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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. Based on measurements of stomach evacuation rates in the appropriate temperature interval and data from a combined Soviet-Norwegian stomach sampling programme, predation mortalities are calculated by a simplified version of the IMR multispecies model for the Barents Sea — MULTSPEC. Cod-capelin interaction parameters and migration parameters for capelin in MULTSPEC are also estimated. The use of the predation mortalities calculated from the multispecies model in a single-species model used for capelin management is discussed.

Introduction.

Up to now, all fish species in the Barents Sea have been managed separately. The single-species management has in the last years failed partly because species interactions were not taken into account (Mehl and Tjelmeland, 1988). This has been the case both for the capelin stock (increased mortality due to predation from cod), and for the cod stock (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.

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.

We think that the work presented in this paper will 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. temperature model, measurement of evacuation rates, measurement of fish stocks in absolute terms) and the management-relevant outcomes must be re-evaluated at a later stage. However, the paper addresses most of the practical problems 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. This paper will serve two purposes: it will (1) explore some possibilities of strengthening the management of Barents Sea capelin by introducing predation from cod on the spawning stock of capelin and (2) it will be an introduction to the MULTSPEC work. Therefore, slightly more material will be covered than are needed to do and discuss the actual estimations performed in the paper.

Description of the Barents Sea ecosystem.

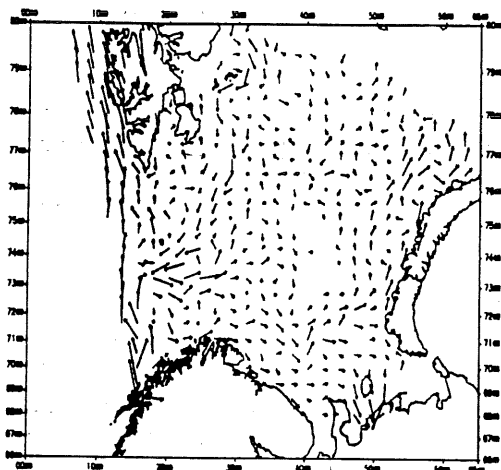
The description of the Barents Sea ecosystem given here is centered on cod and capelin. Only those features of the ecosystem having a bearing on the present and near future use of the MULTSPEC model are dealt with, although we sometimes go a little further than is strictly needed to serve as a basis for the present paper. The herring can have a strong impact on both cod and capelin, see (Hamre, 1989) and (Hamre, 1990), but we will not consider such effects in this paper. A review of the whole ecosystem in the Barents Sea can be found in (Loeng, 1989) and (Skjoldal and Rey, 1989).

Oceanography.

The warm Atlantic current splits into two branches, one branch entering into the southern regions of the Barents Sea and one branch flowing along the western coast of Spitsbergen. The monitoring of the current with current meters and bouys is difficult and costly. A simulation program developed at SINTEF, Trondheim, reveals the general current pattern well and may in the future serve as a basis for ecological modeling (as distinct from "multispecies modeling", where only fish interactions are taken into account), (Slagstad *et al.*, 1989).

The fish spawns at the southern and western borders of the Barents Sea and for some species (cod, herring) far south on the Norwegian coast. The current system determines the drift of the larvae and hence the nursery area. Also, variations in the current system brings about variations in the sea temperature, which in turn strongly influences biological processes (growth and maturation of fish).

Figure 1 Map of the Barents Sea current system — simulations at SINTEF.



The migration of fish, perhaps spawning migration in particular, is probably linked to the physical environment. Therefore, the geographical distribution of fish may be influenced by the currents through the geographical distribution of the spawning stock and the subsequent geographical distribution of the larvae, which in turn is strongly influenced by the currents. Strong variation in the currents may thus lead to a long-term change of geographical overlap between the species due to this feedback loop, as well as having an immediate short-term effect. Because of the geographical nature of inter-species interactions (growth, predation) this may be a major factor behind the natural fluctuation of the species.

Understanding the changes of the physical environment is therefore of paramount importance for modeling. At the IMR, work is done in two different directions:

1. Melting and freezing of water may lead to a build-up of dense bottom water that eventually may trigger exchange of water masses through outflow into the Norwegian Sea, see (Midttun, 1985).
2. The wind system may lead to large shifts in the current pattern of the upper layers. A numerical model (Aadlandsvik, 1989) may in fact explain the overall climatic changes we have had in the 1970s and 1980s.

Capelin

The capelin spends all its life in the Barents Sea. It spawns at the coasts of Norway and USSR along the southern borders of the Barents Sea. The larvae drift north- and eastwards. The nursing area consists of the southern and central parts of the Barents Sea. The juveniles feed on small plankton organisms. Below 10–12 cm length, copepods are the most important food item. At greater body lengths (above 13–14 cm), amphipodes and krill play an important role (Lund, 1981). 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).

Reproduction.

Maturation. During the autumn, immature capelin and maturing capelin may be found in the same areas. The degree of maturation is determined empirically by either a visual scale based on the gonad size or by microscopic investigations of egg size giving a more quantitative index for maturation (Forberg, 1982), hereafter referred to as the Forberg index. The latter method is only applicable on females. The average maturation increases with fish length, both for males and females, see (Forberg and Tjelmeland, 1985). During winter and spring there is a geographical segregation between immature and maturing capelin. Both groups migrate southwards, but the maturing capelin migrates faster.

Spawning. The capelin spawns in two distinct time periods. The main spawning period is in March-April. A part of the capelin stock that does not spawn in this period may gain enough energy during the spring plankton blooming to spawn in June-July. It is not yet known how big this part of the spawning stock is compared to the main spawning stock. In the single-species model that was used with management from 1982 to 1985, the spawning stock included both early and late spawners (Hamre and Tjelmeland, 1982), (Anon., 1983).

In the multispecies modeling project MULTSPEC we attempt to quantify the early spawning component separately from the late spawning component. It should thus be possible to quantify the late spawning component by subtracting the early spawning component from the total spawning component. The latter can be estimated analogously to what was done in (Hamre and Tjelmeland, 1982), by comparing the simulated stock to the total stock next year. However, in order for these calculations to be accurate, the predation from cod in the period April-June should be taken into account. The stomach data material in this period is, however, sparse. In this paper, only the main (early) spawning will be considered.

Natural mortality. Aside from the spawning mortality, the predation from cod is the largest component of the natural mortality on mature capelin. 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.

Geographical distribution and migration.

In the autumn the capelin is distributed in the central and northern parts of the Barents Sea, feeding on krill and copepods. The stock has been surveyed in a joint IMR-PINRO (Murmansk) cruise in September each year since 1972 using acoustic methodology. Figures 2—6 show the distribution in 1983—1987¹. In order to ease the comparison of the model results (i.e. estimations of migration and predation) with the actual initial geographical distributions, we have superposed the geographical divisions used in the model (see page 8).

¹ The maps should be regarded as showing the extent of the geographical distribution each year. Comparisons of abundance between years may not be correct. In the model data, the acoustical information is processed further using data on instrumental characteristics and trawl data.

Figure 2 Geographical distribution of capelin in September 1983.

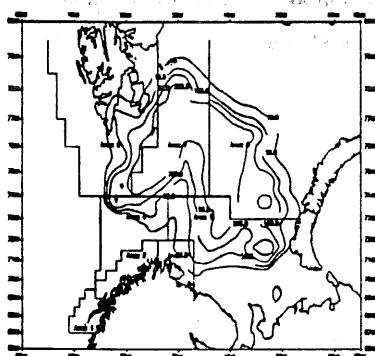


Figure 3 Geographical distribution of capelin in September 1984.

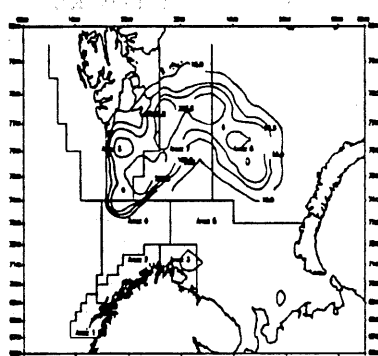


Figure 4 Geographical distribution of capelin in September 1985.

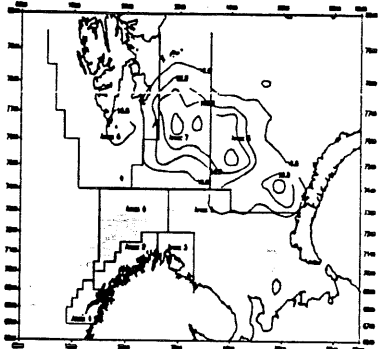


Figure 6 Geographical distribution of capelin in September 1987.

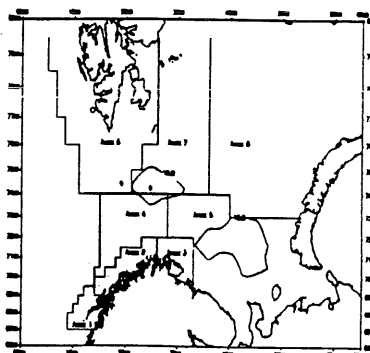
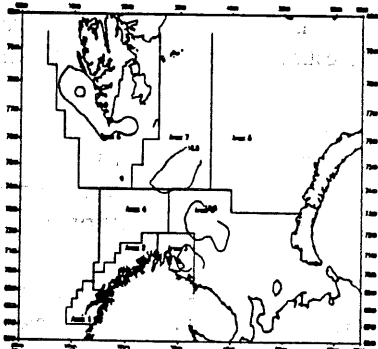


Figure 5 Geographical distribution of capelin in September 1986.



There is a north and westwards displacement from 1983 to 1984. From 1984 to 1985 there is either a bulk westwards displacement, or the most western part has been fished up prior to the cruise and a small eastern component has emerged near Novaja Zemlja.

In 1986 and 1987 the stock was small and southerly distributed. In 1988 the stock is recovering and displaced more northerly than in 1987 and 1986, but further south than in 1983-1985 (figure 7).

Migration of mature capelin. The general features of the spawning migration is well known. Depending on the environmental conditions, the migration according to Soviet investigations may in warm years have an easterly pattern with spawning at the most eastern parts of Norway and along the Kola peninsula and in cold years a westerly pattern with spawning mainly west of 31° longitude (Ozhigin and Luka, 1987).

The geographically distributed stock data that can be used to track the migration of mature capelin are rather sparse. In 1989 we have three consecutive cruises shown in figures 8-10 together with the initial autumn distribution (figure 7).

Figure 7 Geographical distribution of capelin in September 1988.

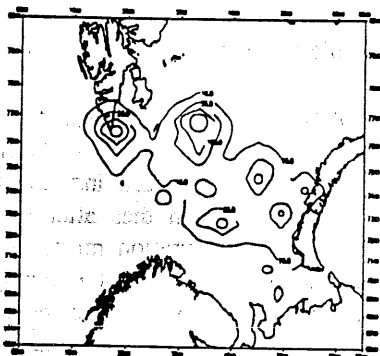


Figure 8 Geographical distribution of capelin in January 1989.

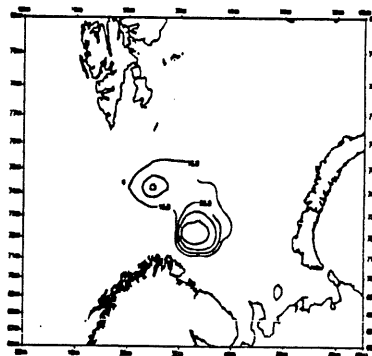


Figure 9 Geographical distribution of capelin in February 1989.

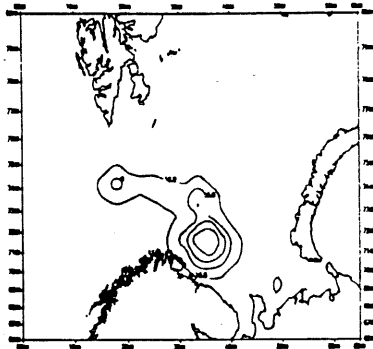
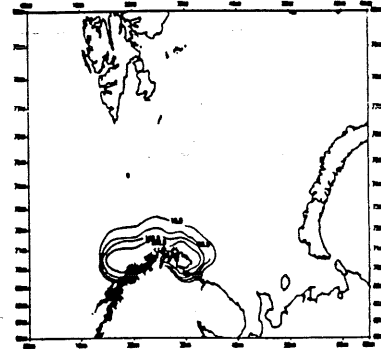


Figure 10 Geographical distribution of capelin in March 1989.



The impression is a mainly southern migration until January, then a south-eastern migration followed by an upstreams (see currents map, page 2) western migration prior to spawning, which takes place in April for the main spawning component. The 1989 data are the only series of acoustic estimate we have on the spawning stock within one year so far.

Both the length and age distributions of the spawning stock have east-to-west gradients that seem to vary irregularly from year to year (Tjelmeland, 1987). A fundamental problem arises in that we are not able to weight the eastern and western parts of the spawning stock properly relative to each other. Thus, old methods attempted by the working group (Anon., 1982) to combine the maturation model and the age distribution in the spawning stock, as measured by the March catches, may be liable to errors.

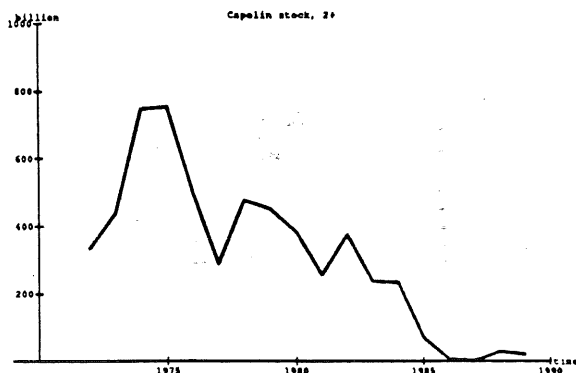
This paper tries to overcome some of these difficulties, partly by using geographically distributed data (stomach content of cod) and partly by letting the ignorance of the geographical variation of the spawning stock length distribution be incorporated into the variance of the maturation parameter estimate.

Growth. The capelin is a fast growing fish. It may increase its weight by 100% during the growth season. The males grow faster than the females (Gjøsæter, 1985). During the September cruises the largest fish is always found in the western regions, even for capelin of the same sex, age and maturity stage (Tjelmeland, 1987), (Gjøsæter, 1985). By relating growth of capelin to the autumn concentration of capelin, it is not possible to verify any density-dependent growth (Gjøsæter, 1986). Of interest to the present study is the growth during the winter season from September to April. However, how the growth varies throughout the year is poorly known.

Stock development

The development of the capelin stock in the period 1972–1989 is dramatic indeed:

Figure 11 The development of the capelin stock 1972–1989, 2+, billion. Acoustic estimates in September.



The period 1972–1989 may be divided into two 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. 1983–1989. The capelin stock collapsed after the strong 1983 yearclass of herring occurred in the Barents Sea and because the cod stock recovered due to the strong 1983 and 1984 yearclasses. The

driving forces are here stock interactions and the development can only be understood in a multi-species context.

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.

Figures 12–16 show the distributions of the Barents Sea component (young cod) in February/March in the period 1984–1988². The data shown are the combined values for cod and haddock from acoustical surveys. At the acoustical surveys it is not possible to distinguish between cod and haddock, the splitting of data is done using additional information from the bottom trawl. Cod and haddock have different behaviour with respect to the trawl. This introduces an additional error. Investigation of these behavioural differences is a separate area of research (Engås and Godø, 1989b), (Engås and Godø, 1989a).

² The data are obtained from two cruises, the young cod cruise in the Barents Sea and the spawning cod cruise in the Lofoten-Vesterålen area. The distributions shown are the acoustical cod-haddock information, not information from the associated trawl survey. In 1985 and 1986, no acoustical measurements were made on the spawning component. The significance for this paper of the distinguishing between the young cod and the spawning component is that one might expect different feeding behaviour between the components. The area distribution of cod used in the model is based on the acoustical data and scaled to the VPA estimations.

Figure 12 Distribution of cod and haddock in the Barents Sea February–March 1984.

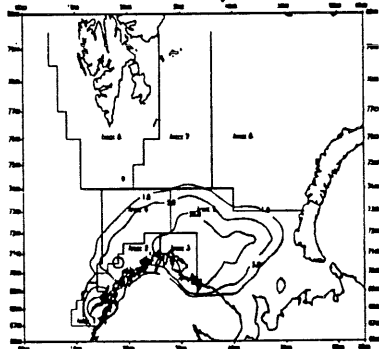


Figure 13 Distribution of cod and haddock in the Barents Sea February–March 1985.

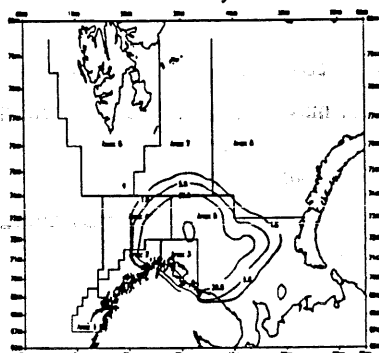


Figure 14 Distribution of cod and haddock in the Barents Sea February–March 1986.

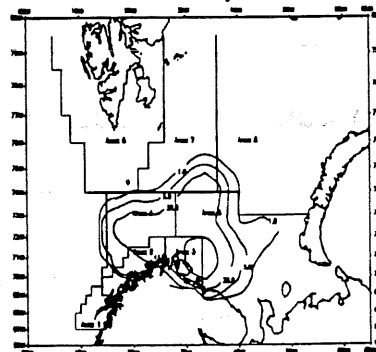


Figure 15 Distribution of cod and haddock in the Barents Sea February–March 1987.

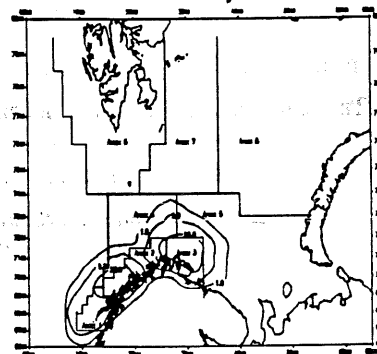
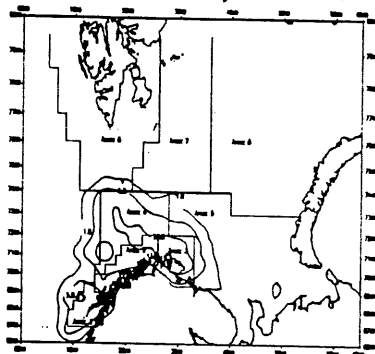


Figure 16 Distribution of cod and haddock in the Barents Sea February—March 1988.



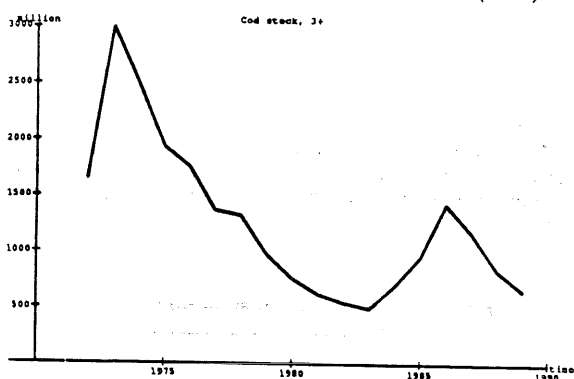
The juveniles grow up in the eastern Barents Sea. A seasonal westwards migration takes part in the first part of the year, followed by a return migration. As the cod grows older, the return migration will not end as far east as where it started. Thus the distribution is shifted to the west as the fish grows older.³

³ The cruise on which these acoustical data have been obtained is the same cruise on which the data underlying the present study have been obtained. The Spitsbergen component is not present in this data material, because the annual young cod survey cannot cover that region because of ice.

Stock development.

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

Figure 17 The development of the cod stock 1972-1989, 3+, million, VPA data (1989).



The decline until 1983 is most probably due to high fishing pressure. The subsequent increase is due to improved recruitment. However, the stock is now declining faster than expected. This may partly be due to cannibalism, unaccounted fishery or discards. Also, the individual growth of the cod declined from 1985 to 1988 (Ajiad *et al.*, 1989). The growth decline was not anticipated by the Arctic Fisheries working group and the quotas amounted to a higher number of individuals than expected. The main reason for the growth decline is probably the collapse of the capelin stock (Ajiad *et al.*, 1989).

Cod-capelin interactions.

There is a considerable overlap between cod and capelin:

1. During the spawning migration of capelin, when the capelin must cross the distribution of cod to reach near-shore waters to spawn. In this paper, we will attempt to quantify the predation by cod on capelin in this period.
2. During the period April-June, when the capelin stock may have feeding migrations far southwards. This migration may, however, be highly variable from year to year, depending on physical conditions and food abundance for capelin.
3. More or less throughout the year in the Spitsbergen area. In this area, some occasions of spawning capelin has been reported, but are believed to be of minor significance.

In this paper, we will only deal the Barents Sea component of cod feeding on the spawning migration.

The cod is to a large extent dependent on capelin for food, as may be inferred from the recent history, when the cod growth was markedly slowed when the capelin stock collapsed. There is also reason to believe that the predation from cod has a substantial impact on the dynamics of the capelin stock.

The migration of capelin is probably not affected by the cod stock. The young cod may migrate following the capelin stock in spring. Cod smaller than 20-30 cm will not eat capelin (Mehl, 1989).

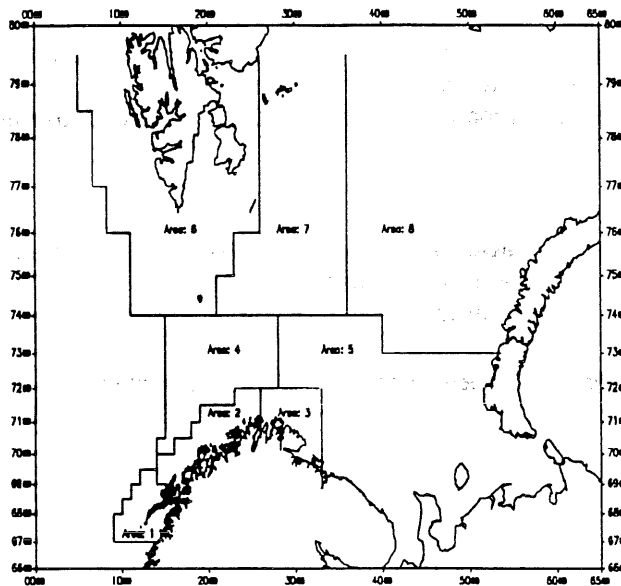
Model.

The model used is a subset of the IMR simulator MULTSPEC. However, in this paper only those parts of MULTSPEC used in the present study are described. The mature capelin-cod subsystem is fairly independent of the rest of the model, no parameters that are not estimated from data are used.

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 18 Model area distribution of the Barents Sea.



As a part of the process of exchanging area distributed catch information between Norway and the Soviet Union, we will switch to a division into seven areas in the near future. A division into these 8 (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:

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

where the 8-dimensional column vector N is the population number in each area for given time, stock and age. The 8×8 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 .

In order to achieve consistency with other written documentation about MULTSPEC, we have kept the same parameter names as in the model software, even though this notation might appear to be unnecessary complicated.

During the estimations of the capelin spawning migration, the number of parameters have been reduced by defining linear relations between the elements of the migration matrices for January, February and March, see page 18. The parameters are:

1. x_1 : The overall east-west migration in January. Larger positive value means migration more to the west.
2. x_2 : The overall north-south migration in February. Larger positive value means stronger southwards migration.
3. x_3 : The overall north-south migration in March. Larger positive value means stronger southwards migration.

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 11.

The number per age and weight per age data used are VPA data from the 1989 Arctic Fisheries working group (Anon., 1990). 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 and σ is the standard deviation. The condition factors used are the same as in the working group prediction, i.e. $c=0.008$ for age 4 and younger and $c=0.009$ for older fish. The standard deviation used is 3 cm for age 1, 4 cm for age 2 and 5 cm for age 3 and older. Only fish of age 3 and older are considered potential predators on mature capelin. Details of the derivation of the mean length-mean weight relationship can be found in (Magnusson and Palsson, 1989). The area distribution is based on data from the annual winter surveys (Dalen *et al.*, 1984), (Høyen *et al.*, 1985), (Nakken *et al.*, 1986), (Godø *et al.*, 1987), (Høyen *et al.*, 1988).

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. The MULTSPEC model has also provision for working with the full length distribution of cod, but this option is not used in the present study.

Stomach data.

About 23000 stomachs of cod have been sampled in the Barents Sea in the years 1984–1988 by Norwegian and Soviet vessels. The methods used for sampling, analysis and data recording are described in (Mehl, 1989). The number of stomachs sampled and the average stomach content of capelin in model areas 2–5 for February and March 1984–1988 are given in the appendix.

Since all predation is considered to be on mature capelin, all capelin below 11 cm is deleted from the stomach data set before any likelihood calculations are carried out.

Capelin.

Stock data.

The input data for the capelin stock are acoustic estimates obtained in September each year, where 5–6 Soviet 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 splitted on area, length and sex using the method described in (Gjøsæter, 1985b).

Maturation.

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

$$m(l) = \frac{1}{1 + e^{4 \times P_1^{cp} \times (P_2^{cp} - l)}} \quad (3)$$

Here:

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

P_1^{cp} : Change in maturation proportion when $l = P_2^{cp}$

P_2^{cp} : 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 6,7 and 8 by the end of the year. In the period January to March, the migration of immature capelin is set to zero.

Catch data

The basic data material on capelin catch is the number per age per month catch as reported in the ICES working group on Atlanto-scandian herring and capelin.

For the time being, problems with the area distribution of catch data forces us to use the assumption that the geographical distribution of the catch is equal to the geographical distribution of fish. In connection with a joint Soviet-Norwegian symposium on fish interactions that is to be held in Murmansk August 1991 we believe that the area distribution of the two countries' catch statistics will be sufficiently accurate to be used in the model.

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 over time and area, so that we get one temperature T (deg C) for each year, area and month. The procedure is documented in (Alvarez and Tjelmeland, 1989).

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:

$$f(\phi(L)) = \frac{\phi(L)}{P_3^{cd}(1) + \phi(L)} \quad (4)$$

where

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

and

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

$G(l, L, species)$ is a piecewise linear suitability function. In the present study, G 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.

$N_{species}(l)$ is the number of fish (millions) per square nautical mile, and $W_{species}(l)$ is the individual fish weight (kg). The unit of $P_3^{cd}(1)$ and of other food thus becomes 1000 tonnes / square nautical mile.

$P_3^{cd}(1)$ 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:

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

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

$$H = P_{22}^{cd}(1) \times e^{0.104 \times T - 0.000112 \times T^3 - 1.5} \times W_{cod}^{P_{22}^{cd}(2)} \quad (7)$$

where W_{cod} is the individual cod weight in kg. We use the value 0.802 for $P_{22}^{cd}(2)$ from Jobling's paper. $P_{22}^{cd}(1)$ will be estimated from the data.

Suitability. Based on the work of Sigbjørn Mehl, we assume that the cod does not start to feed on capelin before it becomes 20–30 cm long (Mehl, 1989). 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. The error made by not using a length distribution for the cod will be tested later.

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

An exponential evacuation rate model is used:

$$\frac{dS(i)}{dt} = -E_{ii}^{cd}(T) \times S(i) + C(i) \quad (8)$$

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

$E_{ii}^{cd}(T)$: Exponential stomach evacuation rate in cod for prey species i , unit h^{-1} .

$E_{ii}^{cd}(T)$ is modeled by a linear temperature regression to empirical evacuation rates determined by fitting an exponential model to laboratory data of gastric evacuation (dos Santos, 1988). The result of this regression for capelin is

$$E_{1cap}(T) = 0.0077 + 0.0072 \times T$$

For other food we use the regression result for krill:

$$E_{1oth}(T) = 0.0090 + 0.0075 \times T$$

We have used Santos' preliminary data (dos Santos, 1988), p.14 for evacuation rates for three different prey groups (unit: grams wet weight/hour) and merely drawn a straight line between the values at two different temperatures, using 2.0 and 5.35 as mean temperatures. For a comparison of different models for stomach evacuation, see Bogstad and Mehl (Bogstad and Mehl, 1990). In (dos Santos, 1990) a more sophisticated model for gastric evacuation is given. In that model, the meal size and the fish size is also taken into account. The consumption rate calculated using this model seems to be somewhat smaller than the consumption rate we calculate in this paper. However, Santos' work was finished so late that we were not able to make use of his results in this paper.

Parameter estimation.

The following parameters will be estimated:

1. Maturation parameters, equation 3. Data used: Acoustical length distributions measured in September, length distributions from biological samples obtained in March.
 - a. P_1^{cp} . Maturation intensity for males and females.
 - b. P_2^{cp} . Length at maturity for males and females.
2. Migration pattern, equation 1. Data used: geographical distribution of capelin in cod stomachs. The migration parameters have been reduced, see page 18.
 - a. $x1$. East-west migration in January.
 - b. $x2$. North-south migration in February.
 - c. $x3$. North-south migration in March.
3. Predation, equations 4 and 7. Data used: geographical distribution of capelin in cod stomachs, experimentally determined digestion rates.
 - a. $P_{22}^{cd}(1)$. Maximum consumption, scaling constant.
 - b. P_3^{cd} . Feeding level half value.
4. Scaling factor. When estimating migration and predation parameters, it was also necessary to introduce a scaling factor on the capelin stock in order not to get inconsistencies in the data, see below.

Scaling of the capelin stock.

The model outlined brings together data that should be reliable in absolute terms (catch, stomach content, stomach evacuation rate) and data that until now have been viewed as stock indices (acoustic estimate of capelin, VPA estimate of cod). The ICES working group on Atlanto-scandian herring and capelin considers the capelin stock to be generally underestimated by the acoustical method (Anon., 1987), (Anon., 1988). When we run the model on unscaled stock data, outfishing or outpredating of the capelin may occur in some areas. Consequently, we have used a scaling factor on the capelin stock in order not to get inconsistencies in the data. The VPA-estimate of the cod stock should also be regarded as correct only to a constant scaling factor. However, in the present analysis we regard these estimates as absolute.

Eide (Eide, 1989), working with biomass based models for the fish species in the Barents Sea also considered this problem and arrived at scaling factors greater than unity for all stocks and higher scaling factors for capelin than for cod.

It is interesting to note that a scaling factor for the acoustic abundance estimate of capelin also was introduced in a simple cod-capelin model described in (Magnusson and Palsson, 1989), although they used a different approach. In Bogstad and Mehl (Bogstad and Mehl, 1990) it is shown that our stomach evacuation model based on Santos' experimental data gives approximately the same consumption estimates as the model used by Magnusson and Palsson. The scaling factor found by Magnusson and Palsson (1.91) is within the range we find for the scaling factor when using different maturation parameters.

Method.

The maximum likelihood method is used. Before we start defining likelihood functions to use with estimation of the various parameters, we will find the admissible parameter space. We define the "admissible parameter space" as the set of parameter for which there is consistency between the parameters and the data sets we use for estimation.

Maturation parameters.

Admissible capelin maturation parameter space.

Before the parameters are estimated, it may be useful to investigate what the possible values of the parameters are, called "admissible parameter space".

If the capelin maturation parameters (page 9) give a too small immature stock, the projected stock to the next year may be smaller than the observed, even when natural mortality is not accounted for. We apply a model where the maturation parameters are constant over time, so the requirement that the immature stock shall sustain next year's total stock must hold for the whole range of years we use. Here the observed catch must also be accounted for. Also, the mature stock must be large enough to account for a nonzero spawning stock when the catch (but not the predation) is accounted for. When those two criteria are applied, an interval in which the length at maturity must lie is found.

In this analysis, the catch is made independent of area but dependent on age. In the period January to April the catch is supposed to be on mature capelin only.

Using a provisional value of 0.55 for P_1^{CP} for both sexes, we have found the minimum length at maturity for age 3 (L3) and 4 (L4) respectively, and also the maximum length at maturity L. The latter is not age-dependent, since the catch is not reported on age. The blanks in the tables indicate that the values found are outside the interval 12–16 cm where we suppose the length at maturity must lie. We suppose that the lengths at maturity thus obtained does not vary much with P_1^{CP} .

Table 1 Admissible length at maturity (cm), females, scaling 1.0.

	Min L3	Min L4	Max L
1974-1975	12.0	13.4	15.5
1975-1976	11.8	12.6	16.0
1976-1977	12.6	13.0	15.0
1977-1978	11.8	13.0	15.1
1978-1979		13.4	14.8
1979-1980		13.6	14.4
1980-1981		13.1	
1981-1982		12.7	16.0
1982-1983		12.6	15.2
1983-1984		12.7	14.6
1984-1985			14.7
1985-1986			14.4
1986-1987			
1987-1988			

Table 2 Admissible length at maturity (cm), males, scaling 1.0.

	Min L3	Min L4	Max L
1974-1975			
1975-1976			
1976-1977		13.5	
1977-1978			
1978-1979			
1979-1980		14.0	15.3
1980-1981		13.9	
1981-1982			
1982-1983			
1983-1984		13.7	15.6
1984-1985			15.9
1985-1986			15.5
1986-1987			
1987-1988			

From these tables, we find that the length at maturity has to be in the interval (13.6,14.4) for females, and (14.0,15.3) for males, for the assumption about age- and time independent length at maturity to be valid.

Estimation of maturation parameters using March length distributions .

The maturation parameters determine both the total biomass and length distribution of the spawning stock. By far the most important entity is the size of the spawning stock, which is important for management. Ideally, the maturation parameters should be estimated using measured values for the spawning stock. However, we have little data, only in 1989 did we obtain a more or less reliable acoustic estimate of the spawning stock, and then only on the early spawning component. We must expect that the crude model operated today would need a timeseries as long as possible for estimation of the most crucial parameters. Using only one year may bias the model. Besides, using direct measurements of the spawning stock makes the maturation parameters and the predation parameters become coupled.

The maturation parameters must refer to the early spawning component, since the late spawning component is supposed not to be present in the stomach material from the period January-March.

For finding values of the maturation parameters that may give acceptable assessments of the spawning stock, we are therefore left with methods that utilizes other data sources.

Because the maturation parameters affect strongly both the mean length and the shape of the length distribution, measured values of the length distribution may be used to estimate these parameters. We may expect some growth during the winter season from September to March. If the growth was the same for all length groups the growth would not affect the shape of the length distribution of the fish. Above a certain length most of the fish will mature, so that the maturation parameters will not affect the right slope of the length distribution. In the length interval that is most affected by the maturation parameters (around the length at maturity) the significance of the growth would be very small compared to the significance of the maturation parameters. Therefore, the growth and the maturation parameters may be reasonably uncorrelated when length distributions are used for estimated both groups of parameters simultaneously. We will invoke the rather weak assumption that the growth is independent of length within the length interval (roughly 13-17 cm) of interest.

We will strengthen the method by using otolith measurements to adjust for growth during the period January-March (rather, from the time of formation of the winter ring to measurement of the otolith).

Method for length adjustments between model and data distributions. Thus, the following assumptions are made:

- the growth is independent of length (later to be slacked),
- the predation does not affect the length distribution
- the catch does not affect the length distribution

Under the assumption above the length distribution in March is determined by the length distribution measured in September and the maturation parameters. The difference in mean length is adjusted for by letting the simulated stock have an overall growth in length equal to the difference in mean length. It is only the difference in shape between the modeled length distribution in March and the length distribution from the biological samples in March which counts.

One important problem is to find the "true" length distribution from the data. The samples are obtained from both the eastern and western part of the spawning migration, where the length distributions may be different. For a summary of the data, see the appendix, where the geographical positions of the samples used are shown in figures 20 — 29 (page ?), a summary of the data is given in tables 21 — 22 (page 26) and plots of the length distributions are shown in figures 30 — 49 (page 27).

Since we have no prior knowledge of the migration (this will be estimated after the maturation parameters have been estimated), just pooling together all the samples will be dubious indeed. Instead we let our ignorance of the geographical distribution of the spawning stock be reflected into the uncertainty interval of the maturation parameters.

This is done by calculating the length distribution as:

$$l = al_{west} + (1 - a)l_{east}$$

then calculating the likelihood of obtaining l given the model represent the "truth". This likelihood is integrated over a to obtain the marginal likelihood, i.e the likelihood of obtaining the measurements no matter what the geographical distribution is, i.e. the likelihood function used in the estimations is:

$$L\alpha \int f(p)^{l(a)} da$$

where :

f = normalized number of model fish in the area

p = maturation parameters

This method has a logical flaw, since the number of fish measured is an artificial construct. We believe, however, that the constructed number of fish reflects the total number of fish measured good enough for the

parameter confidence limits to be reasonable. Anyway, the uncertainty in the estimation of the maturation parameters is by far not the greatest uncertainty we have to cope with.

Once estimates of the migration pattern have been obtained, one might go back to estimate the maturation parameters by using the known values of a and proceed to convergence. Or, alternatively, we might estimate the maturation parameters together with the migration parameters. Neither of these approaches have yet been tried, since the first-step estimation of maturation parameters yields sufficiently precise results.

All the subsequent runs are made for 1979–1988 spring data.

The files of biological samples in March do not include fish that are not age-determined, and all fish are mature (visual index > 3). The Forberg index (Forberg, 1983) has not been used in this respect, because of lack of data in the 70s and because it does not apply to males.

Length distributions for which the number of fish in area 2 or area 3 are smaller than 10 have been rejected. In order to have a robust procedure, 3 and 3 length groups (of 0.5 cm width) are concatenated.

Results without using back-calculation from otoliths.

Table 3 Results — estimation of capelin maturation parameters: Expectations.

	Maturation intensity Pcp1, all ages	Length at maturity Pcp2, all ages
Final	Females: 0.55 Males: 0.80	Females: 14.37 Males: 16.79

Table 4 Results — estimation of capelin maturation parameters: Covariances.

	Pcp2	Pcp1	
Females	0.016	-0.0062	Pcp2
	-0.0062	0.0040	Pcp1
Males	0.0072	0.00016	Pcp2
	0.00016	0.00067	Pcp1

Justification by measured otolith edge. Prior to the evaluation of the likelihood function, a back-calculation of the measured length distribution by sex, age and area has been performed. A length growth of 16 cm pr mm otolith radius has been used, which is averaged from (Gjøsæter, 1986).

Table 5 Results — estimation of capelin maturation parameters: Expectations.

	Maturation intensity Pcp1, all ages	Length at maturity Pcp2, all ages
Final	Females: 0.60 Males: 0.80	Females: 14.28 Males: 15.88

Table 6 Results — estimation of capelin maturation parameters: Covariances.

	Pcp2	Pcp1	
Females	0.00011	-0.000058	Pcp2
	-0.000058	0.000091	Pcp1
Males	0.0015	-0.0012	Pcp2
	-0.0012	0.0014	Pcp1

The length at maturity has been lowered for both sexes. This is consistent with the assumption that there is length dependent growth, smaller fish growing faster than bigger fish. When this is corrected for in the data set, the data length distribution gets broader. In order for the model length distribution to match, the length at maturity has to be lowered.

Since the otoliths only catch up with growth after the winter ring has emerged, only a part of the growth from September to March has been adjusted for. One might then expect that the lengths at maturity should be even lower than the values shown in table 5.

Also, the precision of all estimates has increased, with the exception of maturation intensity for males.

The length at maturity for females falls within the admissible parameter space, whereas the length at maturity for males does not. However, the admissible parameter space was found using a scaling factor of 1.0. When a higher scaling factor is used, the upper bound on the parameter space increases. In this paper we will not pursue this analysis further.

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

Theory

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 weight of the measured stomach content is normally distributed with expectation value $S(L)$ when viewed fish by fish, the following variable will be t-distributed:

$$t = \frac{\sqrt{N_{sample}} \times (\bar{X} - S)}{s} \quad \text{where :} \quad (13)$$

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

Here:

X_i : Stomach content meaned over cod length and the time period and area under consideration.

\bar{X} : Mean stomach content from cod of length L averaged over 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 collect stomachs fish by fish and thereby have the opportunity to calculate the variance, we are in a position to calculate s . Therefore, the maximum likelihood method is applicable. In other words, the probability of measuring what actually is measured is calculated, given that the model represents the "truth". This probability is given by the t-distribution. The mathematical form of the t-distribution is given by:

$$f(t) = \frac{\Gamma(\frac{N+1}{2})}{\sqrt{N\pi} \times \Gamma(\frac{N}{2})} \times \frac{1}{(1 + \frac{t^2}{N})^{\frac{(N+1)}{2}}} \quad (14)$$

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 mean stomach content is normally distributed. However, the stomach content 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 stomach content. Therefore, the mean stomach content 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 3 days making τ equal to 0.1 and the size of a meal to 20 grams. This gives a probability of having zero stomach content of

$$e^{-\frac{S}{2.0}}$$

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.

Other food.

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. When there are no stomach data at hand, an overall other food concentration pattern is used. This is calculated as follows:

Given a year, a month and an area,

1. The total stomach content is fetched from the data.
2. The consumption is then calculated using the model evacuation rate.
3. The maximum consumption per cod is calculated using the model predation parameter $P_{22}^{cd}(1)$, equation 8.
4. The feeding level is calculated by dividing consumption by maximum consumption.
5. The total food abundance is calculated by using the feeding level function (equation 4 inversely).
6. The abundance of other food is calculated by dividing the total food abundance on capelin and other food using the stomach content data.

The calculations are done by area and averaged over month and year. The final result is stored in the other food parameters of the model.

The other food calculations are dependent on the value of the parameter $P_{22}^{cd}(1)$. If a lower limit on this parameter is estimated from the stomach content data directly (see page 18), the calculations of other food should be done after the final estimate of $P_{22}^{cd}(1)$.

Using a value of $P_{22}^{cd}(1)$ of 3.5 the other food pattern becomes:

Table 7 Other food pattern.

Area	2	3	4	5
Other food concentration (1000 t pr sq. n. mi.)	0.0028	0.0016	0.0024	0.0044

Maximum consumption rate. Using results from (Jobling, 1988), we get a value for $P_{22}^{cd}(1)$ 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 $P_{22}^{cd}(1)$ 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 model. The latter is calculated using the model parameter $P_{22}^{cd}(1)$. 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 $P_{22}^{cd}(1)$ is to increase the parameter until the error messages just disappears. 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 was found to be 3.5.

Baseline parameters for migration. Reduction of migration parameters.

Migration In January to March the migration matrix V (equation 18, page 8) of mature capelin is set to:

Table 8 Baseline migration in January.

	1	2	3	4	5	6	7	8
1								
2								
3								
4					1.0	0.5		
5						0.5	1.0	
6								
7								
8								

The adjustment x_1 to the parameters to the left, is defined in the following way:

$$x_1 > 0:$$

$$[7,4] \leftarrow [7,4] + [7,5]x_1$$

$$[7,5] \leftarrow [7,5] - [7,5]x_1$$

$$[8,4] \leftarrow [8,4] + [8,5]x_1$$

$$[8,5] \leftarrow [8,5] - [8,5]x_1$$

$$x_1 < 0:$$

$$[7,4] \leftarrow [7,4] + [7,4]x_1$$

$$[7,5] \leftarrow [7,5] + [7,5]x_1$$

With the values given in the matrix above, this means that x_1 can vary between -1.0 and 1.0 . x_1 is later to be estimated. x_1 has positive values for increased westwards migration with respect to the baseline parameters.

Table 9 Baseline migration in February

	1	2	3	4	5	6	7	8
1								
2				0.5				
3					0.5			
4								
5								
6								
7								
8								

The adjustment x_2 to the parameters to the left, is given in the following way:

$$[4,2] \leftarrow [4,2] + x_2$$

$$[5,3] \leftarrow [5,3] + x_2$$

With the migration matrix above, this means that x_2 can vary between -0.5 and 0.5 . x_2 is later to be estimated. x_2 has positive values for increased southwards migration with respect to the baseline parameters.

Table 10 Baseline migration in March

	1	2	3	4	5	6	7	8
1								
2				0.5				
3					0.5			
4								
5								
6								
7								
8								

The adjustment x_3 to the parameters to the left is given in the following way:

$$[4,2] \leftarrow [4,2] + x_3$$

$$[5,3] \leftarrow [5,3] + x_3$$

With the migration matrix above, this means that x_3 can vary between -0.5 and 0.5 . x_3 is to be estimated. x_3 has positive values for increased southwards migration with respect to the baseline parameters.

Year-by-year estimation of halfvalue and migration.

We are then left with the estimation of 5 parameters, the 3 migration parameters, the feeding level half value parameter and the scaling factor for capelin. 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. Concerning the scaling factor, it was decided to estimate this by increasing it until there is no outpredating or outfishing in any area in February or March. We thus adopt the following scheme:

1. Estimate the 3 migration parameters on a year-to-year basis keeping the half-value parameter and the scaling factor fixed.
2. Estimate the half-value parameter on the whole time range keeping the annual migration parameters fixed. Do this for varying scaling factors, in order to find the lowest scaling factor for which there is no outfishing or outpredating for the most likely value of the half-value parameter.
3. Go to step 1 until convergence.

Reference estimation, using otolith-adjusted spring growth. No scaling factor is needed to avoid outfishing when predation is turned off, although we then get a mortality of 5.04 in 1984.

We estimated the feeding level half value $P_{j^{cd}}$ to be 0.041 ± 0.001 , and the corresponding scaling factor to be 2.02. The migration parameters found are shown in table 11.

Table 11 Migration parameters, otolith adjusted spring growth.

	Param.	1983-84	1984-1985	1985-1986	1986-1987	1987-1988
East-west migration, start January	x1	0.96	0.75	-1.00	-1.00	-0.88
North-south migration, start February	x2	-0.49	0.35	-0.48	-0.43	0.50
North-south migration, start March	x3	-0.14	-0.42	-0.50	-0.50	0.21

Table 12 Spawning biomasses and mortalities, otolith adjusted spring growth.

	1983-1984	1984-1985	1985-1986	1986-1987	1987-1988
Spawning biomass (1000 tonnes)	461	415	56	19	4
Total mortality	0.81	0.86	1.11	0.58	1.07
Natural mortality	0.26	0.42	0.86	0.58	1.07

For these parameter values, we found the spawning biomasses and mortalities to be (Table 12):

Estimation using doubly otolith-adjusted spring growth.

As the otoliths only catch up with growth after the winter ring has emerged, only a part of the growth from September to March has been accounted for. We thus decide also to do the estimations with maturation parameters calculated by doubling the change in parameters from no back-calculation to backcalculation. These values are (table 13):

Table 13 Maturation parameters, doubly otolith-adjusted growth.

Maturation intensity Pcp1, all ages	Length at maturity Pcp2, all ages:
Females: 0.65 Males: 0.80	Females: 14.19 Males: 14.97

We found the feeding level half value P_3^{cd} to be 0.041 ± 0.001 , and the corresponding scaling factor to be 1.66. The migration parameters found are shown in table 14 and the spawning biomasses and mortalities in table 15.

Table 14 Migration parameters, doubly otolith-adjusted spring growth..

	Param.	1983-84	1984-1985	1985-1986	1986-1987	1987-1988
East-west migration, start January	x1	0.96	0.74	-1.00	-0.87	-0.87
North-south migration, start February	x2	-0.49	0.34	-0.48	-0.45	0.24
North-south migration, start March	x3	-0.16	-0.50	-0.50	-0.50	0.33

Table 15 Spawning biomasses and mortalities, doubly otolith-adjusted spring growth.

	1983-1984	1984-1985	1985-1986	1986-1987	1987-1988
Spawning biomass (1000 tonnes)	434	361	61	27	7
Total mortality	0.83	0.92	1.07	0.57	0.96
Natural mortality	0.27	0.45	0.85	0.57	0.96

Parameter estimation results, using the length at maturity used by the working group. Here we have used $P_2^{cp} = 13.94$ for both sexes, which is the knife-edge maturity used by the working group (Anon., 1989). The value of P_1^{cp} was thus set to 10.00 for both sexes. The half value was found to be 0.041 ± 0.001 , with a corresponding scaling factor of 1.25. The migration parameters found are shown in table 16 and the spawning biomasses and mortalities in table 17.

Table 16 Migration parameters, working-group maturation parameters.

	Param.	1983-1984	1984-1985	1985-1986	1986-1987	1987-1988
East-west migration, start January	x1	0.95	0.71	-1.00	-0.85	-0.83
North-south migration, start February	x2	-0.49	0.33	-0.48	-0.45	0.10
North-south migration, start March	x3	-0.18	-0.50	-0.50	-0.50	0.35

Table 17 Spawning biomasses and mortalities, working-group maturation parameters.

	1983-1984	1984-1985	1985-1986	1986-1987	1987-1988
Spawning biomass (1000 tonnes)	348	248	36	19	5
Total mortality	0.91	1.10	1.06	0.56	0.92
Natural mortality	0.29	0.52	0.77	0.56	0.92

Sensitivity tests.

We have used the maximum likelihood method throughout and tried to build likelihood functions based on what we regard as realistic probability distributions of the data used. The estimated standard deviations for the maturation parameters and the predation halfvalue parameter are small. Therefore, the sensitivity will be based on looking into how the most important response variable — the spawning biomass — depends on the migration parameters. The estimated confidence limits are small also on these parameters (not shown), so that errors in the estimation of migration does not severely affect the estimated spawning stock biomasses and mortalities. However, when the model is used for prediction one does not know what the migration pattern is going to be 4–7 months ahead in time. Before any correspondence between migration and environmental indices observable in the autumn is established, one is forced to regard the variation in migration pattern as estimated for the years 1984 to 1988 as the uncertainty range. Table 18 shows how the spawning stock in 1985 and 1986 varies using the 5 sets of migration patterns previously obtained. Table 19 shows how the spawning stock biomass in 1985 varies when

the parameters are changed one at a time by half the maximum change. The reference spawning stock represents baseline migration parameters (all three x zero).

Table 18 Spawning stock variation with migration pattern. Doubly otolith-adjusted model.

Migration pattern	Spawning stock 1985	Spawning stock 1986
1984	407	49
1985	361	30
1986	330	61
1987	318	59
1988	234	17

Table 19 Spawning stock 1985 variation with one-parameter changes. Doubly otolith-adjusted model.

Variation	x1	x2	x3
+50%	284	236	227
zero	227	227	227
-50%	224	238	229

The choice of a 50% of maximum variation in the migration parameters is in itself arbitrary. However, the variation should be compared to the variation in the estimated migration pattern. We may conclude that by far the greatest uncertainty stems from uncertainty in the east-west migration component.

These results pertain to the situation (i.e. cod stock geographical distribution, capelin stock initial geographical distribution) that prevailed in 1985, but we believe that the trend is generally applicable.

Discussion.

The estimates of the total mortality do not differ much. The reason for this is that in all three cases the scaling factor has been determined so that there is just enough capelin to account for the catch and predation from cod. The input capelin stock at January 1. does then not differ very much, and hence neither does the predation mortality. The way the scaling factor is used also explains why the predation half value P_3^d also remains unchanged. One might then argue that not much is gained, except for revealing the incompatibility between the acoustical estimate of capelin, the stomach content data and the VPA estimates of cod. 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.

When using the mortalities obtained here for management of capelin, the question of scaling must be solved. If the old capelin model is to be used, i.e. a model that is scaled to unity, it is not straightforward to scale the mortalities correctly. The way the model is treated, the predation in absolute terms is not much changed, and therefore it seems natural to scale all mortalities in inverse proportion to the scaling of the stock.

The problems of a possible proportional bias has been adressed by the working group (Anon., 1982), and the acoustical measurement of the capelin stock has been treated as an index of abundance rather than as a measurement of the stock in absolute terms. In order to compare the results obtained in this paper from using different values of the capelin maturation parameter, we have scaled the spawning biomasses obtained to an acoustical scaling factor of 1.0.

Table 20 below shows the spawning biomasses and natural mortalities from the three estimation experiments scaled to unity.

Table 20 Spawning biomass and natural mortality 1984–1988 scaled down to 1.0.

	Otolith adjustment	Scaling 2.02 Length at maturity 14.28, 15.88	Double adjustment	Scaling 1.66 Length at maturity 14.19, 14.97	Working group	Scaling 1.25 Length at maturity 13.94, 13.94
	Spawning biomass	Natural mortality	Spawning biomass	Natural mortality	Spawning biomass	Natural mortality
1984	343	0.52	359	0.44	338	0.36
1985	320	0.84	310	0.74	244	0.65
1986	49	1.73	57	1.41	36	0.96
1987	13	1.17	20	0.94	17	0.70
1988	3	2.16	6	1.59	5	1.15

Also, the migration pattern is remarkably consistent between the three methods for obtaining the capelin maturation parameters. However, on several occasions the parameters have been estimated at their

limits, which suggests that a more elaborate migration model or another transformation of parameters could be used.

Implications for capelin management.

The main problem that arises when one tries to use the results from this paper in connection with management is the scaling of capelin that is necessary to make the capelin acoustic measurement, the VPA estimate of the cod stock and the stomach evacuation rates compatible.

The logical method to proceed is to look into how sensitive the scaling is to the management advice. It is shown in (Hamre and Tjelmeland, 1982) that a 50% increase in scaling only leads to a 10% increase in the calculation of the MSY when the single-species model for capelin is used.

The following procedure could be used:

1. Calculate the series of spawning stock biomass each year using different scalings.
2. Build a stock-recruitment relation for each scaling.
3. Calculate the optimal spawning stock in each case, using the single-species capelin model, under reasonable assumptions of the size of the future cod stock.
4. Investigate how the TAC differ between the different scalings.

Ideally, the amount of late spawners, neglected in this paper, should be included in the analysis, and the mortality on immature fish should also be connected to the cod stock.

Is the exponential evacuation rate model applicable when the stomach content is very large?

There is obviously an upper limit to the stomach evacuation rate in grams per hour, which may be exceeded by the exponential evacuation rate (unit: per hour) if the degree of fullness in the stomach is close to maximum. This may occur when the cod feeds heavily on capelin, and may lead to an overestimate of the consumption. If a relationship between the size of cod and the maximum stomach evacuation rate in grams per hour can be found, this problem can be avoided.

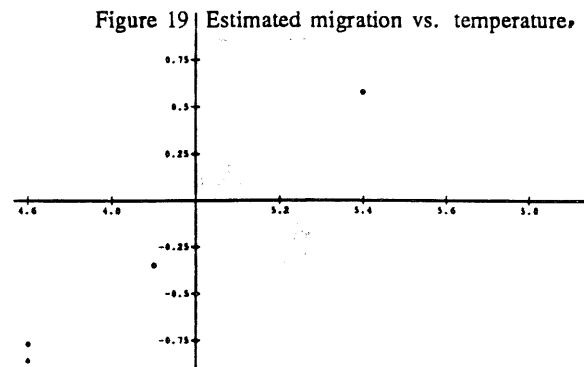
Using the results for prediction: The migration.

When using the model results to predict the spawning biomass of capelin given a certain level of the catch and given the size and geographical distribution of the cod stock, the main difficulties lies with the geographical distribution of the capelin spawning migration.

When using the results from this paper, the capelin stock should be predicted from the measurement in September to the spawning in the following spring. It is natural to look for environmental indices that can be measured in September and that may have some predicting power for the geographical distribution of the capelin spawning stock during the period January-March.

The simplest index would be the temperature. To motivate for such attempts, we have plotted the highest temperature in the autumn as measured along the Kola meridian vs. the estimated value of the east-west

component of the migration pattern the following January (x_1), see figure 19. The almost linear relationship might be deceptive and might be broken when we include more data, but it does not discourage further attempts in this direction.



Further work

We will introduce Santos' new evacuation model (dos Santos, 1990) into MULTSPEC. This model includes the effect of meal size, and we may thus avoid the problem with large stomach content mentioned above. Preliminary calculations (Bogstad and Mehl, 1990) show that the consumption becomes somewhat lower with this new model, which will reduce or eliminate the need for scaling of the capelin stock. We will also switch to the new area distribution (seven areas) and make use of the area distributed catch data. Then we will redo the estimations, with the 1989 stomach data included and using the 1990 VPA estimate for cod. A paper on the implementation of the results of our modeling work into capelin management is also planned, and hopefully this can be used by the capelin and herring working group in 1991.

A long-term goal is to perform sustainable yield assessments for capelin and cod using the full-fledged model.

Conclusion.

The present work is a first attempt to quantify stock interactions in the Barents Sea using a multi-species 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 and area-structured stock data may lead to a quantification of the cod stock's predational impact on the mature capelin. However, considerable work is still to be done in order to utilise the results in practical management. The main uncertainty is the geographical distribution and timing of the capelin spawning migration.

Appendix A Biological samples in March

Geographical distribution of samples.

Figure 20 Distribution capelin samples used — March 1979.

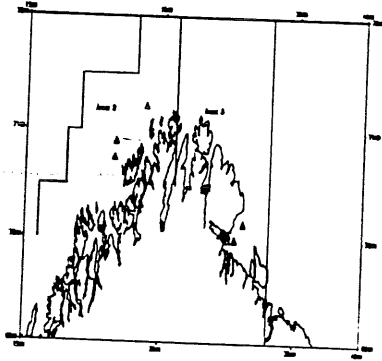


Figure 23 Distribution capelin samples used — March 1982.

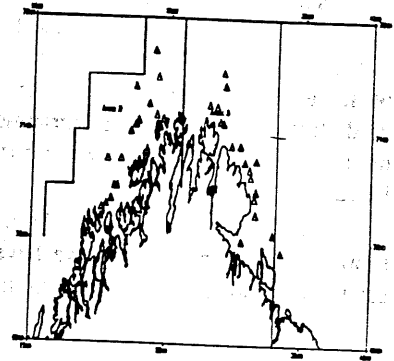


Figure 21 Distribution capelin samples used — March 1980.

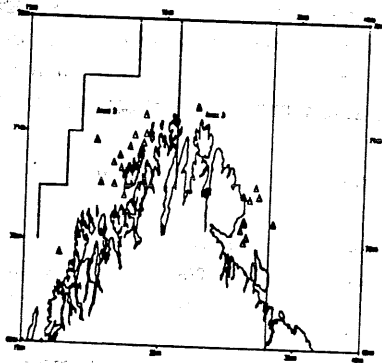


Figure 24 Distribution capelin samples used — March 1983.

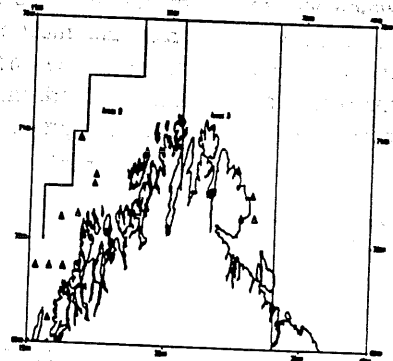


Figure 22 Distribution capelin samples used — March 1981.

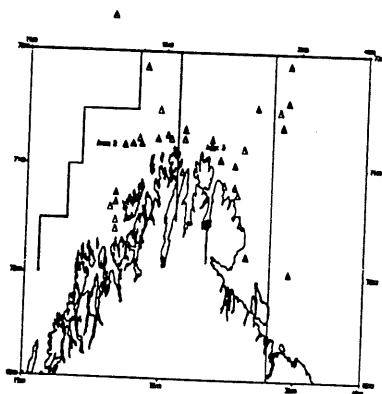


Figure 25 Distribution capelin samples used — March 1984.

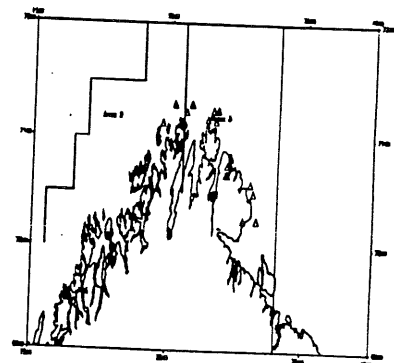


Figure 26 Distribution capelin samples used — March 1985.

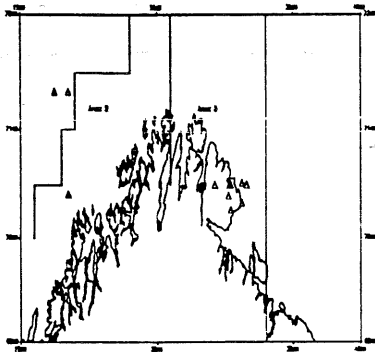


Figure 28 Distribution capelin samples used — March 1987.

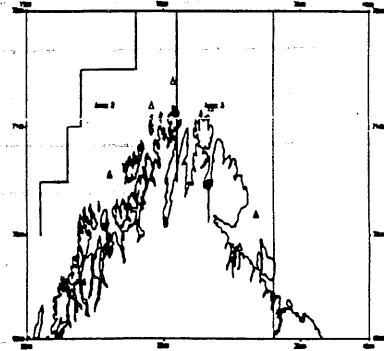


Figure 27 Distribution capelin samples used — March 1986.

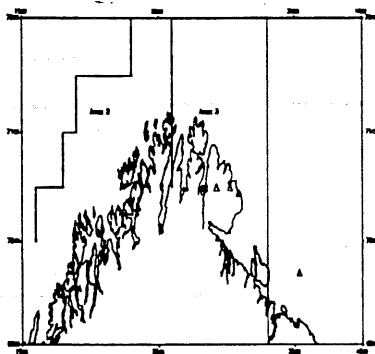
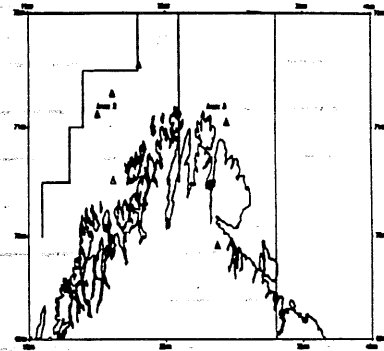


Figure 29 Distribution capelin samples used — March 1988.



Length distributions.

Summary of length distributions.

The estimation of maturation parameters is based upon the length distributions from biological samples obtained in March each year. The length distributions are different in areas 2 and 3. We interpret this difference as a result of changes in maturation, growth and migration from year to year, rather than as random sampling errors. Tables 21 and 22 give a summary of the distributions used in the paper. The length distributions in area 2 and area 3 has been tested for difference. The mean length should be smaller than Δl in order that the two length distributions should have a 90% probability of being drawn from the same parent distribution. They are statistically different with the exception of the years 1981, 1985 and 1987.

Table 21 Summary of biological distributions in March — females.

Year	Area 2			Area 3			Δl , 90%
	Number of samples	Number of fish	Mean length	Number of samples	Number of fish	Mean length	
1979	11	48	14.92±1.06	22	131	15.88±0.85	0.22
1980	15	375	15.07±0.81	14	713	15.51±0.88	0.06
1981	18	510	15.85±0.93	18	822	15.83±0.94	0.06
1982	23	535	15.91±1.16	24	1078	16.08±1.01	0.06
1983	13	392	16.10±1.00	6	286	15.32±0.86	0.08
1984	5	44	15.72±1.08	23	739	15.26±0.84	0.21

Table 21 (Continued) Summary of biological distributions in March — females.

1985	3	90	15.44±0.88	8	287	15.57±0.95	0.14
1986	1			13	416	14.74±0.82	
1987	2	27	14.03±0.74	16	145	14.12±0.65	0.19
1988	6	72	15.01±0.63	15	71	14.52±0.76	0.19

Table 22 Summary of biological distributions in March — males.

Year	Area 2			Area 3			Δl, 90%
	Number of samples	Number of fish	Mean length	Number of samples	Number of fish	Mean length	
1979	11	37	16.43±0.87	22	87	17.48±0.83	0.18
1980	15	273	16.51±0.79	14	500	17.26±0.82	0.07
1981	18	575	17.51±0.89	18	624	17.55±0.93	0.04
1982	23	456	17.83±1.00	24	890	17.91±0.91	0.06
1983	13	170	17.56±1.00	6	121	17.04±0.80	0.13
1984	5	66	17.04±0.71	23	631	16.55±0.89	0.12
1985	3	85	16.64±0.94	8	412	16.91±0.96	0.02
1986	1			13	194	16.06±0.86	
1987	2	12	14.92±0.44	16	105	15.22±0.59	0.18
1988	6	43	16.60±0.55	15	29	15.70±0.87	0.24

Plot of length distributions.

Figure 30 Length distributions March 1979 — females.

Figure 31 Length distributions March 1980 — females.

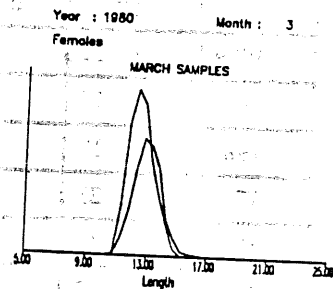
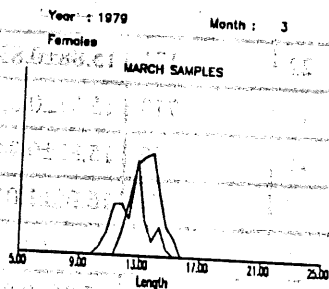


Figure 32 Length distributions March 1981 — females.

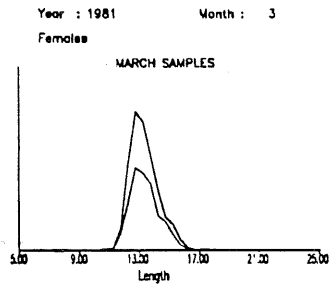


Figure 36 Length distributions March 1985 — females.

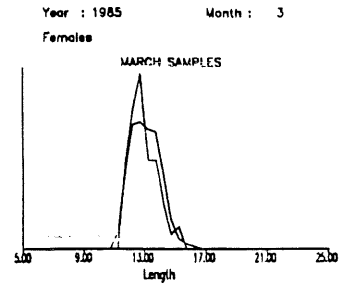


Figure 33 Length distributions March 1982 — females.

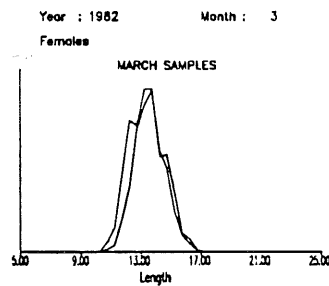


Figure 37 Length distributions March 1986 — females.

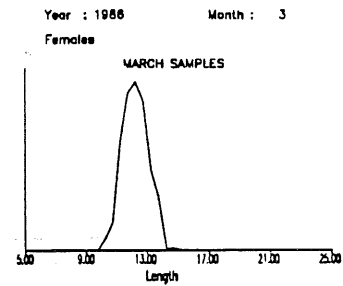


Figure 34 Length distributions March 1983 — females.

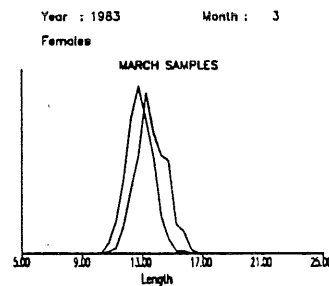


Figure 38 Length distributions March 1987 — females.

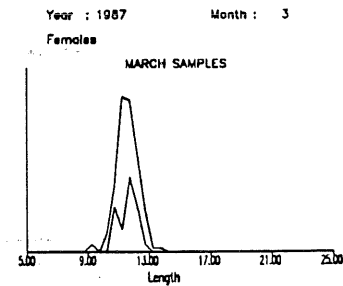


Figure 35 Length distributions March 1984 — females.

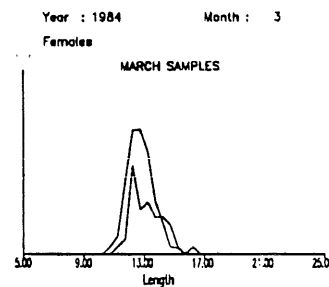


Figure 39 Length distributions March 1988 — females.

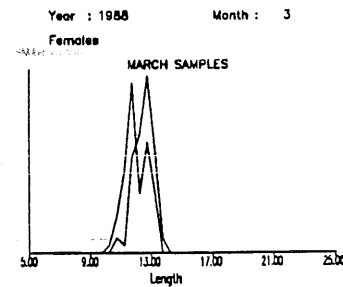


Figure 40 Length distributions March 1979 — males.

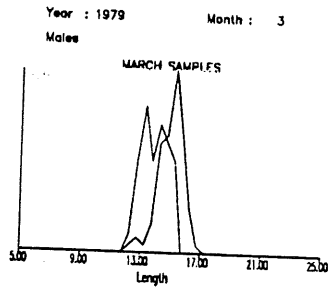


Figure 44 Length distributions March 1983 — males.

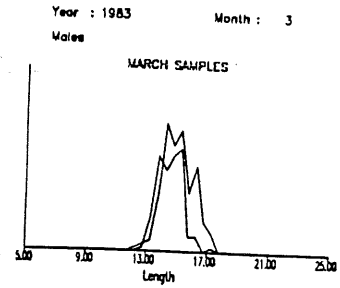


Figure 41 Length distributions March 1980 — males.

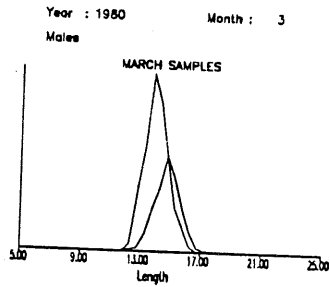


Figure 45 Length distributions March 1984 — males.

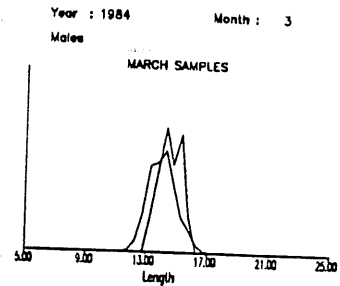


Figure 42 Length distributions March 1981 — males.

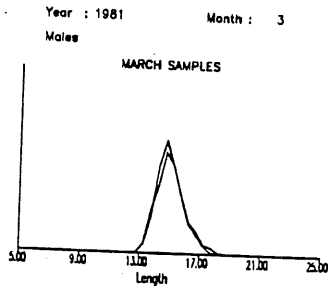


Figure 46 Length distributions March 1985 — males.

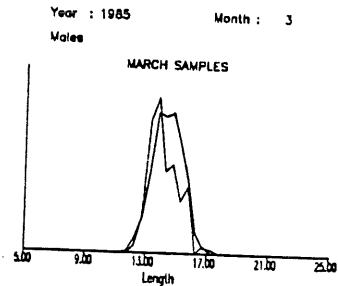


Figure 43 Length distributions March 1982 — males.

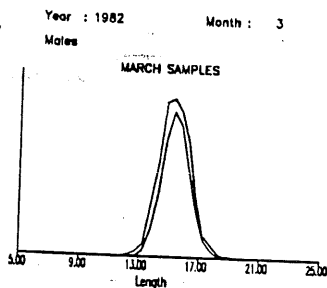


Figure 47 Length distributions March 1986 — males.

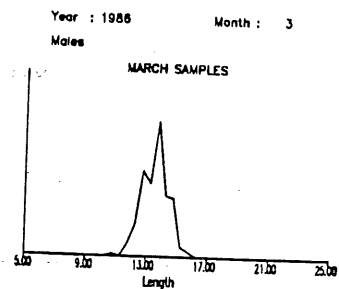


Figure 48 Length distributions March 1987 — males.

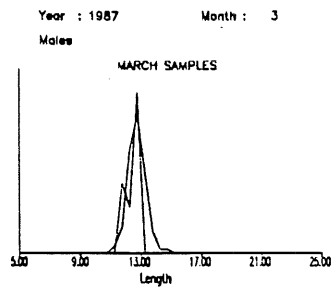
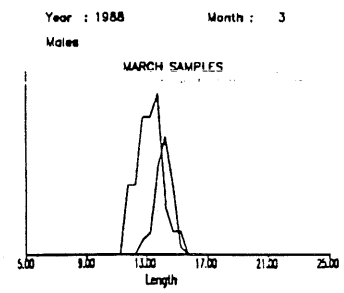


Figure 49

iles.



Appendix B Stomach data.

Number of stomachs sampled and the average stomach content of capelin in model areas 2-5 in February and March 1984-1988:

Table 23 Stomach content — capelin February 1984

Area 4 18.18 74	Area 5 0.89 331
Area 2 1.42 50	Area 3 0.63 270

Table 28 Stomach content — capelin March 1986

Area 4	Area 5 9.31 237
Area 2	Area 3

Table 24 Stomach content — capelin March 1984

Area 4 21.51 44	Area 5
Area 2 30.22 118	Area 3

Table 29 Stomach content — capelin February 1987

Area 4 0.49 306	Area 5 1.33 194
Area 2 0.16 207	Area 3 0.14 386

Table 25 Stomach content — capelin February 1985

Area 4 4.89 109	Area 5 22.73 662
Area 2 31.82 60	Area 3 12.57 398

Table 30 Stomach content — capelin March 1987

Area 4	Area 5
Area 2 0.0 90	Area 3

Table 26 Stomach content — capelin March 1985

Area 4 8.96 103	Area 5
Area 2 118.66 176	Area 3

Table 31 Stomach content — capelin February 1988

Area 4 0.77 180	Area 5 2.49 181
Area 2 0.19 213	Area 3 1.31 775

Table 27 Stomach content — capelin February 1986

Area 4 18.96 132	Area 5 10.07 745
Area 2 0.11 148	Area 3 0.54 180

Table 32 Stomach content — capelin March 1988

Area 4 0.16 51	Area 5 22.87 20
Area 2 0.37 51	Area 3

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