

**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

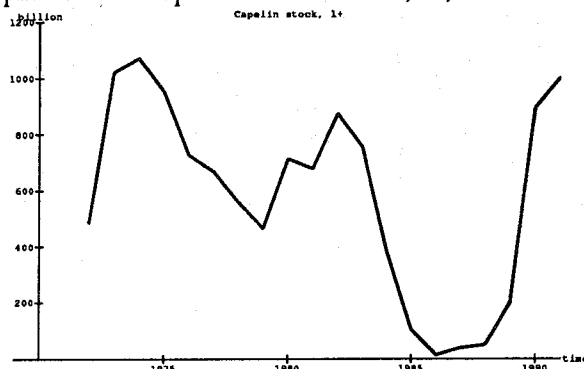
Distribution and migration.

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.

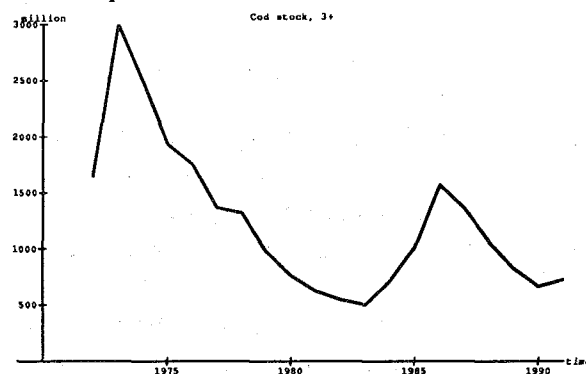
The North-East Arctic cod stock has two components: The Barents Sea component is distributed mainly to the south of the capelin distribution as measured in September. The main spawning area is Vesterålen/Lofoten, but spawning may also occur further south. The Spitsbergen component is distributed in the 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

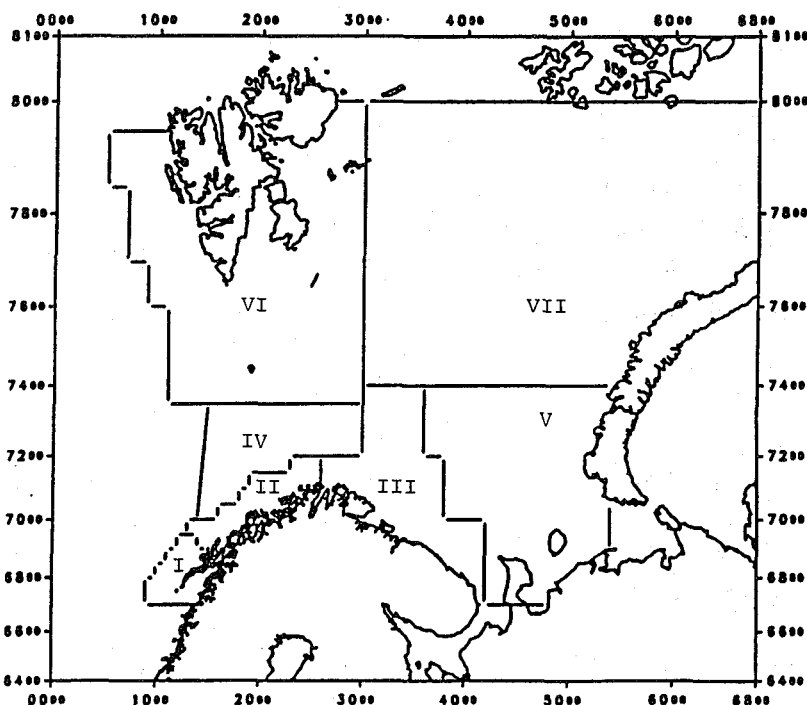
the Arctic Fisheries Working Group and the quotas amounted to a higher number of individuals than expected (Anon, 1989a). The main reason for this growth decline was probably the collapse of the capelin stock (Mehl and Sunnanå, 1991). The fishing mortality was in 1990 brought down to the F_{low} level, 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 (Gjørseter, 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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