents Sea ecosystem. There has been extensive data collection on capelin and other fish stocks through national and joint Soviet-Norwegian surveys. Plankton data have been collected by the Institute of Marine Research with the purpose of describing feeding conditions of capelin since 1979. This research was intensified and broadened with the Norwegian Research Programme on Marine Arctic Ecology (PRO MARE) in 1984-89. Oceanographic data are collected regularly on fixed sections and are part of long time series that for the Kola-section goes back to the beginning of this century. The extensive research and monitoring activities have left us in a good position to examine and analyse in retrospect the ecological events that took place during the 1980s. The climatic events have been reviewed by Loeng et al. (1992). Hamre (1991, 1992) has reviewed the changes in the capelin stock size and considered mechanisms responsible for these changes, involving interactions between the capelin, herring and cod stocks. Here we describe and examine the fluctuations in ocean climate and zooplankton biomass and how these factors were related to variations in growth rate and stock size of capelin.

MATERIAL AND METHODS

The Institute of Marine Research has maintained observations in several standard sections in the Barents Sea in order to map climatic signals in the current system. Since 1977 observations have been carried out six times a year at the Fugloya-Bjornoya section and four times a year at the Vardo-N section (Fig. 1). The longest time series of temperature in the Barents Sea is the Russian recording in the Kola-section (Fig. 1), which started as early as 1900. The data from the Kola-section have been provided by PINRO. Means of temperature and salinity have been calculated for the main Atlantic inflow through the various sections, using the method described by Blindheim and Loeng (1981). These means are prepared for the depth interval of 50-200 m along the parts of the sections which are marked in Fig. 1. In the Kola-section means from 0-200 m are used. By using means over part of sections, small scale spatial variability is filtered out. Zooplankton biomass data have been collected by the Institute of Marine Research since 1979. Data for the period 1979-84 were reported by Skjoldal et al. (1987), and details on methods are given there. Up to 1982 the biomass was recorded as zooplankton volume and these data have been converted to dry weight and ash-free dry weight using standard conversion factors. The samples have been collected with vertical net hauls (Juday or WP-2 nets, 180 m mesh size in most cases), with additional samples collected with MOCNESS multiple net sampler (333 m mesh size) since 1984. There has been a shift in time of sampling from mainly the summer season up to 1984 to more samples from the autumn season from 1986 onwards. This reflects an emphasis

on processes associated with the receding ice edge and summer feeding of capelin in the early period and data collection during the autumn multispecies surveys from 1986. The large data set on zooplankton from the Barents Sea during the 1980s are being analysed and will be reported more extensively elsewhere (H. R. Skjoldal, A. Hassel and L. Omli, unpubl. results). Here we have used calculated mean biomass values for different subareas used in MULTSPEC, a multispecies model being developed for the Barents Sea (Bogstad and Tjelmeland, 1990; Fig. 1). Because most of the research in the first part of the 1980s was conducted in subarea 7 in the central and northern Barents Sea, data from other subregions are available mainly for the latter part of the 80s. Observed weight and length of capelin (*Mallotus villosus*) were analysed based on data from the annual joint Soviet/Norwegian capelin surveys in the autumn. Length and weight at age representative for the whole stock were extracted from detailed stock size tables in the survey reports (Institute of Marine Research, Bergen, unpubl. reports). Measurements representative for the MULTSPEC subareas were extracted from tables of stock size for each of these subareas, calculated by an alternative program for acoustic stock size estimation (Gjøsæter, 1985). In both cases, the two-year-old age group has been used to construct time series, for three reasons. Firstly, this age group is unaffected by any possible size-selective spawning mortality. Secondly, the high number of individuals of this age-group sampled each year ensures a good data base. Thirdly, this age group has experienced only three growth seasons, and its size therefore reflects cumulatively the growth conditions in the current and the two previous seasons. Data of this type illustrate accumulated growth over more than one year. This resolution of growth data is insufficient for many purposes, and growth during the current growth season is a better variate to use to reveal interannual variability. The growth in the current season may also to some degree depend on the previous growth history of the fish, and it is in addition difficult to estimate. We have used two different approaches to derive such estimates. One method has been to subtract the mean length and weight of one year old individuals observed by the end of the former growth season from the values for two years old individuals observed at the end of the current growth season. If size dependent differences in mortality during the season are small, this method may give reliable estimates of growth for the total stock. The method has clear limitations for revealing growth differences related to geographical distribution due to the extensive migration of capelin. The second approach is based on a linear relationship between otolith growth and capelin growth in length (Gjøsæter, 1986). The width of the outer growth zone in the otolith is therefore related to capelin length increment in the current growth season. If one assumes that an individual caught in a certain geographical area in late autumn has spent most of the growth season in that area, such estimates of fish growth can be related to measured environmental factors in the subareas. Length increments in the current growth season were therefore calculated from otolith growth zone measurements from individuals inhabiting the various subareas.

RESULTS

Ocean climate

In order to compare the temperature conditions in the Barents Sea during the 1980s with earlier periods, a three-years running mean is shown in Fig. 2. The period from 1977 to 1982 was the coldest period observed in the Barents Sea since the beginning of the century. Fig. 3 shows more details in the variability in temperature and salinity of the Atlantic inflow to the Barents Sea during the last 15 years. The cold period lasted to the beginning of 1982, but the temperature started to increase already during the summer 1981 in the western part of the Barents Sea. In the eastern part the warming started later during the spring 1982 (Loeng et al. 1992). The warm period lasted for three years (1982-84), and was followed by four years with temperatures just below average (1985-88). In 1989 there was a rapid temperature increase in the whole southwestern Barents Sea (east to about 35E). Since then the temperature has been almost 1 C above the average. In the eastern Barents Sea the temperature increase took part during the winter and spring 1990. The salinity reached a minimum in 1978/79 (Fig. 3). This marked the arrival of the large salinity anomaly that was advected around in the northern North Atlantic during the 1960s and 70s (Dickson et al., 1988; Blindheim and Skjoldal, 1992). There was a marked increase in salinity up to 1980, followed by a slower increase until maximum was reached in 1984. The salinity decreased to a minimum in 1989, followed by a new increase. The main features in the variability of salinity follow the temperature fluctuations, but Fig. 3 also indicates small differences.

Zooplankton biomass

A time series of mean zooplankton biomass obtained with vertical net hauls in subarea 7 (Fig. 1) reveals a minimum in the zooplankton biomass in 1983 and 1984 (Fig. 4). The data up to 1984 have been presented in more details by Skjoldal et al. (1987) and Rey et al. (1987). The minimum in 1984 reflected low abundance of the dominant copepod *Calanus finmarchicus*, which showed a 50-fold decrease from peak numerical abundance in 1982 (Skjoldal et al. 1987). After the minimum in 1984 there was an increase in biomass to a maximum in this data set in 1987, followed by a decrease up to 1990. Size-fractioned biomass data obtained with vertical net hauls (left column) or MOCNESS plankton sampler (right column) from 1985 to 1990 are shown in Fig. 5. The highest mean biomass has typically been found in subarea 8 (northeastern Barents Sea) and the lowest in subarea 5 (southeastern Barents Sea, Fig. 1). The mean biomass in subarea 7 has typically been intermediate between those of areas 8 and 5 (Fig. 5). The total biomass obtained with vertical net and MOCNESS sampler show in most cases quite similar levels. Since the number of samples and the geographical coverage in each subarea have varied considerably, detailed interpretation of the results must be done with some caution. In general, the smaller meshed vertical nets give higher biomass in the size fraction <1 mm, whereas MOCNESS collects more of the organisms >1 mm. The size fractions >1 mm were typically dominant in contributing to the total zooplankton biomass. We have little data available to describe if the zooplankton minimum in subarea 7 in 1983-84 also occurred in other subareas. In subarea 5 the biomass showed an increasing trend from low levels in 1987. In subarea 8 the biomass was relatively high from 1985 onwards (Fig. 5).

Capelin growth

Time series of mean length and weight of two years old capelin for the total stock show that the growth varied considerably in the period from 1977 to 1991 (Fig. 6a). Length and weight fluctuated in parallel, with minima in 1978, 1984 and 1991. The conditions for growth were better in the period 1980-83 and was particularly good in the period 1986 to 1990. The weight probably reflects the growth conditions in a more direct way than the length does, and it also fluctuates to a larger extent. Estimated mean growth in length and weight during the current season for the total stock are shown in Fig. 6b. These growth estimates were calculated by subtracting the observed length and weight of one-year old individuals the previous year from those of 2-years old individuals in a given year. These data should more accurately reflect the growth of the two-year-olds in the year indicated, since the growth at the 0- and 1-group stages of the same year class is subtracted. The variation in growth in current season is much larger than for mean length and weight (Fig. 6), as was to be expected. The maxima in the periods 1982-83 and 1986-90 are more pronounced. Low growth rate, corresponding to weight increments of 5 grams or less, were observed in the years 1977-81, 1984-85, and 1991. Time series of mean length and weight for 2-years old individuals from subareas 5, 7, and 8 are depicted in Fig. 7. The pattern of changes in mean length and weight for subarea 7 from 1979 to 1990 is quite similar to that for the total stock (Figs 6a and 7a). Estimated length increments in the current growth season calculated from otolith growth zones are shown in Fig. 8. The growth pattern obtained from otoliths for the total stock revealed the same main features as the pattern derived from length increments from 1- to 2-years of age ($r = 0.78$; Figs 6b and 8a). However, there were some discrepancies between the two sets of estimates. Thus the otolith method showed higher growth in 1980 and lower growth in 1990 than the observed length increments. The growth pattern from otoliths for subarea 7 showed very close correspondence to that for the total stock (Fig. 8a, c). The otolith growth estimates were typically higher for subarea 5 and lower for subarea 8 than the estimates for the total stock, and their pattern of interannual variability also showed some differences (Fig. 8a, b, d).

DISCUSSION

The variability in temperature and salinity are due to fluctuations in the Atlantic inflow to the Barents Sea. The variability in the currents may be explained by external forcing, but may also be a result of processes taking part in the Barents Sea itself (Midttun and Loeng, 1987). One process of importance is the formation and outflow of bottom water from the eastern basin, a process described in detail by Midttun (1985). The outflowing bottom water have to be replaced by inflowing Atlantic water from the west. The outflowing volume may vary considerably from year to year, and so will the corresponding inflow. Between 1982 and 1983, and between 1989 and 1990 there were extremely large outflows of bottom water from the eastern Barents Sea which coincided with increased Atlantic inflow (Loeng et al., 1992). Ådlandsvik (1989) and Ådlandsvik and Loeng (1991) have shown that the variability in the Atlantic inflow is closely related to the wind conditions. The warm periods in the Barents Sea are related to stable low pressure situations in the area, while cold periods are linked to high pressure situations. It is possible that wind-driven inflow during periods of stable low pressure will push

the bottom water in the eastern basin out of the Barents Sea and into the Arctic Ocean. Results from a laboratory model support this assumption (McClimans and Nilsen, 1990). The combination of an increased inflow caused by the atmospheric circulation and the associated outflow of bottom water allows for large and rapid temperature increases such as observed in 1982/83 and 1989/90 (Fig. 3). The inflow events and the associated variability in the ocean climate are major driving forces for the ecological conditions in the Barents Sea, affecting all trophic levels (Skjoldal and Rey, 1989; Blindheim and Skjoldal, 1992). The Barents Sea ecosystem is a zoogeographical transition zone where the inflowing Atlantic water is gradually transformed into Arctic water. This makes the Barents Sea strongly dependent on advective transport of boreal plankton with the inflowing water. The seasonal vertical migration of the dominant herbivore copepod Calanus finmarchicus interacts with the fluctuations in the ocean currents to determine the transport into the Barents Sea (Fig. 9). Atlantic water flowing into the Barents Sea during late autumn and winter will contain few C. finmarchicus which overwinters in deep water of the Norwegian Sea below the threshold depth at the entrance to the Barents Sea. Water flowing into the Barents Sea during spring and summer will, on the other hand, contain the Calanus population which then resides in the upper layer. This mechanism of low transport of Calanus during the overwintering period contributes to a lower and more variable zooplankton biomass in the southern and central Barents Sea than in the adjoining part of the Norwegian Sea (Degtereva, 1979; Skjoldal and Rey, 1989). The major inflow event in 1982 apparently ended late in the winter 1982/83. The southwestern Barents Sea was by then filled up with Atlantic water that had entered during autumn and winter and that contained few Calanus finmarchicus. This is a likely explanation for the observed low biomass in the central Barents Sea in 1983 and 1984 (Skjoldal and Rey, 1989). We have previously shown that the zooplankton minimum was due primarily to low abundance of C. finmarchicus (Skjoldal et al., 1987). Besides the influence of advective transport, there is also a large influence on zooplankton stocks by growth and predation within the Barents Sea. Most of the data in the time series of zooplankton biomass for subarea 7 (Fig. 4) are from Atlantic water where Calanus finmarchicus is a dominant species. C. finmarchicus spawns in spring and the new cohort develops to reach the overwintering stage V by summer (Hassel, 1986; Skjoldal et al., 1987). After the growth period, predation from capelin and other predators will reduce the abundance and biomass of Calanus during autumn. Due to this cohort development and predation, a considerable seasonal variation in zooplankton biomass is expected. This is exemplified by results from June and August 1981 and from May and September 1987 and 1989 (Fig. 4). The seasonal variation is one reason why a direct comparison between zooplankton biomass and capelin growth is difficult. The growth of capelin has shown large variation during the late 1970s and the 1980s, with minima in 1977, 1984 and 1991 and maxima in 1980, 1982-83 and 1988-90 (Figs 6 and 8). Comparing these results with the temperature and salinity anomalies in the Fugløya-Bjørnøya and Vardo-N sections (Fig. 3), it is seen that the growth minimum in 1977 coincided with the onset of large negative anomalies. The low growth in 1984-85 also appeared in a period of rapidly decreasing anomalies. The periods of high growth in 1980 and 1982-83 occurred under rapidly increasing temperature anomalies. The period of high growth in 1988-90 started under average temperature conditions followed by a rapid increase to high positive anomalies both

in temperature and salinity. Consequently, there is a tendency for high growth to occur during periods of warming and low growth to occur during periods of cooling. This could reflect a general pattern of larger advective transport of plankton with the inflowing current during periods of warming and less transport during cooling periods following inflow events. Temperature may also have a direct influence on growth and distribution of capelin. Gjøsæter and Loeng (1987) found that the mean temperature in the capelin feeding area varied from year to year during the period 1974 to 1985. In periods of increased inflow of warm Atlantic water, the capelin stock would partly compensate for the increased temperature by shifting the feeding area north- and eastwards. Correspondingly, there was a south- and westwards shift in distribution in periods of water cooling. Such shifts in distribution may act to reduce the effects of inflow events on growth rate. Comparison of the temporal pattern of change in capelin growth rate (Figs 6b and 8a) with the time series of zooplankton biomass (Fig. 4) reveals no significant correlation ($r = -0.24$, $n = 12$). A strict relationship between capelin growth rate and zooplankton biomass is not to be anticipated, however, for several reasons. One is the seasonal change in zooplankton biomass already mentioned. A second reason is the dynamical nature of the interaction between capelin and zooplankton, where capelin on its feeding migration can rapidly deplete the zooplankton stocks, particularly the preferred large food organisms distributed in the upper water layer (Hassel et al., 1991). A third reason is the selection in sampling where large forms of zooplankton such as euphausiids and amphipods are not representatively sampled by the vertical net hauls. Despite these limitations, there are some broad similarities between capelin growth rate and mean zooplankton biomass in the subareas. For subarea 7, both variables showed maximum in 1980, minimum in 1984, and maximum again in 1987 or 1988 (Figs 4 and 8c). The patterns were different for subarea 5 in the southeastern Barents Sea where capelin growth rate and zooplankton biomass were low in 1987 (Figs 5a and 8b). In subarea 8 (the northeastern Barents Sea) there was no clear relationship (Figs 5b and 8d). The capelin stock size in numbers fluctuated by a factor of more than 200 during the period 1979-1991 (Fig 10a). One would expect density dependent influence on growth rate to be easily recognizable during such large stock size fluctuation. Such influence has for instance been shown for Atlantic herring where an inverse relationship between growth rate and yearclass strength has been found (Toresen, 1986). However, the density dependency is complex in the present case of the Barents Sea capelin. Fig. 10b depicts the growth history of three selected yearclasses. The 1978 yearclass was chosen as representative for the growth during a period of intermediate to high stock size from 1979- 1982. By comparison, the 1982 yearclass showed considerably lower growth despite the rapid decrease in stock size from 1983 to 1986. We interpret this as an overriding influence by the low availability of zooplankton food on the capelin growth rate. The low growth rate was one factor which contributed to the rapid decline of the capelin stock. The event of inflow of Atlantic water and associated warming of the Barents Sea had thus a marked influence on capelin growth, but in an intricate and non-linear manner. Only through knowledge of the mechanisms involved (Fig. 9) can such relationships be properly explained in hindcast and used for predictive purposes in future models (Giske et al., 1992). The recovery of the capelin stock was surprisingly rapid from the low stock size in 1986 to a high level in 1990 (Hamre, 1991, 1992; Fig. 10a). The high individual growth rate (Figs 6b and 8) and correspondingly early

maturation played an important role for this rapid recovery. The rapid growth of the 1987 yearclass is apparent from Fig. 10b which shows that the mean weight of 3-years old individuals of this yearclass was almost three times that of the 1982 yearclass. The highest capelin growth rates were seen in the period from 1988 to 1990 (Figs 6b and 8). This corresponded to the second inflow event and warm ocean climate in 1989-90. While the capelin stock was at its low level in the late 1980s, the Barents Sea ecosystem was considered to be in a disturbed state with disrupted energy flow to higher trophic levels (Borisov, 1991). As we see now, this situation was transient, and natural regulatory processes caused a rapid recovery of the capelin stock that rectified the "imbalance" of the ecosystem. Reduced predation by capelin is likely to have contributed to a general increase in the amount of zooplankton after the minimum in 1984 (Fig. 4). This increase in zooplankton contributed in turn to high capelin growth rate. Feeding capelin selects larger zooplankters, and euphausiids, amphipods and large copepods such as *Calanus hyperboreus* and *C. glacialis* are important food items for the older yearclasses of capelin (Hassel, 1984; Panasenko, 1984). These large zooplankters have a life cycle of more than one year. Dominant euphausiids in the Barents Sea, such as *Thysanoessa inermis* and *T. raschii*, reach maturity after two years (Dalpadado and Skjoldal, 1991). There will therefore be a delay in their population increases following a decrease in predation mortality. It is likely that the rapid decrease in capelin stock between 1984 and 1986 was associated with a marked reduction in predation and that the populations of euphausiids and amphipods increased in response to this. There is indirect evidence for increase in abundance of *Parathemisto* spp. from stomach content data for cod (Mehl, 1989, 1991). High abundance of large food items was probably a decisive factor for the rapid growth of capelin when the stock recovered from low levels. The growth rate of capelin was again low in 1991 and comparable to growth rates in 1977 and 1981 (Fig. 6b). The large capelin stock size (Fig. 10a) is the probable cause for the reduced growth rate, through its effect on the feeding environment (Hassel et al., 1991; Anon., 1992). The relationship between stock size and feeding conditions is complex, however, as both the total areal distribution as well as smaller scale distributional patterns will determine the available food levels and feeding conditions of capelin. The dynamic nature of the capelin-zooplankton interactions makes it necessary to address the issue of density dependent growth more closely through the use of analytical and numerical models (Giske et al., 1992). In conclusion we can state that variation in growth rate has played a decisive role in the large fluctuation of the capelin stock size in the recent decade. Large-scale changes in the physical conditions caused by the major inflow events and associated variability in ocean climate have been a primary driving force for the ecosystem dynamics (Sherman, 1991a, b). The physical forcing has, however, to a considerable degree acted through various biological interactions in the ecosystem. Thus we can link the major changes in capelin growth rate and stock size fluctuations with changes in zooplankton. Variation in fish recruitment has also had important effects on the ecosystem dynamics. Strong yearclasses of cod and herring in 1983 caused important interactions and effects in the system (Skjoldal and Rey, 1989; Hamre, 1991, 1992; Mehl, 1989, 1991). One probable effect was to cause recruitment failure of capelin in 1984 and 1985 due to predation on capelin larvae from juvenile herring (Fossum, 1992). The zooplankton minimum in 1984 may have contributed to low growth rate and thereby high predation mortality of capelin larvae in this period (Skjoldal and Rey, 1989).

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Appendix A Figure legends

Fig. 1. Map of the Barents Sea showing the MULTSPEC subareas used for calculating mean zooplankton biomass and capelin size and growth rate. The positions of three hydrographic sections are also shown. A: Fugloya - Bjornoya; B: Vardo -N; C: Kola-section.

Fig. 2. Three years running average of yearly temperature in the Kola-section during the period 1900-1990, based on data from Bochkov (1982) and from PINRO, Murmansk (pers. comm.) From Loeng (1991).

Fig. 3. Anomalies of temperature (left) and salinity (right) in the sections Fugloya - Bjornoya (A) and Vardo-N (B). From Loeng et al. (1992).

Fig. 4. Mean zooplankton biomass for vertical net hauls from stations in the MULTSPEC subarea 7 in the Barents Sea. Vertical lines denote twice the standard deviation, with numbers of stations given at top of the figure. Based on cruises in July 1979, June 1980, June and August 1981, June 1982-84, August 1985, September/October 1986-1990, and May 1987 and 1989. Based on data from Skjoldal et al. (1987) and Skjoldal, Hassel, and Omli (unpubl. results).

Fig. 5. Mean zooplankton biomass for samples obtained with vertical net hauls (left columns) and MOCNESS (right columns) for stations in MULTSPEC subareas 5, 7, and 8. The biomass is given for different size fractions as follows: open columns - <1mm; vertically hatched columns - > 1 mm or 1-2 mm; cross-hatched columns - >2 mm. Samples of the >2 mm fraction were not taken in 1985-86 and for the vertical net hauls in 1987. From Skjoldal, Hassel and Omli (unpubl. results).

Fig. 6. a. Length and weight in September for two-years old individuals, averaged for the total stock of Barents Sea capelin from 1977 to 1991. b. Mean increase in length and weight in current year for the total stock of two-years old capelin for the years 1977-91.

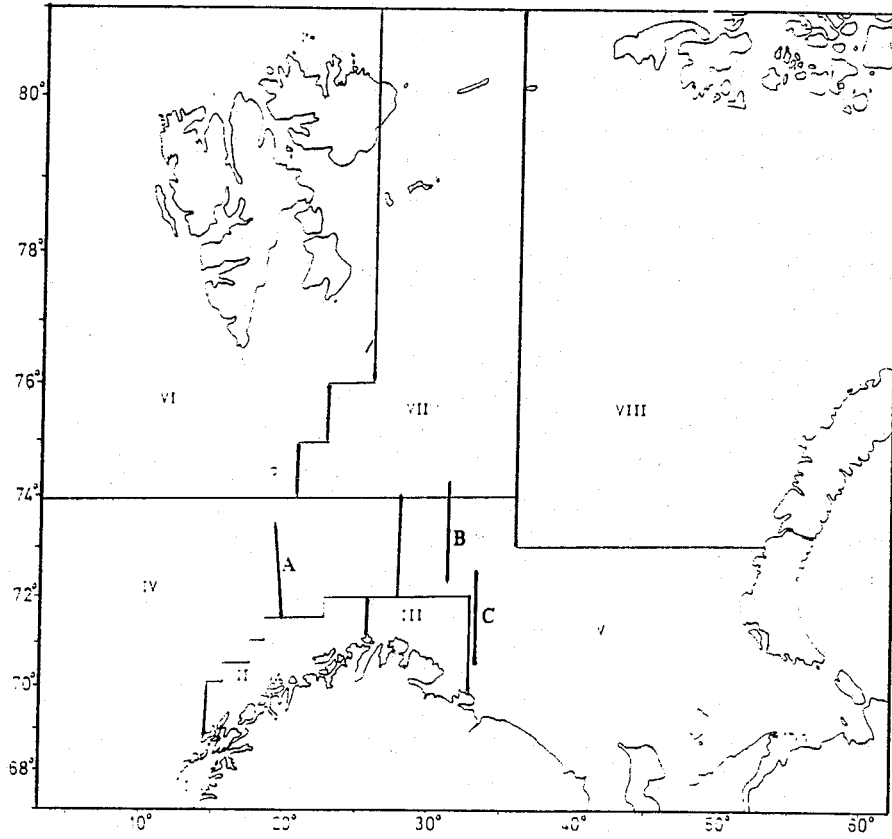
Fig. 7. Mean length and weight in September of two-years old capelin sampled in (a) subarea 7 from 1977 to 1990, (b) subarea 5, and (c) subarea 8 from 1985 to 1990.

Fig. 8. Estimated growth in current year as length increment calculated from otolith growth zones for capelin for the period 1977-90. a. Total area. b. Subarea 5. c. Subarea 7. d. Subarea 8.

Fig. 9. Life cycle and transport of Calanus finmarchicus into the Barents Sea. Animal behaviour, reflected in seasonal vertical migration to overwintering depth in the Norwegian Sea below the threshold depth at the entrance to the Barents Sea, interacts with Atlantic inflow to control the advective transport of Calanus.

Fig. 10. A. Size of the Barents Sea capelin stock of two-years age or older for the period 1979-91. B. Growth curves as mean weights for 1 to 4 years old individuals for three selected yearclasses: 1978, 1982, and 1987.

Figure 1



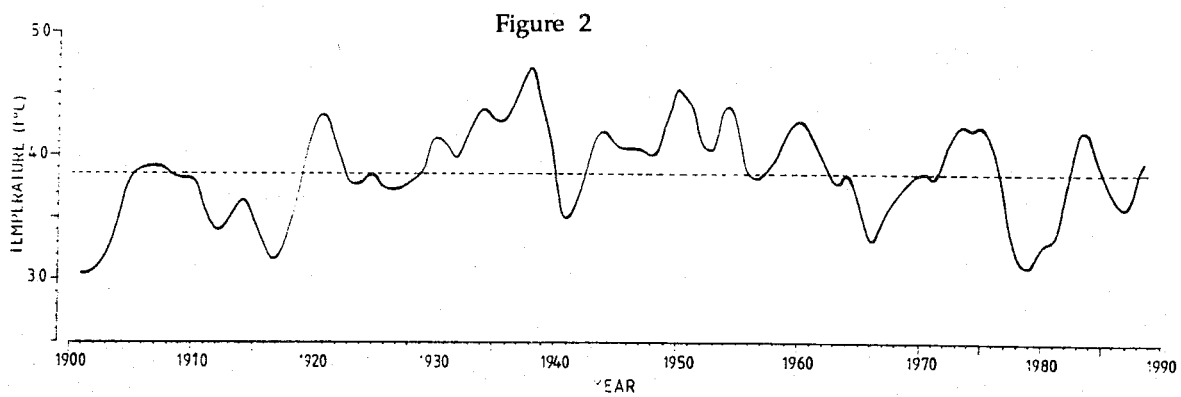


Figure 3

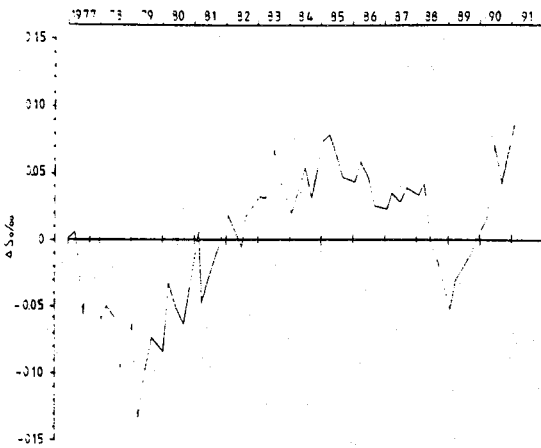
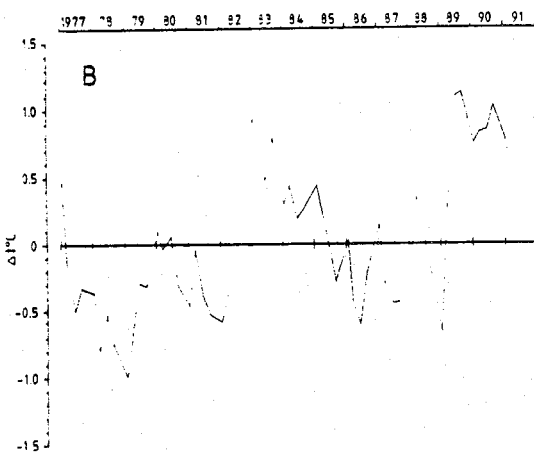
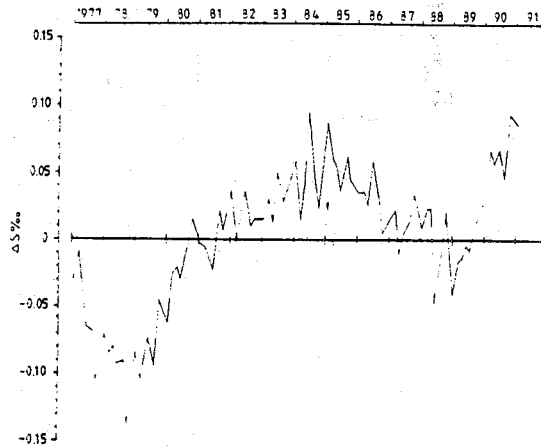
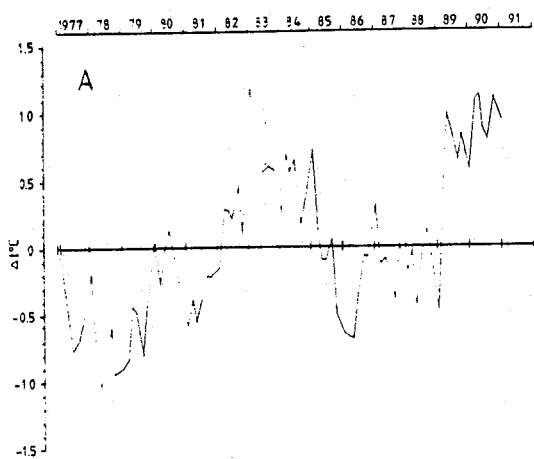
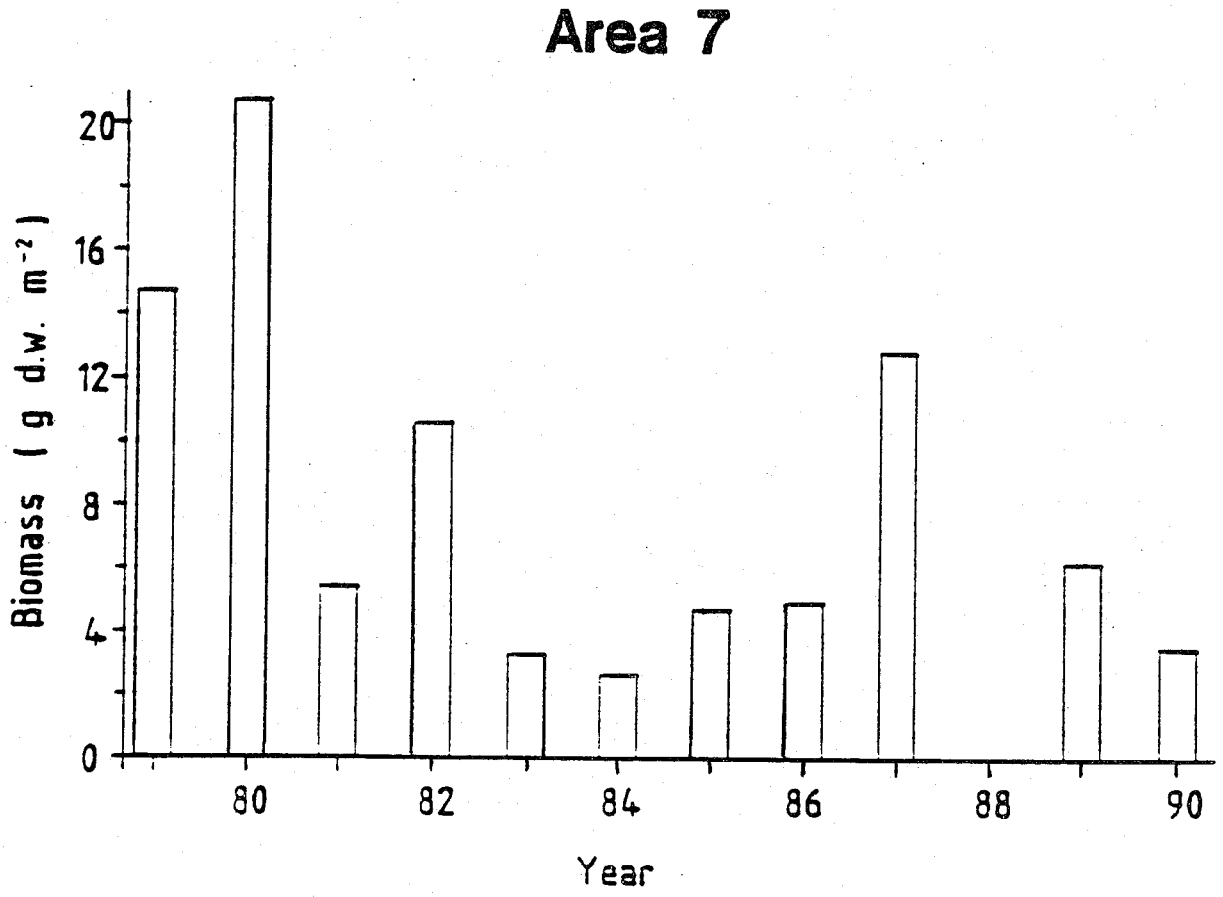
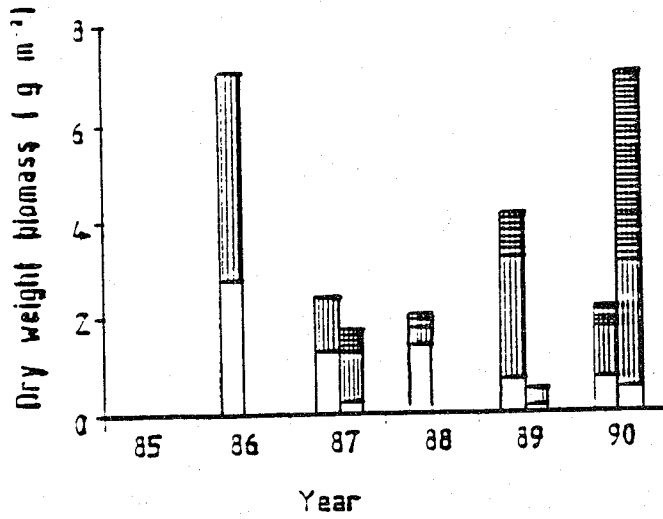


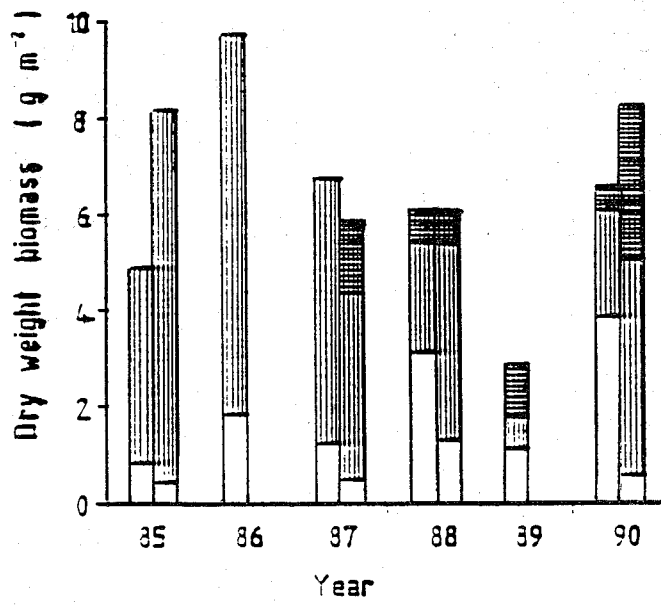
Figure 4



Area 5



Area 8



Area 7

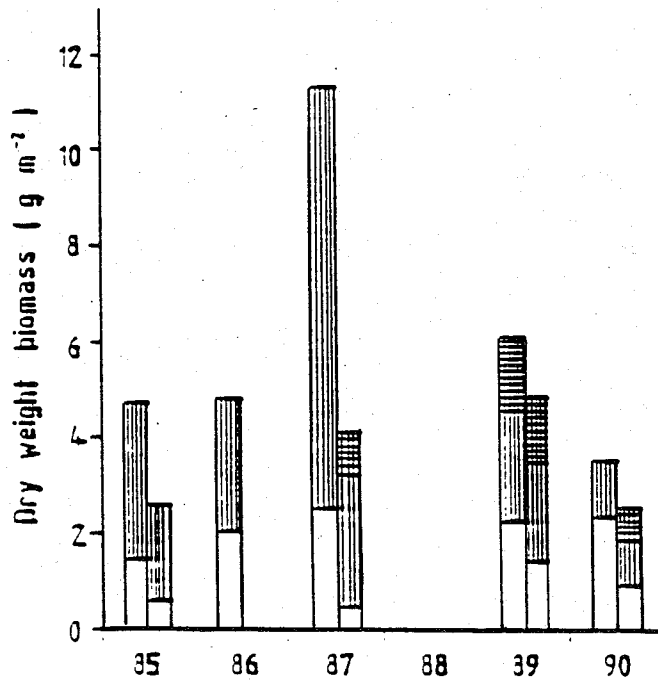
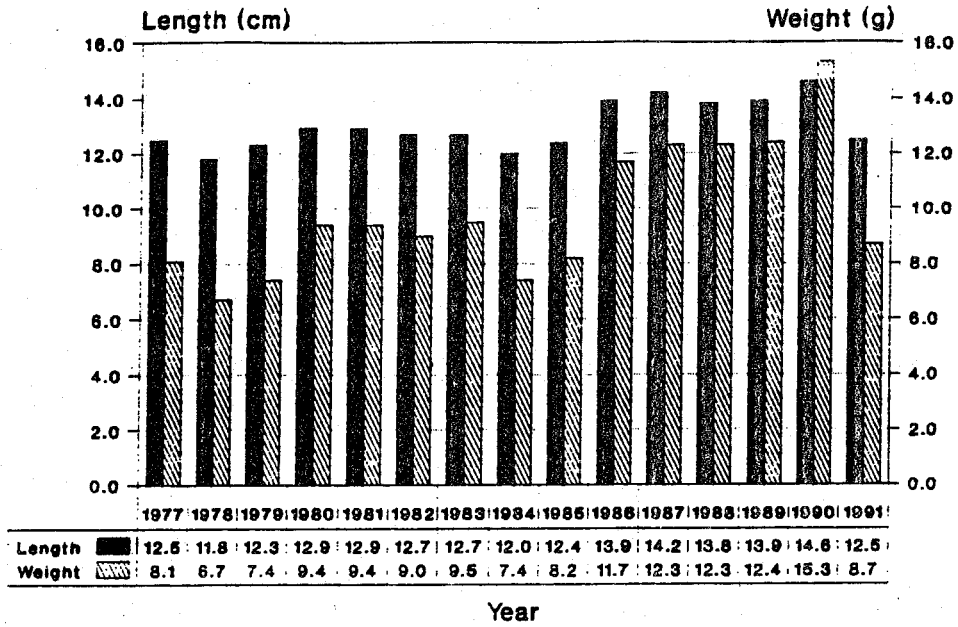


Figure 6

Capelin Age 2
Length and weight at age
Total area



Capelin Age 2
Growth in current year
Total area

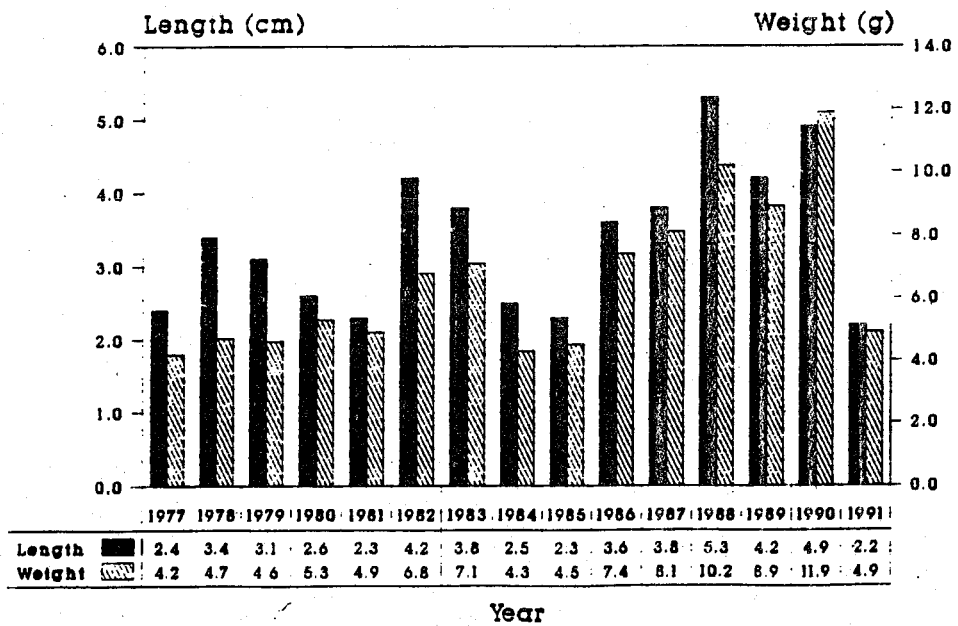
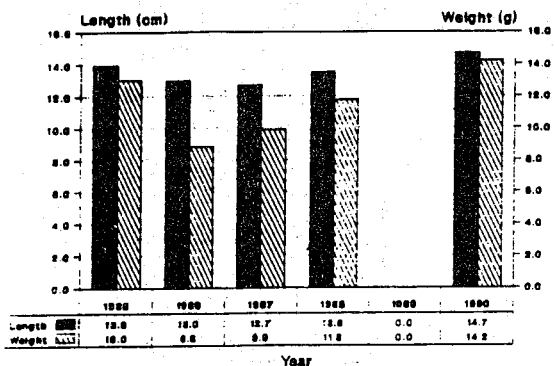
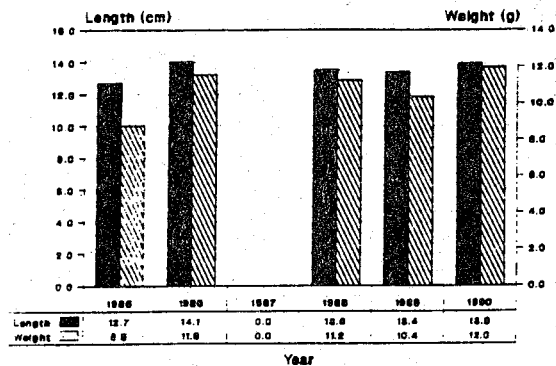


Figure 7

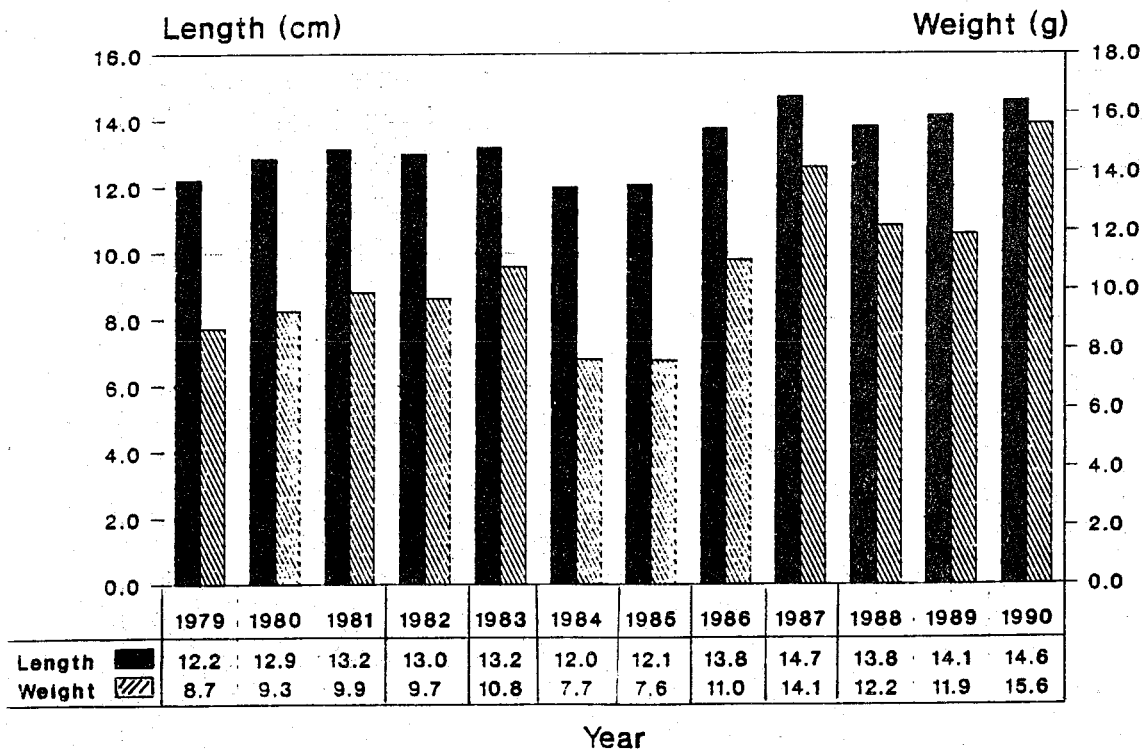
Capelin Age 2
Length and weight at age
Subarea 5



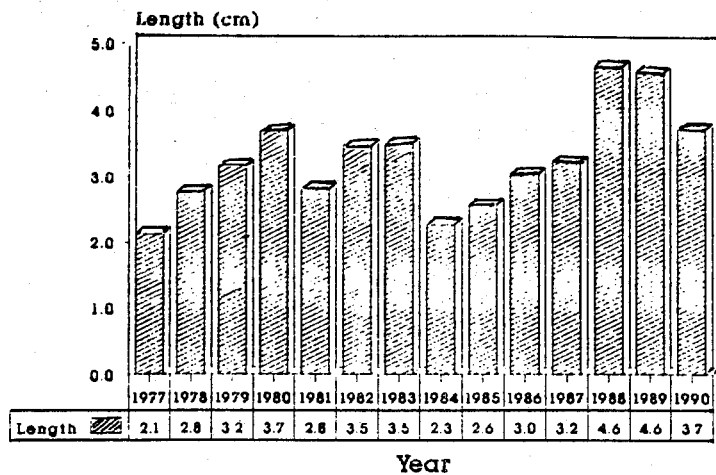
Capelin Age 2
Length and weight at age
Subarea 6



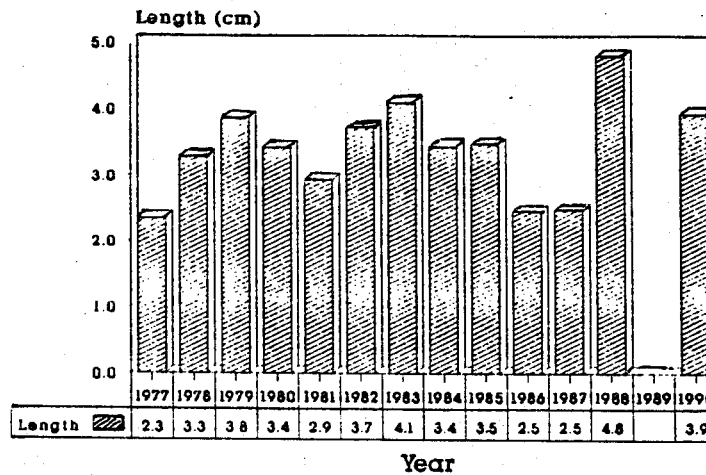
Capelin Age 2
Length and weight at age
Subarea 7



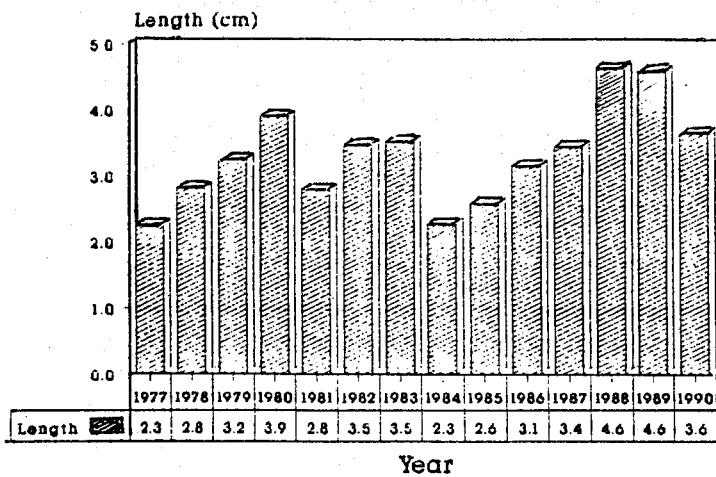
Capelin Age 2
Backcalculated growth in current season
Total area



Capelin Age 2
Backcalculated growth in current season
Subarea 5



Capelin Age 2
Backcalculated growth in current season
Subarea 7



Capelin Age 2
Backcalculated growth in current season
Subarea 8

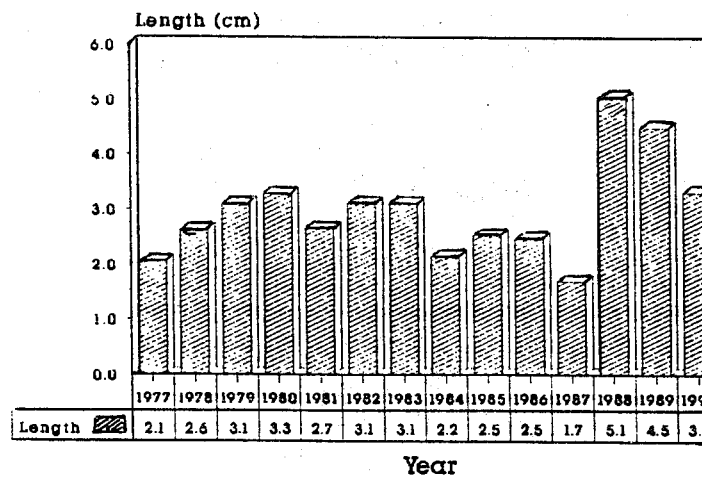


Figure 8

Figure 9

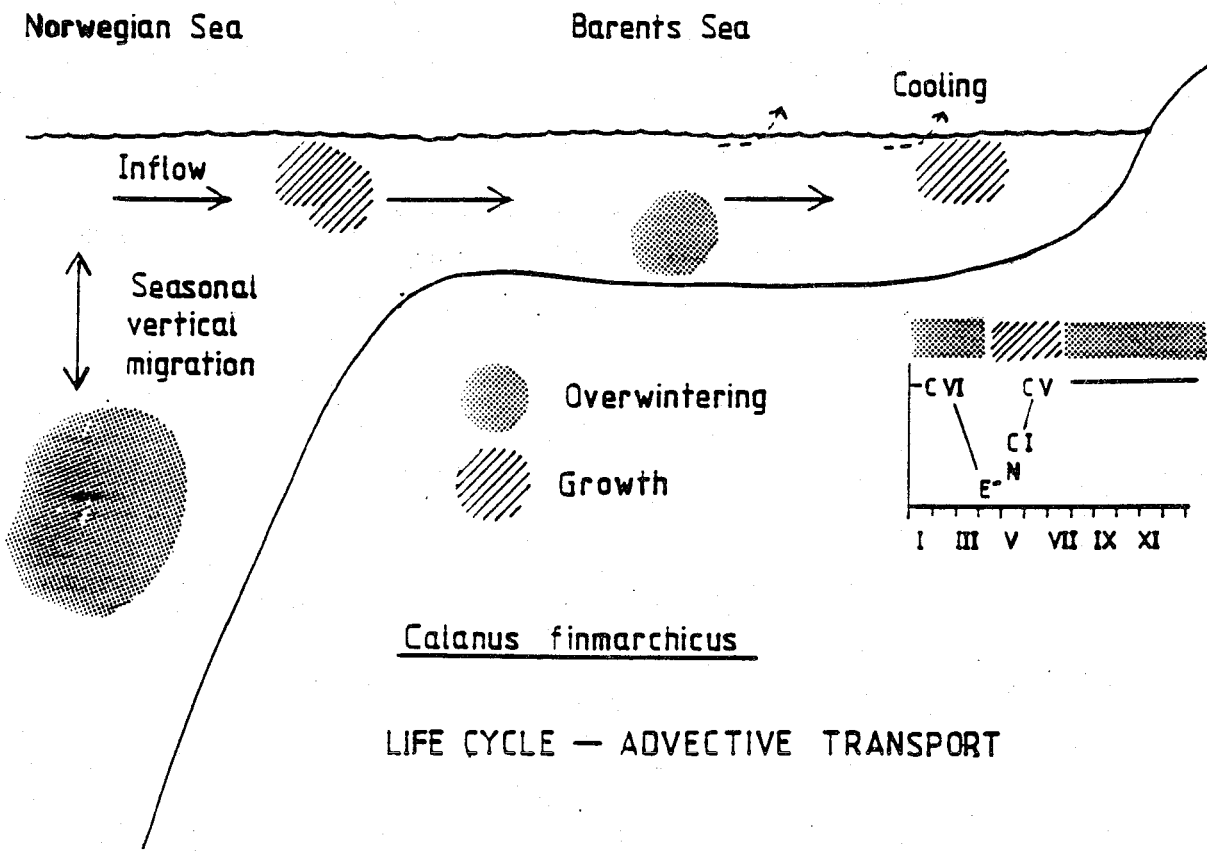


Figure 10

