Who eats whom in the Barents Sea?

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ABSTRACT

An overview of the estimates of consumption by predators on the main fish stocks in the Barents Sea is given. The main predators are cod (*Gadus morhua),* harp seal (*Phoca groenlandica*) and minke whale (*Balaenoptera acutorostrata*). The results indicate that cod is the most important predator, consuming about as much food annually as harp seals and minke whales combined. The consumption estimates, together with data on the amount of fish removed by commercial fisheries, are compared to estimates of the abundance and removal through natural mortality of the various species of fish prey. The consistency between these estimates is discussed. The natural mortality values for cod and haddock used in assessments are found to be reasonably consistent with the consumption estimates. The consumption of capelin is found to be higher than what is available for predation in years of low capelin abundance, while in years of high herring abundance the consumption of herring does not explain all the mortality. The way in which the consumption estimates are and can be utilised in the assessment and management of fish stocks in the Barents Sea using multispecies models and approaches is described.

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Introduction

It is believed that the state of the Barents Sea ecosystem to a large extent will be revealed through the state of the stocks of Northeast Arctic cod (*Gadus morhua*), Barents Sea capelin (*Mallotus villosus*) and Norwegian Spring-Spawning herring (*Clupea harengus*) (Hamre 1994). 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. Cod prey on capelin, herring and young cod (Bogstad and Mehl MS 1997), while herring is an important predator on capelin larvae (Huse and Toresen MS 1995). Cod growth is also affected by prey (especially capelin) abundance (Mehl and Sunnanå 1991).

Studies of the diet of minke whale (*Balaenoptera acutorostrata*) (Fig. 1) and harp seal (*Phoca groenlandica*) in the Barents Sea have indicated that they also are important predators on cod, capelin and herring (Folkow *et al.* this volume, Haug *et al.* MS 1999, Nilssen *et al.* this volume). An overview of the studies of feeding ecology of harp seals and minke whales in the Barents Sea, as well as of the multispecies modelling efforts for the Barents Sea involving these two marine mammal species, is given in NAMMCO (1998).

The present paper provides estimates of consumption by predators (fish, marine mammals, birds) of various prey species in the Barents Sea and adjacent areas. The consumption estimates are compared to estimates of the abundance and removal through natural mortality of the various species of fish prey, and the consistency between these estimates is evaluated. Finally, utilisation of the consumption estimates in multispecies modelling and in the assessment and management of the fish stocks in the Barents Sea is discussed.

ESTIMATES OF PREY STOCK SIZE AND OF M-OUTPUT BIOMASS

Estimates of stock size of some of the most important fish species and shrimp are given in Table 1. The stock estimates for herring, capelin and polar cod (*Boreogadus saida*) in the Barents Sea are from acoustic surveys. For herring, the estimates are from the Norwegian survey on young herring in the Barents Sea in May-June (given in Gjøsæter and Bogstad 1998 for the period 1984-1996). The number at age from these surveys is given in ICES (1999c), while the weight at age is taken from the various survey reports. For capelin and polar cod, estimates from the joint Norwegian/Russian survey in September/October are used (Gjøsæter MS 1997, Gjøsæter and Ushakov MS 1997, Anonymous 1999). For these three species, the estimates are of 1 year old and older (1+) fish. The biomass of 3 year old and older (3+) herring in the Norwegian Sea and Norwegian coastal waters is taken from the VPA-based estimate made by the ICES Northern Pelagic and Blue Whiting Fisheries Working Group (ICES 1999c).

Fig. 1: *Sieves are used to sort the stomach and intestinal contents of a minke whale.*

Photo: Tore Haug

Table 1. Acoustic abundance estimates (1+) of capelin, herring and polar cod, VPA estimates of cod (1+), haddock (1+), herring (3+), Greenland halibut (3+) and deep-sea redfish (6+) and swept area estimates of deep-water shrimp, long rough dab and thorny skate (biomass in 1000's of tonnes).

	Capelin	Herring[1]		Polar cod	Cod	Haddock	Shrimp	Greenland halibut	Deep-sea redfish	Long rough dab	Thorny skate
Year	(1+)	(1+)	(3+)	(1+)	(1+)	(1+)		(3+)	(6+)		
1984	2964	311	647		1028	185	471	115	231		
1985	860	869	547		1185	302	246	112	194		
1986	120	255	1699	308	1420	392	166	116	151		
1987	101	0	3246	382	1180	270	146	111	160		
1988	428	0	4346	86	984	168	181	108	169	22	
1989	864	15	4974	207	950	154	216	107	205	30	
1990	5831	47	5603	127	1092	171	262	92	185	45	41
1991	7287	487	5586	381	1795	294	308	91	180	46	54
1992	5150	1666	6244	594	2162	506	239	54	161	76	34
1993	796	1519	6724	609	2755	605	238	61	199	91	47
1994	200	2864	9298	540	2391	614	161	52	199	55	116
1995	193	633	12744	426	2243	657	193	49	210	73	34
1996	503	94	13582	487	2279	555	276	42	234	76	43
1997	911	12	13519	401	2006	416	300				
1998	2056	146	11858	840	1424	293	341				
1999	2775	331	11730	1142	1314	249	324				
Average 1990-96	2851	1044	8540	452	2102	486	240	63	195	66	53

[1]Acoustic 1+ estimate for juveniles in the Barents Sea, VPA 3+ estimate for the total Norwegian Spring-Spawning herring stock.

Table 2. M-output biomass (MOB) for capelin, herring, polar cod, cod and haddock. (1000's of tonnes)

	Species (age group)				
	Capelin	Herring	Polar cod	Cod	Haddock
Year	(1+)	(Barents Sea 1-3)	(1+)	(1+)	(1+)
1984	3135	1530		226	47
1985	2000	1606		267	71
1986	669	1076		264	64
1987	200	783	828	220	44
1988	80	329	242	201	31
1989	537	524	490	209	33
1990	415	871	291	301	40
1991	3313	1620	711	405	71
1992	7773	2771	1110	486	111
1993	4622	4674	1140	529	120
1994	982	3205	1151	458	121
1995	163	913	965	458	122
1996	261	419	980	461	96
1997	828	560	864	371	72
1998	915	217	1855	290	54
Average 1991-93	**5236**	**3022**	**987**	**473**	**101**
Average 1994-96	**469**	**1512**	**1032**	**459**	**113**

For deep-water shrimp (*Pandalus borealis*), biomass estimates (indices) from bottom trawl surveys in the main shrimp areas were used for comparisons (Aschan 1999 and M. Aschan, Norwegian Institute of Fisheries and Aquaculture, Tromsø, Norway, pers. comm.). These estimates, however, only reflect what was available for the bottom trawl, while the total biomass is believed to be much higher.

For cod and haddock (*Melanogrammus aeglefinus)*, the biomass of 1+ fish from the VPA-based stock estimate made by the ICES Arctic Fisheries Working Group (ICES 2000) is given. For cod and haddock, a natural mortality (M) of 0.2 per year + predation mortality induced by cod is assumed. The biomass estimates of Greenland halibut (*Reinhardtius hippoglossoides*) (3+) and deep-sea redfish (*Sebastes mentella*) (6+) are taken from ICES (1998a). For long rough dab (*Hippoglossoides platessoides*), the biomass estimates are based on indices from shrimp surveys in the Svalbard area (Albert 1999). The biomass indices of thorny skate (*Raja radiata*) are calculated from Russian trawl surveys for demersal fish (Dolgov MS 1997).

The stock abundance does not, however, reflect the amount available for consumption during the year. Thus, the biomass output through natural mortality (M) (called the 'M-output biomass' by Hamre and Tjelmeland (MS 1982), in this paper: MOB) has been calculated (Table 2). In general, the MOB is calculated using the catch equation, but with F and M interchanged, and the calculated number removed by M is multiplied by a relevant mean weight:

$$MOB_t = \sum_a w_{t,a} \frac{N_{t,a} M_{t,a} (1 - e^{-(F_{t,a} + M_{t,a})})}{F_{t,a} + M_{t,a}}$$

where

MOB_t	is the M output biomass in time step t
$N_{t,a}$	is number of fish of age a in the beginning of time step t
$F_{t,a}$ and $M_{t,a}$	are the relevant fishing mortality and natural mortality respectively for age a in time step t
$w_{t,a}$	is the estimated mean weight of age a fish during time step t.

As the abundance, mortality and growth of 0-group fish are very uncertain, it was decided to exclude 0-group fish from the calculations of MOB. The M values are calculated in different ways for the different stocks. In all MOB calculations, the weight of a prey cohort was assumed to increase linearly through the time step.

For capelin, the MOB was calculated in the same way as in Gjøsæter (MS 1997), by calculating the reduction of the abundance of a cohort in the acoustic survey during one year, which is not caused by the fishery, and multiplying this by the mean weight of these individuals. This is done separately for each age group in the stock, for the immature and mature component of each age group, and for three separate seasons. This entity should reflect the amount available to predators. Also, total spawning mortality is assumed for this stock, and the biomass of the spawning capelin is thus included in the calculated MOB:

$$MOB_y(capelin) = \sum_{a=1}^{5} \sum_{s=1}^{2} \sum_{m=1}^{3} \frac{M_{y,a,s,m} N_{y,a,s,m} (1 - e^{-(F_{y,a,s,m} + M_{y,a,sm})}) w_{y,a,s,m}}{F_{y,a,s,m} + M_{y,a,s,m}} + \sum_{a=1}^{5} N_{y,a,2,4} w_{y,a,2,4} +$$
$$\sum_{a=1}^{5} \sum_{m=4}^{9} \frac{M_{y,a,1,m} N_{y,a,1,m} (1 - e^{-(F_{y,a,1,m} + M_{y,a,1,m})}) w_{y,a,1,m}}{F_{y,a,1,m} + M_{y,a,1,m}} + \sum_{a=1}^{5} \sum_{s=1}^{2} \sum_{m=10}^{12} \frac{M_{y,a,s,m} N_{y,a,s,m} (1 - e^{-(F_{y,a,s,m} - M_{y,a,s,m})}) w_{y,a,s,m}}{F_{y,a,s,m} + M_{y,a,s,m}}$$

Where s denotes stock (1 – immature, 2- mature) and m month. Details on the calculations of N, w, M and F for capelin are given in ICES (1995).

The same survey-based approach was taken for polar cod, but the calculations for that stock were not separated by season and by mature/immature stock. The MOB for polar cod is calculated in the following way:

$$MOB_y(herring) = \sum_{a=1}^{3} \left(\frac{N_{y,a} M_{y,a} (1 - e^{-(F_{y,a} + M_{y,a})}) w_{y,a}}{F_{y,a} + M_{y,a}} \right)$$

where:
$Ns_{a,y}$: Survey abundance of age a fish in year y

$Ms_{a,y}$: Survey mortality of fish from age *a-1* in year *y-1* to age a in year *y*:$-\ln(Ns_{a,y}/Ns_{a-1,y-1})$
$Ws_{a,y}$: Average weight of age *a* fish in year *y* in survey
$N_{a,y}=Ns_{a,y}e^{Ms}$:Number of fish of age *a* at start of year *y*
$w_{a,y,1}$: Average weight of fish of age *a* during the period 1 January- 1 October in year *y*: $(15*ws_{a-1,y-1}+9*ws_{a,y})/24$
$w_{a,y,2}$: Average weight of fish of age a during the period 1 October- 31 December in year *y*: $(3*ws_{a,y}+21*ws_{a+1,y+1})/24$
C_y: catch in year *y*

We assume $Ms_{1,y}=Ms_{2,y+1}$, $Ms_{5,y+1}=Ms_{4,y}$, $ws_{0,y-1}=0.4*ws_{1,y}$, $ws_{5,y+1}=ws_{4,y}$

For herring, the MOB was calculated for ages 1-3 using abundance at age, weight at age and mortality figures from the VPA, where yearly M-values of 0.9 for age groups 1 and 2 and 0.15 for age 3 (ICES 1999c) were used. The herring were assumed to leave the Barents Sea on July 1 in their third year of life, so an M-value of 0.075 was applied for this age group in the MOB calculations. An alternative way would be to calculate the MOB for herring in the same way as for capelin and polar cod, based on the annual young herring surveys in the Barents Sea. This was not done because the abundance indices at age for each cohort are less coherent for herring than for capelin and polar cod. Also, much of the herring leaves the Barents Sea before they are surveyed in May/June as three-year-olds, making survey-based mortality calculations for age 2-3 not appropriate for MOB calculations. The MOB is thus calculated in the following way:

$$MOB_y(herring) = \sum_{a=1}^{3} \frac{N_{y,a} M_{y,a} (1-e^{-(F_{y,a}+M_{y,a})}) w_{y,a}}{F_{y,a}+M_{y,a}}$$

The MOB calculated for cod and haddock should be divided into MOB from cod predation and MOB due to residual natural mortality. MOB due to predation by cod is given in Table 2, while MOB due to residual natural mortality for each year y is calculated in the following way:

$$MOB_y(species) = \sum_{a=1}^{a\max} \frac{N_{y,a} M1_{y,a} (1-e^{-(F_{y,a}+M1_{y,a}+M2_{y,a})}) w_{y,a}}{F_{y,a}+M1_{y,a}+M2_{y,a}}$$

where M1 (=0.2) is the residual natural mortality and M2 is the natural mortality due to predation by cod. amax=15 for cod and 14 for haddock.

Table 3. The Northeast Arctic cod stock's consumption of main prey species in 1984 - 1998. (1000's of tonnes)

	Prey species											
Year	**Amphi-pods**	**Krill**	**Shrimp**	**Capelin**	**Herring**	**Polar cod**	**Cod**	**Haddock**	**Redfish**	**Gr. Halibut**	**Others**	**Total**
1984	27	114	443	735	80	15	22	51	370	0	512	2369
1985	172	58	157	1640	185	3	33	47	227	0	1173	3695
1986	1232	109	143	844	135	142	83	110	316	0	670	3784
1987	1064	66	189	226	32	202	25	4	318	0	668	2794
1988	1228	316	128	334	8	90	9	3	220	0	408	2743
1989	816	243	133	585	3	32	8	11	234	0	733	2797
1990	137	83	193	1594	7	6	19	15	241	0	1571	3866
1991	66	76	188	2894	8	12	26	20	309	7	1091	4697
1992	103	159	376	2463	331	97	54	106	188	20	1021	4920
1993	254	720	317	3058	165	278	285	72	100	2	788	6039
1994	579	725	532	1115	150	604	235	50	80	0	691	4761
1995	981	519	368	638	115	256	393	117	194	1	860	4441
1996	637	1181	349	555	48	106	552	70	98	0	676	4272
1997	391	537	324	950	6	120	360	43	38	1	527	3298
1998	537	537	382	881	65	49	154	21	10	0	479	3115
Av. 91-93	**141**	**318**	**294**	**2805**	**168**	**129**	**122**	**66**	**199**	**10**	**967**	**5219**
Av. 94-96	**732**	**808**	**416**	**769**	**104**	**322**	**393**	**79**	**124**	**0**	**742**	**4491**

(Table 3)

Table 4. Consumption by minke whales and harp seals in the Barents Sea. (1000's of tonnes, wet weight) The minke whale calculations are based on data from 1992-1995, while those for harp seals are from 1990-1996. For harp seals, the most conservative estimates (assuming field metabolic rate = 2 • basal metabolic rate) are used.

Prey	Minke whale consumption	Harp seal consumption (low capelin stock)	Harp seal consumption (high capelin stock)
Capelin	142	23	812
Herring	633	394	213
Cod	256	298	101
Haddock	128	47	[1]
Krill	602	550	605
Amphipods	0	304	313[2]
Shrimp	0	[1]	[1]
Polar cod	[1]	880	608
Other fish	55	622	406
Other crustaceans	0	356	312
Total	**1817**	**3491**	**3371**

[1] The prey species is included in the relevant "other" group for this predator

[2] Only *Parathemisto*.

CONSUMPTION BY VARIOUS PREDATORS

Cod

Bogstad and Mehl (MS 1997) calculated the consumption of various prey species by cod using stomach content data from the joint IMR (Bergen)-PINRO (Murmansk) stomach content data base (Mehl and Yaragina MS 1992), a model for the gastric evacuation rate of cod (dos Santos and Jobling 1995) and data on sea temperature and the abundance and geographical distribution of cod. The consumption is calculated for three main areas in the Barents Sea and for the first and second half of the year and for age groups 1-11+ separately. On the average 7,500 stomachs have been sampled annually since 1984. These consumption estimates were updated by ICES (2000), and are given in Table 3. The prey categories given in the table in addition to cod, capelin and herring are deep-sea shrimp, polar cod, redfish (*Sebastes* spp.), amphipods (mainly Hyperiidae), krill (Euphausiacea), and other food. For fish and shrimp as prey, the consumption is calculated by 5 cm prey length groups for prey < 30 cm and 10 cm prey length groups for prey > 30 cm. The consumption estimates in Table 3 do not include the consumption by mature cod in the period when it is outside the Barents Sea, which is assumed to be 3 months during the first half of the year (Godø 1989). During this period it may consume significant amounts of adult herring (Bogstad and Mehl MS 1997).

Work on unifying and improving Russian and Norwegian methods of consumption calculation is in progress (ICES 1999a). Russian qualitative stomach content data (as described e.g. in Ponomarenko *et al.* MS 1978 and Ponomarenko and Yaragina MS 1979) will be utilised in this work.

The food conversion efficiency averaged over the whole period was found to range from 25% for age 1 cod to 13% for age 7 cod. These values are in accordance with results of other investigations (e.g. Jobling 1988). The calculated consumption should also be compared to estimates of energy consumption using bioenergetics models (Ajiad MS 1996).

Harp seals and minke whales

Nilssen *et al.* (this volume) and Folkow *et al.* (this volume) calculated the consumption by harp seals and minke whales, respectively, in the Barents Sea using data on energy intake, diet composition, energy density of prey and predator abundance. For harp seals, the data on diet composition were collected in the period 1990-1996. The food consumption by 2,223,000 harp seals (see ICES 1999b) was calculated both for periods with a high and low capelin stock. The consumption by 85,000 minke whales (Schweder *et al.* 1997) during an assumed 180 days feeding period (mid April – mid October) in the Barents Sea and in Norwegian coastal waters was calculated using data from 1992-1995, but data from 1992 in areas with high capelin abundance were excluded in order to get an estimate for a period with a low capelin stock. The consumption by minke whales and harp seals in the Barents Sea for a situation with a low capelin stock and high herring stock, as calculated for assumed point estimates of abundance, is given in Table 4, together with the consumption by harp seals in a situation with an assumed high capelin stock. The abundance of two of the dominant prey species (capelin and herring) has been very variable, as seen from Table 1. Both capelin and herring may be high or low, giving four possible combinations of the abundance of these two main pelagic species. Data on the diet composition of harp seal and minke whale are only available for two and one of those combinations respectively and great care should be taken when applying these data in other situations. At present, data on prey size composition in harp seal stomachs are not available, but will be in the near future (K. T. Nilssen, Norwegian Institute of Fisheries and Aquaculture, Tromsø, Norway, pers. comm.). The same is true for minke whales, except for herring where we know that the majority of specimens eaten by the whales belong to the young, immature (1-5 years old) cohorts (Lindstrøm *et al.* MS 1999). It is likely that minke whales feed on adult herring during their southward migrations from the Barents Sea in autumn (Folkow *et al.* this volume). This possible consumption is not included in the consumption estimate for minke whales given in Table 4, which should, therefore, be regarded as an underestimate with regard to herring.

Humans

Humans are also important predators on cod, herring, capelin and other stocks (Fig. 2). The catch of Northeast Arctic cod, Barents Sea capelin, Norwegian Spring-Spawning herring, Northeast Arctic haddock, deep-sea shrimp, polar cod, Greenland halibut and redfish (*Sebastes marinus* and *Sebastes mentella* combined) in the period 1984-1998 are given in Table 5. The data are taken from ICES (2000) for cod, haddock, Greenland halibut and redfish and from ICES (1999c) for herring and capelin. It should be noted that the catches of herring are taken outside the Barents Sea (in the Norwegian Sea and Norwegian coastal waters). Aschan (1999) gives shrimp catches by year for the period 1988-1997, and data on shrimp catches for the period 1984-1987 are given by ICES (1987; 1988). Revised catch figures for these years (minor changes) as well as catch data for 1998 were kindly provided by Aschan (pers. comm.). Catch figures for polar cod were provided by H. Gjøsæter, Institute of Marine Research, Bergen, Norway (pers. comm.).

Fig. 2
Minke whales are hunted in the Barents and Norwegian Seas by Norwegian hunters

Photo: Tore Haug

Other predators

Cod, harp seals, minke whales and humans are the main predators on cod, capelin, herring and other abundant fish stocks in the Barents Sea. The consumption by other fish and mammal stocks, as well as birds and invertebrates, is reviewed below:

Other fish

Capelin, herring and polar cod are mainly plankton feeders. Three groups of planktonic crus-

Table 5. Catches (1000's of tonnes) of some commercial stocks in the period 1984 -1998.

Year	Cod	Capelin	Herring	Haddock	Shrimp	Polar cod	Greenland halibut	Redfish
1984	278	1477	54	17	131	0	26	101
1985	308	868	170	41	129	0	23	93
1986	430	123	225	97	70	0	25	53
1987	523	0	127	151	45	0	20	35
1988	435	0	135	92	49	0	10	41
1989	332	0	104	55	63	0	21	47
1990	212	0	86	26	81	0	23	63
1991	319	929	85	34	81	0	33	68
1992	513	1123	104	54	75	0	9	32
1993	582	586	232	78	59	50	12	30
1994	771	0	479	121	30	5	9	31
1995	740	0	902	138	27	20	12	26
1996	732	0	1220	174	31	30	14	25
1997	762	0	1427	149	35	11	10	26
1998	593	0	1223	94	53	1	12	33

taceans dominate the diet of capelin and polar cod: copepods, euphausiids and amphipods. (Gjøsæter 1998, Ajiad and Gjøsæter MS 1990). The consumption of fish by these plankton-feeding species is small. Calanoid copepods dominate the diet of herring in the Barents Sea (Huse MS 1994), but herring is also an important predator on capelin larvae, although these make up a small proportion of the diet (Huse and Toresen MS 1995). Melle (MS 1985) identified herring as a heavy predator on cod eggs, based on studies in Lofoten in April 1983.

Apart from cod, other abundant piscivorous fish stocks in the Barents Sea are haddock, deep-sea redfish, Greenland halibut, long rough dab and thorny skate. Only a few scattered diet studies and consumption estimates are available for these species. The biomass of haddock is much lower than that of cod. In the period 1993-1998, the biomass of three year old and older haddock fluctuated between 300,000 and 650,000 tonnes (Table 1). Also, as benthic organisms are a major part of the diet of haddock (Burgos and Mehl MS 1987, Jiang and Jørgensen 1996), the total consumption of fish prey by haddock should be small compared to that by cod, harp seal and minke whale. Ponomarenko *et al.* (MS 1978) estimated the annual consumption of capelin by haddock as 11.8% to 47.8 % of the haddock biomass, or between 84,000 and 405,000 tonnes in the period 1974-1976. In the same period the biomass of haddock was about 700,000 tonnes. Antipova *et al.* (MS 1980) reports that consumption of capelin by haddock mainly takes place in March and April, and some of this may be of post-spawning capelin.

The biomass estimates of other piscivorous fish species in the Barents Sea has in the period 1984-present been low compared to that of cod and haddock (Table 1). The biomass of Greenland halibut (3+) declined from 115,000 tonnes in 1984 to 42,000 tonnes in 1996. The diet of Greenland halibut consists mostly of fish and cephalopods (Michalsen and Nedreaas 1998).

The biomass of deep-sea redfish (6+) has fluctuated around 200,000 tonnes in the period 1984-1996. Dolgov and Drevetnyak (MS 1990) estimated the annual ration of deep-sea redfish as 125% to 599 % of the body weight. The diet of redfish consists mainly of calanoids, arrow-worms (*Sagitta* spp.) and euphausiids as well as fish prey for larger redfish (Boldovsky 1944, cited in Dolgov and Drevetnyak MS 1990). The biomass of thorny skate has fluctuated between 35,000 and 115,000 tonnes in the period 1990-1996, with a mean annual consumption of

152,000 tonnes in 1994-95 (Dolgov MS 1997). About 25 % of this was fish prey with 1-2 year old cod as the most important group (about 10%).

Survey indices of long rough dab from shrimp surveys in the Barents Sea and the Svalbard area (Table 1) show that the biomass of long rough dab has increased in recent years and is at present about 100,000 tonnes. Cod made up on average about 20% of the diet of long rough dab in the 1990s (Dolgova and Dolgov MS 1997). Other commercial species were of minor importan in the diet of long rough dab.

It seems reasonable to assume that the consumption/biomass ratio of other piscivorous fish species than cod in the Barents Sea is of the same order of magnitude as the ratio for cod. Thus, the biomass of the other piscivorous fish species than cod can be used as an indicator of their total consumption. In the period 1990-96, the average total biomass of haddock, Greenland halibut, deep-sea redfish, long rough dab and thorny skate was about 900,000 tonnes (Table 1) while that of cod was about 2,100,000 tonnes. In the same period the average annual consumption by cod was about 4.7 million tonnes. Applying the same consumption/ biomass ratio for other piscivorous species as for cod gives an average annual consumption of about 2.0 million tonnes in the same period. Based on available information on the diet and consumption of these species, less than half the total consumption is fish prey, and only parts of the Greenland halibut and deep-sea redfish stocks (mainly immature fish) are found in the Barents Sea. It should, however, be kept in mind that the biomass of some of these species has been much larger in the past. The biomass of deep-sea redfish was almost 1 million tonnes at the end of the 1960s and that of Greenland halibut was above 300,000 tonnes in 1970 (ICES 1998a).

Other marine mammals

Our knowledge of the present diet of marine mammals other than harp seals and minke whales in the Barents Sea is fairly fragmented and incomplete. Their consumption of cod, capelin and herring is assumed to differ substantially between species, owing both to their variable importance in the area in terms of biomass, and to their dietary preferences. Common to most of them is that our quantitative knowledge of their abundance and/or diet composition is rather restricted.

Piscivorous baleen whales, other than minke whales, in the Barents Sea include humpback whales (*Megaptera novaeangliae*) and fin whales (*Balaenoptera physalus*) (Christensen *et al.* 1992a). Recent survey results indicate that there are ca. 1,000 humpback whales in the Norwegian and Barents Sea (Christensen *et al.* 1992b). In the past, the species has been reported to pursue and feed on capelin in the Barents Sea for parts of the year (generally from September to January/February) (Ingebrigtsen 1929). In spring and summer, however, the food of humpbacks has been observed to be mainly krill. Krill has also been reported to be the main food for fin whales (Jonsgård 1966), for which an abundance estimate of approximately 3,000 animals was calculated for the Norwegian and Barents Sea from sightings surveys performed in 1995 (NAMMCO 1998). Jonsgård (1966) also acknowledged the importance of fish in the fin whale diet, and emphasised the typical seasonal nature of the food intake of the species: In North Norway, capelin dominated the diet in early spring, whereas the summer diet was comprised mainly of crustaceans and, to a much lesser extent, herring. This was in good agreement with observations that most fin whales disappeared from North Norway in April, the bulk of them presumably moving westward into the Norwegian Sea, while in June-August they were again found off the coast of North Norway and in Bear Island and Spitsbergen waters preying mainly on krill (Ingebrigtsen 1929). Recent observations, made during the 1995 sightings surveys, seem to confirm the previously observed summer distribution of fin whales (NAMMCO 1998), and it is suggested that fin whales may be of some significance as predators on herring in the Norwegian Sea (Misund *et al.* 1997). There is no recent quantitative information on the diet of humpback and fin whales in the Barents Sea area. The other baleen whales that occur in the Barents Sea, blue whales (*Balaenoptera musculus*), sei whales (*Balaenoptera borealis*) and Greenland right whales (*Balaena mysticetus*), are known to be pure plankton feeders in this area (Christensen *et al.* 1992a).

The most numerous species of toothed whale in the Barents Sea area are probably white-beaked dolphins (*Lagenorhynchus albirostris*) and harbour porpoises (*Phocoena phocoena*). Generally, knowledge concerning the biology of white-beaked dolphins is very limited, and there is no information about their feeding habits in the Barents Sea area. From sightings surveys in 1989, it appears that the size of the Barents Sea population may be around 60,000 – 70,000 animals (Øien MS 1993). The same sighting surveys provided a point estimate of nearly 11,000 harbour porpoises for the Lofoten-Barents Sea area (Bjørge and Øien 1995). From analyses of harbour porpoises taken as by-catch in gill nets in the northernmost coastal areas of Norway in 1985-1990, Aarefjord *et al.* (1995) concluded that capelin dominated the diet (a little over 40% of the biomass), which was, however, also comprised of herring, saithe (*Pollachius virens*) and blue whiting (*Micromesistius poutassou*) (all categories with 15% to 20% contributions to the total prey biomass). A third toothed whale that may be of some significance is the killer whale (*Orcinus orca*). From questionnaires in 1982-1987, Christensen (1988) suggested a maximum inshore occurrence of 1,500 killer whales in Norwegian waters, while the 1989 sightings surveys suggested an abundance of approximately 7,000 animals in the northern North Sea and eastern Norwegian Sea up to Bear Island (NAMMCO 1993). Killer whales are known to feed almost exclusively on herring in coastal waters of North Norway (Christensen 1982, Similä *et al.* 1996), whereas both their local abundance and feeding habits in the Barents Sea are unknown. A fourth toothed whale, the Arctic white whale or beluga (*Delphinapterus leucas*), is known to occur seasonally in both the northernmost and south-eastern parts of the Barents Sea (Gurevich 1980). Gurevich (1980) refers to capelin, herring and various gadoids as important beluga food in Arctic waters north of Russia, but no information on abundance (see also Gjertz and Wiig 1994) or quantitative diet composition is available.

Of the more Arctic seal species associated with the Barents Sea (in the northernmost and south-eastern parts) ringed seals (*Phoca hispida*); are known to feed either on pelagic or ice-associated crustaceans and polar cod (Belikov and Boltunov 1998, Lydersen 1998, Wathne *et al.* 2000); bearded seals (*Erignathus barbatus*) and walruses (*Odobenus rosmarus*) feed on Arctic benthic invertebrates and fish (the last species also occasionally feeds on seal pups (Timoshenko and Popov 1990, Gjertz and Wiig 1992, Hjelset *et al.* 1999)). Harbour seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*), both residents in coastal areas in the southern part of the Barents Sea, may feed on herring, cod and other fish species such as saithe, wolffish (*Anarchias spp.*), some flatfishes and sand eels (*Ammodytes spp.*) (Skeie MS 1995, Berg *et al.* MS 1999). The abundance of harbour seals in coastal areas of North Norway (north of Lofoten) and Russia and on Spitsbergen is, however, only 2,500 animals (Henriksen *et al.* 1997, Haug *et al.* MS 1998a). The abundance of grey seals in the same areas (except Spitsbergen) is slightly higher, ca. 4,400 animals (Haug *et al.* 1994, MS 1998b).

Certainly, the total annual consumption of cod, capelin and herring in the Barents Sea by marine mammals other than minke whales and harp seals, particularly fin whales, white-beaked dolphins and harbour porpoises, must be of some magnitude. With our presently very restricted knowledge of their annual distribution, abundance, and relative diet composition, further quantification of their ecological significance must, however, await availability of more data.

Seabirds

Mehlum and Gabrielsen (1995) estimated the total consumption by seabirds in the Barents Sea to be 1.4 million tonnes, but the proportions of various fish species in this total base are not available. The common guillemot (*Uria aalge*) represents about 10% of the total food requirement, and this species eats mostly capelin. The Brünnich's guillemot (*Uria lomvia*) represents 55% of the total food requirement, but has a much lower proportion of capelin in its diet. A total mean capelin consumption in the order of 200,000 to 300,000 tonnes could be a fair guess (Gjøsæter 1998). Other numerous seabird species, e.g. kittiwakes (*Rissa tridactyla*) and puffins (*Fratercula arctica*), are also known to eat capelin and herring, and for all seabird species feeding on pelagic fish in the Barents Sea, it is evident that both their choice of prey and breeding success will change in response to changes in stocks of key forage fishes such as capelin and herring (Krasnov and Barrett 1995, Barrett and Krasnov 1996). Barrett *et al.* (1990) estimated the consumption of gadoids (0-2 year old cod and saithe) by shags (*Phalacrocorax aristotelis*) and cormorants (*Phalacrocorax carbo*) to be about 6,000 tonnes annually, some of this consumption occurs in areas south of the area under consideration in this paper. Erikstad (1990) studied the feeding of four seabird species in the open water of the southeastern Barents Sea, near the ice edge. 1-group cod were recorded in all species, most frequently in Brünnich's guillemot (58.3% frequency of occurrence) and kittiwake (57.7%), followed by glaucous gull (*Larus hyperboreus*) (18.2%) and northern fulmar (*Fulmarus glacialis*).

Invertebrates

Invertebrates are predators on cod eggs, larvae, and 0-group (Pálsson 1994) but their predation on these life stages has not been quantified. As we in this paper mainly consider predation on 1+ fish, we will not take predation by invertebrates into account.

COMPARISON OF ESTIMATES OF CONSUMPTION, PREY ABUNDANCE AND M-OUTPUT BIOMASS OF PREY

The strong fluctuations in prey stock sizes (especially herring and capelin) from year to year indicate that it is dangerous to combine data from several years to obtain a consumption estimate. For harp seals, data for periods when both the capelin and herring stocks are low, are lacking, and for minke whales, data for periods with a high capelin stock are also too sparse to give a reasonable picture of the minke whale's feeding habits in such situations. In periods when preferred prey like capelin and herring are scarce, krill may be an important food item (Haug *et al.* MS 1999). Harp seal invasions on the coast of Northern Norway in 1986-1988 (Haug and Nilssen 1995) were probably related to the low abundance of capelin. During the invasions, the harp seals consumed substantial amounts of gadoids (Haug *et al.* 1991), and it has been suggested that their consumption of saithe may have affected the recruitment to this stock in the period (Ugland *et al.* 1993).

In comparisons of consumption estimates and stock size estimates, the consumption estimates for minke whales may be considered representative for the period 1993-1995, while the consumption estimates for harp seals may be considered representative for the period 1990-1992 (high capelin stock) and 1993-1997 (low capelin stock), respectively. When making comparisons, one should consider that the fishery and predation affect different age groups, at least for cod, haddock, redfish and herring. Data on the size composition of the prey and of the consumption is at present only available for cod as predator. Also, it is difficult to compare annual estimates (cod consumption, catch) with estimates based on aggregating data from several years (seal and whale consumption). In Tables 2 and 3, we have calculated averages for the periods 1991-1993 and 1994-1996, corresponding to periods of high and low capelin abundance, respectively. The abundance and consumption of capelin in the first half of 1993 was so high that it seems reasonable to include this year in the 'high capelin' period, even though the stock estimate in autumn 1993 was low.

The consumption of capelin is higher than both the acoustic abundance estimates of capelin and the calculated MOB in several of the years with low capelin abundance. The reason for this may be both that the annual production by the capelin stock is higher than the measurements of the standing stock in autumn, and possible underestimates of the capelin stock and overestimation of the consumption, particularly by cod (Bogstad and Mehl MS 1997). It is noteworthy that the estimates of the consumption of capelin by predators (particularly cod) are much higher than the catches for the years 1991-1993 when there was a capelin fishery. Problems with the consistency between capelin consumption and capelin abundance have also been encountered for capelin in Icelandic waters. Magnússon and Pálsson (1989, 1991) found that the acoustic abundance estimate of capelin in Icelandic waters had to be scaled up by a factor of 1.9 in order to get consistency between the estimates of capelin stock size, capelin catch and consumption of capelin by cod.

The estimate of consumption of cod by harp seals and minke whales (554,000 tonnes for low capelin stock and less than 357,000 tonnes for high capelin stock, respectively) is fairly close to the estimates of MOB (cannibalism excluded) of around 500,000 tonnes. The predation by other predators on cod is probably quite low compared to the predation by the three main predators cod, harp seal and minke whale. The level of the natural mortality rate used thus seems appropriate, but cod survey data should be used to investigate whether natural mortality increases in periods of low capelin stock, as the consumption estimates presented here indicate. The estimate of 175,000 tonnes of haddock consumed in years of low capelin stock is somewhat above the average MOB value of 121,000 tonnes for the period 1993-1995. The same considerations about the level of natural mortality as mentioned for cod also apply to haddock. For both these stocks the annual removal of fish by predators seems to be at about the same level as the reported landings from the commercial fishery. It should, however, be remembered that the predators prey on a wider range of age groups than the commercial fishery does.

The consumption of herring by the three main predators amounts to about 1.2 million tonnes in years with low capelin abundance. Even taking other predators into account, the total predation seems to be much lower than the MOB in those years. Whether the value of M=0.9 is appropriate also for large year classes, is open to discussion. However, the biomass estimates of young herring given in Table 1 (which do not include 0-group) also indicate that the biomass and hence the 'production' of herring in the Barents Sea is large. Barros (MS 1995) found the mortality of young herring in the Barents Sea to be closely related to abundance of young cod, which seems somewhat strange if harp seals and minke whales are more important predators on herring than cod is. It should also be noted that the frequency of occurrence of herring in cod stomachs was much lower in the 1990s than when large herring year classes occurred in the Barents Sea in the 1950s and 1960s (Ponomarenko and Yaragina MS 1979,Yaragina and Dolgov pers. comm. cited in Gjøsæter and Bogstad 1998).

The consumption of polar cod by harp seal and cod combined is on the same level as the calculated MOB. Predation by other predators (e.g. ringed seal) on this stock should not be neglected when comparing MOB and predation for this stock.

How uncertain are the consumption estimates and the estimates of biomass 'lost' through natural mortality?

The number of predators, the consumption per predator and the diet composition affects the consumption estimates. There is still considerable uncertainty associated with the assessment of cod (ICES 2000, Nakken 1998) using VPA-based assessment methods to determine the current stock size, although no measure of the uncertainty in the stock estimate has been given. The stock estimates of minke whales (Schweder *et al.* 1997) and harp seals (ICES 1999b) have been revised considerably recently, and for these stocks, uncertainty estimates are provided. The prey species composition is probably more uncertain than the estimates of consumption per predator, as the coverage of stomach samples in space and time is limited, especially for marine mammals.

There is also uncertainty associated with the estimates of prey stock size and the MOB estimates derived from those. Although the acoustic estimates of the capelin stock form a coherent time series, there are indications that they may be underestimates (Gjøsæter 1998). The M-values used in the single-species assessments and in calculation of the MOB for cod, haddock and herring are not very well substantiated.

USE OF RESULTS IN MULTISPECIES MODELLING AND IN MANAGEMENT

Using appropriate values for the natural mortality M is important both when assessing the stock size in the past, and for prediction purposes. It is of importance both in single- and multispecies models, as even in multispecies models where the mortality induced by predators is modelled explicitly, there will always be a 'residual' component of the mortality. We will first describe how consumption information have been used in assessment and prediction so far, and also give some perspectives on future developments in this field.

Use of consumption estimates in stock assessment and management

In the Barents Sea, with few species and large variations in recruitment, growth, maturation, mortality and environmental conditions, it is important to take multispecies considerations into account both in the assessment of present and past stock size of the capelin, cod and herring stocks and both when making short-term and long-term predictions of the development of these stocks.

Results of the multispecies research in the Barents Sea have already been utilised in the management of capelin, cod and haddock, by improving the assessments of current stock size and the short- and medium term prognosis. Bogstad and Gjøsæter (1994) described a method for calculating the amount of capelin that can be consumed by cod during the spawning migration of capelin. This method was used in the assessment of capelin in 1991-1993, but is only applicable in periods with high capelin abundance. A better method based on the work presented in Bogstad (MS 1997) and Tjelmeland (1997) is under development (ICES 1999c, Anon. 1999). In this new method, the consumption of mature capelin by cod is modelled as a function of both capelin and cod abundance. The consumption of young age groups of cod and haddock by cod has been included in the VPA for cod and haddock as an additional catch, and including predation in this way gave a better fit between survey data and VPA estimates for both cod and haddock (ICES 1999a). It should also be possible to include predation by cod into the assessment of herring, redfish and shrimp. For shrimp it is especially important since the consumption of shrimp by cod is much larger than the fishery. At present there is no assessment model for shrimp in the Barents Sea, but such models are being developed (Aschan 1999).

Estimates of consumption by predators other than cod can at present not be used directly to provide annual values of consumption and hence natural mortality caused by these species. However, they may be used to improve the values of 'residual' natural mortality. Also, they may be used in prediction models, assuming that there is a relationship between predator stock size and the mortality induced by a predator.

Use of diet information in multispecies modelling for the Barents Sea

Data on diet or who-eats-whom are the backbone of multispecies modelling. However, most of the multispecies models for the Barents Sea have been based on fairly sparse information about diet composition of predators, rather than being calibrated against actual stomach data. Until recently, only data on cod diet were available for such calibration, but the information about harp seal and minke whale diet now available could also be used in this way.

Several multispecies models for the Barents Sea have been constructed. The most comprehensive one is MULTSPEC (Bogstad *et al.* 1997), where cod, harp seal and minke whale are predators on capelin, herring and cod. In addition, herring prey on capelin larvae, and the growth of cod is dependent on the food abundance. In this model, only the parameters describing predation by cod on capelin have been estimated from stomach data (Bogstad MS 1997), while other interaction parameters have been set according to available knowledge without doing any formal parameter estimation. This model is structured by area, age and length and may be too complex for use in, for example, studies of management strategies. Thus, simpler models (CAPSEX, AGGMULT) have been made that are structured by age and length or only by age. Cod stomach data have also been used in parameter estimations in AGGMULT. Tjelmeland and Bogstad (1998) give a description of the models MULTSPEC, CAPSEX and AGGMULT.

Several other multispecies models for the Barents Sea are described in Rødseth (1998).

Use in studies of long-term management strategies

An important use of such models is to investigate the effects of various long-term management strategies for the species involved. Such models have to contain sub-models for maturation, recruitment, growth, natural mortality and catch for each stock, in addition to interaction terms. A minimum set of requirements for a model investigating long-term management strategies for the minke whale-harp seal-cod-herring-capelin system in the Barents Sea, which would take the main interactions into account, could be:

1. An initial stock estimate, with uncertainty and also the uncertainty in the stock estimates made during the simulation period (annual estimates for fish stocks, less frequent estimates for marine mammal stocks). Uncertainty in the stock estimates is now included in the evaluation of single-species harvest control rules both for Norwegian

Spring-Spawning herring (ICES 1999c), Northeast Arctic cod (ICES 2000) and Barents Sea capelin (ICES 1999c, Anon. 1999). Uncertainty estimates are also available for the marine mammal stocks (Schweder *et al.* 1997, ICES 1999b).
2. A model of recruitment for each stock, taking into account the stochastic nature of the recruitment to fish stocks. For capelin the influence of herring on capelin recruitment (Gjøsæter and Bogstad 1998) should be included. Environmental effects on recruitment will implicitly be included here.
3. A model for how cod growth and maturation depends on food (capelin) abundance (Mehl and Sunnanå 1991).
4. A model for cod, harp seal and minke whale predation on capelin, herring and cod, e.g. along the lines of Bogstad *et al.* (1997). Such a model should take account of the predator's functional response to changes in prey abundance and the relative abundance of alternative prey.
5. A harvest control rule for all species.

In order to define an optimal harvest control rule for a multispecies system, the harvest of various species must be given some weight. This could be, for example, economic value. Harvesting costs for various species could also be included. A review of work in this field is given by NAMMCO (1999). As the fish stocks in questions are shared between several countries (primarily Norway and Russia) which may put different values to the catch and to the harvesting costs, such analyses will be important for each country to carry out before agreements on harvesting control rules for the species in question are agreed upon.

The diet data for marine mammals are fairly sparse, so it may seem rather bold at the present stage to include predation by marine mammals on fish in studies of harvesting strategies. However, present knowledge about the diet and consumption of harp seals and minke whales in the Barents Sea is better and more up to date than the knowledge about the diet of marine mammals in Icelandic waters, for which Stefánsson *et al.* (MS 1997a, 1997b) used crude models for the natural mortality of capelin and cod caused by marine mammals (fin whales, minke whales, humpback whales, harbour seals and grey seals) in studies of harvesting strategies. In ICES (1997a) it is indicated how these models can be used in management of fish stocks in Icelandic waters. Medium-term simulations for the development of the Icelandic cod stock were based on the work presented by Stefánsson *et al.* (MS 1997a) and a likely harvesting strategy for all species in that model, i.e. sustainable harvest of seals and no harvest of whales, leading to increasing natural mortality on, for example, cod. The species interactions, modelling efforts and management questions in the Barents Sea are quite similar to those in Icelandic waters, and it is expected that co-operation between the research groups carrying out such studies for the Barents Sea and for Icelandic waters will be very valuable. Stefánsson and Pálsson (1998) have outlined how multispecies models for boreal systems such as the Barents Sea and Icelandic waters should be constructed.

Multispecies interactions should also be included in the development and provision of precautionary advice, as such interactions may significantly impact the values of biological reference points. Also, some of the traditional biological reference points are not well defined in the context of interacting species (see discussion in ICES (1997b, 1999d)). Gislason (1999) studied single- and multispecies reference points for Baltic fish stocks (cod, herring and sprat (*Sprattus sprattus*)). A similar study of the cod-capelin-herring system in the Barents Sea would be interesting.

CONCLUSIONS

Investigations of the diet of the main predators on fish in the Barents Sea: cod, harp seal and minke whales, have provided much information about the importance of the predation by these three species on the main fish stocks in the Barents Sea. Cod is the most important predator, at present consuming about as much food as the two marine mammal species combined. Some other predator species (haddock, fin whales, white-beaked dolphin, killer whale, ringed seal and some birds) may be of importance as predators on the pelagic species capelin, herring and polar cod. The consumption estimates and the estimates of fish biomass available for consumption generally match fairly well, except for when the capelin biomass is low or the herring biomass is high. Estimates of the consumption by cod of various prey species are now being used in assessment and management using both simple and more complex multispecies models and approaches. Estimates of the consumption of fish by marine mammals can at present only be used for evaluating the values of natural mortality used, and for making long-term predictions. It is very important to reduce the uncertainty associated with consumption estimates.

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