

MULTSPEC – A Multi-species Model for Fish and Marine Mammals in the Barents Sea

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Abstract

A detailed description is given of MULTSPEC, which is an area, age and length structured multispecies simulation model for the species capelin (*Mallotus villosus*), herring (*Clupea harengus*), cod (*Gadus morhua*), harp seal (*Phoca groenlandica*) and minke whale (*Balaenoptera acutorostrata*) in the Barents Sea. In the model, both harp seals and minke whale, and cod, prey on capelin, herring and cod, and in addition, herring prey on capelin larvae. Cod is the most important predator. Information on food preferences and food requirements obtained from the Norwegian research program on marine mammals is used to quantify the predation by marine mammals on fish. The sensitivity of the model to the stock sizes and food preferences of harp seals and minke whales is investigated, together with the sensitivity to the food preferences of cod. A tentative conclusion on likely effects of an increasing whale stock is that the herring stock will be most heavily affected. An increasing harp seal stock will most heavily affect the capelin and cod stock. The model is more sensitive to changes in the food preferences of cod than to changes in food preferences or stock sizes of marine mammals.

Key words: Barents Sea, capelin, cod, harp seal, herring, minke whale, multispecies model

Introduction

The MULTSPEC project has as its aim to improve the scientific basis for management of the main stocks of fish and marine mammals in the Barents Sea by taking into account multi-species interactions. Our approach is basically an extension of Beverton and Holt's (1957) single species model, modelling predation mortality as a separate component of natural mortality and making individual growth dependent of the amount of available food. The present study is not an attempt to model all parts of the ecological system of the Barents Sea. The model is directed towards the biological system consisting of the stocks of Northeast Arctic cod (*Gadus morhua*), Norwegian spring-spawning herring (*Clupea harengus*) and Barents Sea capelin (*Mallotus villosus*) and parts of the biological and physical environment having a direct and significant effect on the development of these stocks. In the future, more fish species may be added to the model. However, both total fish production in the Norwegian-Barents Sea area (including Norwegian coastal waters), and also other aspects of the total ecosystem, are believed to be closely linked to the

development of these stocks in the sense that they have a dominating effect on the rest of the ecosystem, and that the state of the total ecosystem to a large extent will be "revealed" through the state of these three stocks. The reader is referred to some further comments on the modelling philosophy and the underlying cod-herring-capelin system in Ulltang (1995).

Of the top predators, only the stocks of harp seals (*Phoca groenlandica*) and minke whales (*Balaenoptera acutorostrata*) are currently included as modelled populations. These two stocks were selected because of their known importance as predators on fish (see e.g. Haug *et al.*, 1996; Nilssen, 1995; Nordøy *et al.*, 1995a, 1995b), and also because they have a long history of exploitation and can be expected to be the target of regulated exploitation in the future. In a management context, there are a number of possible purposes for including marine mammals in a multispecies model. Disregarding for the moment the scientific limitations of what is possible at present to predict with the model, a selection of possible purposes can be listed as follows:

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- 1) To investigate strategies for optimising the total yield of harvested marine mammals and fish resources.
- 2) To estimate and predict marine mammals' effects on harvested fish resources in order to improve the quality of management advice on the latter.
- 3) To predict effects on marine mammal stocks by varying exploitation strategies on their (harvested) prey stocks.

The strategy aimed at here is to gradually implement a multi-species approach to the management (Ulltang, 1995). With respect to marine mammals, emphasis has been on purpose (2). In the present study, MULTSPEC is used as a simulation model to deal with some more limited aspects of purpose (1), namely:

- i) to investigate long-term effects on the cod-herring-capelin system of different stock sizes of minke whales and harp seals
- ii) to investigate how sensitive such effects are to food preference parameters of minke whales and harp seals
- iii) to compare the importance of minke whales and harp seals as predators relative to the main fish predator in the ecosystem, namely cod.

Under i), runs were included where one or both of the marine mammal stocks were suddenly totally removed from the system as an attempt to further illustrate their role as predators.

For the fish stocks, recruitment functions and values of natural mortality covering other sources than predation from the modelled species cannot be taken from earlier single species assessments but have to be evaluated within the multispecies model itself. In the simulations, functions and values have been chosen which give results in broad agreement with historical stock dynamics as estimated in single species models, but further estimation work in the multispecies model is required. Where appropriate, possible significant effects on the results arising from errors in the assumed relationships are discussed.

Materials and Methods

Model structure

The MULTSPEC is an area-structured simulation model which includes capelin, herring, cod,

harp seal and minke whale. The characteristics of the model are presented here, while details on model structure and assumed functional relationships are given in Appendix 1.

The stocks which are included in MULTSPEC are represented by tree structures where each branch in each level defines a sub-population. A level may be divided by migration route, area, sex, age or length. How many levels a modelled species is represented by varies somewhat. All stocks are age-structured, and calculations on survival and mortalities are done on age groups or subdivisions of age-groups. The area division used in the model is shown in Fig. 1. Depending on the time of the year, a large portion of the minke whale stock may be distributed outside the Barents Sea. Therefore, an 'area 0' has been included in addition to the seven areas defined in the Barents Sea.

The model includes discontinuous processes like reproduction, which are handled on a yearly basis, and continuous processes like predation and natural mortality, which occur at 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 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. This is carried out by running the two models together like a zipper, the models waiting for each other's output files before starting the simulations each time step.

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). We use climatological data adjusted by the yearly variations in the Kola section.

The plankton supply for capelin and herring is given by a bell shaped (with respect to time of year) function. Cod is modelled to prey upon capelin, herring, cod and other food.

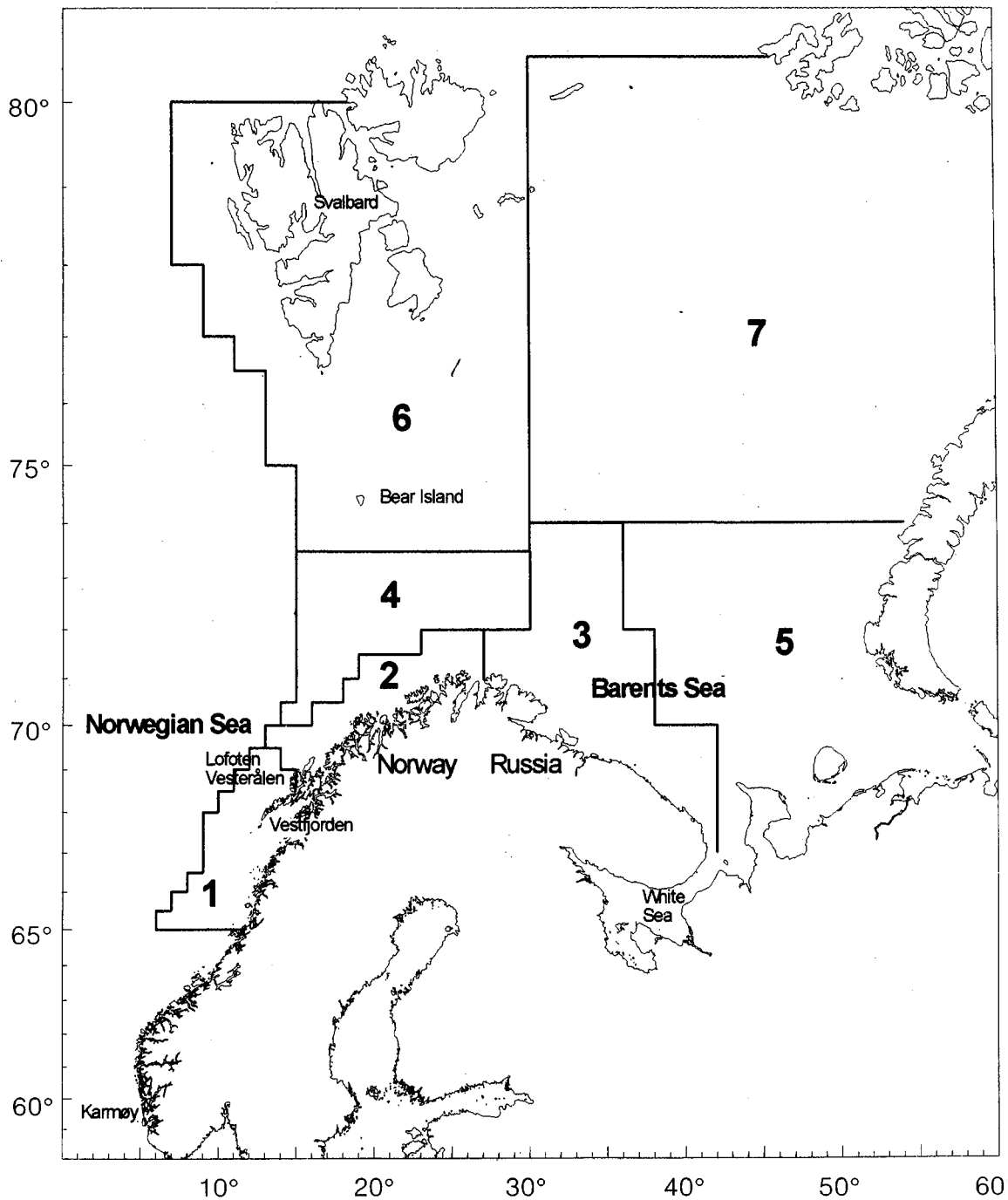


Fig. 1. Geographical scope and area division of MULTSPEC.

Some processes are modelled similarly for two or all three fish species. Individual growth (in both length and weight) of capelin, cod and herring within the MULTSPEC areas is made dependent on the size of the fish, the feeding level and temperature. Outside the MULTSPEC areas, the growth of herring is expressed by a linear function, depend-

ing on length only. The fishing mortalities assumed correspond to a relatively modest fishery. The natural mortalities have their basis in ICES working group reports (e.g. Anon., MS 1995a, b), but have been adjusted downward to compensate for the predation mortalities generated by the modelled species which are calculated separately (all

mortalities are given as instantaneous mortality coefficients).

A Beverton-Holt function is used to express the spawning stock biomass-recruitment relationship for capelin and for cod. For herring, a depensatory spawning stock-recruitment curve is used (Ulltang, 1980) with the inflection point at a spawning biomass of 2.5 million tons (Fig. 2). In order to model the fluctuations in strength of herring year-classes, strong recruitment is implemented two years in a row every eight years by increasing the parameter for maximum recruitment. The number of herring that mature is determined by a function which is length-dependent only.

For all species, migration between areas is implemented using migration matrices which are variable by month, and for fish by age group, but constant from year to year:

$$N_{s,t+1,a} = M_{s,t,a} N_{s,t,a}$$

where s is stock (cod, harp seal, minke whale) or substock (mature/immature capelin, six 'life stages' of herring (see below)), t is time (month number), a is age, m is number of areas, $N_{s,t,a}$ is an m -dimensional vector, containing the number of fish of (sub)stock s at time t of age a for each area, and $M_{s,t,a}$ is an m by m migration matrix, where the matrix elements m_{ij} indicate the proportion of the (sub)stock s in area i at time t which migrate to area j during this time step.

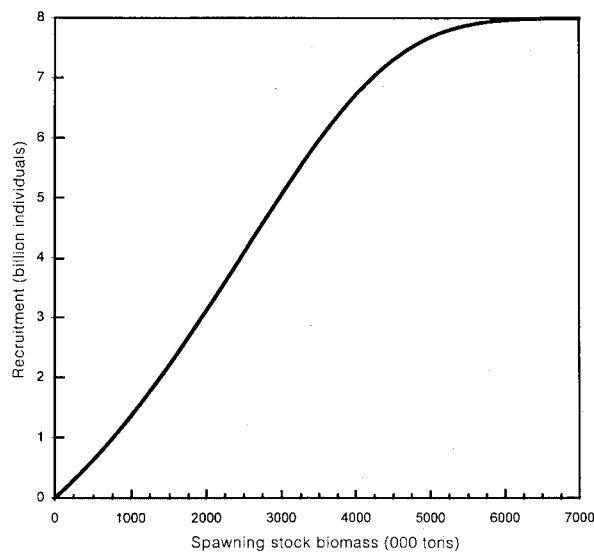


Fig. 2. Spawning stock-recruitment relationship used for herring.

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 1 April, when spawning takes place. In October the capelin stock is divided into a mature and an immature part by a length dependent function.

The herring switch migration pattern several times during its life time. For this reason, six different sets of migration parameters are implemented. The parameters are set so that the spawning areas are placed along the Norwegian coast from Karmøy to Vestfjorden. The 0-group then drifts north and into 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. There is an option in the program which makes it possible to choose a migration pattern for the mature stock similar to the one observed in the 1950s. This option is not used in the current paper.

The migration parameters for cod are set so that the larvae drifts 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 1 April, when spawning takes place. All cod in area 1 at 1 April is assumed to be mature.

The sub-models 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 fish. 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.

In October–January, the entire minke whale stock is found outside the model areas 1–7 (Norwegian catch statistics, unpubl. data). The model provides for a northward- and eastward migration during spring and early summer, and a reversed migration during late summer and autumn. The July distribution is calculated from the findings of the

July 1989 sighting survey (Øien, 1991). The distribution in the other months is interpolated between the July distribution and the October–January distribution, based on information from incidental sightings and catch statistics. 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.

The distribution patterns resulting from the migration procedures are shown in Tables 1 (harp seals) and 2 (minke whales). The tables specify the fraction of the population present in a given area at a given time.

Recruitment takes place once a year, during January in the whale model, and during March in the seal model. The sex ratio of newly borns is assumed to be 1:1.

At present the weight is treated as a function of age (in whole years) only. The weight-at-age is thus not affected by prey abundance.

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 is either a function of the predator's weight alone (whales present in the Barents Sea only in summer) or a function of weight and month (seals).

In the reference run, the catches of marine mammals are set so that the marine mammal populations stay approximately constant.

Different natural mortality parameters apply for age group 0 and older animals (see Appendix 2).

Initial stock data

The initial stock data for capelin used in the runs are taken from the joint Norwegian-Russian acoustic survey in September–October 1993 (Anon., MS 1994b). 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 1 January 1994 were available (Anon., MS 1995a). The numbers of 1- and 2-year old cod have been calculated by back-calculating the prognosticated number at age 3 by a yearly natural mortality $M = 0.2$, as was done by Mehl (1989) and Bogstad and Mehl (1992) when calculating the cod stock's consumption of various prey species. (A fluctuating and generally considerably higher value of M for 1- and 2-year old cod due to cod cannibalism was found from Anon., MS 1997). The area distribution of immature cod 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 cod are in area 1 in January. The size distribution has been calculated from the weights in the stock at 1 January (taken from Anon., MS 1995a), as described by Bogstad and Tjelmeland (MS 1990, 1992). The herring stock number-at-age at 1 January 1994 is taken (from Anon., MS 1995b), and the area distribution and length-at-age is calculated based on data from

TABLE 1. Area distribution (fraction of total stock present) of harp seals by month.

Month	Area 1	Area 2	Area 3	Area 4	Area 5	Area 6	Area 7
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. Area distribution (fraction of total stock present) of minke whales by month.

Month	Area 0	Area 1	Area 2	Area 3	Area 4	Area 5	Area 6	Area 7
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

several Norwegian surveys (all described in Anon., MS 1995b).

The acoustic estimate of the capelin stock only provides abundance estimates for 1 year and older capelin. In order to obtain an initial value of the number of 0-group capelin, it was decided to start MULTSPEC in October 1992, with capelin stock data from the 1992 autumn survey (Anon., MS 1993) and cod stock data for January 1992 (given in Anon., MS 1995a), prognosticated forward in time from January to October. The herring stock data in October 1992 was calculated by running HERMOD as a single species model from January to October 1992, using the stock number and weight-at-age estimate at 1 January 1992 (given in Anon., MS 1995b) as initial value. The model was then run to January 1993, when it was updated with data for the herring and cod stock abundance and weight-at-age at 1 January 1993. In April 1993, cod, capelin and herring spawn, so that the 1993 year-class for these species is generated. The capelin stock in the model was updated with 1993 capelin survey data in October 1993, and finally, the model was updated with cod stock data in January 1994.

The harp seal population at age 0 and at age 3 and older at 1 March 1991, was calculated from a pup production estimate of 142 000 (Russian aerial survey reported in Anon., MS 1994a), age composition data from samples of Norwegian catches, and reproductivity parameters given in Appendix B. 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 1986–88 (Haug and Nilssen, 1995). The pup production in 1989–90 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 1 March 1991. The harp seal stock size at 1 October 1993 was then calculated by projecting the stock at 1 March 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 parameters.

The age distribution of minke whales is taken from historical single-species simulations of this stock. This has been scaled to an initial population totaling 80 000 whales in 1990 (Schweder *et al.*, 1991), and then projected forward in time, correcting for catches and natural mortality. The estimate of 80 000 whales is under revision.

Results

Reference run

A reference run (Run 1) was chosen for the simulation using the parameter values given in Appendix B for fish, seals and whales. A period of 20 years was used for all runs. A summary table of the stock sizes, catches and consumption figures in the reference run is given in Table 3. Figure 3 shows the development (in biomass) of capelin, cod and herring (in the Barents Sea and of the total herring stock).

The variation in the biomass of cod, herring and capelin was generally within the range observed for the period where stock estimates were available. The herring spawning biomass, which is not shown in Table 3, reached a peak of 9.5 million tons in 1998 and 1999, and this was at the same level as estimated by VPA for the 1950s (Dragesund *et al.*, 1980). The strong decrease in capelin stock when the strong 1999–2000 and 2007–2008 year classes of herring enter the Barents Sea, illustrated clearly the assumed herring-capelin dynamics, and the influence of capelin on the cod stock can also be seen relatively clearly. The total consumption by cod and the fraction of capelin, herring and cod in the diet of cod seemed reasonable when compared to the results of Mehl (1989) and Bogstad and Mehl (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.* (1996). 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.* (1996). The food preferences of harp seals were set equal

to those of minke whales, except for the preference for other food which was set higher for harp seals.

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 stocks of marine mammals from the ecosystem (Run 2), removing only minke whales (Run 3), removing harp seals only (Run 4), or alternatively assuming no whale catch (Run 5), no seal catch (Run 6) or no marine mammal catch (Run 7), the latter three runs leading to an increase in one or both of the marine mammal populations. Effects of varying food preferences for marine mammals were studied by doubling the suitability of cod for whales (Run 8) and by doubling the suitability of herring for seals (Run 9). Run 8 was chosen since cod is a key species being both a heavy predator and a prey in the simulated system, while Run 9 was chosen in order to get an indication of to what extent seal consumption of herring is limited by lack of geographical overlap. The effects of varying food preferences for cod were studied by reducing suitability of herring for cod by 50% (Run 10). The results of the simulations are summarised in Table 4.

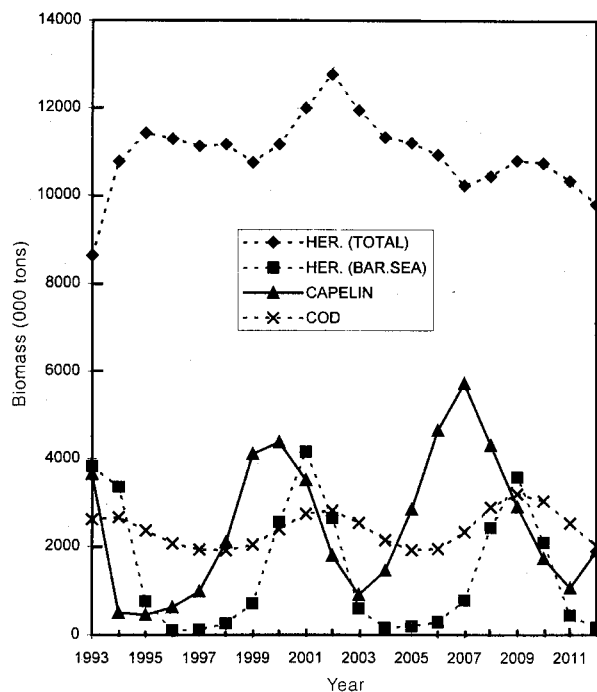


Fig. 3. Development in biomass of capelin, cod, herring in the Barents Sea and the total herring stock in the reference run (Run 1).

When comparing the effect of changing the suitability of herring for seals and the effect of changing the suitability of herring for cod, it was important to note the relationship between available food and cod. For marine mammals, the total consumption (in energy terms) was constant and thus not affected by the changes in suitability, while for cod, changing the suitability of a prey species changed the total amount consumed because the feeding level was changed.

The main effects of varying stock sizes of harp seals and minke whales may be summarised as follows:

The herring stock increased as predation from marine mammals decreased (Runs 2–4) and decreased as predation from marine mammals increased (Runs 5–7). With suitabilities as in the reference run, the herring stock was 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 Fig. 4 comparing Runs 3 and 4 to the reference run. The quantity of herring consumed in the Barents Sea by whales and

TABLE 3. Stocks, consumption and catches, Run 1 (reference run). State of stocks at 30 September. Capelin spawning stock at 1 April. Consumption and catches for 12 last months. Fish and other food in 1 000 tons. Mammals in numbers. CAP capelin, S.CAP = Capelin spawning stock, B.HER = Herring biomass in MULTISPEC 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 seals: capelin 1.00, cod 0.20, herring 1.00, other food 0.50.

YEAR	IM. CAP	SP. CAP	B. HER	TOT. HER	WHA LES	SEALS			CC.			WC.			SC.			C.						
						CAP	COD	OTH	CAP	COD	OTH	CAP	COD	OTH	CAP	COD	OTH	CAP	COD	OTH	CAP	COD	OTH	
1993	3647	1519	2612	3826	8635	83520	2371	74	1536	3689	141	74	228	143	545	70	68	573	489	605	419	213	40368	
1994	446	66	2664	3347	10774	85328	660	118	1380	4960	35	111	265	219	198	107	119	956	74	700	546	237	42000	
1995	493	65	2363	755	11421	85024	453	136	778	4956	17	140	213	285	44	108	107	1197	180	824	722	2501	34733	
1996	618	1	2072	96	11288	84687	623501	550	103	359	4456	61	161	113	344	174	100	50	1115	3	705	908	2491	33052
1997	977	5	1933	114	11128	85037	616898	596	82	282	4002	92	156	83	349	253	84	8	1070	16	537	1068	2505	32122
1998	2100	80	1909	250	11167	85151	610919	1048	84	258	3637	114	135	90	328	282	84	8	1036	192	500	1216	2508	31937
1999	4103	62	2045	704	10753	85164	606357	1931	83	321	3305	175	96	119	246	508	65	10	736	163	537	1284	2508	32076
2000	4368	69	2392	2554	11168	85097	604382	2437	87	699	3393	170	67	205	160	603	57	50	550	209	511	1155	2505	32686
2001	3511	124	2742	4151	11998	84964	604525	2482	98	1160	3889	112	76	242	177	521	75	97	573	448	560	993	2501	33300
2002	1793	257	2809	2645	12773	84812	605827	1977	113	1156	4513	69	102	236	218	400	94	107	703	680	685	897	2496	33712
2003	900	185	2532	590	11943	84639	607588	1223	111	715	4767	54	137	183	275	213	105	93	969	507	764	948	2491	33948
2004	1455	34	2144	150	11326	84526	609236	966	92	352	4292	81	154	113	319	218	100	41	1044	134	731	1035	2488	34014
2005	2840	3	1921	192	11199	84439	610404	1398	76	291	3486	143	127	90	293	442	75	9	807	17	641	1159	2485	33947
2006	4643	88	1947	290	10930	84363	611018	1995	75	285	3068	223	92	88	221	551	59	10	672	220	556	1265	2483	33825
2007	5720	337	2333	778	10235	84289	611119	3243	81	333	3024	247	74	112	172	660	49	13	531	641	504	1243	2481	33685
2008	4307	403	2893	2426	10444	84208	610847	3749	104	741	3638	194	66	193	140	642	58	48	499	841	518	1087	2479	33562
2009	2899	122	3192	3579	10803	84119	610398	2869	125	1243	4670	111	90	233	170	496	95	93	595	524	631	917	2476	33485
2010	1730	131	3032	2086	10744	84021	609937	1734	118	1136	5205	58	123	222	224	384	112	103	719	426	789	820	2473	33454
2011	1061	152	2531	438	10334	83921	609578	1226	100	664	4847	59	146	165	278	223	111	84	968	450	879	865	2470	33462
2012	1903	33	2011	164	9806	83823	609372	1137	82	352	3933	98	145	105	311	278	92	31	989	140	810	946	2467	33493

TABLE 4. Extracts from runs 1-10. Unit = 1 000 tons. Yearly average (bold) and value last year.

Run	Consumption by whales						Consumption by seals						Consumption by cod						Catch						Stock size					
	cap	cod	her	cap	cod	her	cap	cod	her	cap	cod	her	cap	cod	her	cap	cod	her	cap	cod	her	cap	cod	her	cap	cod	her			
1 Reference	113	114	165	382	86	57	1 702	97	702	318	649	975	2 476	2 404	10 943															
2 Only cod, capelin and herring	98	145	105	278	92	31	1 137	82	352	140	810	946	1 903	2 011	9 806															
3 Cod, capelin, herring and harp seals	120	120	161	30	119	68	2 120	108	785	440	755	988	3 244	2 735	11 300															
4 Cod, capelin, herring and minke whales	91	171	100	416	81	54	1 399	98	419	356	1 001	993	1 919	2 556	10 739															
5 No whale catch	175	145	202	371	82	20	1 939	92	650	368	636	941	2 966	2 372	10 385															
6 No seal catch	217	237	148	478	111	76	1 470	69	286	256	791	838	2 779	1 859	8 220															
7 No marine mammal catch	107	113	167	445	146	53	1 513	94	677	266	616	970	2 138	2 293	10 817															
8 High suitability (0.4) of cod for whales	93	137	107	445	146	53	879	74	305	44	698	931	1 397	1 756	9 493															
9 High suitability (2.0) of herring for seals	168	143	204	536	128	31	1 751	89	629	316	605	937	2 609	2 266	10 287															
10 Low suitability (0.1) of herring for cod	221	220	144	628	128	31	1 242	61	246	109	684	820	2 483	1 611	7 880															
	118	164	155	416	77	60	1 980	86	708	410	616	1 056	2 957	2 322	12 091															
	71	217	103	228	87	41	847	71	369	136	789	1 108	1 537	1 760	12 008															
	121	114	158	398	82	75	1 868	97	678	345	661	931	2 768	2 444	10 314															
	112	146	95	321	90	42	1 362	81	334	203	842	856	2 383	2 066	8 569															
	54	108	209	213	86	81	770	95	587	152	575	1 447	1 036	2 154	18 101															
	8	129	204	28	97	85	90	91	421	12	693	2 096	103	1 952	23 476															

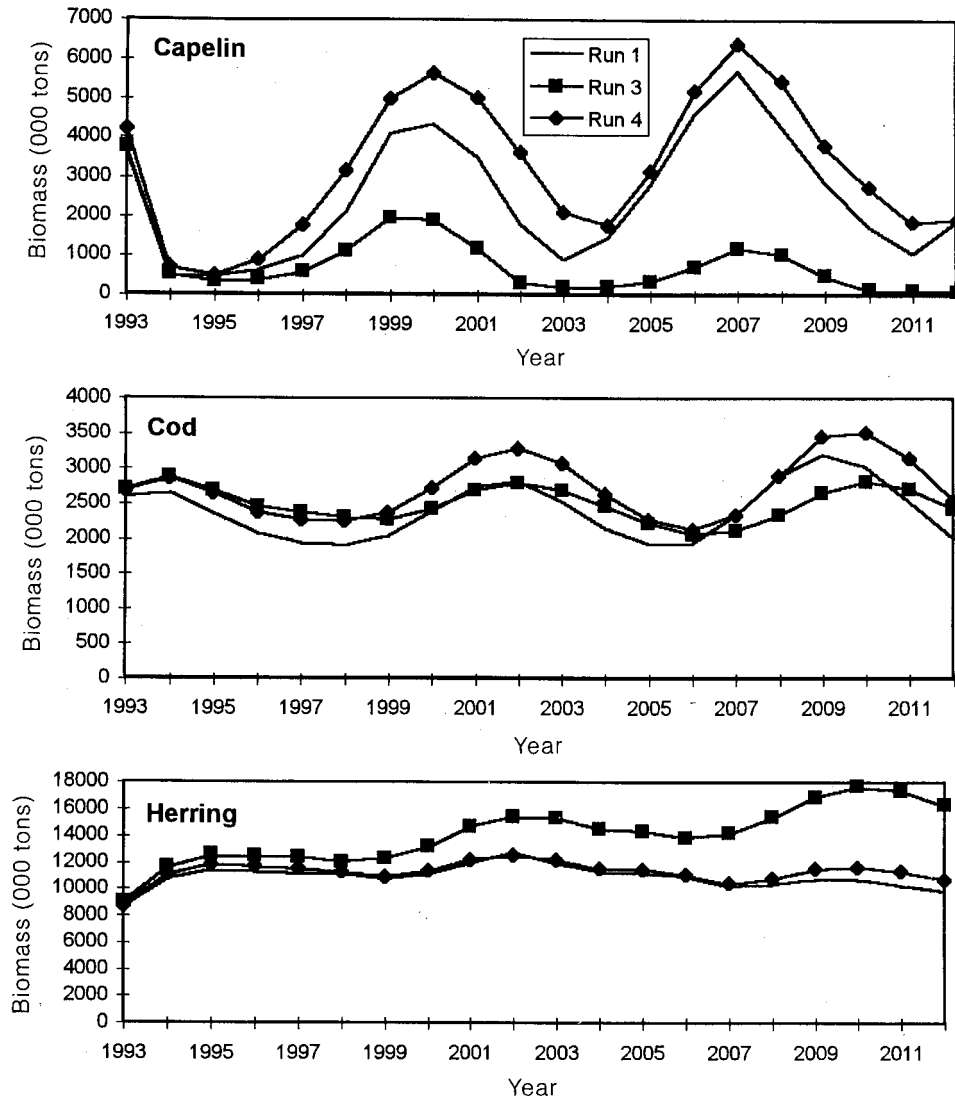


Fig. 4. Development in biomass of capelin, cod and herring for Run 1 (reference run), Run 3 (no minke whales) and Run 4 (no harp seals).

seals was moderate or negligible compared to the total herring stock biomass (Table 4). The reason why the herring stock was so sensitive to changes in the whale stock was that predation reduced the number of recruits to the mature stock by an amount which was not negligible, and this had both an immediate effect on the total stock and a long-term effect through the spawning stock-recruitment relationship.

The development in the capelin stock was mainly determined by changes in the herring and

cod stock. The effect on capelin of changes in these stocks generally was in the opposite direction of effects from changes in marine mammal predation on capelin. This resulted in an increase or decrease in the capelin stock when the minke whale stock increased (Run 5) or decreased (Run 3). Since herring was less sensitive to changes in the harp seal stock than to changes in the minke whale stock, and since predation on capelin from harp seals was high, an increase (Run 6) or decrease (Run 4) in the harp seal stock led to a decrease or increase in the capelin stock.

The effects on the cod stock from changes in the marine mammal stocks were more difficult to summarise in few words. Generally, the cod stock increased or decreased when marine mammal stocks decreased or increased, as intuitively expected. For example, if the seal population was not exploited and was allowed to increase (Run 6), the mean annual cod catch decreased by 33 000 tons over the simulation period (Table 4), and the catch in the last year was 112 000 tons 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. For example, removing the two mammal stocks (Run 2) led to a reduced cod stock in two years (2008–2009) due to reduced capelin stock.

One interesting feature which reflects the complexity of the system was 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.

Figure 5 showed the results of increasing the suitability of cod for whales (Run 8), or increasing the suitability of herring for seals (Run 9), keeping all other parameters as in the reference run. This figure again illustrated the complexity of the system. Initially, a higher suitability of cod for whales 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 slightly 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). A higher suitability of herring for seals led to a decrease in the herring stock and an increase in the capelin stock, while the cod stock increased marginally. Even with a higher suitability, herring is the prey species of which the harp seals eat in smallest quantity due to low geographical overlap.

Run 10 was included to illustrate 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 and 9) and even more dramatic effects than removing both marine mammal stocks from the system (Fig. 6). 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.

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.

Yodzis (1994) discussed the influence of differing biological assumptions as to predator interference on the forms of two-species predator-prey models, and the importance of these issues for the effects of marine mammals on fisheries. In the simulations, a marine mammal's functional response (the total number of prey individuals consumed per unit area per unit time by an individual predator (Yodzis, 1994)) is independent of the predator stock and also in terms of total weight consumed independent of the prey stocks. The marine mammals feed until their energy requirement is satisfied, and then stop. This may of course lead to pathological results if the total biomass of the prey stocks (the three fish species and other food) is approaching or getting below the total energy requirement of the marine mammals. However, this never occurred in the simulations. There was in all months and areas, a large excess of food.

The predator consumption of each prey species is in the simulations a function of relative prey stock size and the assumed suitabilities. The model formulation does not take into account the possibility

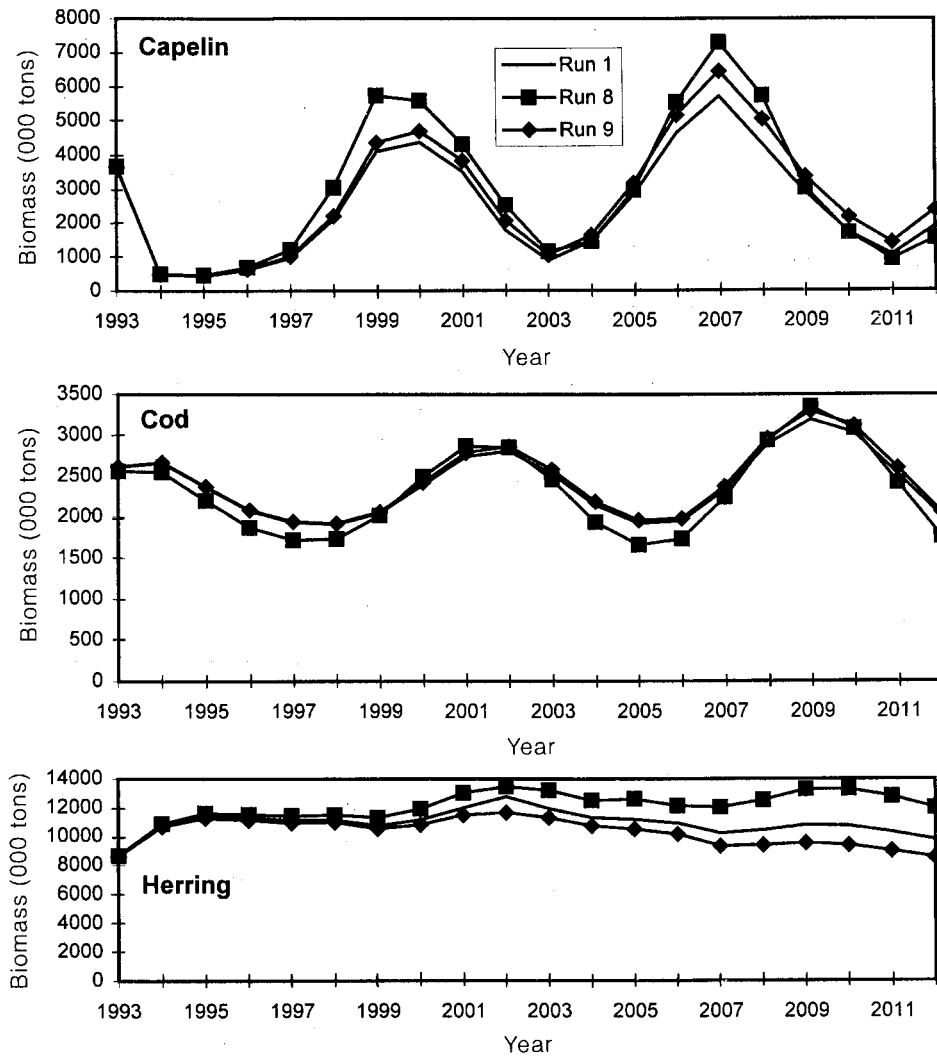


Fig. 5. Development in biomass of capelin, cod and herring for Run 1 (reference run), Run 8 (high suitability of cod for whales) and Run 9 (high suitability of herring for seals).

of a specialist feeding behaviour where the predator tries to maintain its daily ration of a preferred prey species irrespective of its abundance, or a highly opportunistic behaviour where the predator switches over to the more abundant prey to a larger extent than results from using constant suitabilities. Effects of both possibilities in a marine mammal-fish context are discussed by Beverton (1985).

The main conclusion from the simulations in relation to Yodzis (1994) discussion is that simple two-species models (e.g. a whale-capelin model) could lead to highly erroneous results, since inter-

actions at the fish level are crucial for the end result for each fish species.

A critical scientific question is whether the simulations give predictions which can be used for testing basic model assumptions of species interactions and especially the effects of marine mammal predation. Almost needless to say, the predicted stock sizes for any given year, say year 2000, in any run can not be used for such testing because we know with almost certainty that such a prediction is wrong. Of an infinite number of possibilities with respect to for example herring recruitment,

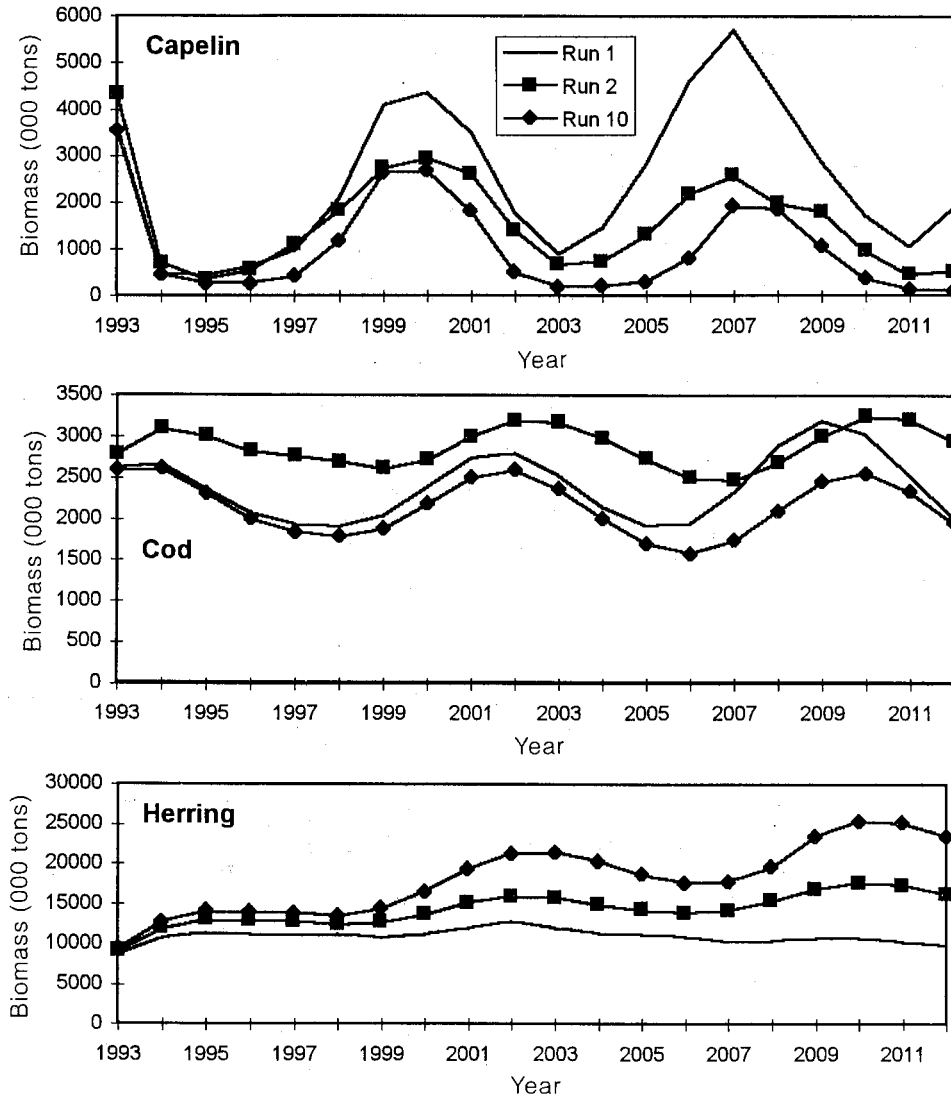


Fig. 6. Development in biomass of capelin, cod and herring for Run 1 (reference run), Run 2 (no marine mammals) and Run 10 (low suitability of herring for cod).

we have chosen one scenario. The underlying stock-recruitment curves for the fish stocks have not been tested, and there will in any case be a large stochastic variation around the curves. The same is true for individual growth. Neither can the estimated difference in future development of the fish stocks between, for example a run with a stable whale stock, and a run with an increasing whale stock be tested against observations for evaluating the model. The predictions in, say the reference run and Run 5 (no whale catch), do not show features that differ to the extent that any realised future development will falsify assumptions on whale predation. The simulations thus give us no future tests

of the model with respect to the effects of the marine mammal predation.

However, the MULTSPEC model can be used for making a different type of predictions for testing purposes. From a set of estimated initial conditions the model can make short-term predictions on details such as size- and species-composition of stomach content of an individual in a given area, and such predictions can be tested against observations. This has been utilised in estimation of for example predation parameters in a cod-capelin system (see e.g. Bogstad and Tjelmeland, 1992; Tjelmeland and Bogstad, 1993). In principle, stom-

ach content data for seals and whales can be used in a similar way, but methodological problems exist in estimating food preference parameters from the available data (see e.g. Skaug *et al.*, 1998).

In the MULTSPEC project, the main emphasis has been placed on modelling the population dynamics of the three selected fish species, the interaction between them and the predation from the minke whales and harp seals. There are other apex predators (other marine mammals and birds), and there are other fish which could influence the development of the three modelled species. However, our modelling philosophy is based on the assumption that main features of the dynamics of the Barents Sea ecosystem at the fish level are captured by including the selected species.

Both errors in the marine mammal total food composition and food preferences and inaccurate modelling of the interactions at the fish level could significantly affect the estimated effects of the mammal predation. Extensive investigations to estimate the minke whale and harp seal 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, the stomach sampling of the minke whale stock during 1992–94 (Haug *et al.*, 1996) has shown a high proportion of fish in the diet (except for the Bear Island-Spitsbergen area where krill dominated in 1993–94), with a large contribution of herring from Norwegian coastal areas. 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 consumption of capelin is in general agreement with direct calculation from stomach sampling data (Anon., MS 1996). The cod consumption of herring in 1993–94 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 content data do not properly reflect 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 capelin recruitment (Hamre, 1991), and sampling of herring stomachs has confirmed that young herring feed extensively on capelin larvae (Huse and Toresen, 1995). However, the modelled predation needs further evaluation.

Concerning herring, it should be recognised that only part of the minke whale-herring interactions are at present taken into account. 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 into account, since this could significantly affect the dynamics of the whole system. 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 80 minutes of computer time (on a HP 9000/755), which limits large-scale stochastic simulations somewhat.

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 the proper modelling of migration is equally important for 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 searches for herring or krill over large areas, the model should reflect this. If some minke whales go for herring, they may not be in the Barents Sea in years when there is 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 into account the mortalities generated by main predators which are now explicitly 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 into account 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 the opposite direction. The size of effects illustrates the importance of marine mammals, but compared to Run 10 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 predation should still have the highest priority. It is also important to study how important cod is as food item for marine mammals (see Run 8).

When no marine mammals are caught, the stock size in year 2012 will be 1.1 million harp seals and 144 000 minke whales, respectively. Although this is not above historical stock levels, density-dependent effects on growth etc. may to some extent slow down the estimated stock increase. The aim of the simulations was not, however, to estimate how fast the stocks would increase under a zero catch regime, but to estimate the effect of such increases when they occur.

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 avoiding a situation where substantial gains in one fishery are achieved at the expense 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 by using decision rules where expected stock development of all three fish species over the coming years is taken into account.

A tentative conclusion on the 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 sub-adult and adult herring in Norwegian coastal waters south of the MULTSPEC area and in the Norwegian Sea is included. How sensitive this conclusion is to model formulations and parameter values can only be thoroughly investigated by more extensive simulations. However, if it is accepted that minke whales are heavy predators on herring and that the main features of the cod-herring-capelin interactions have been captured, the conclusion could only be changed by much stronger compensatory mechanisms in the population dynamics of the herring stock, e.g. much slower individual growth at high stock sizes and a dome-shaped stock-recruitment curve. Probably only the latter could drastically change the results, but there is no support for such a stock-recruitment relationship for this stock (for a discussion of stock-recruitment relationship for this and some other herring stocks in the northeast Atlantic, see Ulltang (1980)). An increasing harp seal stock will most heavily affect the capelin and cod stock. The magnitude of these effects in the present study may be an under-estimate due to the assumed large proportion of other food in the diet of harp seals.

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Appendix 1: Model Structure

The parameter files specifying the values used in the present simulations are given in Appendix B.

Notation used in this appendix are: p is predator species, s is sex, a is age (years), A is area, m is month, N is number of fish (millions) and mammals, W is individual weight (kg), B is biomass (thousand tons), and T is temperature ($^{\circ}\text{C}$).

Temperature

The following positions are used to represent areas 1–7: 68 $^{\circ}$ 00'N, 12 $^{\circ}$ 00'E; 70 $^{\circ}$ 30' N, 20 $^{\circ}$ 00'E; 71 $^{\circ}$ 00'N, 34 $^{\circ}$ 00'E; 72 $^{\circ}$ 30'N, 20 $^{\circ}$ 00'E; 72 $^{\circ}$ 00'N, 45 $^{\circ}$ 00'E; 74 $^{\circ}$ 30'N, 22 $^{\circ}$ 00'E; 76 $^{\circ}$ 00'N, 40 $^{\circ}$ 00'E. A depth of 100 m is used. The adjustment to the yearly variation is done in the following way:

$$T(\text{year}, m, \text{position}) = T_1(m, \text{position}) + T_2(\text{year}, m) - T_3(m) \quad (1)$$

where, $T_1(m, \text{position})$ is temperature from climatology (Ottersen and Ådlandsvik, 1993), $T_2(\text{year}, m)$ is temperature in Kola section (Bochkov, 1982 and PINRO, Murmansk, pers. comm.) and $T_3(m)$ is temperature from climatology at Kola section.

The temperature in the years after 1994 has been set equal to the temperature from the climatology.

Plankton

The plankton supply for capelin and herring is given by the following function:

$$F(A, t) = P_1(A) e^{-4 \ln 2 \frac{(P_2(A) - t)^2}{P_3(A)}} \quad (2)$$

where F is the plankton abundance in grams dry weight per square meter, t is time (month number (1–12)), $P_1(A)$ is the maximum plankton abundance in area A , $P_2(A)$ is the time for maximum plankton abundance in area A , and $P_3(A)$ is 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 g dry weight per m^2 , which is somewhat higher than the values given by Skjoldal *et al.* (1992).

Capelin

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.

Proportion of maturing stock (Forberg and Tjelmeland, 1985) is calculated as:

$$m(l) = \frac{1}{1 + e^{4C_1(a,s) \times (C_2(a,s) - l)}} \quad (3)$$

where $m(l)$ is proportion of stock maturing at length l , $C_1(a,s)$ is change in maturation with length when $l = C_2(a,s)$, $C_2(a,s)$ is fish length at 50% maturity, referred to as "length-at-maturity", and the values of C_1 and C_2 are taken from Tjelmeland and Bogstad (1993).

Spawning stock biomass – recruitment relationship:

$$R(B) = \frac{C_{13} B}{C_{14} + B} \quad (4)$$

where R is recruitment-at-age 0 in June, B is Spawning stock biomass, C_{13} is maximum recruitment (number of larvae in June), and C_{14} is 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. Feeding level (Andersen and Ursin, 1977):

$$f(\phi) = \frac{\phi}{C_3 + \phi} \quad (5)$$

where ϕ is relative food abundance (plankton biomass divided by capelin biomass), and C_3 is the value of ϕ when a capelin consumes half of maximum.

Individual growth:

$$\frac{dl}{dt} = C_4(s)l^{C_5(s)}f(\phi)(C_6T + C_7) \quad (6)$$

$$\frac{dW}{dt} = C_8(s)W^{C_9(s)}(f(\phi) - C_{10})(C_{11}T + C_{12}) \quad (7)$$

The parameters C_4 , C_5 , C_8 and C_9 are sex-dependent.

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.

It is assumed that the only natural mortality is predation mortality generated by the species included in the model. The 0–3 group herring are predators on 0-group capelin, and may significantly hamper the capelin recruitment (Huse and Toresen, 1995). This is accounted for by introducing an additional predation mortality on 0-group capelin in each area:

$$M_{0, cap} = C_{15}N_{0, her} + C_{16}N_{1, her} + C_{17}N_{2, her} + C_{18}N_{3, her} \quad (8)$$

where $N_{a, her}$ is the number of herring of age a . We assume that all capelin die after spawning.

Herring

The herring stock is divided into 16 age groups (0–15+) and 42 length groups of 1.0 cm (4–45 cm). It is not divided by sex.

Feeding level inside the MULTSPEC areas (Andersen and Ursin, 1977):

$$f(\phi) = \frac{\phi}{H_3 + \phi} \quad (9)$$

where ϕ is relative food abundance (plankton biomass divided by herring biomass), and H_3 is the value of ϕ when a herring consumes half of maximum.

Individual growth inside the MULTSPEC areas:

$$\frac{dl}{dt} = H_4l^{H_5}f(\phi)(H_6T + H_7) \quad (10)$$

$$\frac{dW}{dt} = H_8W^{H_9}(f(\phi) - H_{10})(H_{11}T + H_{12}) \quad (11)$$

Growth outside the MULTSPEC areas:

$$\frac{dl}{dt} = H_{18}l + H_{19} \quad (12)$$

where H_{18} and H_{19} are constant for all age-groups.

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

$$m_a(l) = \frac{N_a}{1 + e^{4H_1(H_2 - l)}} \quad (13)$$

where $m_a(l)$ is number that matures at age a , H_2 is fish length at 50% maturity, referred as "length-at-maturity", H_1 is change in maturation when $l = H_2$, N_a is number of herring at age a , and l is mean length at age a .

Spawning takes place in March, and the resulting number of larvae is calculated by:

$$R(B) = H_{15} (1 - e^{(e^{-H_{16}H_{17}} - e^{H_{16}(B-H_{17})})}) \quad (14)$$

where R is recruitment in June, B is spawning stock biomass, H_{15} is maximum recruitment, and H_{17} is inflection point.

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 recruiting 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 per 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 per year, which is the natural mortality used for age 3 and older herring in the ICES stock assessments (Anon., MS 1995b).

Cod

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

Spawning stock biomass – recruitment relationship:

$$R(B) = \frac{G_{13}B}{G_{14} + B} \quad (15)$$

where R is recruitment at age 0 in June, B is spawning stock biomass, G_{13} is maximum recruitment (number of larvae in June), and G_{14} is the value of B giving half of maximum recruitment.

The value 6 000 million for the maximum recruitment, G_{13} , should be seen in relation to the maximum recruitment at age 3 for the year-classes 1966 and onwards (Anon., MS 1995a) which is 1 818 million fish (the 1970 year-class). The second strongest year-class is the 1969 year-class (1 015 million). The value of the spawning stock biomass giving half of maximum recruitment, G_{14} , has been set to 150 000 tons, which is close to the lowest level in the period from 1946 onwards.

Feeding level concept (Andersen and Ursin, 1977):

$$f(\phi(L, A)) = \frac{\phi(L, A)}{G_3 + \phi(L, A)} \quad (16)$$

where G_3 is the value of the food density f when a cod eats half of maximum consumption,

$$\phi(L, A) = \sum_{prey} \phi(preyl, L, A) + otherfood(A, a),$$

$$\phi(preyl, L, A) = S(preyl, L) N(preyl, A) W(preyl, A) / areaisize(A)$$

and: $S(preyl, L)$ is suitability of prey of length l as food for cod of length L ,

$$N(preyl, A) \text{ is number of prey group } l \text{ in area } A,$$

$$W(preyl, A) \text{ is individual weight of prey group } l \text{ in area } A, \text{ and}$$

$$otherfood(A, a) = G_{23}(A) + aG_{23}(0)$$

and: $areaisize(A)$: size of area A (naut. miles²).

The amount of prey (capelin, herring and cod) of length l eaten per unit time by a cod of length L is given by (the size- and temperature-dependency in this formula is taken from Jobling (1988)).

$$R_{cod}(preyl, L, A) = H_{cod} f(\phi(L, A)) \frac{\phi(preyl, l, L, A)}{\phi(L, A)} \quad (17)$$

where $H_{cod} = G_{22}(1)e^{0.104T - 0.000112T^3} W_{cod}^{G_{22}(2)}$, and

H_{cod} is maximum food uptake (size and temperature dependent).

The values for G_3 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 1996) for cod preying on mature capelin, using mainly the same methodology as in Bogstad and Tjelmeland (MS 1990, 1992). The value of $G_{22}(1)$ given by (Anon., MS 1996) has been multiplied by $e^{-1.5}$ for use in the work presented here, due to a reordering of the equation. The suitability $S(\text{prey}, l, L)$ for some values of l and L for each prey is given in Appendix B. The suitability for l - L combinations which are not given in these tables, is found by linear interpolation. 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.

Individual growth of cod:

$$\frac{dl}{dt} = G_4 l^{G_5} f(\phi)(G_6 T + G_7) \quad (18)$$

$$\frac{dW}{dt} = G_8 W^{G_9} (f(\phi) - G_{10})(G_{11} T + G_{12}) \quad (19)$$

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 of G_4 , G_5 , G_8 , G_9 and G_{10} are the same as those used in the studies of cod growth (Anon., MS 1996), 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.

Sea Mammals

The minke whale stock is divided into 2 sexes and 21 age groups (0–20+). The harp seal stock is divided into 17 age-groups (0–16+) assuming a sex ratio of 1:1 in stock and catch. At present, the migration procedures for sea mammals make no distinction with respect to sex or age-group.

In the following equations, the index p denotes marine mammal stocks (harp seal or minke whale).

The number of 0-year olds of sex s recruited to the stock p is given as:

$$N_{p,A,s,0} = \frac{1}{2} \sum_{a=1}^{a_{\max}} R_{p,a} N_{p,A,females,a} \quad (20)$$

where $R_{p,a}$ is reproductivity for females age a of stock p ; and equals the fraction of age group 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 (Christensen, 1981) and 0.94 for seals (Bowen *et al.*, 1981).

For seals, the fractions recruited to the breeding stock are the ones found by Kjellqwist *et al.* (1995) for the period 1990–93. For whales, a knife-edge maturation at age 7 is applied (Christensen, 1981). Recruitment takes place at 1 January for minke whales and at 1 March for harp seals.

For whales, the length at age a is:

$$l_{a,males} = 8.33(1 - e^{-0.169(a+4.3)}) \quad (21)$$

$$l_{a, females} = 9.07(1 - e^{-0.142(a+4.3)}) \quad (22)$$

Length-weight relationship (Folkow and Blix, 1992):

$$W(l) = 8.148 l^{3.163} \quad (23)$$

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

$$W_{a, males} = 6654 (1 - e^{-0.169(a+4.8)})^{3.163} \quad (24)$$

$$W_{a, females} = 8709 (1 - e^{-0.142(a+4.8)})^{3.163} \quad (25)$$

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

$$W_a = 129.9e^{-1.458e^{-0.384(a+0.5)}} \quad (26)$$

Catches of minke whales are subtracted from the population of age 1 and older whales present in MULTSPEC areas in June. For harp seals different catch rates are applied on pups (0 years old) and age 1 and older seals. The catches are subtracted in March, after the breeding season. The values of natural mortality used for marine mammals correspond to those used in single-species assessment by ICES (for harp seals) and IWC (for minke whales).

The normal energy requirement (J) of a predator p in month m is set to:

$$E_{p,s,a,m} = P_{p,m} W_{p,s,a} \Delta t \quad (27)$$

where $P_{p,m}$ is average rate of energy consumption of the species p in month m (W/kg), and Δt is number of seconds in month m .

The 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 C from a predator p on prey species i in an area to:

$$C_{p,s,a,m,i} = E_{p,s,a,m} \frac{S_{p,i} B_i}{\sum_j \eta_j S_{p,j} B_j} \quad (28)$$

where $S_{p,i}$ is suitability of prey i to predator p , B_i is biomass of prey i , and η_i is energy content of prey i .

As for minke whales, Blix and Folkow (1995) have estimated the daily energy expenditure or field metabolic rate to 80 kJ per kg per day. 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 (the last value is calculated using the information in Table 1 in Nordøy *et al.* (1995a)). When multiplying the field metabolic rate by this ratio between gross energy intake and field metabolic rate, we get a gross energy intake of 125 kJ per kg per day or 1.45 W per kg.

The energy consumption rate parameter for harp seal is an array with one value for each month. The average gross energy intake of harp seals is set to 343 kJ per kg per day or 3.97 W per kg according to Lager *et al.* (1994), who carried out an experiment where the harp seals were fed capelin. 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 in the months from July to September, as it is known that the harp seals improve in condition from June to September (Nilssen, 1995).

The energy content of the various prey species is taken from Nordøy *et al.* (1995b). For cod, the value for polar cod is used, while for other food, the value for *Crustacea* is used.

Appendix 2: Parameter Files

These are parts of parameter files used by MULTSPEC and HERMOD.

Oceanographic parameters

Effective area size (nautical miles²)

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 (where P_i is maximum plankton abundance, g per m², P_2 is time for maximum plankton abundance (month), and P_3 is duration of high plankton abundance (months)).

Area	1	2	3	4	5	6	7
P_1	15.0	15.0	15.0	15.0	15.0	15.0	15.0
P_2	6.5	6.5	7.0	7.0	8.0	8.0	8.0
P_3	4.0	4.0	4.0	4.0	4.0	4.0	4.0

Capelin parameters

Maturing (where C_1 determines steepness of maturation curve and C_2 is length where 50% are mature.)

Age	2		3		4	
Sex	Female	Male	Female	Male	Female	Male
C_1	0.60	0.60	0.60	0.60	0.60	0.60
C_2	13.65	14.04	13.65	14.04	13.65	14.04

Feeding level

C_3	1.20	Feeding level half value relative food abundance (plankton biomass/plankton feeder biomass)
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Growth

C_4	0.285	0.305	Maximum length change (female/male)
C_5	-0.10	-0.10	Length dependence of length change (female/male)
C_6	1.00		Temperature dependence of length change
C_7	1.90		Temperature offset of length change
C_8	0.0133	0.0142	Maximum weight change (female/male)
C_9	0.6700	0.6700	Weight dependence of weight change (female/male)
C_{10}	0.00		Feeding level offset of weight change
C_{11}	1.00		Temperature dependence of weight change
C_{12}	1.90		Temperature offset of weight change

Larval production

C_{13}	12000000.0	Maximum recruitment
C_{14}	30.0	Value of spawning biomass giving half of maximum recruitment

Larval death rates

C_{15}	0.00001	Larvae mortality induced by 0-group herring
C_{16}	0.00006	Larvae mortality induced by 1-group herring
C_{17}	0.00006	Larvae mortality induced by 2-group herring
C_{18}	0.00006	Larvae mortality induced by 3-group herring

Fishing mortality

C_{21}	0.00 for immature	0.10 for mature
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Herring parameters

Feeding level

H_3	0.20	Feeding level half value relative food abundance (plankton biomass/plankton feeder biomass)
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Growth

H_4	0.23	Maximum length change
H_5	-0.10	Length dependence of length change
H_6	1.00	Temperature dependence of length change
H_7	1.90	Temperature offset of length change
H_8	0.011	Maximum weight change
H_9	0.67	Weight dependence of weight change
H_{10}	0.00	Feeding level offset of weight change
H_{11}	1.00	Temperature dependence of weight change
H_{12}	1.90	Temperature offset of weight change

Natural mortality

H_{20}	0.01
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HERMOD parameters

H_1	31.2	Length where 50% are mature
H_2	0.55	Determines steepness of maturation curve
H_{15}	8000.0	(low value) Maximum recruitment
H_{15}	100000.0	(high value) Maximum of maximum recruitment
H_{16}	0.0005	recruitment parameter
H_{17}	2500.0	Inflection point for spawning stock-recruitment relationship, 1 000 tons
H_{18}	0.39	growth parameter
H_{19}	14.31	growth parameter

Cod parameters

Feeding level

G_3	0.0054	Feeding level half value (1000 ton per naut. miles ²)
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Growth

G_4	0.860	Maximum length change
G_5	-0.300	Length dependence of length change
G_6	1.00	Temperature dependence of length change
G_7	1.90	Temperature offset of length change
G_8	0.018	Maximum weight change
G_9	0.480	Weight dependence of weight change
G_{10}	0.03	Feeding level offset of weight change
G_{11}	1.00	Temperature dependence of weight change
G_{12}	1.90	Temperature offset of weight change

Larvae production

G_{13}	6000.0	Maximum recruitment
G_{14}	200.0	Value of spawning biomass giving half of maximum recruitment

Natural mortality

G_{20}	0.012
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Fishing mortality

G_{21}	0.089
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Feeding

$G_{22}(1)$	0.27	Maximum feeding per cod (kg per month)
$G_{22}(2)$	0.802	Maximum feeding per cod, body weight dependency (exponent)
$G_{23}(0)$	-0.0005	Other food, 1 000 tons per naut. mile ² , age dependence
$G_{23}(1-7)$	0.007	0.007 0.007 0.007 0.007 0.007 0.007 0.007 Other food, 1 000 tons per naut. mile ² , by area

Fishing pattern

G_{32} (age 0-10)	0.000	0.000	0.000	0.016	0.102	0.377	0.749	0.511	0.327	0.299	0.328
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Suitability of capelin for cod

Capelin length	Cod length				
	10 cm	20 cm	30 cm	40 cm	50 cm
5 cm	0.10	0.50	1.00	1.00	1.00
10 cm	0.00	0.10	1.00	1.00	1.00
15 cm	0.00	0.00	1.00	1.00	1.00
20 cm	0.00	0.00	1.00	1.00	1.00

Suitability of herring for cod

Herring length	Cod length				
	12 cm	25 cm	40 cm	55 cm	70 cm
5 cm	0.00	0.20	0.20	0.20	0.20
15 cm	0.00	0.00	0.20	0.20	0.20
25 cm	0.00	0.00	0.00	0.20	0.20
35 cm	0.00	0.00	0.00	0.00	0.20

Suitability of cod for cod

Cod (prey) length	Cod length				
	15 cm	30 cm	40 cm	50 cm	70 cm
5 cm	0.00	0.05	0.15	0.25	0.25
15 cm	0.00	0.00	0.08	0.25	0.25
25 cm	0.00	0.00	0.00	0.13	0.25
40 cm	0.00	0.00	0.00	0.00	0.00

Marine Mammal Parameters

η_{cap}	6.9	energy content of capelin (kJ per g)
η_{her}	7.1	energy content of herring (kJ per g)
η_{cod}	5.3	energy content of cod (kJ per g)

Harp seal parameters

0.025		instantaneous natural mortality per month, age = 0
0.0083		instantaneous natural mortality per month, age > 0
21.5		% caught, age = 0
1.8		% caught, age > 0
$P_{\text{seal,m}}$	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 per kg, month 1–12
$R_{\text{seal,a}}$	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, age 0–16
$\eta_{\text{seal,oth}}$	5.0	energy content of other food, kJ per g
$B_{\text{seal,oth,A}}$	0.02 0.02 0.02 0.02 0.02 0.02 0.02	other food density, 1 000 tons per naut. mile ² area 1–7
$s_{\text{seal,cap}}$	1.0	suitability of capelin as prey
$s_{\text{seal,her}}$	1.0	suitability of herring as prey
$s_{\text{seal,cod}}$	0.2	suitability of cod as prey
$s_{\text{seal,oth}}$	0.5	suitability of other food

Minke whale parameters

0.0583		instantaneous natural mortality per month, age = 0
0.0075		instantaneous natural mortality per month, age > 0
2.7		% caught, age > 0
$P_{\text{wha,m}}$	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 per kg, month 1–12
$R_{\text{wha,a}}$	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	reproductivity, age 0–20
$\eta_{\text{wha,oth}}$	5.0	energy content of other food, kJ per g
$B_{\text{wha,oth,A}}$	0.03 0.03 0.03 0.03 0.03 0.03 0.03	other food density, 1 000 tons per naut. mile ² , area 1–7
$s_{\text{wha,cap}}$	1.0	suitability of capelin as prey
$s_{\text{wha,her}}$	1.0	suitability of herring as prey
$s_{\text{wha,cod}}$	0.2	suitability of cod as prey
$s_{\text{wha,oth}}$	0.1	suitability of other food
