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MULTSPEC - A Multispecies Model for Fish and Marine Mammals in the Barents Sea

by

Bjarte Bogstad, Kjellrun Hiis Hauge and Øyvind Ulltang

Institute of Marine Research, P. O. Box 1860 Nordnes
N-5024 Bergen, Norway

Abstract

MULTSPEC is an area-structured multispecies simulation model for the species capelin, herring, cod, harp seal and minke whale in the Barents Sea. Information on food preferences and food requirements obtained from the Norwegian research programme on marine mammals is used to quantify the predation by marine mammals on fish. The importance of harp seals and minke whales as predators relative to the main fish predator in the ecosystem, cod, is discussed. The sensitivity of the model to the food preferences and stock sizes of harp seals and minke whales is investigated.

1 Introduction

In Bogstad *et al.* (MS 1992) results of some simulation studies with a multispecies model for the Barents Sea (MULTSPEC) were given with the aim of studying the sensitivity of the model to assumptions on food preferences and stock sizes of minke whales and harp seals. At that time, herring (*Clupea harengus*) was not included in MULTSPEC as a separate species, and results of the scientific whaling operations conducted in 1992-1994 were not available.

The present paper gives results of new simulation studies with herring included. When choosing food preference parameters for minke whales and harp seals, results of the diet studies reported in Haug *et al.* (MS 1995), Skaug *et al.* (MS 1995) and Nilssen (1995) have been used for setting likely ranges of parameter values. Also new data on total energy requirements of seals and whales have been utilized when setting the parameters determining total consumption. No fine tuning of the model parameters to the new data has been aimed at. The main aim of the paper is to demonstrate the model's behaviour when herring as an important prey item is included and study the sensitivity of the model to food preference parameters and stock sizes of minke whales and harp seals. Also, the relative importance of harp seals and minke whales as predators relative to the main fish predator in the ecosystem, cod, is discussed.

A preliminary version of this paper (Bogstad *et al.* MS 1995) was presented at the IWC meeting in May 1995. The most important change in the model since that paper was written is that cod now may prey on all stock components of herring in the MULTSPEC area. Also, some of the parameters for cod and capelin have been changed based on parameter estimations presented at the last meeting of the ICES Multispecies Assessment Working Group (Anon., MS 1995c). MULTSPEC has so far mainly been used for estimating predation mortalities of mature capelin generated by cod (Bogstad and Tjelmeland MS 1990, 1992). Basic philosophy and modelling approach is described in Ulltang (1995). In Bogstad *et al.* (MS 1992) a description of model structure and basic equations determining the population dynamics of each species included were given. The present paper includes an updated description of the model.

2 Model structure

The multispecies model for the Barents Sea (MULTSPEC) is an area-structured simulation model which includes the species capelin (*Mallotus villosus*), herring (*Clupea harengus*), cod (*Gadus morhua)*, harp seal (*Phoca groenlandica*) and minke whale (*Balanoptera acutorostrata*).

The stocks which are included in MULTSPEC are represented by tree structures where each level denotes sub-populations distributed over a given dimension, which may be area, sex, age or length. The area division used in the model is shown in Figure 1.

Fig. 1

As the minke whale stock, depending upon the time of the year, to a large extent is distributed outside the Barents Sea, we have included an 'area 0' in addition to the seven areas in the Barents Sea. The model comprises discontinuous processes like reproduction, which is handled on a yearly basis, and continuous processes like predation and natural mortality, which are performed for each time step. The ordering of these processes is as follows: Migration - Fishing- Predation - Growth. The time step used in these simulations is one month.

The basic units in the model are:

- Number of fish and larvae: Millions.
- Weight of individual fish and mammals: kg
- Temperature: deg C

- Time : month
- Length of individual fish : cm

We use the subscripts A for area, s for sex (1: female, 2: male), and a for age. W denotes individual weight, l individual length and N stock size in numbers.

The main changes in the MULTSPEC model since the paper by Bogstad *et al.* (MS 1992) was written are:

1. Herring is included, as MULTSPEC can now be linked to the single-species model HERMOD (Dommasnes and Hiis Hauge, MS 1994).

2. 0-group dynamics for fish is now modelled. Especially important here is the predation by young herring on 0-group capelin.

3. Changes have been made in the equations describing growth and food requirements for harp seals and minke whales.

4. A new temperature model has been implemented.

The parameter files are given in Appendix.

3 Oceanography

Sea temperature is included in the equations for growth and maximal food consumption by fish. It also enters the equation for cod stomach evacuation rate (Bogstad and Tjelmeland, 1992), and will certainly be included in energetics models for marine mammals. Temperature may also prove to be important in a future development of migration models.

We use climatological data (Ottersen and Ådlandsvik, 1993), adjusted by the yearly variations in the Kola section (Bochkov, 1982 and PINRO, Murmansk, pers. comm.). The following positions are used to represent areas 1-7:

6800N, 1200 E; 7030N, 2000E; 7100N, 3400E; 7230N, 2000E; 7200N, 4500E;

7430N, 2200E; 7600N, 4000E

A depth of 100m is used. The adjustment to the yearly variation is done in the following way:
T(year, month, position)= T(position) from climatology + T(year, month) from Kola section - T(month) from climatology at Kola section. The temperature in the years after 1994 has been set equal to the temperature from the climatology.

4 Plankton

The plankton parameters are here denoted by P (Ppl in the parameter file). The food supply for capelin and herring is given by the following function:

$$F(A, t) = P_1(A) \times e^{-4\frac{(P_2(A) - t)^2}{P_3(A)} ln2} \quad \text{(EQ 1)}$$

where

F: the plankton abundance in grams dry weight per square meter,
t: time (month number (1-12))
$P_1(A)$: the maximum plankton abundance in area A
$P_2(A)$: the time for maximum plankton abundance in area A
$P_3(A)$: Duration of the time period when the plankton abundance exceeds half the maximum abundance in area A.

The value of P_1 is set to 15.0 grams dry weight per square meter, which is somewhat higher than the values given by Skjoldal *et al.* (1992).

5 Capelin

The capelin parameters are here denoted by C_i (Pcp in the parameter file). The capelin stock is divided into 6 age groups (0-5), 50 length groups of 0.5 cm (0-25 cm) and 2 sexes. In addition, the stock is divided into a mature and an immature part.

The migration parameters for capelin are the same for all age groups, but they differ between immature and mature capelin. The migration parameters for mature capelin are set so that all the mature capelin will be in areas 2 and 3 at April 1, when spawning takes place. In October the capelin stock is divided into a mature and an immature part by the following function (Forberg and Tjelmeland, 1985):

$$m(l) = \frac{1}{1 + e^{4C_1(a,s) \times (C_2(a,s) - l)}} \quad \text{(EQ 2)}$$

Here:

$m(l)$: Proportion of stock maturing at length l
$C_1(a,s)$: Change in maturation with length when $l = C_2(a,s)$
$C_2(a,s)$: Fish length at 50% maturity, referred to as "length at maturity"

The values of C_1 and C_2 are taken from Tjelmeland and Bogstad (1993).

The following spawning stock biomass - recruitment relationship for capelin is used (Beverton and Holt, 1957):

$$R(B) = \frac{C_{13} \times B}{C_{14} + B} \quad \text{(EQ 3)}$$

where

R:	recruitment at age 0 in June
B:	Spawning stock biomass
C_{13}:	Maximum recruitment (number of larvae in June)
C_{14}:	The value of B giving half of maximum recruitment.

This relationship is applied for each of the areas 2 and 3, where spawning takes place.

The spawning stock- recruitment relationship given by Hamre and Tjelmeland (MS 1982) is of the same form, but applied to recruitment at age 2 in September for the whole stock (no area distribution). They give the values 440 million for C_{13} and 450 thousand tonnes for C_{14} . This relationship was calculated based on a single-species model, and can thus not be assumed to be valid in a multispecies context. The values of C_{13} and C_{14} are adjusted so that we get a reasonable development of the capelin stock. C_{14} was set to 30 thousand tonnes, as it has been observed that good capelin year classes (e.g. the 1989 year class) can be produced by relatively small spawning stocks.

The feeding level (Andersen and Ursin, 1977) is defined in the following way:

$$f(\phi) = \frac{\phi}{C_3 + \phi} \qquad \text{(EQ 4)}$$

where

ϕ:	Relative food abundance (plankton biomass divided by capelin biomass)
C_3:	The value of ϕ when a capelin consumes half of maximum.

The individual growth is made dependent on the size of the fish, the feeding level, and the temperature:

$$\frac{dl}{dt} = C_4(s) \times l^{C_5} \times f(\phi) \times (C_6 \times T + C_7) \qquad \text{(EQ 5)}$$

$$\frac{dW}{dt} = C_8(s) \times W^{C_9} \times (f(\phi) - C_{10}) \times (C_{11} \times T + C_{12}) \qquad \text{(EQ 6)}$$

The parameters C_4 and C_8 are sex-dependent, because the growth of male capelin is faster than the growth of female capelin. The parameters C_6 and C_{11} have been set to 1.0, and the parameters C_7 and C_{12} to 1.9, resulting in no growth when the temperature T in the sea is equal to -1.9 C (freezing). The growth in length is implemented so that a fish in a given length group will grow into the next length group with a probability proportional to the growth.

We assume that fishing is carried out only on mature capelin in the period October-March. The fishing mortality of mature capelin is the same in all areas and months, and for all age groups, sizes and sexes. A monthly fishing mortality of 0.10 is used (all mortalities are given as instantaneous mortality coefficients),, which corresponds to a relatively modest fishery.

For capelin, it is assumed that there is no other natural mortality than predation mortality generated by the species included in the model. 0-3 group herring are predators on 0-group capelin, and may significantly hamper the capelin recruitment, (Huse and Toresen, MS 1994). This is accounted for by introducing an additional predation mortality on 0-group capelin in each area:

$$M_{0cap} = C_{15} \times H_0 + C_{16} \times H_1 + C_{17} \times H_2 + C_{18} \times H_3$$

where H_i is the number of herring of age i. We assume that all capelin die after spawning.

6 Herring

The Norwegian Spring Spawning Herring Stock is included by running MULTSPEC together with HERMOD, a single species model for the herring stock (Dommasnes and Hiis Hauge, MS 1994). The HERMOD areas include the Norwegian Sea, the Norwegian Coast and the Barents Sea. While the herring is immature it stays mainly either in the Barents Sea or in coastal areas. In the Barents Sea growth and natural mortality are taken care of by MULTSPEC while HERMOD simulates all other processes.

The herring parameters are denoted by *H* (Phe in the parameter file).

The herring stock is divided into 6 stock components, 16 age groups (0-15+) and 42 length groups of 1.0 cm (4-45 cm). It is not divided by sex. The reason for dividing the stock into stock components is the complexity of the migration patterns within the stock.

Six different sets of migration parameters are implemented, each corresponding to a stock component. The parameters are set so that the spawning areas are placed along the Norwegian coast from Karmøy to Ofotfjord. The 0-group then drifts north to the Barents Sea where it stays for about two years before the herring heads west and south to coastal areas. Here it stays until it matures. The mature stock migrates to the Norwegian Sea after spawning. An additional parameter makes it possible to choose another migration pattern for the mature stock. This parameter describes the pattern of the mature stock in the 1950s. The reason for this additional option is that parts of the stock tend to readopt this old migration pattern. This option is not used in the current paper.

The function that determines the number of each age group that matures is dependent on length only:

$$m(a, l) = \frac{n(a)}{1 + e^{H_2 \times (H_1 - ml[a])}},$$

where:

$m(a,l)$:	Number that matures at age a.
H_1:	Fish length at 50% maturity, referred as "length at maturity".
H_2:	Change in maturation when $l = H_1$
$n(a)$:	Number of herring at age a.
$ml(a)$:	Mean length at age a.

Spawning takes place in March, and the resulting number of larvae is calculated from the biomass of the spawning stock at that time.

$$R(B) = H_3\left(1 - e^{\left(e^{(-0.17377)} - e^{(0.0005)(B-2500)}\right)}\right), \qquad \text{(EQ 7)}$$

where

R:	Recruitment in June.
B:	Spawning stock biomass.
H_3:	Maximum recruitment.

This is a depensatory stock-recruitment curve (Ulltang, 1980) with inflection point at B = 2.5 million tonnes. In order to model the fluctuations in the recruitment, H_3 is set higher two succeeding years every 8 years.

Inside the MULTSPEC areas the growth function for herring is the same as for capelin. Outside the MULTSPEC areas the growth is expressed as follows:

$$\frac{dl}{dt} = H_4 l + H_5.$$

H_4 and H_5 are constant for all age groups.

We assume that fishing is carried out only during September, October, February and March. The yearly fishing mortality is set to 0.15 and is the same in all areas. The herring starts to recruit to the fishery at 25 cm length and is fully recruited at 35 cm length.

In order to account for predation by other predators, we assume that there is a natural mortality of 0.02/month in the MULTSPEC areas in addition to the mortality generated by predation by cod, harp seals and minke whales. Outside the MULTSPEC areas natural mortality is set to 0.23/ year, which is the natural mortality used for age 3 and older herring in the ICES stock assessments (Anon., MS 1995b).

7 Cod

The cod parameters are denoted by G.

The cod stock is divided into 11 age groups (0-10+) and 20 5 cm length groups (0-100 cm).

The migration parameters for cod are set so that the larvae drift into the Barents Sea, and the cod then moves westwards as it becomes older. There is also a migration southwards to the coast in the months October-March, and a migration to the north and east in the months April-September. In particular, the migration parameters are set so that a part of the age groups 6 and 7 and all cod of age 8+, will be in area 1 (Lofoten/ Vesterålen) by April 1, when spawning takes place. All cod found in area 1 at April 1, is assumed to be mature.

The spawning stock biomass - recruitment relationship used is of the same form as for capelin:

$$R = \frac{G_{13} \times B}{G_{14} + B} \qquad \text{(EQ 8)}$$

The value 6000 million for the maximum recruitment G_{13} at age 0 (in June) should be seen in relation to the maximum recruitment at age 3 for the year classes 1966 and onwards (Anon., 1995a) which is 1818 million fish (the 1970 year class). The second strongest year class is the 1969 year class (1015 million). G_{14}, the value of the spawning stock biomass giving half of maximum recruitment, has been set to 150 thousand tonnes, which is close to the lowest level in the period from 1946 onwards.

The feeding level concept (Andersen and Ursin, 1977) is defined in the following way for cod:

$$f(\phi(L)) = \frac{\phi(L)}{\phi(L) + G_3(1)} \quad \text{(EQ 9)}$$

where $\phi(L)$ is the total food abundance (capelin + herring + cod + other food, 1000 tonnes per square nautical mile) and $G_3(1)$ is the value of $\phi(L)$ when a cod eats half of maximum consumption. The amount of prey (capelin, herring and cod) of length l eaten per unit time by a cod of length L is given by:

$$R_{cod}(l, L, prey) = H_{cod} \times f(\phi(L)) \times \frac{\phi(l, L, prey)}{\phi(L)} \quad \text{(EQ 10)}$$

where H_{cod} is the maximum food uptake and $\phi(l, L)$ is the availability of prey of length l as food for cod of length L.

H_{cod} is made size- and temperature dependent:

$$H_{cod} = G_{22}(1) \times e^{0.104 \times T - 0.000112 \times T^3} \times W_{cod}^{G_{22}(2)} \quad \text{(EQ 11)}$$

and $\phi(l, L)$ is defined by:

$$\phi(l, L) = S(l, L) \times N(l) \times W(l) \quad \text{(EQ 12)}$$

The size- and temperature dependency in this formula is taken from Jobling (1988). The values for $G_3(1)$ and $G_{22}(1)$ and for other food are the same as those estimated at the last meeting of the Multispecies Assessment Working Group (Anon., MS 1995c) for cod preying on mature capelin, using mainly the same methodology as in Bogstad and Tjelmeland (MS 1990, 1992). The suitability S(l,L) is implemented as a piecewise linear function. The suitabilities of different sizes of capelin, herring and cod as prey for different sizes of cod as predator are based on studies of the diet of North-East Arctic cod (Mehl, 1989, Bogstad *et al.* (1994)). The amount of other food has been set equal in all areas, but decreasing with cod age. Because the herring in area 1 stays in the Tysfjord/Ofotfjord area for some months in late autumn and early winter, where it is not available as food for Northeast Arctic cod , we assume that in Area 1 there is predation by cod on herring only in February, March and April.

The growth of cod is modelled in the same way as the growth of capelin.

$$\frac{dl}{dt} = G_4 \times l^{G_5} \times f(\phi) \times (G_6 \times T + G_7) \quad \text{(EQ 13)}$$

$$\frac{dW}{dt} = G_8 \times W^{G_9} \times (f(\phi) - G_{10}) \times (G_{11} \times T + G_{12}) \quad \text{(EQ 14)}$$

The parameters describing the relationship between growth and temperature, G_6, G_7, G_{11} and G_{12}, have the same values as for capelin. The values for G_4, G_5, G_8 and G_9 are the same as those used in the studies of cod growth presented in Anon. (1995c), where it was shown that MULTSPEC could reproduce the observed changes in growth quite well.

The fishing pattern ($G_{32}(a)$) is the same as the one estimated for 1993 by the ICES Arctic Fisheries Working Group at its 1994 meeting (Anon., MS 1995a). The fishing mortality (G_{21}) is set so that the yearly fishing mortality becomes 0.46 (mean over ages 5-10, unweighted). This corresponds to F_{med}, which is used by ICES as a biological reference point for this stock (Anon., MS 1995a). The fishing mortality is the same for all months and areas. No length selectivity of the catch within an age group is included, giving the same weight at age in the catch as in the stock, and consequently the catch in weight corresponding to a given fishing mortality becomes too low.

The ICES Arctic Fisheries Working Group uses a natural mortality of 0.2 per year (0.0167 per month) for cod. When predation from mammals is calculated by the model and is no longer included in the natural mortality, a lower value should be used. We have chosen 0.012 per month.

8 Sea Mammals

The submodels for harp seals and minke whales are basically area-structured one-species models. Interactions with the fish species are limited to the effects of mammal predation on the fish stocks. Tentative formulations of how the fluctuations of prey stocks are likely to affect the behaviour and condition of the sea mammal populations have been made, but are not included in the present paper.

The minke whale and harp seal parameters have prefixes *pmi* and *pha*, respectively. See Appendix for details on parameters.

The minke whale stock is divided into 8 areas, MULTSPEC areas 1 - 7 and an area 0 (see Introduction), 2 sexes and 21 age groups (0-20+).

The harp seal stock is divided into 7 areas and 17 age groups (0-16+).

At present, the migration procedures for sea mammals make no distinction with respect to sex or age group.

The minke whale stock spends most of the time south of the model areas 1 - 7. The model provides for a northward migration during spring and early summer, and a southward migration during late summer and autumn. The distribution is an extrapolation from the findings of the July 1989 sighting survey (Øien, 1991). The fraction of the stock present in the model areas 1-7 never exceeds 55%.

The harp seal stock spends late winter and spring in coastal areas (mainly 3 and 5), and migrates northward during summer and autumn (Haug *et al.* 1994). In this context the White Sea is regarded as belonging to area 5.

Tabs. 1 - 2

The distribution patterns resulting from the migration procedures are shown in Tables 1 and 2. The tables specify the fraction of the population being present in a given area at a given month. The migration parameters have been chosen so as to give this distribution. The pattern for minke whales is the same as used in Bogstad *et al.* (MS 1992), while the migration pattern for harp seals has been somewhat adjusted.

Recruitment takes place once a year, during January in the whale model, and during March in the seal model. Equal numbers of males and females are born. The number of 0-year olds of sex s recruited to the stock is given as:

$$\Delta N_{A,s,0} = \frac{1}{2} \times \sum_{a=1}^{a_{max}} R_a \times N_{A,1,a}$$

where R_a=(P_repro) =reproductivity for females age a; equals the fraction of age groups *a* recruited to the breeding stock, multiplied by a fertility parameter specifying the average number of recruits born by a mature female (0.95 for whales and 0.94 for seals).

The weight of sea mammals is an essential variable for computing their food consumption. At present the weight is treated as a function of age in whole years only. The weight at age for minke whales is calculated using a von Bertalanffy function for length at age from Christensen (1981), combined with a length-weight relationship obtained by Folkow and Blix (1992). The length at age function is

$$L_t = 833(1 - e^{-0.169(t+4.3)})$$

for males and

$$L_t = 907(1 - e^{-0.142(t+4.3)})$$

for females, and the length-weight relationship is

$$W = 8.148l^{3.163}.$$

This gives the following formulas for the weight at age at July 1 (used as a representative weight for the part of the year when the minke whales stays in the Barents Sea):

$$W = 6654\,(1 - e^{-0.169\,(a+4.8)})^{3.163}$$

for males and

$$W = 8709\,(1 - e^{-0.142\,(a+4.8)})^{3.163}$$

for females.

According to Innes *et al.* (1981) the average weight of a normally growing harp seal is set to

$$W = 129.9 \times e^{-1.458 \times e^{-0.394 \times (a+0.5)}} \quad \textbf{(EQ 15)}$$

For both seals and whales, the model has a tentative formulation for how the condition factor depends on the food supply, but this feature has not been included in the runs presented in this paper.

Catches of minke whales are subtracted from the population of age 1 and older whales present in MULTSPEC areas in June.

For harp seals the distinction is made between pups (0 years old) and age 1 and older seals. The catches are subtracted in March, after the breeding season.

In the reference run, the catches are set so that the populations stay approximately constant.

Different natural mortality parameters apply for age group 0 and older animals (see Appendix).

The computation of predation by sea mammals is based upon their energy requirement. The model assumes that the normal energy requirement of an individual during a time step of length Δt is either a function of the predator's weight alone (whales present only in summer) or a function of weight and month (seals). The normal energy requirement of a predator subpopulation $N^{p}_{A,s,a}$ during a time step of duration Δt is set to

$$E^{p}_{A,s,a} = N^{p}_{A,s,a} \times P_p \times W \times \Delta t \quad \textbf{(EQ 16)}$$

where P_p is a parameter expressing the average rate of energy consumption of the species at the time. This consumption is distributed over the various prey populations, including exogenous "other food", in proportion to the mass density of the prey weighted by its suitability for the predator. Provided that the time step is sufficiently short, the consumption of each prey will be small compared to prey stock size, and we set the consumption from the predator subpopulation $N^{p}_{A,s,a}$ on prey species i in area A to

$$C_{A,s,a}^{p,i} = E_{A,s,a}^{p} \times \frac{s_{p,i} B_{i,A}}{\sum_j \eta_j s_{p,j} B_{j,A}} \qquad \text{(EQ 17)}$$

where

$s_{p,i}$: suitability of prey i to predator p
$B_{i,A}$: biomass of prey i in area A
η_i: energy density of prey i

As for whales, Blix and Folkow (1995) have estimated the daily energy expenditure or field metabolic rate to to 80 kJ kg^{-1} day^{-1}. Nordøy *et al.* (1995a) estimate the gross energy intake of the entire whale population during the summer to 8.64 10^{12} kJ, of which the field metabolic rate accounts for 5.51 10^{12} kJ. Taking this ratio between gross energy intake and field metabolic rate into account, we get a gross energy intake of 125 kJ kg^{-1} day^{-1} or 1.45 W kg^{-1}.

The energy consumption rate parameter for seal, *pha_ereq*, is an array with one value for each month. The average gross energy intake is 343 kJ kg^{-1} day^{-1} or 3.97 W kg^{-1}, according to Nordøy *et al.* (1995b). The monthly values have been set so that the yearly average becomes equal to this value, and so that most of the feeding takes place from July to September.

9 Running the model

9.1 Initiation.

The initial data for capelin used in the runs reported on in this paper are data from the joint Norwegian-Russian acoustic survey in September-October 1993 (Anon., MS 1994). These data give the number of fish by area, sex, age and length, and also the mean weight for each length group. The cod stock numbers by age and size at age at January 1, 1994 are taken from the ICES Arctic Fisheries Working Group report (Anon., MS 1995a). The numbers of 1-and 2-year old fish have been calculated by back-calculating the prognosticated number at age 3 by a yearly natural mortality M=0.2 (this is probably too low, but has been used by Mehl (1989) and Bogstad and Mehl (1992) when calculating the cod stock's consumption of various prey species). The area distribution of immature fish is based on data from the Norwegian winter survey in the Barents Sea and the autumn Svalbard survey, and it is assumed that all the mature fish are in area 1 in January. The size distribution has been calculated from the weights in the stock at January 1 taken from the working group report, as described by Bogstad and Tjelmeland (MS 1990, 1992).

The model was started in October 1992, with capelin data from the 1992 autumn survey (Anon., MS 1993) and cod data for January 1993 from the working group report (Anon., MS 1995a), prognosticated forward in time from January to October. The model was then run to January 1993, when it was updated with 1993 cod data. In April 1993, cod and capelin spawn, so that a 1993 year class is generated. The capelin stock in the model was updated with 1993 capelin survey data in October 1993.

The herring stock number at age is taken from the assessment made by the ICES Atlanto-Scandian Herring and Capelin Working Group (Anon., MS 1995b), and the area distribution and length at age is calculated based on data from several Norwegian surveys (all described in Anon., MS 1995b).

The harp seal population at age 0 and at age 3 and older at March 1, 1991, was calculated from a pup production estimate of 142 000 (Russian aerial survey), age composition data from samples of Norwegian catches, and reproductivity parameters given in Appendix. This resulted in a population of 3 year and older seals of 377 000, with a very low number of 3-5 year old seals and also reduced numbers of 6-9 year old seals compared to older age groups. This is in agreement with the expected high mortality suffered by young seals during the 'seal invasions' to the Norwegian coast in the 1980s, especially the years 1986-1988.

The pup production in 1989-1990 was assumed to be at the 1991 level. The number of 1 and 2 year old seals in 1991 was calculated by subtracting pup catches from the production and correcting for later natural mortality and catches of 1 year old seals. This gave a total population of 1 year and older seals of 537 000 at March 1, 1991. The harp seal stock size at October 1, 1993 was then calculated by projecting the stock at March 1, 1991, forward in time correcting for catches and natural mortality. The number of pups produced in 1992 and later has been calculated from the model reproductivity rates. The total harp seal stock number at the start of the simulations is about 50% larger than in the simulations carried out by Bogstad *et al.* (MS 1992).

As in Bogstad *et al.* (MS 1992), the minke whale population has been scaled to a initial population totalling 80000 whales in 1990, and then projected forward in time correcting for catches and natural mortality. The number of calves produced in 1992 and later has been calculated from the model reproductivity parameters.

10 Results

10.1 Reference run.

As reference run (run 1) was chosen the simulation using the parameter values given in the parameter files in the Appendix for fish, seals and whales. A period of 20 years was used for all

Tab. 3 Fig. 2

runs. A summary table of the stock sizes, catches and consumption figures in the reference run is given in Table 3. In Figure 2 is plotted biomass development of immature capelin, cod, herring in the Barents Sea and total herring stock.

Differences between results of the present reference run and the reference run in Bogstad *et al.* (MS 1995) are mainly due to that predation by cod on maturing and adult herring in MULTSPEC area 1 now is taken account of and that the recruitment function for herring has been changed. Further, a fishing mortality of 0.15 has now been applied on the herring stock compared to 0.05 in Bogstad *et al.* (MS 1995).

The variation in the biomass of cod, herring and capelin is generally within the range observed for the period where stock estimates are available. The herring spawning biomass, which is not shown in Table 3, reaches a peak of about 9.4 mill. tonnes in 1998, and this is at the same level as estimated by VPA for the 1950s (Dragesund *et al.* 1980). The fluctuations in stock size indicate that the main features in the herring-capelin dynamics have been captured (strong decrease in capelin stock when the strong 1999 and 2000 year classes of herring enter the Barents Sea), and the influence of capelin on the cod stock can also be seen relatively clearly. The total consumption by cod and fraction of capelin, herring and cod in the diet of cod also seems reasonable when compared to the results of Mehl (1989) and Bogstad and Mehl (1992). The total consumption of seals and whales has been changed due to the new models for food requirement. This gave an increase in the total consumption by harp seals of about 50 % (equal to the increase in stock number) and a decrease of 25 % in the consumption by minke whales compared to the figures given in Bogstad *et al.* (MS 1992). The minke whale's food preferences were set at levels which gave results consistent with the general pattern in the whale diet as reported in Haug *et al.* (MS 1995). The biomass of capelin, herring, cod and other food consumed by minke whales during 1993 and 1994 broken down by areas and months was shown in Bogstad *et al.* (MS 1995) and compared with the diet reported in Haug *et al.* (MS 1995).

10.2 Effects of varying stock size of minke whales and harp seals, and food preferences of minke whales, harp seals and cod

The effects of varying stock size of minke whales and harp seals were studied by completely removing both stock of marine mammals from the ecosystem (run 2), removing only minke whales (run 3) or harp seals (run 4), alternatively assuming no whale catch (run 5), seal catch (run 6) or marine mammal catch (run 7), the latter three runs leading to increase in one or both of the marine mammal populations. Effects of varying food preferences were studied by doubling the suitability of cod for whales (run 8) or other food for whales (run 9), doubling the suitability of herring for seals (run 10), and finally by reducing suitability of herring for cod by 50 % (run 11). The results of the simulations are given in Tables 4-13. In Table 14 some results are summarized.

Some effects were as intuitively expected, while others were not equally obvious. For example, removing the two mammal stocks (run 2) led as expected to a higher herring stock and in most years a higher cod stock. However, except for the first years (1993-1997), it led to a lower capelin stock which must be seen as a result of the effect an increasing herring stock has on capelin recruitment. The reduced capelin stock led in turn to a reduced cod stock in two years (2008 - 2009). The complexity of the system is illustrated in Figure 3 where results of increasing the suitability of cod for whales (run 8), keeping all other parameters as in the reference run, are shown. Initially, a higher suitability of cod led to a lower cod biomass and higher capelin and herring biomasses. Herring biomass continued to increase compared to the reference run throughout the whole simulation period. Because of the detrimental effect this had on capelin recruitment, capelin biomass got below its reference run values in some years (years 2004 and 2010 - 2012). Increases in herring and capelin biomasses led in turn to a higher cod biomass in some years (years 2000 - 2002 and 2008 - 2010).

The main effects may be summarized as follows:

The herring stock increases or decreases as predation from marine mammals decreases (runs 2-4) or increases (runs 5-7). With suitabilities as in reference run, the herring stock is much more sensitive to changes in the minke whale stock (runs 3 and 5) than to changes in the harp seal stock (runs 4 and 6). This is illustrated in Figure 4 comparing runs 3 and 4.

The development in the capelin stock is mainly determined by changes in the herring and cod stock. The effect on capelin of changes in these stocks generally goes in the opposite direction of effects from changes in marine mammals predation on capelin. This results in an increase or decrease in the capelin stock when the minke whale stock increases (run 5) or decreases (run 3) i.e. a counterintuitive effect. Since herring is less sensitive to changes in the seal stock than to changes in the minke whale stock, and since predation on capelin from seals is high, an increase (run 6) or decrease (run 4) in the seal stock lead to a decrease or increase in the capelin stock, i.e. the effect intuitively expected.

The effects on the cod stock from changes in the marine mammal stocks are more difficult to summarize in few words. Generally, the cod stock will increase or decrease when marine mammal stocks decrease or increase, as intuitively expected. For example, if the seal population is not exploited and is allowed to increase (run 6), mean annual cod catch will decrease by 32000 tonnes over the simulation period (Table 14), and the catch in the last year will be 112000 tonnes lower than in the reference run. This would be a substantial loss to the fishery taking into account the high value of cod. However, because of the strong cod-capelin interactions, resulting in a tendency of cyclic variations in the two stocks with a time lag between the two stock trajectories, the changes in the cod stock may in some years be in the opposite direction than expected when compared to the reference run.

One interesting feature which again reflects the complexity of the system is that there would be larger gains on average in the cod fishery by removing the seals than by removing the whales, despite the fact that whales eat more cod than seals do in the reference run. The explanation lies in the herring-capelin-cod dynamics: Removing whales have a large effect on the herring stock, leading to strongly reduced capelin stock and thereby reduced cod growth.

Run 11 was included for illustrating how sensitive the whole system is to changes in assumed food preferences of cod. Decreasing the suitability of herring as food for cod had much larger effects than changing some of the marine mammal preferences (runs 8-10) and even more dramatic effects than removing both marine mammal stocks from the system (Figure 5). The herring stock increased above historic levels, with resulting detrimental effects on the capelin stock. Also the cod stock decreased due to low capelin stock.

Fig.5

11 Discussion and conclusions

The role of marine mammals in the ecosystems can not be described by any single, or indeed any finite number of features. All we can do is to describe and possibly quantify some effects of the mammals' presence on parts of the ecosystem. This paper considers effects of predation. Predation is at least in theory quantifiable and is also considered to be of potentially high importance with respect to effects on long term fishery yield.

However, even when restricting the considerations to predation, drastic simplifications have to be made in the model compared to the processes going on in nature. For example, the concept of constant food suitabilities is such a simplification.

The selection of species in the multispecies model is based on the hypothesis that total fish production in the Barents Sea area (including Norwegian coastal waters) to a large extent is determined by the development in the stocks of North-East Arctic cod, Norwegian Spring-Spawning herring and Barents Sea capelin. Accordingly, main emphasis has been placed on modelling the population dynamics of these species, the interaction between them and parts of the biological and physical environment having a direct and significant impact on their development. The apex predators are an important part of this environment. There are other apex predators than minke whales and harp seals (other marine mammal stocks and birds) , and there are other fish stocks which could influence the development of the three modelled species (e.g. polar cod). More species may be added to the model later (polar cod is already formally included in the model but has been turned off in the simulations presented because of poor knowledge of its population dynamics), but it is considered very unlikely that this could reverse the directions of effects on fish yield from increasing or decreasing stocks of minke whales and harp seals. However, the size of the effects could be affected (in both directions).

Concerning the modelled interactions, both errors in the marine mammals' total food composition and food preferences and inaccurate modelling of the interactions at the fish level could affect the size of the estimated effects. Also with respect to such errors, it is considered very unlikely that they could reverse the direction of main effects. Extensive investigations to estimate the minke whales and harp seals' total food consumption have been conducted (Blix and Folkow, 1995; Nordøy *et al.*, 1995 a,b) , and the available estimates are probably among the best compared with estimates for marine mammal stocks in other parts of the world. This does not preclude that errors still may be considerable due to methodological difficulties in estimation. Concerning food preferences, methodological problems exist in estimating these from available data (see for example Skaug *et al.*, MS 1995). For the minke whale stock, the stomach sampling during 1992-1994 (Haug *et al., MS* 1995) has shown a high proportion of fish in the diet except for the Bear Island-Spitsbergen area where krill dominated in 1993-1994, and there is also some consistency between years with respect to areas with large contribution from the modelled species. For harp seals, larger uncertainties exist with regard to the proportion of commercially important fish species in the diet.

Of the interactions at the fish level, the cod-capelin interactions have been most extensively studied (see e.g Bogstad and Tjelmeland, 1992; Tjelmeland and Bogstad, 1993), and the model calculation of cod's consumption of capelin is in general agreement with direct calculation from stomach sampling data (Anon., MS 1995c). Cod's consumption of herring in 1993-1994 in the simulation runs is high compared to direct calculations from stomach content data. However, it has been shown by regression techniques that cod may generate a very high mortality on 0-group herring in years with low capelin stock (Barros, 1995), and it is possible that the stomach data do not properly reflct the predation by cod on herring because cod in the pelagic layers are under-represented in the stomach samples. Quantitatively, the largest uncertainty is probably connected to the herring-capelin interactions. Historical time series of herring and capelin recruitment support the hypothesis that presence of strong year classes of herring in the Barents Sea have a detrimental effect on caplein recruitment (Hamre, 1991), and sampling of herring stomachs has confirmed that young herring feed extensively on capelin larvae (Huse and Toresen, MS 1994). However, the modelled predation needs further evaluation.

The simulation results presented are of a preliminary nature since too little time has been available for experimenting with the model after herring was included. In addition to further studies of herring's predation on capelin larvae, more work has to be done on the recruitment functions and the suitability of herring as prey for cod. Also the functions used for individual growth of herring need further considerations.

Concerning herring, it should be recognized that only part of the minke whale-herring interactions are at present taken account of. The mature component of the herring stock has its main spawning and feeding area south of the MULTSPEC area and in the Norwegian Sea. The effect of this predation could not be included in the present study. The coupling of MULTSPEC to the herring model HERMOD should be regarded as a first step towards extending the MULTSPEC model itself to the Norwegian Sea and thereby making it possible to study predation processes in that area.

In the simulations, strong herring recruitment has been assumed to occur at regular intervals. Strong herring year classes seem to be connected with warm periods in the Barents Sea, and strong cod and herring year classes have shown a tendency to appear in the same years (Sætersdal and Loeng, 1987). In further simulations this should be taken account of. The model allows for stochasticity in recruitment (although still using a spawning stock-recruitment relationship) for all fish species, and the effects of this should be investigated by carrying out a large number of simulations. A 20-year run requires about 2 hours of computer time (on a HP 9000/755), which may limit the number of simulations somewhat.

Mammal predation on cod and capelin has been assumed to be non-selective with respect to prey size. This assumption is probably not valid and should be modified based on data on prey size selection. The effects of predation on the prey stocks will depend on the size or age composition of the consumed prey. Particularly the predation on 0-group fish should be calculated by separate suitabilities.

Constant migration patterns have been assumed in the simulations, and the sensitivity to variations in migration patterns has not been tested. It is, however, obvious that the model results will depend heavily on the degree of overlap between the species, and proper modelling of migration is equally important as estimating a predator's preferences given a certain menu card in a local area. Models of migration and food preferences have to be combined. If for example part of the minke whale stock actively search for herring or krill over large areas, the model should reflect this. If some minke whales go for herring, they will probably not be in the Barents Sea in years with no herring in that area. For capelin and cod, we know that there have been large changes in the geographical distributions, and there is a connection between temperature changes and changes in migration pattern.

In the simulations, adjustments have been made to values of natural mortality for the fish stocks compared to traditional values in single stock assessments to take account of that mortalities generated by main predators are now explicitely calculated. These adjustments have been kept unchanged in all simulations. Runs 2-4 therefore do not simulate a situation where marine mammals are not taken account of in the assessments, but a situation where they are actually removed. The main purpose of including runs 2-4 was to see how the model behaved under a wide range of marine mammal abundances, taking zero abundance as one extreme. The results were as expected compared with results of those runs where marine mammals were allowed to increase above their present level, giving effects in opposite direction. The size of effects illustrates the importance of marine mammals, but compared to run 11 it also illustrates that cod is the key predator on fish in the Barents Sea system. It is important to include marine mammals in a multispecies model, but proper modelling of cod's predation should still have the highest priority.

The fishing mortalities on capelin, cod and herring have been assumed constant between runs and years and not dependent on the state of the stocks. In practice, an adaptive management policy will be aimed at. When for example cod is available in larger quantities due to decreased predation from minke whales, this could be taken out as fish catch instead of being left in the sea and creating extra predation pressure on the capelin and herring. This could possibly increase the total gain from reduced minke whale predation and also contribute to avoid a situation where substantial gains in one fishery were achieved at the expence of losses in other fisheries. For estimating the potential gains of such an adaptive strategy, simulations should be carried out where fishing mortality on each stock next year is decided upon using decision rules where expected stock development of all three fish species over the coming years is taken account of.

A tentative conclusion on likely effects of an increasing whale stock on important fish stocks is that the herring stock will be most heavily affected . All effects demonstrated on herring in the present simulations will be substantially enlarged when minke whale's predation on subadult and adult herring in Norwegian coastal waters south of the MULTSPEC area and in the Norwegian Sea is included. An increasing harp seal stock will most heavily affect the capelin and cod stock. The estimated size of the effects in the present study may be underestimated due to the assumed large proportion of other food in seals' diet.

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Table 1. Distribution of harp seals

Month	Area1	Area2	Area3	Area4	Area5	Area6	Area7
1	0.00	0.00	0.20	0.00	0.80	0.00	0.00
2	0.00	0.00	0.30	0.10	0.60	0.00	0.00
3	0.00	0.00	0.25	0.00	0.75	0.00	0.00
4	0.00	0.00	0.25	0.00	0.75	0.00	0.00
5	0.00	0.00	0.00	0.00	0.75	0.25	0.00
6	0.00	0.00	0.00	0.00	0.30	0.50	0.20
7	0.00	0.00	0.00	0.00	0.20	0.50	0.30
8	0.00	0.00	0.00	0.00	0.00	0.20	0.80
9	0.00	0.00	0.00	0.00	0.00	0.10	0.90
10	0.00	0.00	0.00	0.00	0.10	0.00	0.90
11	0.00	0.00	0.10	0.05	0.15	0.00	0.70
12	0.00	0.00	0.30	0.10	0.60	0.00	0.00

Table 2. Distribution of minke whales

Month	Area0	Area1	Area2	Area3	Area4	Area5	Area6	Area7
1	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2	0.92	0.04	0.04	0.00	0.00	0.00	0.00	0.00
3	0.74	0.04	0.05	0.12	0.00	0.00	0.06	0.00
4	0.60	0.04	0.05	0.18	0.03	0.00	0.11	0.00
5	0.49	0.04	0.05	0.21	0.03	0.03	0.13	0.02
6	0.45	0.05	0.07	0.19	0.02	0.05	0.14	0.03
7	0.45	0.05	0.07	0.22	0.02	0.02	0.16	0.02
8	0.56	0.06	0.10	0.13	0.05	0.00	0.10	0.00
9	0.82	0.05	0.11	0.00	0.03	0.00	0.00	0.00
10	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
11	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
12	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 3. Stocks, consumption and catches, run 1 (reference run) State of stocks at Septermber 30. Mature capelin at April 1. Consumption and catches for 12 last months. Fish and other food in million kg. Mammals in numbers. IM.CAP = Immature capelin, MA.CAP = Mature capelin, B.HER = Herring biomass in MULTSPEC areas, TOT.HER = Total herring biomass, OTH = other food, CC = consumed by cod, WC = consumed by whales, SC = consumed by seals, C = catch. Suitabilities for whales: capelin 1.00, cod 0.20, herring 1.00, other food 0.10 Suitabilities for seals: capelin 1.00, cod 0.20, herring 1.00, other food 0.50.

YEAR	IM.CAP	MA.CAP	COD	B.HER	TOT. HER	WHALES	SEALS	CC.CAP	CC. COD	CC. HER	CC. OTH	WC. CAP	WC. COD	WC. HER	WC. OTH	SC.CAP	SC.COD	SC.HER	SC.OTH	C.CAP	C.COD	C.HER	C. WHAL	C.SEAL
1993	3661	1493	2649	3745	8531	83520	626068	2439	75	1598	3640	148	70	227	139	540	61	67	544	489	605	418	213	40368
1994	474	59	2715	3178	10511	85328	627857	710	120	1422	4989	38	111	264	217	191	103	118	923	75	705	545	237	42000
1995	452	58	2398	698	11063	85024	628240	451	138	782	5020	18	143	210	285	43	107	105	1155	170	834	719	2501	34733
1996	662	1	2093	99	10923	84687	623501	573	102	356	4481	64	162	112	340	175	99	47	1071	3	717	900	2491	33052
1997	1102	6	1938	112	10734	85037	616898	623	81	288	3988	96	155	82	345	257	91	8	1019	17	550	1056	2505	32122
1998	2365	92	1914	252	10866	85151	610919	1151	83	263	3571	124	132	88	321	300	80	8	968	213	507	1208	2508	31937
1999	4455	71	2079	691	10341	85164	606357	2116	83	321	3252	192	92	117	229	521	60	10	675	185	536	1252	2508	32076
2000	4714	80	2454	2479	10701	85097	604382	2651	88	684	3401	178	67	201	155	602	54	48	510	255	512	1111	2505	32686
2001	3809	127	2823	3981	11431	84964	604525	2712	100	1137	3933	120	77	237	173	520	73	93	535	478	568	946	2501	33300
2002	2099	247	2882	2496	11657	84812	605827	2148	113	1130	4576	75	105	230	215	410	92	104	649	675	703	851	2496	33712
2003	1074	213	2577	546	11337	84639	607588	1394	110	703	4774	62	139	175	273	237	102	89	897	577	793	906	2491	33948
2004	1664	38	2159	153	10792	84526	609236	1085	91	352	4255	89	153	110	314	238	96	38	979	166	760	996	2488	34014
2005	3255	4	1929	180	10626	84439	610404	1517	76	299	3422	153	124	88	286	454	70	9	748	23	654	1123	2485	33947
2006	5342	97	1980	287	10270	84363	611018	2204	75	280	2995	241	89	82	208	570	54	10	605	239	558	1215	2483	33825
2007	6531	394	2419	746	9483	84289	611119	3615	83	326	2974	262	72	108	160	677	44	12	467	721	507	1165	2481	33685
2008	4848	539	3031	2263	9608	84208	610847	4230	106	710	3652	207	66	184	134	650	54	44	450	1006	527	1004	2479	33562
2009	3127	143	3340	3261	9811	84119	610398	3306	128	1188	4763	124	91	225	162	501	93	88	550	614	554	836	2476	33485
2010	1989	112	3124	1851	9690	84021	609937	1851	118	1079	5371	62	129	213	224	390	111	98	670	406	326	742	2473	33454
2011	1310	162	2567	379	9305	83921	609578	1383	98	630	4860	69	149	153	277	251	108	79	893	485	919	791	2470	33462
2012	2307	38	2015	163	8814	83823	609372	1309	80	344	3845	109	144	99	305	310	87	26	910	178	340	875	2467	33493

Table 4. Results of run 2. Only cod, capelin and herring. Notations as in Table 3.

YEAR	IM.CAP	MA.CAP	COD	B.HER	TOT.HER	CC.CAP	CC.COD	CC.HER	CC.OTH	C.CAP	C.COD	C.HER
1993	4372	1572	2807	4125	8986	2567	76	1633	3634	487	611	420
1994	663	64	3133	3862	11620	781	139	1648	5359	77	760	555
1995	366	96	3046	1031	12580	602	170	1023	5822	263	981	751
1996	600	3	2873	150	12469	484	137	522	5744	7	942	961
1997	1225	6	2785	230	12347	751	113	448	5297	15	828	1132
1998	2029	82	2684	366	11879	1309	116	484	4772	204	835	1249
1999	2941	130	2591	902	11985	1991	113	586	4202	314	876	1367
2000	3187	82	2704	3085	12827	1949	113	1106	4063	221	757	1289
2001	2850	131	3003	5127	14350	1915	124	1604	4371	391	703	1136
2002	1574	238	3236	3437	15174	1752	145	1541	5059	628	779	1056
2003	746	161	3218	932	15065	1176	153	1017	5723	464	873	1116
2004	819	46	3006	248	14252	799	134	550	5756	176	923	1206
2005	1483	2	2734	357	13847	1061	116	475	5093	12	936	1279
2006	2453	45	2496	401	13402	1313	109	544	4413	120	890	1413
2007	2864	199	2479	1056	13665	1946	106	585	3934	428	784	1511
2008	2179	223	2720	3332	14793	1935	117	1176	4048	493	686	1484
2009	1917	94	3071	5409	16294	1461	138	1715	4715	301	674	1330
2010	1045	157	3319	3560	17041	1285	149	1617	5446	438	764	1245
2011	493	101	3269	968	16766	859	151	1060	5991	321	893	1279
2012	573	30	2969	284	15739	582	132	592	5821	111	975	1338

Table 5. Results of run 3. Only cod, capelin, herring and harp seals. Notations as in Table 3. Suitabilities for seals: capelin 1.00, cod 0.20, herring 1.00 other food 0.50.

YEAR	IM.CAP	MA.CAP	COD	B.HER	TOT.HER	SEALS	CC.CAP	CC.COD	CC.HER	CC.OTH	SC.CAP	SC.COD	SC.HER	SC.OTH	C.CAP	C.COD	C.HER	C.SEAL
1993	3783	1512	2739	4053	8898	626068	2503	76	1627	3642	553	59	67	527	489	609	420	40368
1994	473	60	2936	3706	11336	627857	724	132	1578	5209	195	109	121	907	74	738	554	42000
1995	333	59	2736	981	12181	628240	445	158	942	5484	41	118	111	1138	175	913	744	34733
1996	406	1	2510	155	12078	623501	408	125	465	5224	116	116	62	1113	3	830	948	33052
1997	640	4	2396	226	11983	616898	472	104	390	4833	183	113	15	1088	10	688	1119	32122
1998	1249	56	2311	383	11754	610919	814	109	401	4445	185	103	18	1087	137	670	1248	31937
1999	2174	35	2279	922	11711	606357	1384	106	487	4020	353	85	21	864	90	702	1347	32076
2000	2124	43	2450	3107	12572	604382	1462	105	977	3949	419	75	68	712	122	621	1251	32686
2001	1405	110	2729	5066	14031	604525	1290	116	1477	4343	345	84	116	732	315	607	1105	33300
2002	389	153	2859	3351	14787	605827	907	135	1394	5002	180	102	122	929	412	690	1034	33712
2003	238	37	2733	919	14700	607588	362	136	858	5434	50	114	107	1118	121	760	1105	33948
2004	293	4	2485	256	13925	609236	282	120	467	5175	72	115	62	1153	14	772	1201	34014
2005	478	3	2230	373	13903	610404	382	107	408	4595	142	105	26	1117	8	746	1307	33947
2006	926	35	2077	441	13460	611018	588	101	455	4093	161	93	27	1105	84	680	1444	33825
2007	1458	42	2137	1091	13656	611119	986	103	492	3890	274	82	30	956	98	590	1532	33685
2008	1275	35	2406	3370	14745	610847	979	110	1037	4088	323	79	80	824	95	537	1484	33562
2009	691	91	2738	5392	16205	610398	837	124	1548	4596	244	91	123	858	246	569	1328	33485
2010	191	68	2884	3558	16899	609937	510	135	1442	5254	109	108	128	1019	203	670	1248	33454
2011	124	18	2747	991	16625	609578	191	133	910	5539	22	117	110	1154	62	771	1287	33462
2012	117	1	2442	303	15604	609372	124	117	509	5180	41	116	66	1194	2	803	1346	33493

Table 6. Results run 4. Only cod, capelin, herring and minke whales. Notation as in Table 3. Suitabilities for whales: capelin 1.00, cod 0.20, herring 1.00, other food 0.10

YEAR	IM.CAP	MA.CAP	COD	B.HER	TOT.HER	WHALES	CC.CAP	CC.COD	CC.HER	CC.OTH	WC.CAP	WC.COD	WC.HER	WC.OTH	C.CAP	C.COD	C.HER	C.WHAL
1993	4230	1553	2719	3818	8620	83520	2502	75	1604	3632	150	70	227	138	487	607	418	213
1994	659	64	2905	3335	10796	85328	766	127	1492	5142	38	113	265	213	78	727	547	237
1995	490	93	2686	754	11472	85024	606	148	853	5345	20	148	211	275	257	900	728	2501
1996	926	3	2413	97	11329	84687	667	114	406	4949	66	172	112	327	7	819	915	2491
1997	1915	8	2277	121	11113	85037	934	90	336	4372	110	162	80	321	23	669	1074	2505
1998	3424	117	2248	259	11124	85151	1675	92	327	3848	142	137	88	292	283	644	1217	2508
1999	5370	241	2374	717	10655	85164	2777	90	397	3410	193	99	111	229	507	682	1275	2508
2000	6145	121	2745	2579	11066	85097	3297	100	794	3529	192	67	197	141	355	629	1140	2505
2001	5382	234	3211	4185	11933	84964	3730	112	1257	3978	151	71	228	148	684	661	975	2501
2002	3919	233	3375	2614	12264	84812	3100	133	1270	4856	100	107	219	193	727	803	875	2496
2003	2332	306	3153	589	11986	84639	2389	125	821	5205	91	145	161	246	849	925	927	2491
2004	1784	48	2661	128	11330	84526	1385	109	429	5019	88	174	104	301	441	937	1018	2488
2005	3081	1	2254	190	11307	84439	1598	87	361	4016	134	149	85	289	99	848	1148	2485
2006	5160	53	2093	274	10920	84363	2025	83	369	3322	202	104	96	227	159	712	1260	2483
2007	6404	483	2309	782	10233	84289	3026	83	395	3067	216	84	110	208	776	603	1238	2481
2008	5534	598	2896	2588	10619	84208	3805	102	780	3497	203	61	192	134	1003	550	1085	2479
2009	3878	279	3484	3979	11337	84119	3825	130	1292	4467	144	76	230	144	853	629	919	2476
2010	2805	102	3561	2308	11507	84021	2339	146	1290	5687	70	127	220	207	466	823	831	2473
2011	1877	200	3185	485	11182	83921	1908	119	787	5594	78	157	157	251	601	996	889	2470
2012	1967	56	2568	128	10583	83823	1430	97	423	4842	92	171	99	298	361	1018	982	2467

Table 7. Results of run 5. No whale catch. Notation as in Table 3. Suitabilities for whales: capelin 1.00, cod 0.20, herring 1.00, other food 0.10. Suitabilities for seals : capelin 1.00, cod 0.20, herring 1.00, other food 0.50.

YEAR	IM.CAP	MA. CAP	COD	B.HER	TOT. HER	WHALES	SEALS	CC.CAP	CC. COD	CC. HER	CC. OTH	WC. CAP	WC. COD	WC. HER	WC. OTH	SC.CAP	SC.COD	SC.HER	SC.OTH	C.CAP	C.COD	C.HER	C. WHAL	C.SEAL
1993	3661	1493	2649	3745	8531	83520	626068	2439	75	1598	3640	148	70	227	139	540	61	67	544	489	605	418	213	40368
1994	474	59	2715	3178	10511	85328	627857	710	120	1422	4989	38	111	264	217	191	103	118	923	75	705	545	237	42000
1995	450	58	2393	692	11056	87451	628240	450	137	781	5018	19	148	215	296	43	106	105	1155	170	833	719	0	34733
1996	656	1	2077	96	10910	89676	623501	569	102	354	4467	69	172	117	365	175	98	47	1072	3	715	899	0	33052
1997	1085	6	1906	104	10717	92745	616898	609	80	283	3953	106	169	88	383	256	90	8	1022	17	544	1055	0	32122
1998	2390	91	1870	239	10838	95685	610919	1134	79	255	3510	144	148	96	367	299	78	7	972	210	497	1206	0	31937
1999	4616	70	2033	664	10296	98628	606357	2120	80	303	3173	233	104	133	264	530	58	9	666	183	521	1249	0	32076
2000	4951	80	2412	2387	10575	101589	604382	2697	85	649	3314	222	79	237	186	614	52	46	499	262	498	1108	0	32686
2001	4046	140	2786	3829	11198	104579	604525	2840	96	1073	3830	160	92	287	212	532	70	91	524	501	553	941	0	33300
2002	2292	254	2839	2376	11326	107604	605827	2264	110	1073	4483	105	132	288	273	425	89	102	634	694	687	841	0	33712
2003	1209	230	2508	486	10944	110674	607588	1484	106	659	4655	90	182	222	364	256	99	87	878	617	775	890	0	33948
2004	1876	42	2064	134	10395	113902	609236	1171	85	323	4075	134	202	140	429	264	92	33	954	187	735	974	0	34014
2005	3709	4	1821	139	10132	117257	610404	1580	69	270	3210	232	166	111	401	482	65	7	719	28	619	1093	0	33947
2006	6406	110	1887	237	9728	120727	611018	2343	66	241	2740	391	117	97	286	608	48	7	563	258	522	1172	0	33825
2007	8418	488	2383	650	8837	124306	611119	4014	73	281	2684	434	96	143	216	739	35	9	395	809	476	1109	0	33685
2008	6934	754	3071	1951	8708	127989	610847	5021	97	588	3324	370	93	252	186	728	42	36	367	1191	502	938	0	33562
2009	4391	306	3496	2766	8632	131770	610398	4920	113	974	4244	297	116	312	210	598	77	76	451	959	642	763	0	33485
2010	2846	102	3215	1487	8287	135648	609937	2667	117	937	5317	146	213	314	347	448	111	89	603	466	827	660	0	33454
2011	2059	190	2534	262	7816	139636	609578	1797	91	524	4755	160	253	216	462	339	105	68	789	571	919	697	0	33462
2012	3081	44	1881	105	7382	143742	609372	1592	67	284	3549	229	239	139	529	385	80	17	826	298	823	778	0	33493

Table 8. Results of run 6. No seal catch. Notations as in Table 3. Suitabilities for whales: capelin 1.00, cod 0.20 herring 1.00 other food 0.10. Suitabilities for seals: capelin 1.00, cod 0.20, herring 1.00, other food 0.50.

YEAR	IM.CAP	MA.CAP	COD	B.HER	TOT. HER	WHALES	SEALS	CC.CAP	CC. COD	CC. HER	CC. OTH	WC. CAP	WC. COD	WC. HER	WC. OTH	SC.CAP	SC.COD	SC.HER	SC.OTH	C.CAP	C.COD	C.HER	C. WHAL	C.SEAL
1993	3661	1493	2649	3745	8531	83520	626068	2439	75	1598	3640	148	70	227	139	540	61	67	544	489	605	418	213	40368
1994	474	59	2715	3178	10511	85328	627857	710	120	1422	4989	38	111	264	217	191	103	118	923	75	705	545	237	42000
1995	451	58	2396	697	11061	85024	658519	451	137	782	5019	18	143	210	285	43	109	107	1186	170	834	719	2501	0
1996	647	1	2085	99	10919	84687	680482	570	102	356	4475	64	162	112	341	184	104	49	1134	3	716	899	2491	0
1997	1050	6	1921	111	10730	85037	698753	607	81	287	3976	95	155	82	347	275	99	9	1121	17	547	1056	2505	0
1998	2275	87	1886	250	10861	85151	716661	1108	82	261	3555	122	132	88	324	327	89	9	1110	203	501	1207	2508	0
1999	4317	63	2039	689	10342	85164	735445	2032	82	312	3234	189	92	117	233	600	70	11	801	167	525	1251	2508	0
2000	4474	76	2404	2475	10697	85097	757031	2554	87	673	3372	176	67	201	157	718	65	57	628	239	499	1111	2505	0
2001	3471	122	2753	3966	11407	84964	781300	2562	99	1119	3913	116	77	239	176	632	90	116	689	459	551	946	2501	0
2002	1721	239	2790	2478	11603	84812	807276	1960	112	1110	4542	69	104	232	220	495	117	134	881	649	679	851	2496	0
2003	891	173	2462	537	11255	84639	834677	1178	108	678	4713	54	139	178	280	260	134	119	1270	482	761	906	2491	0
2004	1477	28	2045	155	10714	84526	863172	974	87	334	4124	86	150	111	319	307	127	51	1376	111	720	995	2488	0
2005	2741	4	1819	177	10530	84439	892220	1348	73	283	3327	149	121	90	292	605	97	13	1113	18	611	1121	2485	0
2006	4528	98	1867	282	10201	84363	921940	1942	72	261	2948	230	90	82	223	763	80	15	978	233	515	1212	2483	0
2007	5711	299	2304	733	9407	84289	952208	3311	80	304	2939	258	71	110	164	982	65	18	758	592	464	1162	2481	0
2008	4076	372	2876	2230	9503	84208	982998	3843	102	676	3620	200	66	188	139	967	86	70	758	810	489	998	2479	0
2009	2520	97	3098	3199	9648	84119	1014491	2749	122	1129	4710	110	93	229	174	748	150	143	961	456	611	828	2476	0
2010	1248	126	2843	1807	9467	84021	1046894	1518	110	1006	5114	54	124	219	232	555	177	162	1248	400	760	735	2473	0
2011	912	107	2271	362	9035	83921	1080400	937	92	565	4611	51	146	160	296	262	175	136	1769	329	824	784	2470	0
2012	1828	17	1774	161	8614	83823	1115146	1054	73	301	3544	106	136	99	317	502	139	44	1692	64	728	870	2467	0

Table 9. Results of run 7. No marine mammal catch. Notation as in Table 3. Suitabilities for whales; capelin 1.00, cod 0.20, herring 1.00, other food 0.10. Suitabilities for seals : capelin 1.00, cod 0.20, herring 1.00, other food 0.50.

YEAR	IM.CAP	MA. CAP	COD	B.HER	TOT. HER	WHALES	SEALS	CC.CAP	CC. COD	CC. HER	CC. OTH	WC. CAP	WC. COD	WC. HER	WC. OTH	SC.CAP	SC.COD	SC.HER	SC.OTH	C.CAP	C.COD	C.HER	C. WHAL	C.SEAL
1993	3661	1493	2649	3745	8531	83520	626068	2439	75	1598	3640	148	70	227	139	540	61	67	544	489	605	418	213	40368
1994	474	59	2715	3178	10511	85328	627857	710	120	1422	4989	38	111	264	217	191	103	118	923	75	705	545	237	42000
1995	450	58	2390	692	11054	87451	658519	450	137	781	5018	19	148	215	296	43	109	107	1186	170	833	719	0	0
1996	641	1	2069	95	10906	89676	680482	567	101	354	4461	69	172	117	365	184	104	49	1136	3	714	899	0	0
1997	1033	6	1889	103	10713	92745	698753	594	79	282	3942	105	169	88	385	273	98	8	1125	17	541	1055	0	0
1998	2296	87	1842	237	10834	95685	716661	1090	79	253	3494	142	148	96	370	326	88	8	1114	201	491	1206	0	0
1999	4454	63	1994	662	10292	98628	735445	2040	79	299	3151	230	104	133	268	609	67	10	791	165	511	1249	0	0
2000	4680	76	2360	2382	10567	101589	757031	2588	84	639	3288	220	78	238	188	731	62	55	616	244	485	1108	0	0
2001	3675	134	2713	3812	11170	104579	781300	2674	95	1057	3811	154	93	290	217	646	88	113	677	479	537	941	0	0
2002	1878	246	2742	2356	11265	107604	807276	2060	108	1053	4448	98	131	292	279	514	114	132	863	667	663	841	0	0
2003	1001	188	2390	475	10852	110674	834677	1255	103	635	4593	79	181	226	374	281	130	115	1250	518	741	890	0	0
2004	1690	31	1952	136	10303	113902	863172	1060	81	305	3942	132	198	141	435	343	121	45	1341	126	694	972	0	0
2005	3193	4	1717	136	10000	117257	892220	1421	66	255	3116	228	162	113	409	650	89	10	1065	21	578	1087	0	0
2006	5573	114	1780	231	9566	120727	921940	2094	63	224	2694	376	118	97	305	826	71	11	907	257	481	1159	0	0
2007	7644	373	2274	634	8657	124306	952208	3728	70	259	2644	429	96	144	222	1085	51	13	638	677	436	1091	0	0
2008	6186	588	2932	1898	8479	127989	982998	4707	93	555	3265	365	92	255	190	1108	64	56	606	1014	469	918	0	0
2009	3720	208	3281	2663	8331	131770	1014491	4448	107	917	4192	288	117	316	218	918	126	122	781	804	506	742	0	0
2010	2092	124	2949	1416	7931	135648	1046894	2303	110	859	5114	137	208	319	359	685	178	145	1091	451	759	641	0	0
2011	1478	164	2250	232	7418	139636	1080400	1378	86	468	4513	136	249	221	492	435	172	115	1564	484	531	677	0	0
2012	2853	31	1661	98	7001	143742	1115146	1391	61	243	3237	234	224	134	546	658	125	26	1516	150	718	756	0	0

Table 10. Results of run 8. High suitability of cod for whale. Notations as in Table 3. Suitabilities for whales: capelin 1.00, cod 0.40, herring 1.00, other food 0.10. Suitabilities for seals : capelin 1.00, cod 0.20, herring 1.00, other food 0.50.

YEAR	IM.CAP	MA.CAP	COD	B.HER	TOT. HER	WHALES	SEALS	CC.CAP	CC. COD	CC. HER	CC. OTH	WC. CAP	WC. COD	WC. HER	WC OTH	SC.CAP	SC.COD	SC.HER	SC.OTH	C.CAP	C.COD	C.HER	C. WHAL	C.SEAL
1993	3685	1494	2596	3769	8559	83520	626068	2434	74	1593	3614	137	118	214	121	542	59	67	542	489	603	418	213	40368
1994	481	60	2597	3243	10621	85328	627857	710	113	1400	4828	34	169	249	181	194	99	118	924	75	686	546	237	42000
1995	469	60	2228	742	11257	85024	628240	446	126	759	4754	15	212	193	239	43	100	106	1160	174	793	725	2501	34733
1996	764	1	1883	115	11163	84687	623501	572	91	336	4123	59	231	103	287	185	89	50	1064	3	660	911	2491	33052
1997	1385	7	1718	143	11037	85037	616898	694	68	259	3553	99	213	79	284	288	79	10	986	21	484	1073	2505	32122
1998	3426	132	1744	306	11260	85151	610919	1396	66	226	3083	144	175	77	264	356	67	10	902	258	435	1231	2508	31937
1999	6374	105	2065	813	10932	85164	606357	2904	71	284	2748	240	114	111	148	655	39	12	511	247	470	1297	2508	32076
2000	6212	392	2585	2736	11508	85097	604382	3789	75	651	3023	206	93	181	117	687	41	47	408	696	480	1169	2505	32686
2001	4594	318	2992	4352	12506	84964	604525	3730	92	1156	3747	141	113	219	131	576	68	93	463	791	564	1012	2501	33300
2002	2816	244	2955	2725	12885	84812	605827	2555	106	1198	4552	78	165	213	170	455	92	105	585	687	712	916	2496	33712
2003	1360	289	2514	632	12638	84639	607588	1699	97	743	4558	66	206	161	217	298	98	90	817	734	814	965	2491	33948
2004	1600	37	1937	154	11975	84526	609236	995	80	358	3966	74	228	99	269	236	90	43	981	234	760	1056	2488	34014
2005	3264	3	1649	249	12057	84439	610404	1341	62	274	2996	143	177	85	247	453	61	11	757	33	588	1179	2485	33947
2006	6146	117	1741	346	11594	84363	611018	2095	58	258	2545	246	115	82	173	598	43	12	576	236	467	1295	2483	33825
2007	8065	579	2300	909	11283	84289	611119	3827	68	298	2592	267	99	106	128	731	31	15	402	864	420	1317	2481	33685
2008	6685	663	3059	2616	11699	84208	610847	4891	93	695	3282	217	92	176	105	712	37	48	377	1122	455	1200	2479	33562
2009	3270	645	3508	3879	12297	84119	610398	4734	106	1271	4238	147	118	213	119	555	80	92	485	1249	617	1044	2476	33485
2010	1900	123	3189	2277	12253	84021	609937	2009	110	1257	5447	54	192	209	174	386	115	105	661	450	827	943	2473	33454
2011	1102	172	2466	517	11788	83921	609578	1265	89	733	4802	53	220	155	222	237	107	86	902	486	933	970	2470	33462
2012	1814	33	1767	170	11112	83823	609372	966	69	364	3636	80	215	98	270	254	83	37	975	161	817	1042	2467	33493

Table 11. Results of run 9. High suitability of other food for whales. Notations as in Table 3. Suitabilities for whales: capelin 1.00, cod 0.20, herring 1.00, other food 0.20. Suitabilities for seals : capelin 1.00, cod 0.20, herring 1.00, other food 0.50.

YEAR	IM.CAP	MA. CAP	COD	B.HER	TOT. HER	WHALES	SEALS	CC.CAP	CC. COD	CC. HER	CC. OTH	WC. CAP	WC. COD	WC HER	WC. OTH	SC.CAP	SC.COD	SC.HER	SC.OTH	C.CAP	C.COD	C.HER	C. WHAL	C.SEAL
1993	3681	1494	2668	3763	8551	83520	626068	2453	76	1600	3642	126	55	213	205	543	60	67	540	489	606	418	213	40368
1994	477	59	2768	3211	10552	85328	627857	716	123	1439	5048	29	81	246	287	193	105	118	919	74	712	545	237	42000
1995	439	58	2486	725	11119	85024	628240	455	143	803	5145	15	104	189	361	43	110	106	1150	172	852	721	2501	34733
1996	634	1	2212	112	10983	84687	623501	564	109	376	4675	46	118	97	434	168	104	49	1073	3	745	903	2491	33052
1997	1042	6	2078	134	10789	85037	616898	626	88	313	4224	69	113	73	441	249	97	10	1022	16	587	1060	2505	32122
1998	2065	84	2042	275	10924	85151	610919	1102	91	295	3838	88	101	83	411	283	86	10	981	201	554	1211	2508	31937
1999	3790	64	2138	713	10408	85164	606357	1895	91	355	3506	131	78	109	340	472	69	12	731	168	583	1256	2508	32076
2000	3910	72	2444	2514	10781	85097	604382	2319	93	739	3565	133	59	191	240	554	60	52	564	209	543	1117	2505	32686
2001	3081	116	2772	4021	11522	84964	604525	2255	105	1186	4065	83	63	229	250	479	76	98	582	414	578	953	2501	33300
2002	1494	233	2847	2530	11748	84812	605827	1787	119	1159	4668	51	78	221	289	358	94	107	713	630	698	861	2496	33712
2003	808	149	2593	576	11436	84639	607588	1077	117	707	4933	39	103	164	359	179	106	92	969	428	778	919	2491	33948
2004	1383	29	2245	177	10893	84526	609236	950	97	367	4450	63	113	99	408	208	101	40	1011	107	754	1010	2488	34014
2005	2608	4	2032	204	10693	84439	610404	1372	84	321	3694	112	95	81	383	412	78	11	796	16	677	1136	2485	33947
2006	4043	88	2030	309	10373	84363	611018	1895	83	310	3299	163	78	83	327	502	64	12	685	225	593	1227	2483	33825
2007	4893	287	2344	756	9575	84289	611119	2914	88	354	3247	185	68	104	277	583	57	15	579	579	532	1179	2481	33685
2008	3791	256	2832	2333	9749	84208	610847	3296	107	750	3784	154	60	181	217	586	61	49	524	645	537	1016	2479	33562
2009	2648	107	3113	3434	10062	84119	610398	2512	128	1208	4702	81	74	219	249	458	92	93	603	456	637	847	2476	33485
2010	1510	137	3011	1997	10041	84021	609937	1626	122	1095	5196	47	90	207	295	351	107	102	721	431	782	759	2473	33454
2011	990	133	2588	433	9692	83921	609578	1125	107	645	4966	45	108	146	364	194	110	83	962	401	866	817	2470	33462
2012	1891	32	2140	184	9211	83823	609372	1168	89	357	4125	78	108	90	398	268	94	30	954	120	816	904	2467	33493

Table 12. Results of run 10. High suitabilities of herring for seals. Notations as in Table 3. Suitabilities for whales: capelin 1.00, cod 0.20, herring 1.00, other food 0.10. Suitabilities for seals : capelin 1.00, cod 0.20, herring 2.00, other food 0.50.

YEAR	IM.CAP	MA. CAP	COD	B.HER	TOT. HER	WHALES	SEALS	CC.CAP	CC. COD	CC. HER	CC. OTH	WC. CAP	WC. COD	WC. HER	WC. OTH	SC.CAP	SC.COD	SC.HER	SC.OTH	C.CAP	C.COD	C.HER	C. WHAL	C.SEAL
1993	3665	1497	2651	3722	8502	83520	626068	2443	75	1595	3642	148	70	226	140	532	57	91	523	489	605	418	213	40368
1994	475	60	2722	3124	10415	85328	627857	716	121	1412	5002	39	111	263	217	189	98	145	893	75	706	544	237	42000
1995	462	58	2406	677	10918	85024	628240	456	138	773	5037	18	145	208	286	41	102	129	1128	170	837	715	2501	34733
1996	691	1	2102	97	10757	84687	623501	596	103	352	4487	66	162	109	340	176	96	69	1042	3	721	891	2491	33052
1997	1155	6	1946	103	10555	85037	616898	650	81	287	3991	99	156	78	345	263	90	14	1003	18	553	1046	2505	32122
1998	2496	95	1926	238	10635	85151	610919	1203	82	260	3564	129	133	83	321	310	79	13	949	219	511	1193	2508	31937
1999	4740	75	2099	660	10038	85164	606357	2215	83	315	3235	199	92	112	226	532	59	16	653	195	540	1224	2508	32076
2000	5072	84	2489	2351	10287	85097	604382	2812	89	660	3386	186	68	194	153	607	50	73	473	269	518	1079	2505	32686
2001	4154	136	2876	3759	10859	84964	604525	2956	101	1087	3919	131	76	230	168	525	67	123	491	506	576	910	2501	33300
2002	2411	246	2942	2350	10982	84812	605827	2358	115	1086	4601	84	106	223	211	424	87	128	600	686	715	810	2496	33712
2003	1270	237	2632	508	10628	84639	607588	1577	111	683	4797	70	141	167	271	263	99	110	835	636	811	862	2491	33948
2004	1867	43	2205	157	10121	84526	609236	1224	91	346	4273	96	154	106	309	257	94	55	931	202	780	950	2488	34014
2005	3595	4	1967	157	9785	84439	610404	1649	76	301	3422	160	124	84	282	473	69	14	716	29	671	1065	2485	33947
2006	5868	97	2013	257	9310	84363	611018	2379	75	271	2967	253	90	74	202	592	52	16	569	246	572	1131	2483	33825
2007	7297	440	2458	663	8412	84289	611119	3855	81	310	2922	274	72	99	157	695	42	19	434	774	520	1055	2481	33685
2008	5703	626	3096	1993	8346	84208	610847	4619	106	640	3589	223	67	169	131	671	48	63	400	1092	537	886	2479	33562
2009	3664	163	3450	2810	8340	84119	610398	3950	129	1055	4678	149	88	211	152	536	83	110	482	725	667	717	2476	33485
2010	2461	100	3220	1560	8154	84021	609937	2153	121	958	5472	73	135	198	223	414	108	117	612	415	845	628	2473	33454
2011	1766	175	2648	307	7790	83921	609578	1673	96	560	4899	85	154	136	275	300	105	95	803	529	944	681	2470	33462
2012	2919	47	2077	135	7415	83823	609372	1603	78	320	3821	125	145	86	300	358	85	35	834	252	873	775	2467	33493

Table 13. Results of run 11. Low suitabilities of herring for cod. Notations as in Table 3. Suitabilities for whales: capelin 1.00, cod 0.20, herring 1.00, other food 0.10. Suitabilities for seals : capelin 1.00, cod 0.20, herring 1.00, other food 0.50

YEAR	IM.CAP	MA. CAP	COD	B.HER	TOT. HER	WHALES	SEALS	CC.CAP	CC. COD	CC. HER	CC. OTH	WC. CAP	WC. COD	WC. HER	WC .OTH	SC.CAP	SC.COD	SC.HER	SC.OTH	C.CAP	C.COD	C.HER	C. WHAL	C.SEAL
1993	3552	1465	2626	4331	9345	83520	626068	2494	80	1084	3816	144	68	233	138	536	61	69	546	488	604	423	213	40368
1994	431	57	2656	4396	12609	85328	627857	661	120	1041	5087	31	105	277	213	187	100	128	918	74	697	576	237	42000
1995	262	56	2350	1147	13831	85024	628240	379	135	655	4992	12	129	235	272	37	102	120	1147	166	821	790	2501	34733
1996	281	1	2018	131	13664	84687	623501	255	103	327	4527	31	161	136	353	86	98	71	1161	2	705	1005	2491	33052
1997	461	2	1834	181	13591	85037	616898	291	81	259	3996	55	157	107	365	146	92	15	1161	6	532	1172	2505	32122
1998	1301	47	1773	237	13196	85151	610919	584	82	231	3643	77	132	115	348	158	82	15	1152	107	473	1321	2508	31937
1999	2845	31	1884	951	14186	85164	606357	1335	81	240	3360	132	101	134	278	398	66	15	832	76	480	1508	2508	32076
2000	2928	40	2215	3867	16167	85097	604382	1711	87	549	3533	127	58	246	170	488	59	69	632	121	453	1573	2505	32686
2001	2063	122	2561	6997	19012	84964	604525	1647	99	994	4080	66	71	280	192	404	73	128	646	376	505	1438	2501	33300
2002	621	214	2661	5014	20883	84812	605827	1202	112	1101	4646	35	89	278	219	245	90	137	831	553	633	1375	2496	33712
2003	224	67	2410	1410	21040	84639	607588	464	110	731	4900	16	118	241	265	80	99	123	1069	203	724	1430	2491	33948
2004	250	11	2011	370	19909	84526	609236	194	93	388	4440	17	143	178	326	40	96	81	1190	34	701	1488	2488	34014
2005	386	0	1696	288	18456	84439	610404	275	81	288	3728	39	136	146	347	126	82	37	1149	2	601	1498	2485	33947
2006	995	22	1582	317	17405	84363	611018	410	75	252	3330	70	117	138	335	153	72	30	1134	50	480	1516	2483	33825
2007	2223	62	1781	775	17545	84289	611119	1103	75	250	3222	124	91	143	281	328	62	21	916	131	393	1656	2481	33685
2008	2167	20	2180	3241	19348	84208	610847	1378	90	484	3696	110	66	240	189	425	64	65	721	74	383	1758	2479	33562
2009	1349	123	2553	6121	23187	84119	610398	1322	105	914	4319	53	72	283	199	340	79	123	737	352	468	1910	2476	33485
2010	462	120	2645	4644	24977	84021	609937	869	108	1019	4847	26	87	284	217	203	95	135	893	337	616	2021	2473	33454
2011	168	50	2379	1468	24673	83921	609578	356	103	715	4900	12	114	247	260	60	101	122	1102	154	731	2068	2470	33462
2012	146	7	1958	562	23089	83823	609372	126	90	431	4338	11	130	201	310	31	94	84	1204	22	721	2051	2467	33493

Table 14.. Extracts from Tables 3-13 (runs 1-11). Unit = million kg. Yearly average/value last year.

Run	Consumption by whales			Consumption by seals			Consumption by cod			Catch		
	capelin	cod	herring	capelin	cod	herring	capelin	cod	herring	capelin	cod	herring
1 Reference	122 109	114 144	160 99	392 310	82 87	55 26	1873 1309	97 80	695 344	349 178	664 840	933 875
2 Only cod, capelin and herring							1326 582	128 132	996 592	274 111	824 975	1156 1338
3 Cod, capelin, herring and harp seals				200 41	99 116	74 66	783 124	118 117	893 509	138 2	698 803	1153 1346
4 Cod, capelin, herring and minke whales	124 92	120 171	160 99				2189 1430	108 97	784 423	451 361	759 1018	973 982
5 No whale catch	186 229	145 239	195 139	423 385	78 80	51 17	2121 1592	92 67	644 284	399 298	650 823	903 778
6 No seal catch	117 106	112 136	162 99	498 502	107 139	72 44	1692 1054	95 73	673 301	298 64	632 728	931 870
7 No marine mammal catch	181 234	143 224	196 134	552 658	101 125	66 26	1950 1391	90 61	623 243	351 150	620 718	896 756
8 High suit. of cod for whales	125 80	163 215	151 98	422 254	74 83	58 37	2153 966	86 69	706 364	451 161	629 817	1015 1042
9 High suit. of other food for whales	87 78	87 108	151 90	354 268	87 94	58 30	1605 1168	103 89	719 357	289 120	672 816	943 904
10 High suit. of herring for seals	130 125	114 145	153 86	408 358	79 85	72 35	2054 1603	98 78	664 320	377 252	675 873	879 775
11 Low suit. of herring for cod	59 11	107 130	207 201	224 31	83 94	79 84	853 126	96 90	598 431	166 22	586 721	1429 2051

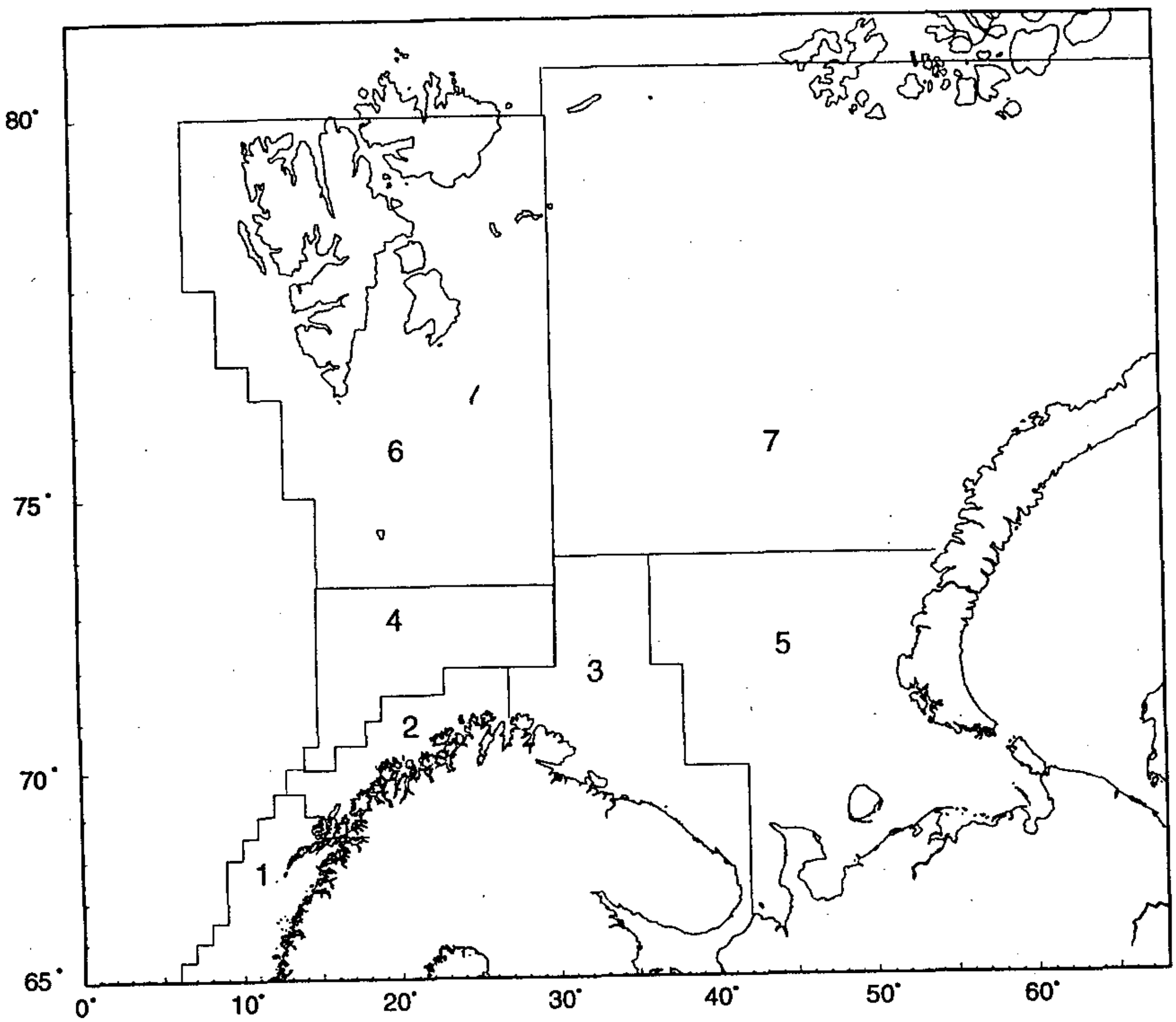

Figure 1. Area division in Multspec.

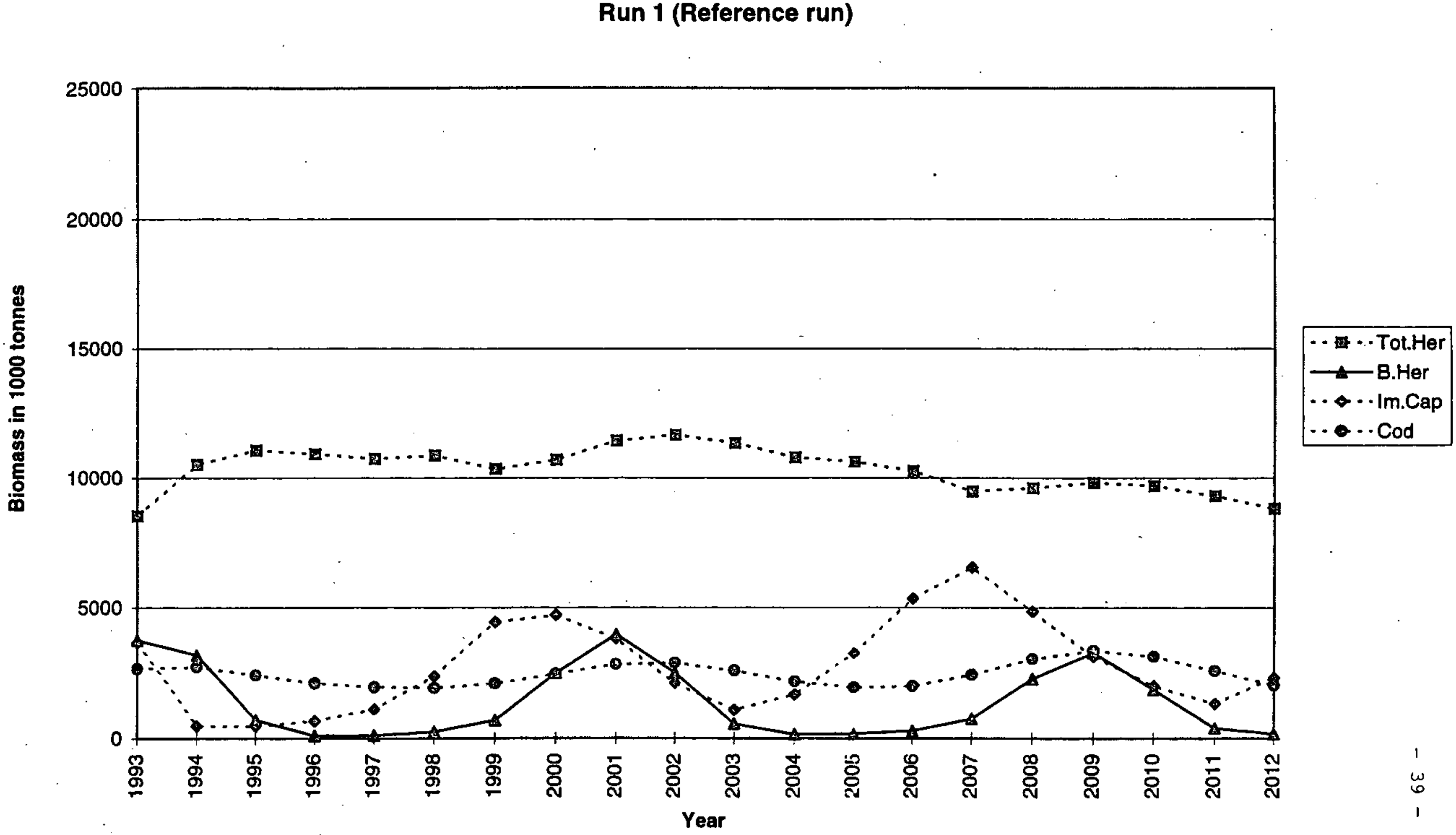

Figure 2 Development in biomass of immature capelin (Im.Cap), cod, herring in the Barents Sea (B.her) and total herring stock (Tot.Her) in the reference run (run 1).

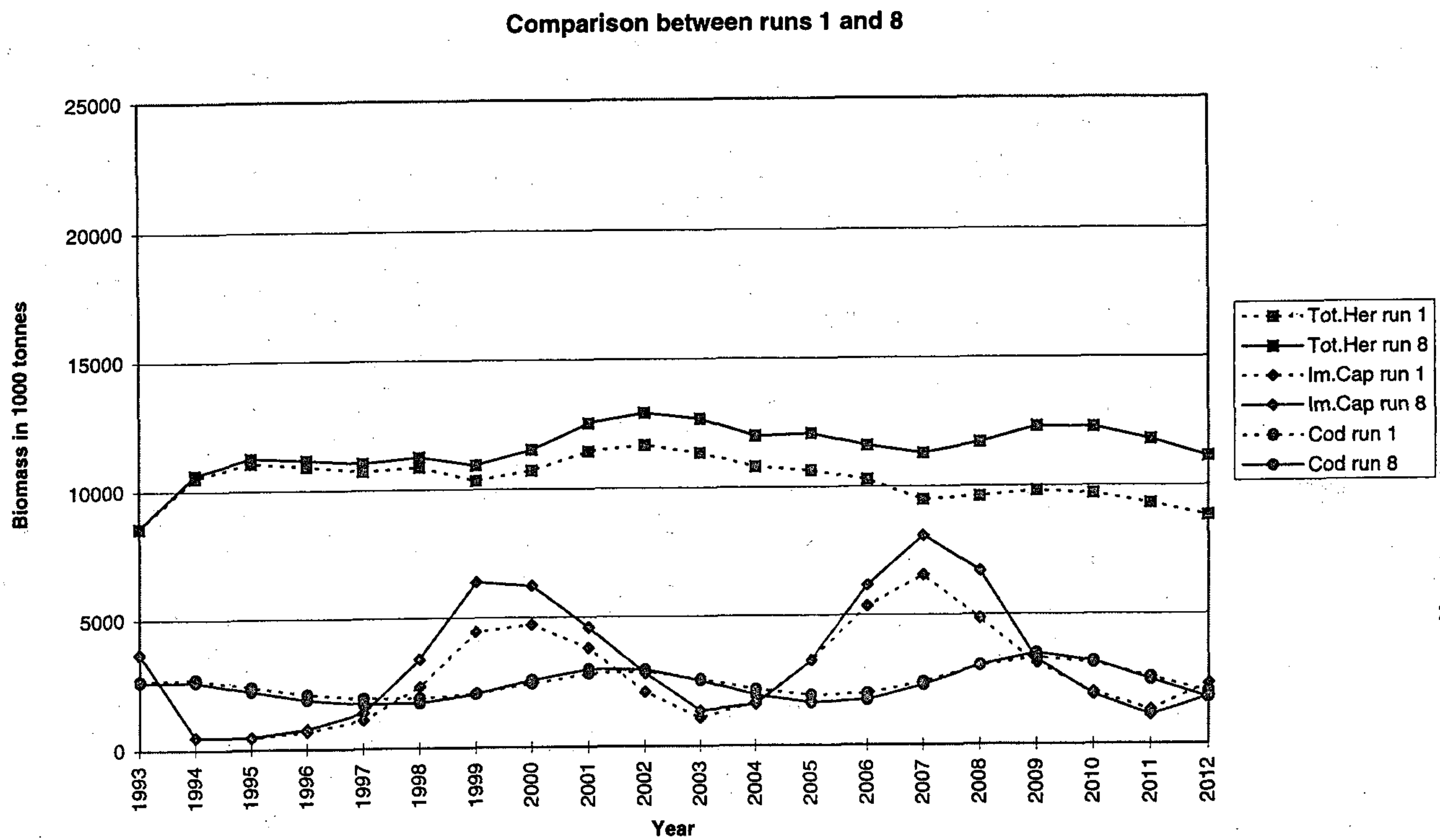

Figure 3. Development in biomass of immature capelin (Im.Cap), cod and herring (Tot.Her) for run 1 (reference run) and run 8 (high suitability of cod for whales).

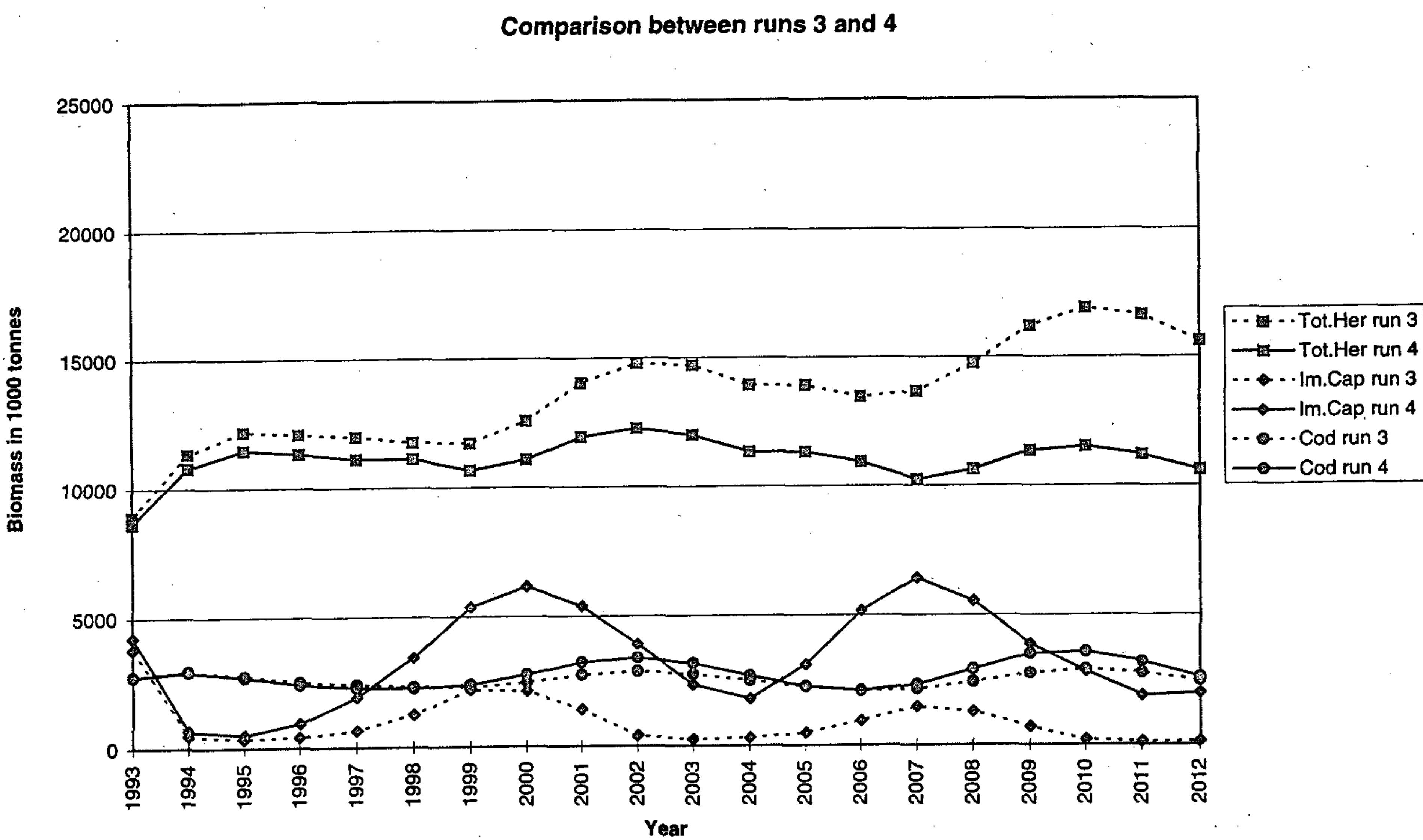

Figure 4. Development in biomass of immature capelin (Im.Cap), cod and herring (Tot.Her) for run 3 (no minke whales) and run 4 (no harp seals).

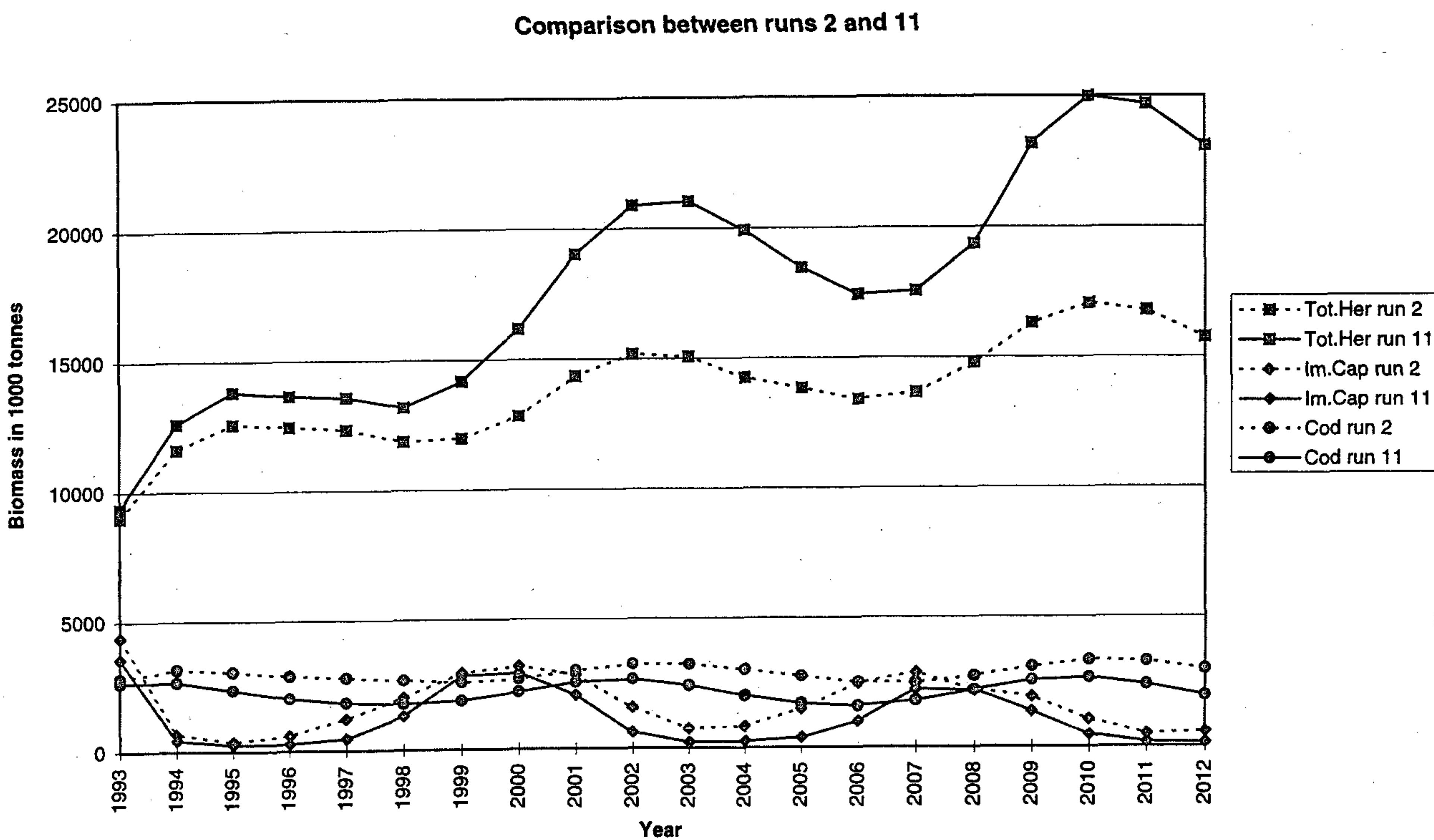

Figure 5. Development in biomass of immature capelin (Im.Cap), cod and herring (Tot.Her) for run 2 (no marine mammals) and run 11 (low suitabilities of herring for cod).

1 Appendix

1.1 Parameter files

Parts of parameter files used by MULTSPEC and HERMOD are given below :

MULTSPEC parameters

Oceanographic parameters

Effective area size (square nautical miles)

Area 1	Area 2	Area 3	Area 4	Area 5	Area 6	Area 7
14000.0	21000.0	50000.0	34000.0	90000.0	60000.0	90000.0

Food availability for plankton feeders. Upper line : grammes pr square meter

Area	1	2	3	4	5	6	7
Ppl1	15.0	15.0	15.0	15.0	15.0	15.0	15.0
Ppl2	6.5	6.5	7.0	7.0	8.0	8.0	8.0
Ppl3	4.0	4.0	4.0	4.0	4.0	4.0	4.0

Capelin parameters

Maturing

Age	2		3		4	
Sex	female	male	female	male	female	male
Pcp1	0.60	0.60	0.60	0.60	0.60	0.60
Pcp2	13.65	14.04	13.65	14.04	13.65	14.04

Feeding level parameter

Pcp3 1.20 Feeding level half value relative food abundance (plankton biomass/plankton feeder biomass)

Growth parameters

Pcp4	0.285	0.305	Maximum length change (female/male)
Pcp5	-0.10	-0.10	Length dependence of length change
Pcp6	1.00		Temperature dependence of length change
Pcp7	1.90		Temperature offset of length change
Pcp8	0.0133	0.0142	Maximum weight change(female/male)
Pcp9	0.6700	0.6700	Weight dependence of weight change
Pcp10	0.00		Feeding level offset of weight change
Pcp11	1.00		Temperature dependence of weight change
Pcp12	1.90		Temperature offset of weight change

Larval production

Pcp13	12000000.0	Maximum recruitment
Pcp14	30.0	Value of spawning biomass giving half of maximum recruitment

Larval death rates

Pcp15	0.00001	Larvae mortality induced by 0-group herring
Pcp16	0.00006	Larvae mortality induced by 1-group herring
Pcp17	0.00006	Larvae mortality induced by 2-group herring
Pcp18	0.00006	Larvae mortality induced by 3-group herring
Pcp19	0.00000	Larvae mortality induced by 0-group cod

Natural mortality

	Age	modf
Pcp20	0.00	0.00

Fishing mortality

	Immature	mature
Pcp21	0.00	0.10

Initializing parameters

Pcp30	0.0000024	Initial condition factor(kg/cm^3)
Pcp31	3.30	Initial weight/length exponent

Energy content

Pcp40 6.9 kJ/g

Herring parameters

Feeding level parameter

Phe3 0.20 Feeding level half value relative food abundance (plankton biomass/plankton feeder biomass)

Growth parameters

Phe4	0.23	Maximum length change
Phe5	-0.10	Length dependence of length change
Phe6	1.00	Temperature dependence of length change
Phe7	1.90	Temperature offset of length change
Phe8	0.011	Maximum weight change
Phe9	0.67	Weight dependence of weight change
Phe10	0.00	Feeding level offset of weight change
Phe11	1.00	Temperature dependence of weight change
Phe12	1.90	Temperature offset of weight change

Natural mortality

	Age	modf
Phe20	0.01	0.00

Fishing mortality

Phe21 0.00

Initializing parameters

Phe30	0.0000024	Initial condition factor(kg/cm^3)
Phe31	3.30	Initial weight/length exponent

Energy content

Phe40 7.1 kJ/g

Cod parameters

Feeding level parameter

Age modf

Pcd3 0.0054 0.00 Feeding level half value(1000 tonnes/sq. nmi)

Growth parameters

Pcd4	0.860	Maximum length change
Pcd5	-0.300	Length dependence of length change
Pcd6	1.00	Temperature dependence of length change
Pcd7	1.90	Temperature offset of length change
Pcd8	0.018	Maximum weight change
Pcd9	0.480	Weight dependence of weight change
Pcd10	0.03	Feeding level offset of weight change
Pcd11	1.00	Temperature dependence of weight change
Pcd12	1.90	Temperature offset of weight change

Larvae production

Pcd13	6000.0	Maximum recruitment
Pcd14	200.0	Value of spawning biomass giving half of maximum recruitment

Larval death rates

Pcd15	0.00	Larvae mortality induced by 0-group herring
Pcd16	0.00	Larvae mortality induced by 1-group herring
Pcd17	0.00	Larvae mortality induced by 2-group herring
Pcd18	0.00	Larvae mortality induced by 3-group herring
Pcd19	0.00	Larvae mortality induced by 0-group cod

Natural mortality

	Age modf	
Pcd20	0.012	0.00

Fishing mortality

Pcd21 0.089

Feeding parameters

Weight modf

Pcd22 1.21 0.802 Max feeding pr cod, kg pr month

Pcd23 -0.0005 0.007 0.007 0.007 0.007 0.007 0.007 0.007

Other food, 1000 tonnes pr sqr nmi by area and age dependence

Initializing parameters

Pcd30 0.000009 Initial condition factor(kg/cm^3)

Pcd31 3.00 Initial weight/length exponent

Fishing pattern

Pcd32 0.000 0.000 0.000 0.016 0.102 0.377 0.749 0.511 0.327 0.299 0.328

Energy content

Pcd40 5.3 kJ/g

Suitability of capelin

Cod lengths 10.0 20.0 30.0 40.0 50.0

Capelin lengths	Suitabilities				
5.0	0.10	0.50	1.00	1.00	1.00
10.0	0.00	0.10	1.00	1.00	1.00
15.0	0.00	0.00	1.00	1.00	1.00
20.0	0.00	0.00	1.00	1.00	1.00

Suitability of herring

Cod lengths 12.0 25.0 40.0 55.0 70.0

Herring lengths	Suitabilities				
5.0	0.00	0.20	0.20	0.20	0.20
15.0	0.00	0.00	0.20	0.20	0.20
25.0	0.00	0.00	0.00	0.20	0.20
35.0	0.00	0.00	0.00	0.00	0.20

Suitability of cod

Cod lengths 15.0 30.0 40.0 50.0 70.0

Cod lengths (prey)	Suitabilities				
5.0	0.00	0.05	0.15	0.25	0.25
15.0	0.00	0.00	0.08	0.25	0.25
25.0	0.00	0.00	0.00	0.13	0.25
40.0	0.00	0.00	0.00	0.00	0.00

Harp seal parameters

pha_mort0 0.025 instantaneous natural mortality pr month, age = 0
pha_mort 0.0083 instantaneous natural mortality pr month, age > 0
pha_mort1 0.3 high mortality in areas 1 & 2 during invations
pha_catch0 21.5 % default catch, age = 0
pha_catch 1.8 % default catch, age > 0
pha_ereq 1.985 1.985 1.985 1.985 1.985 1.985 9.425 9.425 9.425 1.985 1.985 1.985 * energy requirement, W/kg
pha_repro 0 0 0 0 0 0.0188 0.0846 0.1504 0.3478 0.564 0.6768 0.8742 0.94 0.94 0.94 0.94 0.94 * reproductivity
pha_eoth 5.0 energy content of other food, kJ/g
pha_doth 0.02 0.02 0.02 0.02 0.02 0.02 0.02 * ktonnes/sq.naut.mile
pha_scap 1.0 suitability of capelin as prey
pha_sher 1.0 suitability of herring as prey
pha_spol 0.2 suitability of polar cod as prey
pha_scod 0.2 suitability of cod as prey
pha_soth 0.5 suitability of other food
pha_dprey 0.08 prey energy density required, TJ/sq.naut.mile
pha_flev 0.95 feeding level at normal growth
pha_equiv 50 energy/weight, kJ/g

Minke whale parameters.

pmi_mort0 0.0583 instantaneous natural mortality pr month, age = 0
pmi_mort 0.0075 instantaneous natural mortality pr month, age > 0
pmi_catch 2.7 % default catch
pmi_ereq 1.45 1.45 1.45 1.45 1.45 1.45 1.45 1.45 1.45 1.45 1.45 1.45 energy requirement, W/kg
pmi_repro 0 0 0 0 0 0 0 0 0.95 0.95 0.95 0.95 0.95 0.95 0.95 0.95 0.95 0.95 0.95 0.95 0.95 0.95 * reproductivity
pmi_eoth 5.0 energy content of other food, kJ/g
pmi_doth 0.03 0.03 0.03 0.03 0.03 0.03 0.03 0.03 * ktonnes/sq.naut.mile

pmi_scap 1.0	suitability of capelin as prey
pmi_sher 1.0	suitability of herring as prey
pmi_spol 0.2	suitability of polar cod as prey
pmi_scod 0.2	suitability of cod as prey
pmi_soth 0.1	suitability of other food
pmi_dprey 0.01	prey energy density required, TJ/sq.naut.mile
pmi_flev 0.95	feeding level at normal growth
pmi_equiv 50	*energy/weight, kJ/g*

Hermod parameters

2.2 { matchange Determines steepness of maturation curve }
31.2 { matlm50 Length where 50% are maturation }
8.0 { maxrecruitment Maximum recruitment }
100.0 { maxmaxrecruitment Maximum of maximum recruitment }
0.5 { recruitpar1 Recruitment parameter }
2.5 { recruitpar2 Recruitment parameter }