AN ECOPATH MODEL FOR THE NORWEGIAN SEA AND BARENTS SEA

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ABSTRACT

This report documents the construction and basic input data used to generate a 1997 Ecopath with Ecosim model for the Norwegian Sea and Barents Sea, initially assembled during a workshop held at the Institute of Marine Research in Bergen, Norway, in November 2000. This was part of the ocean-wide assessment of ecosystem effects of fishing in the North Atlantic conducted by the *Sea Around Us* project at the University of British Columbia in cooperation with the 'Ecosystem Norwegian Sea' program of the Institute of Marine Research, Bergen. The model area covers 3,116,000 km^2 of Atlantic, arctic and shelf waters. Thirty functional groups were included, ranging from marine mammals to phytoplankton and detritus. In the future, this model can be used to evaluate specific local and regional questions of interest to the Institute of Marine Research, Norway.

INTRODUCTION

At the Institute of Marine Research in Bergen, Norway, an internal project 'Flux of biomasses', under the program 'Ecosystem Norwegian Sea', has been aimed at the quantification of biomass fluxes between trophic levels in the Norwegian Sea. In June 2000, Villy Christensen at the University of British Columbia, Vancouver, Canada, offered to cooperate in the construction of an Ecopath model for the Norwegian Sea and the Barents Sea. Such a model was needed for the project *Sea Around Us* which aims to present material documenting large-scale fisheries impact on marine ecosystems, and to show how such impacts may be mitigated and reversed. It was decided to carry out this cooperation as a workshop, which was held in Bergen 15-17 November 2000, with the following as participants: Villy Christensen and Dirk Zeller, University of British Columbia, Vancouver, Canada; and Sigurd Tjelmeland, Leif Nøttestad, Webjørn Melle, Bjørnar Ellertsen, Are Dommasnes, Institute of Marine Research, Bergen. In addition to these workshop participants, Torstein Pedersen from the Norwegian College of Fisheries Sciences in Tromsø, a member of the modeling group, helped prepare the workshop and supplied data. Cecilie Kvamme from the Institute of Marine Research cooperated with Leif Nøttestad in the preparation of data on benthic fish and squid.

Biological data on primary and secondary production, fishes, seabirds and marine mammals were collected prior to the workshop. Fisheries landings for the most important species were obtained from ICES files, and time series for many species of fish were available from ICES Working Group reports. An Ecopath with Ecosim model (Christensen and Pauly, 1993; Christensen, 1995; Pauly and Christensen, 1996; Christensen, Walters and Pauly, 2000) covering ICES areas I, IIa and IIb was constructed for the year 1997 (Figure 1). In addition, using the time series data and working backwards from the 1997 model, a similar model was constructed for 1950.

Plans for future simulations in order to increase understanding of the food chains in the Norwegian Sea and Barents Sea, and publication of the results, will be formulated once the Technical Report of the Institute of Marine Research, Bergen, Norway is completed.

MODEL AREA

The model covers ICES areas I, IIa and IIb north to approximately 81° N, which includes the Barents Sea (area 1) and the Norwegian Sea (area 2) west to 11° W and south to 63°-64° N (Figure 1). The total surface area is 3,116,000 km^2 (see Table 1 and Figure 1 for sub-areas).

Table 1. Surface area (km^2) of ICES fisheries statistical areas incorporated into the model.

Area	All depths	< 200 m	200-500 m	500-1000 m	1000-2000 m	2000-3000 m	> 3000 m
ICES Area I	1,006,100	472,867	533,233	-	-	-	-
ICES Area IIa	1,348,000	67,400	229,160	80,880	242,640	525,720	202,200
ICES Area IIb	761,900	190,475	152,380	83,810	68,570	175,237	91,428
Total	3,116,000	730,742	914,773	164,690	311,210	700,957	293,628

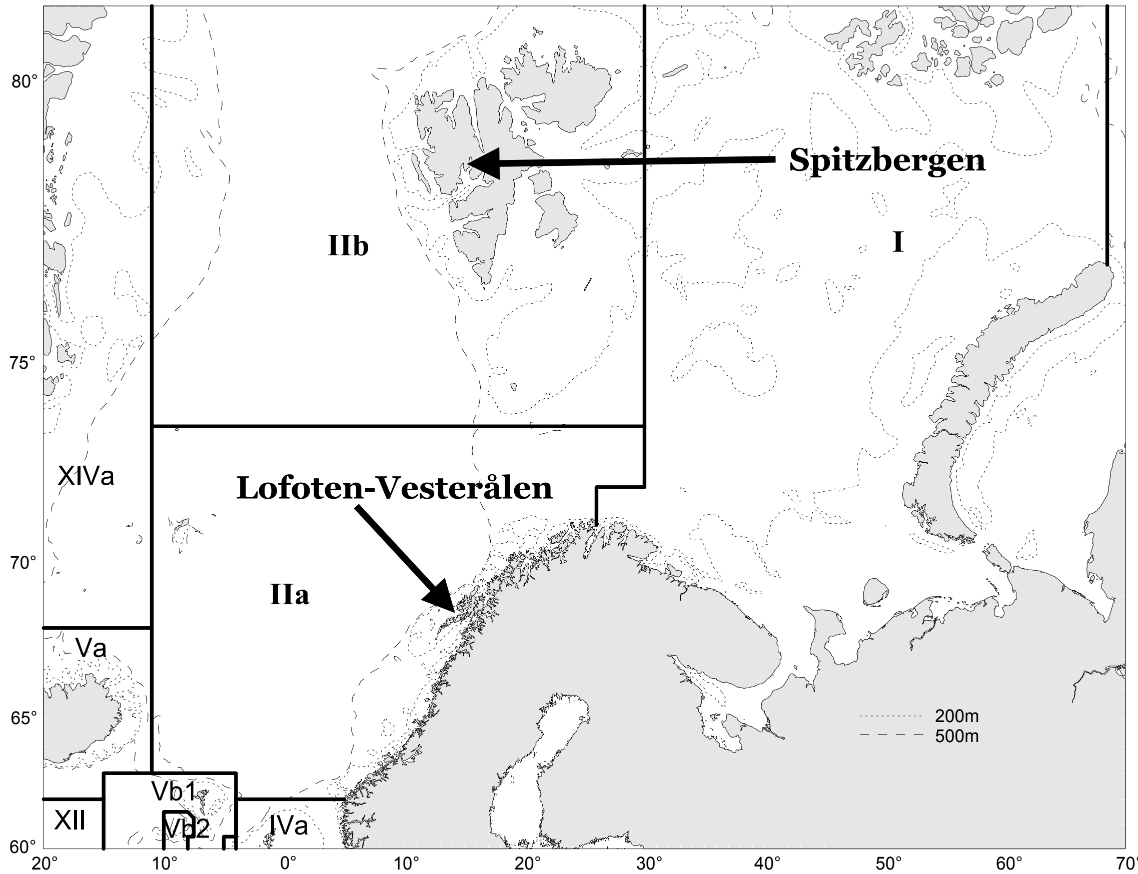

Figure 1. Map of model area, ICES areas I (Barents Sea), IIa and IIb (Norwegian Sea). 200m and 500m depth contours are indicated.

A submarine ridge between Scotland and Greenland forms the border between the Norwegian Sea and the North Atlantic. Iceland and the Faroe Islands form part of the ridge while the deepest sills are located in the Faroe Bank Channel (840 m; area Vb) and in the Denmark Strait (620 m). Topographic structures within the Nordic Seas divide the area into three subareas, the Greenland, Iceland and Norwegian Seas.

The Norwegian and Spitsbergen continental shelf borders the Norwegian Sea to the east, from 62°N to north of 80°N. From 62°N to approximately 64°N the shelf is rather narrow and shelf break depths are generally less than 200 m. Further north the shelf break depth is 500-600 m, and from 64°N to the Lofoten peninsula (67°N) the shelf is wider as well. The Barents Sea is a shelf sea where bottom depths are generally less than 300 m.

The hydrographic conditions in the eastern Norwegian Sea were described by Bjørke *et al.* (1999). The surface circulation is constrained by the bathymetry. In general the large scale circulation is cyclonic with a northward flow of Atlantic and coastal water (7-8°C) in the eastern part of the Norwegian Sea and a southward flow of arctic water along the coast of East Greenland. A branch of the East Greenland current flows into the Norwegian Sea north and east of Iceland as the East Iceland current. In the north-western part of the model area (west of the Spitsbergen shelf) and along the western part of the model area the water is generally cold and arctic (less than 2°C). The coastal water over the Norwegian shelf is generally 7-8°C, with somewhat higher temperatures in summer. Between the coastal water in the east and the arctic water in the west and north, the water in the Norwegian Sea is of Atlantic origin, entering from the south. Typical temperatures for the Atlantic water during summer are 5-7°C.

Atlantic water enters the Barents Sea from the west in the North Cape Current, which divides into a northern and a southern branch. In the northern Barents Sea low-salinity and cold arctic water generally flows from north east to south west. In the west the Atlantic and arctic water meets in a well defined front held in place by the shallow banks of the region. Over the deeper east basin the front is less definite and a substantial mixing of water masses occurs. Over the Norwegian shelf low-salinity coastal water flows northward, entering the Barents Sea along the Norwegian coast.

TIME SERIES DATA

The time series data on biomass, catch and fishing mortalities are based on ICES Working Group reports wherever possible. We have used the latest working groups reports available to us at the time of writing, generally for the year 2000. In most cases, biomass data from the working groups have been produced by Virtual Population Analysis (VPA) carried out by the working groups, and represent the situation at the start of the year. In some cases, catch data from the ICES Fisheries Statistics database has been used when no catch data from working groups were available, or to extend such data.

The time series for biomass and catch are given as tonnes per square kilometer. The values obtained from working groups or other sources have been divided by the area covered by the model (3,116,000 km^2).

SPECIES AND SPECIES GROUPS

Thirty functional groups or species were defined for the purpose of this model, ranging from marine mammals to phytoplankton and detritus (Table 2). The diet matrix for the thirty groups is presented in Table 3.

Table 2. Basic parameters used to describe the 1997 Ecopath model for the Norwegian Sea and Barents Sea, with 29 functional groups, plus detritus. P/B and Q/B are the production/biomass and consumption/biomass ratios, respectively. Trophic level and values in brackets were estimated by the model.

Group	Biomass (t·km^{-2})	P/B (year^{-1})	Q/B (year^{-1})	Ecotrophic Efficiency	Biomass accumulation (t·km^{-1}·year^{-1})	Trophic level
Toothed whales	0.067	0.06	4.90	(0.000)	0.000	4.2
Baleen whales	0.134	0.03	6.56	(0.249)	0.000	3.9
Seals	0.087	0.07	14.52	(0.042)	0.000	4.0
Seabirds	0.005	1.00	99.29	(0.000)	0.000	4.2
Cod 4+	0.448	1.20	2.50	(0.681)	-0.105	4.2
Cod juveniles	(0.351)	1.00	3.50	0.900	0.000	4.1
Haddock	0.134	1.00	2.80	(0.571)	-0.036	3.2
Saithe	0.181	1.00	5.00	(0.861)	0.016	3.5
Other benthic fish	0.700	1.00	5.00	(0.685)	0.000	3.5
Redfish	0.257	0.35	4.50	(0.895)	0.000	3.4
Blue whiting	0.925	0.60	6.00	(0.341)	0.020	3.4
Mackerel	0.180	0.60	6.00	(0.576)	0.009	3.1
Herring 4+	3.261	0.38	4.47	(0.092)	-0.430	3.2
Herring juveniles	(0.326)	0.80	4.47	0.950	-0.002	3.1
Polar cod	(0.472)	1.50	5.00	0.950	0.000	3.4
Capelin	(1.132)	1.00	5.00	0.950	0.000	3.3
Large pelagic fish	(1.652)	0.50	2.50	0.950	0.000	3.1
Small pelagic fish	(0.068)	1.50	5.50	0.950	0.000	3.6
Mesopel fish	(2.079)	2.00	10.00	0.950	0.000	3.3
Squid	2.632	2.44	12.00	(0.059)	0.000	3.3
Benthos	66.000	1.50	9.75	(0.997)	0.000	2.3
Prawns	0.300	1.25	5.00	(0.851)	0.000	2.9
Krill	47.000	2.50	15.00	(0.217)	0.000	2.3
Amphipods	16.000	2.50	15.00	(0.421)	0.000	2.8
Large zooplankton	(16.882)	4.00	15.00	0.950	0.000	2.2
Small zooplankton	50.000	10.00	25.00	(0.909)	0.000	2.0
Jellyfish	4.000	3.00	10.00	(0.339)	0.000	3.2
Seaweeds	4.400	0.65	-	(0.000)	0.000	1.0
Phytoplankton	15.000	117.73	-	0.950	0.000	1.0

Table 3. Diet matrix for the Norwegian Sea-Barents Sea ecosystem model.

Group		Predator															
	Prey	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	Toothed whales																
2	Baleen whales																
3	Seals																
4	Seabirds																
5	Cod 4+		0.099	0.076													
6	Cod juveniles				0.005	0.150	0.024			0.033							
7	Haddock					0.030	0.003			0.006							
8	Saithe					0.045	0.032										
9	Other benthic fish	0.002	0.052	0.012	0.030		0.214				0.100						
10	Redfish	0.065		0.009		0.034											
11	Blue whiting	0.294	0.010	0.010	0.039												
12	Mackerel	0.011															
13	Herring 4+	0.125	0.020	< 0.001													
14	Herring juveniles	0.057	0.100	0.020	0.200	0.007											
15	Polar cod			0.246	0.202	0.017	0.001			0.067							
16	Capelin	0.138	0.106	0.014	0.227	0.313	0.166			0.067							
17	Large pelagic fish		0.041	0.100	0.124	0.045	0.100		0.350				0.050				
18	Small pelagic fish	0.002		0.070													
19	Mesopel fish				0.049	0.045	0.032			0.033		0.050					
20	Squid	0.177		0.015	0.049					0.067							
21	Benthos					0.045	0.032	0.900	0.050	0.329	0.200						
22	Prawns	0.050		< 0.001		0.116	0.072				0.050						
23	Krill	0.080	0.420	0.155	0.075	0.071	0.125			0.067	0.250	0.550	0.100	0.400	0.140	0.500	0.297
24	Amphipods		0.152	0.099		0.083	0.200					0.200		0.050	0.050	0.300	0.297
25	Large zooplankton			0.172				0.100	0.500	0.197	0.300	0.100	0.050	0.350	0.110	0.100	0.099
26	Small zooplankton								0.100	0.132	0.100	0.100	0.800	0.200	0.700	0.100	0.297
27	Jellyfish																0.010
28	Seaweeds																
29	Phytoplankton																
30	Detritus																

Table 3. Diet matrix for the Norwegian Sea-Barents Sea ecosystem model (cont.).

Group	Prey	Predator 17	18	19	20	21	22	23	24	25	26	27
1	Toothed whales											
2	Baleen whales											
3	Seals											
4	Seabirds											
5	Cod 4+											
6	Cod juveniles											
7	Haddock											
8	Saithe											
9	Other benthic fish											
10	Redfish											
11	Blue whiting		0.040									
12	Mackerel		0.040									
13	Herring 4+											
14	Herring juveniles		0.020									
15	Polar cod											
16	Capelin		0.020									
17	Large pelagic fish		0.040									
18	Small pelagic fish											
19	Mesopel fish		0.040	0.048	0.077							
20	Squid		0.120									
21	Benthos					0.150	0.250					
22	Prawns		0.040									
23	Krill	0.100	0.200	0.238	0.153							0.044
24	Amphipods	0.100		0.238	0.153							0.044
25	Large zooplankton	0.100	0.200	0.238	0.463	0.030	0.250		0.050			0.100
26	Small zooplankton	0.700	0.200	0.238	0.153	0.030	0.250	0.250	0.700	0.164		0.712
27	Jellyfish		0.040									0.100
28	Seaweeds											
29	Phytoplankton					0.021		0.500		0.736	0.900	
30	Detritus					0.769	0.250	0.250	0.250	0.100	0.100	

Toothed whales

The toothed whales included in the model are the following four species: White-beaked dolphin (*Lagenorhynchus albirostris)*, Harbor porpoise (*Phocoena phocoena*), Killer whale (*Orcinus orca*) and Sperm whale (*Physeter macrocephalus*). The most numerous species in the Barents Sea are believed to be the white-beaked dolphin and harbor porpoise. The available data are summarized in Tables 4 and 5, and the model input data for this group can be found in Table 2.

*White-beaked dolphins (*Lagenorhynchus albirostris*)*

Sighting surveys indicate that the population size of white-beaked dolphins may be about 60,000-70,000 animals in the Barents Sea (Øien, 1993). There are no data on the feeding habits of this species (Bogstad *et al.*, 2000). Average body weight is 225 kg (Sigurjonsson and Vikingsson, 1997). With an assumed population size of 65,000, this gives a biomass of 14,625 tonnes. Assuming a Q/B similar to harp seals (Q/B = 15), gives a consumption of 219,000 t·year^{-1}.

*Harbor porpoises (*Phocoena phocoena*)*

Sighting surveys estimated the abundance of harbor porpoises to be nearly 11,000 animals for the Lofoten-Barents Sea area (Bjørge and Øien, 1995). Diet of harbor porpoises from coastal areas north of Lofoten was estimated from animals captured as by-catch in commercial fisheries (Aarefjord and Bjørge, 1995). The average body weight is set to be 39 kg (Sigurjonsson and Vikingsson, 1997). The biomass is then 429 tonnes, and assuming a Q/B of 15·year^{-1} gives a consumption of 6000 t·year^{-1}.

*Killer whales (*Orcinus orca*)*

The abundance of killer whales was estimated from sightings to be about 7,000 animals in the northern North Sea and the Barents Sea up to Bear Island (NAMMCO, 1998). Killer whales feed almost exclusively on herring in coastal waters off north Norway (Christensen, 1982; Simila *et al.*, 1996). Average body weight was assumed to be 2,350 kg (Sigurjonsson and Vikingsson, 1997), resulting in an estimated biomass of 16,450 tonnes. With an assumed Q/B of 6.0·year^{-1} (slightly higher than for minke whales), a consumption of 99,000 t·year^{-1} is calculated.

Sperm whales (Physeter macrocephalus)

Christensen *et al.* (1992a) used the 1989 sightings survey to estimate an abundance of 5,231 sperm whales in the Norwegian Sea. Sperm whales were not sighted in the Barents Sea. Sigurjonsson and Vikingsson (1997) used a mean weight of 34,322 kg for sperm whales in Icelandic and adjacent waters, based on Lockyer (1976), and we also use that value here. Sigurjonsson and Vikingsson (1997) also calculated consumption, based on two methods: (a) actual feeding rates of cetaceans in captivity, and (b) energy requirements based on physiological parameters and body weight. Their results correspond to consumption/biomass ratios (Q/B) varying from 1.55 to 2.20·year^{-1}. This seems a very low value, even if we account for the large body size, and in our calculations we have used a value of 4.0·year^{-1} instead.

Sperm whales occurring at latitudes above 45° N are males, whereas females and immatures remain in family groups in warmer water throughout the year (Martin and Clarke, 1986). Thus, even the males will be outside the model area for certain periods of time. In most areas cephalopods form the bulk of the food, with fish forming a relatively small part. In a few areas the situation is reversed and fish assume a higher importance (Kawakami, 1980; in Martin and Clarke, 1986). Martin and Clarke (1986) studied the diet of sperm whales captured between Iceland and Greenland during the years 1978-1981, and demonstrated that this is one area where fish dominates in the diet. Common species found in the stomachs were lumpsucker, redfish, cod and blue whiting, with the lumpfish providing almost half of the total biomass taken by sperm whales in the area. Sigurjonsson and Vikingsson (1997) interpreted their data as showing that fish made up 76% of the stomach content and cephalopods 24%. We have used this as a basis for the diet used in the model.

Table 4. Data for major species of toothed whales present in the Norwegian Sea and Barents Sea.

Species	Abundance	Body weight (kg)	Biomass (tonnes)	Q/B	Consumption ('000 tonnes)
White-beaked dolphin	65,000	225	14,625	15.0	219
Harbor porpoise	11,000	39	429	15.0	6
Killer whale	7,000	2,350	16,450	6.0	99
Sperm whale	5,231	34,322	179,538	4.0	718
Totals (mean)	88,231	-	211,042	(4.9)	1,042

*Beluga (*Delphinapterus leucas*)*

White whale or beluga occurs in the Barents Sea, but there is no data on abundance of this species. Capelin, herring and gadoids have been observed in their diet. This species has not been taken into account for this model.

In 1997 there were no catches of toothed whales from this area. However, catches for other years are included in the time series.

Table 5. Diet composition for the toothed whales. Predation by toothed whales in tonnes by species, and total predation in tonnes and by fraction. Note that for white-beaked dolphin and sperm whales, diet compositions are based on Icelandic data.

Prey	Predator				Total	
	White-beaked dolphin	Harbor porpoise	Killer whale	Sperm whale	Tonnes	Fraction
Toothed whales	0	0	0	0	0	0.00
Baleen whales	0	0	0	0	0	0.00
Seals	0	0	0	0	0	0.00
Seabirds	0	0	0	0	0	0.00
Cod 4+	0	0	0	0	0	0.00
Cod juveniles	0	0	0	0	0	0.00
Haddock	0	0	0	0	0	0.00
Saithe	0	1	0	0	1	0.00
Other benthic fish	0	1	0	0	1	0.00
Redfish	0	0	0	144	144	0.14
Blue whiting	0	0	0	287	287	0.28
Mackerel	0	0	0	0	0	0.00
Herring 4+	22	1	99	0	121	0.12
Herring juv.	55	1	0	0	55	0.05
Polar cod	0	0	0	0	0	0.00
Capelin	132	1	0	0	133	0.13
Large pelagic fish	0	0	0	0	0	0.00
Small pelagic fish	0	2	0	0	2	0.00
Mesopelagic fish	0	0	0	0	0	0.00
Squid	0	0	0	172	172	0.17
Benthos	0	0	0	0	0	0.00
Prawns	0	0	0	115	115	0.11
Krill	0	0	0	0	0	0.00
Amphipods	0	0	0	0	0	0.00
Large zooplankton	11	0	0	0	11	0.01
Small zooplankton	0	0	0	0	0	0.00
Jellyfish	0	0	0	0	0	0.00
Seaweeds	0	0	0	0	0	0.00
Phytoplankton	0	0	0	0	0	0.00
Detritus	0	0	0	0	0	0.00
Sum	219	6	99	718	1,042	1.00

Baleen whales

In the Barents Sea and the Norwegian sea the main baleen whale species is the minke whale (*Balenoptera acutorostrata*). There are also humpback whales (*Megaptera novaeangliae*) and fin whales (*Balaenoptera physalus*) (Christensen *et al.*, 1992a).

*Minke whales (*Balenoptera acutorostrata*)*

Minke whales in the Barents Sea
Minke whales migrate into the model area and feed there between mid-April and mid-October (Bogstad *et al.*, 2000). Consumption data for minke whales is based on the consumption from 85,000 individuals (Schweder *et al.*, 1996) during an assumed 180 days feeding period (mid-April to mid-October) in the Barents Sea and in Norwegian coastal waters using data from 1992-1995 (Bogstad *et al.*, 2000). Total consumption was 1,817,000 tonnes. Average body weight of minke whales is 5,251 kg (Sigurjonsson and Vikingsson, 1997). The average biomass for the model area is the product of the abundance and individual weight divided by two, as this group only stays in the model area during the 6 month feeding period. This gives a Q/B of 8.14·year^{-1}, which we have used in our calculations.

Minke whales in the Norwegian Sea
The abundance is obtained from the difference between the total abundance in the Norwegian blocks of the North Atlantic Sighting Survey-95 and the Barents Sea and North Sea estimate (NAMMCO, 1998). The estimate for Norwegian blocks also includes the North Sea block (south of 62^{o}N). This gives an abundance estimate of 13,000 individuals for the Norwegian Sea.

Sigurjonsson and Vikingsson (1997) also calculated consumption for minke whales in Icelandic and adjacent waters. Assuming that baleen whales feed in Icelandic waters for four months each year, and that the daily energy intake during this period was 10 times the daily energy intake during the remaining eight months of the year, their population and consumption data give a Q/B of about 6.3·year^{-1}. It is not clear from their publication whether the consumption data refer to the feeding in Icelandic waters only. But if that is the case, and if one also compensates for the absence of minke whales from Icelandic waters for $^2/_3$ of the year, the Q/B ratio for that area could be set as high as 18.9·year^{-1}. This indicates that the consumption data should be considered as highly uncertain.

At present, data on prey size composition in minke whale stomachs are not available, but will be in the near future (Bogstad *et al.*, 2000). It was assumed that 70% of the consumed cod were from the age 4+ group. It is known that the majority of herring eaten are immature 1-5 years old (Lindstrøm *et al.*, 1999). It is also likely that minke whales feed on adult herring during their southward migrations from the Barents Sea (Folkow *et al.*, 2000). Note that minke whales are opportunistic feeders, and prey will vary significantly in space and time (see Nordøy *et al.*, 1995; Pauly *et al.*, 1998; Bogstad *et al.*, 2000). The diet for minke whales in the model area is summed from the data from the Barents Sea and from the assumed values from the Norwegian Sea.

*Humpback whales (*Megaptera novaeangliae*)*

It has been suggested that humpback whales stay in their northern feeding areas during most of the year (Ingebrigtsen, 1929). There are about 1,000 humpback whales in the Norwegian and the Barents Sea (Christensen *et al.*, 1992b). This species feeds on capelin in the Barents Sea usually from September to January/February and on krill for the rest of the year (Bogstad *et al.*, 2000). Average body weight is 32 tonnes based on Sigurjonsson and Vikingsson (1997). With a Q/B of 4·year^{-1}, this give a total consumption of 127,000 t·year^{-1}. According to Sigurjonsson and Vikingsson (1997), data from Canadian waters indicate a diet with 60% fish and 40% crustaceans (probably krill) (Mitchell, 1973, in Sigurjonsson and Vikingsson, 1997).

*Fin whales (*Balaenoptera physalus*)*

Data on distribution and stock structure do not suggest that the fin whales have a pattern of migration in and out of the model area similar to that of minke whales (Christensen *et al.*, 1992a). The abundance has been estimated to be about 3,000 individuals for the Norwegian and the Barents Sea (NAMMCO, 1998). It does appear that the area defined as 'Iceland' by NAMMCO (1998) overlaps with ICES area IIa (about 10%), and the abundance of fin whales in the area 'Iceland' was 9,867 in 1995. Krill has been reported to be the main food item for fin whales (Johnsgård, 1966). This species also feeds on fish, and in north Norway, capelin dominate the diet in early spring, while in summer crustaceans comprise most of the diet. Some herring is also consumed in summer. The fin whales disappear from the coastal waters in April, probably moving westwards into the Norwegian Sea. In

June/August, they again appear at the coast feeding on krill (Ingebrigtsen, 1929). In recent years it has been suggested that fin whales may be significant predators of herring in the Norwegian Sea (Misund *et al.*, 1997). Average body weight is 42 tonnes (Sigurjonsson and Vikingsson, 1997), giving a total biomass of 127,000 tonnes. With a Q/B of 4·year^{-1} (Bonner, 1993, pp. 47) the consumption is 507,000 t·year^{-1}. The fraction of the diet made up of fish (only 0.03, based on Icelandic data) used in this calculation may be too low and not reflect that they probably feed on herring in the Norwegian Sea.

Other baleen whales

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). Abundance estimates are not available, but numbers are less than for humpback and fin whales.

The baleen whales included in the model are the following three species: minke whale, humpback whale, and fin whale. Data for baleen whales from the model area are summarized in Table 6, and model input data are in Table 2. Diet composition data for baleen whales used in the model are given in Table 3, and are based on Bogstad *et al.* (2000) data from 1992-1995 and the data presented in Table 7. A total of 2,817 tonnes of baleen whales were caught in 1997, which represents 0.000904 t·km^{-2} for the model area (Gjert Dingsoer, University of Bergen, Norway).

Table 6. Summary data for baleen whales in the study area.

Species	Abundance	Body weight (kg)	Biomass (tonnes)	Q/B	Consumption (‘000 tonnes)
Minke whale[a)]	98,000	5,251	257,299	8.14	2,094
Humpback whale	1,000	31,782	31,782	4.00	127
Fin whale	3,000	42,279	126,837	4.00	507
Totals	117,000	-	415,918	6.56	2,728

a) Biomass for minke whale is (Abundance * Body weight)/ 2, as they only stay in the model area during the half year feeding period.

Table 7. Food composition (% weight) of baleen whales in Icelandic and adjacent waters. ‘MRI’ refers to data from Marine Research Institute, Iceland.

Species	Fish	Crustaceans	Source
Minke whale	59	41	Sigurjonsson and Galan (1991)
Humpback whale	60	40	Mitchell (1973)
Fin whales	3	97	MRI

Seals

*Harp seal (*Phoca groenlandica*)*

The harp seals in the model area are divided into two populations. One breeds in the White Sea (the ‘East Ice’), feeds along the ice edge in the Barents Sea, and occasionally migrates south to the Norwegian Coast. The other population breeds on the ice along the east coast of Greenland (the ‘West Ice’, partly outside the model area), and feeds in the Norwegian Sea. In years with low food abundance, individuals of this population may also migrate to the Norwegian coast.

Harp seal in the ‘East Ice’

Harp seal is the main species of seal in the Barents Sea (Bogstad *et al.*, 2000). At present, data on prey size composition in harp seal stomachs are not available (Bogstad *et al.*, 2000). Consumption is calculated on the basis of an abundance estimate of 2,223,000 individuals (Anon., 1999). Assuming an average body weight of 100 kg (pp. 97 in Haug *et al.*, 1998) this gives a Q/B of 15.7 and 15.16·year^{-1} for the periods with low and high capelin biomass, respectively (Bogstad *et al.*, 2000, data from 1990-1996). The prey item groups ‘Other fish’ (622,000 t) and ‘Other crustaceans’ (356,000 t) given by Bogstad *et al.* (2000) have been distributed amongst model groups based on working group opinion.

Harp seal in the 'West Ice'
In 1998 it was estimated that the abundance was 379,000 individuals (age 1+) and there was a pup production of 67,000 individuals (pp. 37 in Øien, 2000). This gives a biomass of 37,900 tonnes (assuming average body weight of 100 kg), and with a Q/B of 15·year^{-1} this gives a consumption of 569,000 t·year^{-1}. According to Haug *et al.* (1998), polar cod is an important prey during the summer. During the spring, amphipods and krill are important prey. Generally, there is little knowledge of the diet composition. It was assumed that the population takes half of its consumption (284,000 t) within the model area.

*Harbor seal (*Phoca vitulina*)*

This species is found in coastal areas, where it feeds on herring, cod, saithe, wolffish, flatfishes and sand eels. Abundance in the Norwegian coastal waters is between 2,500 and 6,680 animals (Øien, 2000). Estimates of average body weight are not available, but Markussen *et al.* (1989) reported an asymptotic weight of about 74.8 kg for females and 89.6 kg for males. Taking an average for both sexes and assuming that the average population body weight is 70% of the asymptotic weight (Bonner, 1994) gives an average body weight of 58 kg. Thus, population biomass is approximately 388 tonnes, and with a Q/B of 15·year^{-1} this gives a total consumption of 6,000 t·year^{-1}.

*Grey seal (*Halichoerus grypus*)*

Grey seals are found in coastal areas, and feed on herring, cod, saithe, wolffish, flatfishes and sand eels. However, they feed more on benthic fish than do harbor seals. Total abundance along the coast is about 4,413 animals (Øien, 2000). Average body weight is 134 kg based on 70% of the adult weight of the range (170-310 kg, males and 105-186 kg, females, given by Bonner, 1994). This gives a population biomass of 590 tonnes, and with a Q/B of 15·year^{-1} gives a consumption of 9,000 t·year^{-1}.

*Hooded seal (*Cystophora cristata*)*

Within the model area, the hooded seals breed on the ice east of Greenland (the 'West Ice') and feed in the Norwegian Sea. In 1998 the 'West Ice' abundance of age 1+ was 109,100 individuals and the pup production was 26,300 individuals (Øien, 2000). Average body weight is 262 kg based on 70% of the adult weight of the average range (350 kg females, and 400 kg males) as given by Bonner (1994) and Øien (2000). In areas with ice, polar cod is an important prey (Haug *et al.*, 1998). In the Norwegian Sea, squid (*Gonatus* spp.), redfish (*Sebastes* spp.), blue whiting and Greenland halibut are important prey (Øien, 2000). The biomass was calculated as 28,600 tonnes, and a with an assumed Q/B of 10·year^{-1} (somewhat lower than in harp seals) this gives a consumption of 286,000 t·year^{-1}. It is uncertain how much of the stock is distributed in the Norwegian Sea within the area of interest (ICES area IIa). It was assumed that half the total consumption (143,000 tonnes) was taken within the model area.

Other seals

Ringed seal (*Phoca hispida*), bearded seal (*Erignathus barbatus*) and walrus (*Odebenus rosmarus*) are also known to occur in this area (e.g., Bonner, 1994). Abundance estimates are not available, but numbers are thought to be less than for the species mentioned above.

Data for all species of seals are given in Table 8, and the final model input data is in Table 2. The diet composition for seals is given in Table 3, and was based on Table 9. For Harp seal in the Barents Sea the composition of the diet depends on the size of the capelin stock (Nilssen *et al.*, 2000). This model represents the year 1997, when the capelin stock was relatively low, and this is reflected in Table 3.

Table 8. Data summary for all species of seals occurring in the model area.

Species	Abundance	Body weight (kg)	Biomass (tonnes)	Q/B	Consumption ('000 tonnes)
Harp seals 'East Ice'	2,223,000	100	222,300	15.70	3,491
Harp seals 'West Ice'[a]	379,000	100	18,950	15.00	284
Harbor seals	2,500-6,684	58	388	15.00	6
Grey seals	4,413	134	591	15.00	9
Hooded seal	109,000	262	28,558	10.00	143
Total	2,722,097	-	270,787	14.52	3,933

[a]It is assumed that the harp seals in the West Ice stay in the model area for half the year – hence the mean biomass during the year is half the total biomass of the stock.

Table 9. Diet composition for seals in the Norwegian Sea and Barents Sea.

Prey	Harp seals 'East Ice'	Harp seals 'West Ice'	Harbor seals	Grey seals	Hooded seals	Total ('000 tonnes)	Fraction
Toothed whales						0	0.00
Baleen whales						0	0.00
Seals						0	0.00
Seabirds						0	0.00
Cod 4+	149			1.0		150	0.04
Cod juveniles	149			1.0		150	0.04
Haddock	47			1.0		48	0.01
Saithe	20		1.7	1.0		23	0.01
Other benth fish	50			4.9		55	0.01
Redfish	50				36	86	0.02
Blue whiting	50				36	86	0.02
Mackerel						0	0.00
Herring 4+						0	0.00
Herring juv	394		1.5			395	0.10
Polar cod	880	85	0.6			966	0.25
Capelin	55	28	1.7			85	0.02
Large pel fish	50					50	0.01
Small pel fish	150	28			14	193	0.05
Mesopel fish	178					178	0.05
Squid	59				57	116	0.03
Benthos	156					156	0.04
Prawns	200					200	0.05
Krill	550	57	0.3			607	0.15
Amphipods	304	85				389	0.10
Large zoopl						0	0.00
Small zoopl						0	0.00
Jellyfish						0	0.00
Seaweeds						0	0.00
Phytoplankton						0	0.00
Detritus						0	0.00
Totals	3,491	284	5.8	8.9	143	3,933	1.00

The catch of seals for 1997 was reported as 0.000261 $t \cdot km^{-2}$, which equates to 813 tons for the total model area (K. Kaschner, Marine Mammal Unit, Fisheries Centre, University of British Columbia, pers. comm.).

P/B values for marine mammal groups

Estimates of natural mortality for marine mammals are difficult to obtain. In the present model P/B values used for marine mammals were based on consensus expert opinion of total mortality (Z) estimates obtained from scientists in the Institute of Marine Research, Bergen. Future re-evaluations of the model input data should especially re-examine mortality rates for seals.

Sea birds

Seabirds (Barents Sea)

It is estimated that 5,400,000 pairs of seabirds are breeding in the Barents Sea (Anon., 2000a). Consumption in the Barents Sea (ICES area I and the eastern part of areas IIa and IIb) was estimated at 1,000,000 $t \cdot year^{-1}$, with approximately 480,000 tonnes of this being fish and the rest being invertebrates (Anon., 2000a).

The common guillemot (*Uria algae*) accounts for about 10% of the consumption, and this species eats mainly capelin. The Brünnich's guillemot (*Uria lomvia*) accounts for 61% of the fatty fish and 56% of the invertebrates consumed. This species has a much lower proportion of capelin in the diet than *Uria algae*. The total consumption of capelin by these two species has been assumed to be in the order of 200,000 to 300,000 t·year^{-1} (Gjøsæter, 1998). Polar cod and pelagic crustaceans are also important prey species for several species of birds (Mehlum and Gabrielsen, 1995). The Q/B ratio was calculated so as to reflect that some birds were present only part of the year in the Barents Sea.

Seabirds (Norwegian coast / Norwegian Sea)

Puffins (*Fratercula arctica*) are numerous, and breed along the Norwegian coast. They are known to feed on small pelagic fish (e.g., herring and sand eel) and 0-group pelagic gadoids. The total number of puffins and other sea birds (except for cormorants and shags) breeding along the Norwegian coast are estimated to be about 10,000,000 individuals (Anon., 2000a). The consumption from cormorants and shags are included in the estimate for consumption both for the Barents Sea and for the Norwegian Sea.

The diet composition is uncertain and has been estimated for the Barents Sea as well as for the Norwegian coast and the Norwegian Sea. However, we have tried to use the information given in Anon. (2000a). The ICES report points out that the consumption estimate does not include "the very large but unknown number of fulmars that are spread over most of the area throughout the year". In addition, an unknown but similarly very large, number of little auks from the Barents Sea spend the winter in the Norwegian Sea. As well, the estimate "does not include the large numbers of seabirds which breed on Shetland and Faroe Islands, many of which probably also forage in the Norwegian Sea a large part of the year" (Anon., 2000a). This means that the estimates for the Norwegian Sea are most likely underestimated.

The biological data for seabirds are summarized in Table 10, and the model input data is found in Table 2. The diet composition for Barents Sea and Norwegian Sea are in Tables 11 and 12, respectively, while the model diet compositions are in Table 3.

Table 11. Diet composition and consumption data for seabirds in the Barents Sea. Source: Anon. (2000).

				Consumption (t·year^{-1})			
Species	**Body weight (g)**	**Abundance**	**Biomass (tonnes)**	**Fat fish**	**Other fish**	**Invertebrates**	**Sum**
Northern fulmar	820	1,650,000	1,353	0	41,518	107,638	149,156
Northern gannet	3,204	4,950	16	865	0	0	865
Great cormorant	3,250	13,000	42	896	1,344	299	2,539
Shag	1,836	15,600	29	882	1,058	0	1,940
Great skua	1,400	780	1	0	7	0	7
Arctic skua	350	15,600	5	135	0	0	135
Mew gull	380	52,000	20	0	499	740	1,239
Herring gull	1,000	260,000	260	0	11,999	8,888	20,887
Lesser black-backed gull	800	1,300	1	0	22	0	22
Great black-backed gull	1,680	65,000	109	3,103	2,979	0	6,082
Glacous gull	1,800	31,200	56	0	326	362	688
Black-legged kittiwake	409	2,210,000	904	73,130	0	10,834	83,964
Common tern	125	2,600	0	0	26	0	26
Arctic tern	110	130,000	14	0	589	654	1,243
Razorbill	711	66,000	47	3,465	0	0	3,465
Common guillemot	1,028	396,000	407	33,354	0	0	33,354
Brunnich guillemot	998	5,940,000	5,928	293,658	0	261,029	554,687
Black guillemot	410	130,000	53	2,727	0	5,453	8,180
Atlantic puffin	480	1,650,000	792	63,757	0	0	63,757
Little auk	160	4,290,000	686	5,838	0	70,053	75,891
Total	-	16,924,030	10,725	481,810	60,367	465,950	1,008,127

Table 10. Data summary for seabirds in the Norwegian Sea and Barents Sea.

Area	Abundance	Body weight (kg)	Biomass (tonnes)	Q/B	Consumption ('000 tonnes)
Barents Sea	16,924,030	0.63	10,725	93.99	1,008
Norwegian Sea	10,774,015	0.50	5,390	109.83	592
Totals	27,698,045	-	16,115	99.29	1,600

Table 12. Diet composition and consumption data for seabirds in the Norwegian Sea. Source ICES (2000).

				Consumption (tonnes)			
Species	**Body weight (g)**	**Abundance**	**Biomass (tonnes)**	**Fat fish**	**Other fish**	**Invertebrates**	**Sum**
Northern fulmar (residents)	810	24,750	20	0	618	1,601	2,219
Northern fulmar (visitors)	810	2,000,000	1,620	0	47,557	123,295	170,852
European storm petrel	24	16,500	0	0	0	91	91
Leach's storm petrel	42	1,650	0	0	0	14	14
Northern gannet	3,204	7,425	24	1,297	0	0	1,297
Great cormorant	3,250	54,000	176	10,326	0	3,442	13,768
Shag	1,836	45,000	83	1,056	5,915	939	7,910
Great skua	1,400	90	0	0	1	0	1
Arctic skua	350	18,000	6	148	0	0	148
Common gull	380	270,000	103	0	2,850	4,222	7,072
Herring gull	1,000	45,000	45	0	3,206	2,375	5,581
Lesser black-backed gull	800	6,300	5	0	102	0	102
Great black-backed gull	1,680	117,000	197	8,570	8,227	0	16,797
Black-legged kittiwake	409	585,000	239	0	19,873	5,520	25,393
Common tern	125	10,800	1	76	0	11	87
Arctic tern	110	90,000	10	0	769	0	769
Razorbill	711	49,500	35	2,870	0	0	2,870
Common guillemot	1,028	16,500	17	1,385	0	0	1,385
Black guillemot	410	54,000	22	1,195	1,753	0	2,948
Atlantic puffin	460	5,362,500	2,467	36,376	266,399	0	302,775
Little auk	160	2,000,000	320	0	8,443	21,890	30,333
Total	-	10,774,015	5,390	63,299	365,713	163,400	592,412

Cod 4+ (*Gadus morhua*)

Within the model area there is one large stock of cod, the North East Arctic Cod (also called Barents Sea cod). In addition there is a smaller stock, the Norwegian Coastal Cod, and possibly other and still smaller stocks.

The North East Arctic Cod spawns along the Norwegian Coast from 62° N and northwards, with the main spawning at Lofoten - Vesterålen (67°-69° N). Eggs and larvae drift into the Barents Sea, and the juveniles feed there until they mature at an age of 6-7 years. Maturing cod migrate to the Norwegian coast to spawn, and back to the Barents Sea after spawning. Recruitment to the fishery starts at age 3.

The Norwegian Coastal Cod (which may consists of several stocks) has only in recent years been subject to research, and little is known about stock sizes as yet. It is also difficult to differentiate the catches of this stock from those of North East Arctic Cod - although landings in some statistical areas in specific months are recorded as being Norwegian Coastal Cod. In the present model, all catches of cod are treated as one unit.

As there is a considerable amount of cannibalism by large cod upon smaller cod, this species is split in two groups for modeling: Cod 4+ years and Cod juveniles (1-3 years).

The ICES Arctic Fisheries Working Group (Anon., 2001a) gives a time series of biomass by age for ages 3-13+, calculated by VPA, which includes the years 1950-1997. The biomass of Cod 4+ for 1997 has been calculated as the sum of the biomasses for ages 4-13+ in 1997, and divided by the model area (3,116,000 km²) gives a biomass of 0.448 t·km⁻² (Table 2). The biomass for 1998 has been calculated in the same way to 0.344 t·km⁻², and the biomass accumulation is 0.104 t·km⁻² (Table 2).

Bogstad *et al.* (2000) give biomass and consumption for cod in the Barents Sea for the years 1984-1989. The Q/B ratios calculated from these data vary from 3.118 to 1.644·year⁻¹, with a mean of 2.433·year⁻¹. These figures do not include consumption by mature cod in the period when they are outside the Barents Sea, which, according to Bogstad *et al.*, may be significant. The Q/B ratio used (Table 2) should therefore be considered a minimum value.

Bogstad *et al.* (2000) give the diet composition for the years 1984-1998 for cod in the Barents Sea, with averages for the years 1991-1993 when the capelin stock was high, and for the years 1994-1996 when the capelin stock was low. The consumption data are summarized in Table 13. During 1997, the capelin stock was low (Anon, 2000b; Bogstad *et al.*, 2000), and the average diet for 1994-1996 has been used as a basis for the diet composition for Cod 4+ in the model (Table 3).

The ICES Arctic Fisheries Working Group (Anon, 2001a) gives a time series of biomass for ages 3-13+ calculated by VPA, as well as catch in numbers by age and weight in catch by age, for a period which includes the years 1950-1997. Using the data from Anon. (2001a), biomass for each of the years 1950-1997 has been calculated as the sum of the biomasses for ages 4-13+.

Catch for each age for the years 1950-1997 has been calculated as the product of catch in numbers by age and weight in catch for that age, whereupon the catches for ages 4-13+ were summed to give catch for that year.

Table 13. Diet composition of cod 4+ for the Barents Sea.

	High capelin stock years Average for 1991-1993		Low capelin stock Average for 1994-1996	
Prey	**Fraction**	**‘000 tonnes**	**Fraction**	**‘000 tonnes**
Amphipods	0.027	141	0.163	732
Krill	0.061	318	0.180	808
Shrimp	0.056	294	0.093	416
Capelin	0.538	2,805	0.171	769
Herring	0.032	168	0.023	104
Polar cod	0.025	129	0.072	322
Cod	0.023	122	0.088	393
Haddock	0.013	66	0.018	79
Redfish	0.038	199	0.028	124
Greenland halibut	0.000	10	0.000	0
Others	0.185	967	0.165	742
Total	-	5,219	-	4,491

Cod juveniles (1-3 years)

According to the ICES Arctic Fisheries Working Group (Anon., 2001a), biomass for 3 year old cod in 1997 was 146,245 tonnes, corresponding to 0.047 t·km^{-2}. Biomass for 1 and 2 year old cod is not known. Mortality rates for juvenile cod are uncertain, and back-calculation from 3 years to younger ages would also be uncertain. We therefore let Ecopath calculate the biomass, using an ecotrophic efficiency of 0.9 (Table 2).

For 1997, the Working Group report (Anon., 2001a) gives M=0.5·year^{-1} and M=0.3·year^{-1}, as well as F=0.02 and F=0.2 for 3 and 4 year old cod, respectively. Based on this, we estimated a production/biomass ratio of 1.0·year^{-1} for juvenile cod (Table 2). The Q/B ratio was also estimated at 3.5·year^{-1} (Table 2). The diet composition was based on Bogstad *et al.* (2000) and on the expert opinions of model working group participants.

Haddock (*Melanogrammus aeglefinus*)

Haddock is distributed along the coast of Norway from 62° N northwards, and into the Barents Sea. They mature at an age of 4-7 years, and the spawning area is along the continental slope from approximately 66° N to approx. 74° N (Torsvik *et al.*, 1995).

Biomass and catch for haddock (3+ years) are given in Anon. (2001a), who presents time series back to 1950. Bogstad *et al.* (2000) give stock size for 1+ haddock for the years 1984-1998, based on the VPA in Anon. (2001a), and M = 0.2 per year. According to their calculations, the biomass of 1+ haddock in 1997 was 416,000 tonnes, corresponding to 0.134 t·km^{-2} (Table 2). In 1998 , the biomass of 1+ haddock was 293,000 tonnes, corresponding to 0.094 t·km^{-2}. Therefore, biomass accumulation of haddock was 0.036 t·km^{-2} (Table 2).

Fishing pressure on haddock is lower than for cod (Anon, 2001a), but the group 'haddock' includes all 1+ fish, while cod was split in juveniles and 4+ fish. Estimating the production/biomass ratio for haddock as 1.0 year^{-1} appears reasonable (Table 2). It is likely that the consumption/biomass ratio for cod and haddock of the same size is similar, and a value for haddock that is in between those for Cod juveniles (3.500) and Cod 4+ (2.500) seems reasonable. The value was estimated to 2.8·year^{-1} (Table 2).

Diet composition is estimated to be mostly benthos organisms, and some large zooplankton (Table 3). Jiang and Jørgensen (1996) described the food composition of haddock in the Barents Sea on a quarterly basis during the years 1984-1991. Crustaceans and echinoderms were important food items, followed in importance by fish, molluscs and annelids. There was considerable variation between years and seasons, and the authors warned that the precision of data from this kind of investigations is low.

The ICES Arctic Fisheries Working Group (Anon., 2001a) ran a VPA for ages 3-13+ for the years 1950-1999. The stock summary table in Anon. (2001a) gives total biomass and landings for each of the years 1950-1999, and we have used these data as the basis for our time series for biomass and catch. We have made no attempt to estimate data for 1-3 year old haddock.

Saithe (*Pollachius virens*)

Saithe is found along the Norwegian coast and on the continental shelf from approximately 62° N to the border with Russia. Spawning takes place on the shelf from 62° N to 69° N (Torsvik *et al.*, 1995).

Biomass and catch for saithe 2+ back to 1960 were taken from the ICES Arctic Fisheries Working Group report (Anon., 2001a). Data for age 1 saithe are not given. Biomass of the stock in 1997 was 564,750 tonnes, corresponding to 0.181 t·km^{-2} (Table 2). Biomass in 1998 was 612,836 tonnes, corresponding to 0.197 t·km^{-2}. The biomass accumulation was therefore 0.016 t·km^{-2} (Table 2).

Production/biomass ratio and consumption/biomass ratio were estimated as 1.0·year^{-1} and 5.0·year^{-1}, respectively (Table 2). Diet composition was based on Robb and Hislop (1980) and Robb (1981), with pelagic fish and zooplankton as the most important prey (Table 3).

The ICES Arctic Fisheries Working Group (Anon., 2001a) ran a VPA for ages 2-11+ for the years 1960-1999. The stock summary table calculated by the VPA program (Anon., 2001a) gives total biomass and landings for each of the years 1960-1999, and we have used these data as the basis for our time series for the years 1960-1997. Fishing mortality for those years has been calculated as the ratio catch/biomass.

The ICES Fisheries Statistics database gives catches for the years 1950-1959, and these catches have been used to supplement the catches given by Anon. (2001a), in order to extend the time series for catches back to 1950. Noting that the ratio of catch to biomass (C/B) for the years 1960-69, while varying from 0.10 to 0.22, has no clear trend, we have calculated the mean C/B for these years to be 0.164 year^{-1}. We then used this value to represent the C/B ratio for the years 1950-1959. Having thus established a C/B ratio for the 1950s, we have calculated biomass densities for those years using equation (1):

$$B = \frac{C}{(C/B)} \qquad \ldots 1)$$

We have made no attempt to estimate time series data for 1-2 years old saithe.

Other benthic fish

The group 'Other benthic fish' has been used to represent all benthic fish not already included in one of the other groups. Species of major fisheries importance in this group include: Atlantic halibut (*Hippoglossus hippoglossus*), Greenland halibut (*Reinhardtius hippoglossoides*), European plaice (*Pleuronectes platessus*), long rough dab (*Hippoglossoides platessoides*), monkfish (*Lophius piscatorius*), wolffishes (*Anarhichas* spp.), pollack (*Pollachius pollachius*), whiting (*Merlangius merlangus*), ling (*Molva molva*), blue ling (*M. dypterygia*), cusk (*Brosme brosme*) and skates (*Raja* spp.). Apart from catch statistics, parameters for this group can only be assumed, which is reflected in the input to the model (Table 2). The biomass density used (0.700 t·km^{-2}) is fairly high, and the diet composition is spread over a wide range of groups (Table 3), which is reasonable when the predator group itself is so diverse.

A time series for catch of this group was prepared for the years 1973-1997 from the ICES Fisheries Statistics database. We have tried to include in the catch statistics of this group all species of benthic fish which are important in the fishery and which are not already included in one of the other groups.

Redfish (*Sebastes* spp.)

There are three species of redfish in the model area, *Sebastes marinus*, *S. mentella* and *S. viviparus*. There are some differences in the distribution area and depth preferences of these species, but in general 'redfish' are found on the continental shelf (also to some extent in the Barents Sea), along the continental slope, and westwards from the slope as pelagics (Torsvik *et al.*, 1995).

Sebastes marinus and *S. mentella* are the main species targeted by the fishery. The last analytical assessment of *S. mentella* in the model area was done by the ICES Arctic Fisheries Working Group in 1997 (Anon., 1998). They calculated that the biomass of age 6+ *S. mentella* was 233,938 tonnes in 1996. There is no analytical assessment available for the two other species, and it is assumed that the total biomass of all three species of redfish, including the younger ages, is 800,000 tonnes, corresponding to 0.257 t·km^{-2} (Table 2). Production/biomass and consumption/biomass ratios (Table 2) were taken from the Icelandic model (Mendy and Buchary *et al.*, this volume).

The diet composition used in the model was estimated (Table 3), and consists mainly of large and small zooplankton, krill and benthos (see also Hureau and Litvinenko, 1986).

The ICES Arctic Fisheries Working Group in 1997 (Anon., 1998) carried out an analytical assessment for *Sebastes mentella*, and the stock summary table calculated by the VPA program (for ages 1-19+) gives a time series of stock biomass and landings for the years 1965-1996. However, there are no corresponding data for the other redfish species, and a time series of biomass for the complete group 'redfish' is therefore not available. However, a time series of catch data for 'redfish' for the years 1950-1997 is available from the ICES Fisheries Statistics database and has been used.

Blue Whiting (*Micromesistius poutassou*)

There is possibly more than one stock of Blue Whiting in the model area. However, the ICES Northern Pelagic and Blue Whiting Fisheries Working Group treats all Blue Whiting in the North East Atlantic north of Gibraltar as one stock (Anon., 2000b). This stock has its main spawning area west of the British Isles, but there seems to be at least one smaller spawning area within the model area, west of the Norwegian continental slope at about 67° N. At least part of the juveniles grow up in the North Sea, and a large part of the stock feeds in the Norwegian Sea during summer, but migrates to the south of the model area for spawning.

The ICES Northern Pelagic and Blue Whiting Fisheries Working Group (Anon., 2000b) calculated the 1997 stock biomass (0-10+ years) of Blue Whiting as 5,763,250 tonnes, corresponding to 1.850 $t \cdot km^{-2}$. Only 2+ year fish will be in the Norwegian Sea, and the spawning stock will be out of the model area during the migration to and from the spawning area. To compensate for this, it is assumed that 50% of the biomass of blue whiting is found in the model area, giving a value of 0.925 $t \cdot km^{-2}$ for the biomass density (Table 2). The stock biomass in 1998 was calculated to 5,889,000 tonnes, and assuming that 50% of the biomass is found in the model area, this corresponds to 0.945 $t \cdot km^{-2}$ in 1998. Hence, a biomass accumulation of 0.020 $t \cdot km^{-2}$ was estimated (Table 2). Production/biomass and consumption/biomass ratios were based on working group opinion (Table 2).

Timokhina (1974) presented approximate diet composition for blue whiting, showing that the main food items are euphausids and copepods, with a small proportion of amphipods and chaetognaths. This data formed the basis for the model diet composition for this species (Table 3).

The ICES Northern Pelagic and Blue Whiting Fisheries Working Group (Anon., 2000b) has a Stock Summary table for blue whiting that gives stock biomass for the years 1981-1999. This table has been used as a basis for the time series of biomass density for those years, assuming that 50% of the biomass is found within the model area. Most of the catches of blue whiting are taken outside the model area, west of the British Isles (spawning fish) or in the North Sea (juveniles). The time series of catches for the years 1950-1979 used here comes from the ICES Fisheries Statistics database and only includes catches within the model area.

Mackerel (*Scomber scombrus*)

Mackerel are common in the model area from the south and into the western part of the Barents Sea, and comes from the western mackerel stock which spawns west of the Ireland. Part of the stock migrates into the Norwegian Sea during summer to feed, but moves to the south of the model area for spawning. In the model, the main food items are zooplankton, krill and pelagic fish (Table 3).

The ICES Working Group on the Assessment of Mackerel, Horse Mackerel, Sardine and Anchovy (Anon., 2001b) assessed the stock of the North East Atlantic Mackerel stocks (ages 0-12+) for the years 1984-1998. The total biomass in 1997 was calculated as 4,474,264 tonnes, corresponding to 1.436 $t \cdot km^{-2}$. However, mackerel are found within the model area only for part of the year, and then it is only part of the stock that feeds in the area. It is assumed that 25% of the stock feeds in the Norwegian Sea during the summer season (6 months). Consequently, 12.5% of the biomass (0.180 $t \cdot km^{-2}$, Table 2) was allocated to the model area. The total biomass in 1998 was 4,732,194 tonnes, and allocating 12.5% of the biomass to the model area gives 0.189 $t \cdot km^{-2}$. Hence, a biomass accumulation of 0.009 $t \cdot km^{-2}$ was estimated (Table 2).

The ICES Working Group on the Assessment of Mackerel, Horse Mackerel, Sardine and Anchovy (Anon., 2001b) has a Stock Summary table for mackerel that gives biomasses for the years 1981-1997. This table has been used as a basis to calculate a time series of biomass density, assuming that 12.5% of the biomass is found within the model area. Most of the catches of mackerel are taken outside the model area. The time series of catch data used here is based on the ICES Fisheries Statistics database and only includes catches within the model area.

Large pelagic fish

The pelagic species that are not specifically named were split into two groups, smaller and larger than approximately 50 cm, in order to make it easier to estimate the diet composition. The species of large pelagics of major fisheries interest include: porbeagle (*Lamna nasus*), basking shark (*Cetorhinus maximus*), Greenland shark (*Somniosus microcephalus*), spiny dogfish (*Squalus acanthius*), Northern bluefin tuna (*Thunnus thunnus*), hake (*Merluccius merluccius*) and Atlantic salmon (*Salmo salar*).

We have let the model calculate the biomass of the group of large pelagic fish, using an ecotrophic efficiency of 0.950 (Table 2). Consumption/biomass has been set at $2.500 \cdot year^{-1}$ and a total mortality rate of $0.5 \cdot year^{-1}$ was assumed (Table 2). The food items for this group has been estimated through expert opinion during the workshop, and covers a large number of items, from fish like mackerel and blue whiting to zooplankton (Table 3).

A time series for catch of this group was prepared for the years 1973-1997 from the ICES Fisheries Statistics database. We have included all species of large pelagic fish (larger than approximately 50 cm) which are important in the fishery and which are not already included in one of the other groups.

Small pelagic fish

This group consists of pelagic fishes smaller than 50 cm. Species in this group that are of commercial importance include: Atlantic eel (*Anguilla anguilla*), sprat (*Sprattus sprattus*), greater argentine (*Argentina silus*), Norway pout (*Trisopterus esmarckii*), horse mackerel (*Trachurus trachurus*) and lumpsucker (*Cyclopterus lumpus*).

We have let the model calculate the biomass of small pelagic fish, using an ecotrophic efficiency of 0.950 (Table 2). Consumption/biomass has been set at 5.000 and production/biomass to 1.500 (Table 2).

The diet is assumed to be krill, amphipods and other zooplankton (Table 3).

A time series for catch of this group was prepared for the years 1973-1997 from the ICES Fisheries Statistics database. Included are all species of small pelagic fish (smaller than approximately 50 cm) which are important in the fishery and which are not already included in one of the other groups.

Herring 4+ (*Clupea harengus*)

During their first 3 years of life, young herring of the Norwegian Spring Spawning Herring stock feed in the Barents Sea and in Norwegian fjords (Devold, 1963; Dragesund *et al.*, 1980). In the summer of their third year they migrate out of the Barents Sea and into the Norwegian Sea. These immature herring feed mostly in the eastern part of the Norwegian Sea on or near the continental shelf, while older and larger herring tend to feed further west (Anon., 1995, 1996; Vilhjalmsson *et al.*, 1997; Holst *et al.*, 1998, 1999). Most of the herring mature as 5 years old fish, and they spawn in February-April on the shelf along the Norwegian coast, from Lindesnes (58°N, 7°E) in the south to Vesterålen (69°N, 15°E) in the north (e. g. Slotte and Dommasnes, 1998). After spawning, adults migrate into the Norwegian Sea and feed from April to September (Anon., 1995, 1996; Vilhjalmsson *et al.*, 1997; Holst *et al.*, 1998). The exception to this pattern occurred from 1970-1990 when the stock was very small, and fed along the Norwegian coast (Anon., 1979, 1982, 1986, 1991; Dragesund *et al.*, 1997). From October until the spawning migration starts in January the herring stay in deep water. In the period 1950-1969 they over-wintered in the Norwegian Sea. During the years from 1970 until the late 1980s the stock was split in two components which over-wintered in western Norway and in Lofoten, respectively. Since 1987 the herring has over-wintered in the Vestfjord fjord system (North of Lofoten) (Dommasnes *et al.*, 1994).

As the young herring ('juveniles' 1-3 years old) are found in a different area from the older ones (4 years and older), the herring has been split into two groups in the model.

Biomass and catch data for Norwegian Spring Spawning herring for ages 0-15+ back to 1950 were taken from the VPA tables in the annual reports from the ICES Northern Pelagic and Blue Whiting Fisheries Working Group (Anon., 2000b). Based on data in this Working Group report, the biomass of 4-16+ herring in 1997 was 10,161,650 tonnes, corresponding to 3.261 $t \cdot km^{-2}$ (Table 2). By 1998 the biomass of 4-16+ herring was calculated to 8,820,590 tonnes, corresponding to 2.831 $t \cdot km^{-2}$. Thus, biomass accumulation during 1997 was –0.430 $t \cdot km^{-2}$ (Table 2).

Fishing mortality for 5-16+ herring is given as 0.23 and the natural mortality as 0.15, giving a total instantaneous mortality of $0.38 \cdot year^{-1}$ (Anon., 2000b). If this is assumed to be valid also for 4 years old herring, this gives a production/biomass ratio of $0.38 \cdot year^{-1}$ for the part of the stock that is in the Norwegian Sea (Table 2).

According to Palomares and Pauly (1989) the following formula can be utilized to estimate the consumption/biomass ratio:

$$Q/B = 3.06 * W_{\infty}^{-0.2018} * T_c^{0.6121} * A_r^{0.5156} * 3.53^{Hd} \qquad \ldots 2)$$

where:
W_{∞} = the asymptotic weight (in g) as defined by the von Bertalanffy equation;
T_c = the mean habitat temperature in °C;
A_r = the aspect ratio for the caudal fin (see Pauly, 1989);
Hd = the food type (0 for carnivores and 1 for herbivores and detritivores).

Analysis of age-length data at the Institute of Marine Research (A. Dommasnes, unpublished data) gives L_{∞} = 36.7 cm. The corresponding weight is approximately 330 g (Slotte, 1998). The habitat temperature varies from year to year, particularly in the feeding areas (Anon., 1995, 1996; Vilhjalmsson *et al.*, 1997; Holst *et al.*, 1998, 1999), but an acceptable average is 6.0° C. Pauly (1989) gives a value of A_r = 1.9 for herring from Georges Bank and Scotland. That value is also used here.

Pauly *et al.* (1990) give an alternative formula for calculating the consumption/biomass ratio:

$$Q/B = 10^{6.37} * 0.0313^{Tk} * W_\infty^{-0.168} x * 1.38^{Pf} * 1.89Hd \quad ....3)$$

where:
Tk = an expression for mean annual temperature, Tk = 1000 / (temperature +273.1);
Pf = 1 for apex or pelagic predators and/or zooplankton feeders.

Formulas (2) and (3) give consumption/biomass ratios of 3.96 and 4.97 respectively. The mean of these, 4.47, is used in the present model (Table 2). It should be noted that according to Pavshtiks and Timokhina (1972) one tonne of herring consumes, on average, 6-8 tonnes of plankton per year. The value used for Q/B in the model may therefore be rather low.

Diet composition for herring in the Norwegian Sea has been investigated by Dalpadado *et al.* (2000) and is summarized in Table 14. Krill and copepods were dominant food items, amphipods were also important in the autumn, and the stomach samples also contained some other zooplankton and some fish larvae (Table 3).

The ICES Northern Pelagic and Blue Whiting Fisheries Working Group (Anon., 2000b) gives a time series of biomass for ages 0-16+ calculated by VPA, as well as catch in numbers by age and weight in catch by age, for the years 1950-1999. Using the data from Anon. (2000b), biomass for each of the years 1950-1997 has been calculated as the sum of the biomasses for ages 4-16+. Catch for each age has been calculated as the product of catch in numbers by age and weight in catch for that age, whereupon the catches for ages 4-16+ were summed to give catch for that year. Fishing mortality time series has been calculated as the ratio catch/biomass.

Herring juveniles

Herring juveniles are 1-3 years old herring, living mainly in the Barents Sea.

The VPA tables in the annual reports from the ICES Northern Pelagic and Blue Whiting Fisheries Working Group (ICES, 2000b) give biomass for 1-3 years old herring of 979,560 tonnes, corresponding to 0.275 t·km^{-2}. By 1998 the corresponding value was 973,570 tonnes, corresponding to 0.275 t·km^{-2}, and the biomass accumulation during 1997 was –0.002 t·km^{-2}. Upon balancing the model, however, it was noted that a biomass of 0.275 was too low to satisfy the demand for herring juveniles as prey. Thus, Ecopath estimated a biomass of 0.323 t·km^{-2} using an ecotrophic efficiency of 0.950 (Table 2).

A production/biomass ratio of 0.8·year^{-1} was assumed based on expert opinion (Table 2). The ICES Working Group report uses M=0.9·year^{-1} for ages 0-2, and M=0.15·year^{-1} for older ages (Anon., 2000b). The consumption/biomass ratio was set at 4.470·year^{-1}, as for the older herring (Table 2).

An investigation by Huse and Toresen (1996) on the feeding habits of herring and capelin in the Barents Sea in 1992 and 1993 showed that copepods and krill were the most important prey items, accounting for over 80% of the diet. The diet composition used in the model is given in Table 3.

Using VPA data Anon. (2000b), biomasses for the years 1950-1997 have been calculated as the sum of the biomasses for ages 1-3. Catch for each age has been calculated as the sum of the product of catch in numbers by age and weight in catch for that age. Fishing mortality time series has been calculated as the ratio catch/biomass.

Table 14. Diet fraction for herring in the Norwegian Sea, based on Dalpadado *et al.* (2000).

Fish larvae	Copepods	Amphipods	Krill	Other zooplankton
0.1	0.4	0.05	0.4	0.05

Polar cod (*Boreogadus saida*)

Polar cod is an important stock in the Barents Sea, but is also found to a smaller extent in the northern and western part of the Norwegian Sea. Only the stock in the Barents Sea is taken into account in the model.

An acoustic estimate in the Barents Sea in September-October 1997 gave a total stock biomass of 400,700 tonnes (Anon., 2000), corresponding to 0.129 t·km^{-2} for the whole model area. Upon balancing the model, the initial biomass estimate based on the acoustic survey was too low to sustain the demands for polar cod as prey. Thus, we let the model calculate the biomass density, using an ecotrophic efficiency of 0.950. The biomass calculated by the model was 0.4727 t·km^{-2} (Table 2). Production/biomass ratio and consumption/biomass ratio have been estimated based on expert opinion during the workshop (Table 2).

Ajiad and Gjøsæter (1990) showed that, in the north-eastern part of the Barents Sea, amphipods made up 89% of the diet of polar cod. In the central part amphipods and krill were most important, and in the south-eastern part of the Barents Sea copepods, amphipods and krill were most important. In addition, prawns and fish larvae were taken. This information has been used to specify the diet in the model (Table 3).

Anon. (2000) gives a time series of acoustic estimates of the biomass of polar cod in the Barents Sea for the years 1986-2000, which has been used here. The time series for catch of this group comes from the ICES Fisheries Statistics database.

Capelin (*Mallotus villosus*)

There are two capelin stocks in the model area: The Iceland-East Greenland-Jan Mayen stock and the Barents Sea stock.

The Iceland-East Greenland-Jan Mayen stock spawns along the south east and west coasts of Iceland and feeds in the area between Iceland, East Greenland and Jan Mayen. This stock will migrate into the model area in significant numbers only in some years for a brief period in summer/autumn (the last record in the 1980s). Data from this stock were not included in the model.

The Barents Sea stock spawns along the coasts of northern Norway, and sometimes also along the coasts of northern Russia. This stock feeds in the Barents Sea.

Estimates of biomass (ages 1-5+) for the years 1972-1999, and landings for the years 1965-1999 were obtained from the ICES Northern Pelagic and Blue Whiting Fisheries Working Group (Anon., 2000b). The biomass for capelin given by the Working Group are based on acoustic estimates in September-October, and the biomass estimated for 1997 was 866,000 tonnes, corresponding to a biomass density of 0.276 t·km^{-2}. The model could not be balanced with the estimate of biomass for 1997, indicating that it was too low. We therefore let the model calculate the biomass, using an ecotrophic efficiency of 0.950. The biomass density calculated by the model was 1.132 t·km^{-2} (Table 2). Production/biomass ratio and consumption/biomass ratio have been estimated by the working group (Table 2).

The investigation by Huse and Toresen (1996) on the feeding habits of herring and capelin in the Barents Sea in 1992 and 1993 showed that capelin feed mainly on copepods and krill, which accounts for nearly 80% of their diet. An approximate representation of the findings of Huse and Toresen (1996) was used for the present model (Table 3).

The report of the ICES Northern Pelagic and Blue Whiting Fisheries Working Group (Anon., 2000b) gives a time series of acoustic estimates of the biomass of Barents Sea capelin for the years 1990-1999. The report of the ICES Atlanto-Scandian Herring, Capelin and Blue Whiting Assessment Working Group in 1995 (Anon., 1995b) extends this time series back to 1973. The time series for biomass for these two working groups is the basis for our time series of biomass for the years 1973-1997.

Anon., (2000b) gives catches of Barents Sea capelin for the years 1965-1999. The ICES Fisheries Statistics database is used to extend the catches back to 1958. The catches before 1958, if any, were very small, and we have set those catches to zero.

Mesopelagic fish

The mesopelagic fish in this area are mainly Müller's pearlside (*Maurolicus muelleri*) and lanternfish (*Benthosema glaciale* and *Notoscopelus* spp.). Dalpadado *et al.* (1998) reported on densities of *Benthosema glaciale*, *Maurolicus mülleri* and *Notolepis rissoi* in different water-masses in the Norwegian Sea based on cruises during the summers of 1993-1995. *Benthosema glaciale* occurred in lowest densities in arctic water, and highest in Atlantic waters. *Maurolicus mülleri* and *Notolepis rissoi* were mainly restricted to coastal and Atlantic waters. The total biomass for the three species was estimated as 3.85 million tonnes wet weight. The area investigated was 1.7 million km^2, giving a mean biomass of 2.26 $t \cdot km^{-2}$. A lower biomass density of 1.840 $t \cdot km^{-2}$ was initially used for this model, considering that the density of mesopelagic fish in the Barents Sea is low. However, a biomass of 1.840 $t \cdot km^{-2}$ was not sufficient to sustain the demand from predation, and instead we let the program calculate the biomass density, using an ecotrophic efficiency of 0.950. The model estimated biomass of 2.079 $t \cdot km^{-2}$ (Table 2) was close to the estimate based on Dalpadado *et al.* (1998).

The values used for production/biomass and consumption/biomass ratio have been estimated during the workshop (Table 2).

Mesopelagic fish appear to feed mainly on copepods and krill (Gjøsæter, 1973, 1981a,b; Kawaguchi and Mauchline, 1982; Sameoto, 1988, 1989; Giske *et al.*, in Skjoldal *et al.*, 1993). In the model, predation by mesopelagic fish was distributed evenly between krill, amphipods, and large and small zooplankton, and a small fraction was allocated to cannibalism (Table 3).

Squid

The boreo-Atlantic gonate squid *Gonatus fabricii* is one of the most abundant nektonic organisms in the subarctic North Atlantic and Arctic Oceans (Nesis, 1971; Kristensen, 1984). In the pelagic and mesopelagic phase juvenile *Gonatus* (0-group) are very active. The subadult squid migrate to larger depths where the males and immature females remain active, while maturing, mature and spent females reduce their activity and cease feeding. Bjørke and Gjøsæter (1998) have made rough calculations of biomass, production and predation on *Gonatus fabricii* in the Norwegian Sea. They assumed a life cycle of 24 months, meaning that two cohorts are present at any time. Using their figure 3, it is possible to calculate that the mean biomass present during the first year of a cohort is 1.8 million tonnes, and during the second year the mean biomass present for the cohort is 6.4 million tonnes. The mean biomass during the year of the two cohorts present is then 8.2 million tonnes. This results in a biomass estimate of 2.632 $t \cdot km^{-2}$ (Table 2).

The mean production of *Gonatus fabricii* during a year was calculated to 20 million tonnes. If we assume that *Gonatus* makes up the larger part of the squids and that the lack of precision in the *Gonatus* data covers the other species, we can let the data for *Gonatus* represent all the squid species in the model area. The production/biomass ratio is 20,000,000/ 8,200,000 = 2.44$\cdot year^{-1}$ (Table 2).

Sennikov *et al.* (1989) investigated stomach content of juvenile and adult *Gonatus fabricii* in the Norwegian and Barents Seas, and found that their food items changed with age (Table 15). A preliminary investigations of 141 *Gonatus fabricii* (50-337 mm length) caught in the Norwegian Sea in 1999 indicated that amphipods (*Themisto* ssp.) constituted 42% of the stomach content, euphausids 17%, remains of mesopelagic fishes 11%, and other remains (decapods, *Gonatus,* etc.) 30% (H. Bjørke, Institute of Marine Research, Bergen, pers. comm.). The diet composition used in the model is listed in Table 3.

The feeding rates of squids are usually high, a number of estimations are made in captive and wild *Illex illecebrosus* giving feeding rates varying from 3.6-6.7% of the body weight per day (see O´Dor and Dawe, 1998). The feeding rates are usually higher in juvenile squid. At present we suggest a daily feeding rate of 5% of the body weight in the pelagic juvenile *Gonatus fabricii*, and an average daily feeding rate of 2% in bathy- and mesopelagic adults.

Table 15. Diet of the squid *Gonatus fabricii*, based on Sennikov *et al.* (1989) in percent.

Prey	**0-200 m depth (mainly juveniles)**	**350-450 m (mainly adults)**
Copepods	28	1
Amphipods	36	5
Euphausiids	11	33
Decapods	1	19
Chaetognaths	13	-
Gonatus	2	5
Pteropods	3	-
Fish	3	38

Using Bjørke and Gjøsæter´s (1998) estimate of biomass, the above mentioned feeding rates and the stomach content found by Sennikov *et al.* (1989) and H. Bjørke (pers. comm.) we estimated the annual consumption of different prey by *Gonatus fabricii* in the Norwegian Sea to 99.4 million tonnes (Table 16). Combined with the biomass estimate by Bjørke and Gjøsæter (1998), this gives a consumption/biomass ratio of 12.0·year^{-1} (Table 2).

The time series for catch of this group comes from the ICES Fisheries Statistics database.

Table 16. Estimates of consumption for *Gonatus fabricii* in the Norwegian Sea, based on Bjørke and Gjøsæter (1998) and Sennikov *et al.* (1989).

Prey	Juveniles (10^6 tonnes)	Adults (10^6 tonnes)
Copepods	9.2	1.3
Amphipods	12.8	11.0
Euphausiids	4.6	11.7
Decapods	0.3	22.3
Chaetognaths	4.3	-
Gonatus	0.5	5.3
Pteropods	0.9	1.2
Fish	2.0	12.0
Sum	34.6	64.8

Benthos

Christensen (1995), in his model for the North Sea, used the groups echinoderms, polychaetes and other macrobenthos, and the sum of the biomasses for these groups is 105 t·km^{-2}. The production/biomass ratio used for the three benthos groups was 2.0·year^{-1}, and the consumption/biomass ratio used for the three groups was was 13.0·year^{-1}.

Zatsepin & Rittikh (1976) investigated the quantitative distribution of macrobenthos in the Norwegian Sea and southern part of the Greenland Sea using grab sampling, and found that biomass was closely related to depth (Table 17). Romero-Wetzel (1989) used a box-corer at the Vøring Plateau (about 67°N 5°E), the continental slope, and the deep sea off the plateau, and found the highest biomass 8 g·m^{-2} at about 600 m depth, and a biomass of 0.5 g·m^{-2} at 2-3000 m depth.

The box-corer sampling may be less efficient than sampling with a grab and may explain the lower values observed by Romero-Wetzel (1989). The grab data may also be underestimated, as the grab catches fewer organisms than a sledge that covered the same area (T. Brattegard, Institute of Marine Research, Bergen, pers. comm.)

Using the data from the Norwegian/Greenland Seas given by Zatsepin & Rittikh (1976) and the depth distribution given in Table 1, we estimated the approximate biomass by interpolating the Zatsepin & Rittikh biomass data to fit the depth intervals. This gave a total biomass in the modelled area of 205,699,671 tonnes, or 66.0 t·km^{-2}, all depths included.

The average biomass in the upper 500 m was about 120-140 g·m^{-2}, which is not too far from the biomass observed by Christensen (105 g·m^{-2}, 1985), who excluded the less important groups from the biomass estimates.

The production/biomass and consumption/biomass ratios are likely to be lower due to lower temperatures, and tentatively we have reduced the North Sea values by about 25%. This gives a production/biomass ratio of 1.50·year^{-1} and a consumption/biomass ratio of 9.75·year^{-1}.

The diet composition parallels that of Christensen (1995), with mainly detritus, plankton and some cannibalism (Table 3).

The time series for catch of this group comes from the ICES Fisheries Statistics database.

Table 17. Biomass (wet weight) of macrobenthos at different depths in the Norwegian Sea and southern part of the Greenland Sea based on grab sampling. From Zatsepin & Rittikh (1976).

Depth range (m)	0-100	100-200	200-400	400 -600	600-800	800-1,500	> 1,500
Biomass (g·m^{-2})	217	111	60	54	27	11	2.2

Prawns (*Pandalus borealis*)

Bogstad *et al.* (2000) give biomass estimates for prawns in the Barents Sea for the years 1984-1999. The value for 1997 is 300,000 tonnes, corresponding to 0.096 t·km^{-2}. However, the estimates were obtained by the swept area method and only reflect what was available to the bottom trawl. The total biomass is believed to be higher. In order to compensate for the underestimate, a biomass density of 0.300 t·km^{-2} was used in the model (Table 2). The values used for production/biomass and consumption/biomass ratios were estimated by the working group (Table 2).

In the model, prawns feed on benthic organisms, large and small zooplankton, and detritus (Table 3).

The ICES Arctic Fisheries Working Group (Anon., 2001a) gives catches for prawns in the Barents Sea for the years 1970-1999. We have extended this time series back to 1950, using catches from the ICES Fisheries Statistics database. Anon. (2001a) also gives two series for catch per unit of effort, for the Russian and Norwegian Prawn fishery in the Barents Sea. The two series follow each other very well. The series for the Norwegian fishery goes back to 1980, one year longer than the Russian series, and we use the Norwegian series as a relative measure for biomass density of prawns for the years 1980-1997. These numbers have not been divided by area, as have been done for the other time series of biomass.

Krill (Euphausiidae)

Of the species found, *Meganyctiphanes norvegica* is widely distributed, and most abundant in Atlantic and coastal waters. *Thysanoessa inermis* is more of a cold water species. The smallest of the dominant krill species, *T. longicaudata*, was widespread with large abundances in arctic waters.

Dalpadado *et al.* (1998) reported a total biomass of krill in a selected area of the Norwegian Sea (1,700,000 km^2) during summer of 50 million t, with the highest biomass in arctic waters. This corresponds to a density of 29.41 t·km^{-2}.

A new estimate of the total biomass of krill within ICES areas I, II and III was calculated by horizontal integration of the biomass of krill in trawl stations within 6 depth layers from 0 to 500 m during the time period 1990-2000. The krill was sampled with a large pelagic trawl (Åkra trawl) equipped with a fine meshed (16 mm) net in the cod end. These mesh sizes are too large to retain the 0-group and most of the 1-group, and calibration by simultaneous hauls with a fine-meshed plankton trawl (7.5 mm stretched mesh size) indicated that the krill populations were underestimated by 60% with the pelagic trawl (Hassel and Melle, 2000). Thus, all catches were multiplied by 1.6. Total biomass of krill within the area (3,116,000 km^2) was estimated at 161 million t, corresponding to 52 t·km^{-2}. Dalpadado et *al.* (1998) obtained their results with the Åkra trawl as well and after adjusting their result due to loss of small individuals (multiplying by 1.6) the total biomass was 47 t·km^{-2}. That is very similar to our new estimate at 52 t·km^{-2} which we used in the model (Table 2).

Pavshtiks and Timokhina (1972) calculated the approximate production of the predominating zooplankton organisms in the Norwegian Sea for some of the years 1959-1969. According to their calculations the production of juvenile krill varied between 3.3 and 13.0 million tonnes (average 7.1 million t). The authors point out that this is a minimum value, and given the gears they used they probably did not sample the larger krill (Dalpadado *et al.*, 1998). The value seems very low if used together with the biomass estimate by Dalpadado *et al.* (1998) for a limited region of the Norwegian Sea it gives a production/biomass ratio of only 0.14 year^{-1}.

Given the life history of krill, and the likely high predation levels, it would be reasonable to expect a production/biomass ratio similar to *Gonatus fabricii* (i.e., 2.5 year^{-1}, Table 2). Lacking other data, we also used a consumption/biomass ratio of 15.0·year^{-1} that was similar to *Gonatus fabricii* (Table 2).

The diet of krill was assumed to consist of small zooplankton, phytoplankton, and detritus (Table 3).

Amphipods

The large *Themisto libellula*, reported to be a typical cold water species, dominated the trawl catches in Arctic water in the survey by Dalpadado *et al.* (1998). The smaller species *T. abyssorum* and *T. compressa,* being most abundant in Atlantic water, were probably not efficiently collected by the trawl and therefore underestimated. Juveniles of *Themisto libellula* were probably underestimated to the same extent as krill of similar size.

Dalpadado *et al.* (1998) found that the total biomass of hyperid amphipods (*Themisto* spp.) in the Norwegian Sea (1,700,000 km^2) was 110 million tonnes. This corresponds to a density of 64.71 $t{\cdot}km^{-2}$.

The unpublished data set used for krill in the previous section also includes catches of amphipods. By the same procedure of horizontal integration the total biomass of amphipods in the ICES areas I, II and III was estimated at 49 million t, corresponding to 16 $t{\cdot}km^{-2}$, which was the input biomass to the model (Table 2). Even though a loss of juvenile *T. libellula* and the smaller species of the genus *Themisto* through the meshes of the trawl is probable, no correction factor to account for this loss was available to us.

No data was available for mean production/biomass or consumption/biomass, but as a 'guesstimate' we used the same value as for krill, $2.5{\cdot}year^{-1}$ and $15.00{\cdot}year^{-1}$, respectively (Table 2).

Large zooplankton

Dalpadado *et al.* (1998) found that the total biomass of the small shrimps *Sergestes* spp. and *Pasiphaea* spp. in the Norwegian Sea (1,700,000 km^2) was 1.60 million t, mainly in coastal and Atlantic waters. This corresponds to a density of 0.94 $t{\cdot}km^{-2}$.

Zooplankton biomass in the ICES areas I, II and III was measured with MOCNESS hauls to 700 m or to the bottom during several annual cruises conducted by IMR (Wiebe *et al.,* 1985). During these cruises the samples were size fractioned by sieving on 180, 1000 and 2000 µm sieves. From the size fraction larger than 2000 µm shrimps, krill and small fishes which are not sampled quantitatively were removed. The rest is termed 'large zooplankton'. No single cruise covered all areas, and a complete annual coverage from all areas was not available to us. Thus, biomass measured during the June-July cruise in ICES area II and the September-October cruise in ICES area I was used to calculate the average biomass for all areas. It was also assumed that this biomass was representative for the whole year. The biomass of large zooplankton in area I and II was estimated at 40 million t, corresponding to 13 $t{\cdot}km^{-2}$, when used for the total model area. The biomass of 13 $t{\cdot}km^{-2}$ was not sufficient to account for the predation, and we enabled the model to estimate the biomass using a P/B of $4{\cdot}year^{-1}$, Q/B of $15{\cdot}year^{-1}$ and EE of 0.95. The calculated biomass was 16.9 $t{\cdot}km^{-2}$ (Table 2).

Small zooplankton

Sakshaug *et al.* (1994) estimated biomass of *Calanus* in the Barents Sea to 2 t $C{\cdot}km^{-2}$. Using their conversion factors, this corresponds to 15 $t{\cdot}km^{-2}$ wet weight. They also estimated the production/biomass ratio for *Calanus* in the Barents Sea to 4.0 $year^{-1}$.

Timokhina (1964, translation by Serebryakov, 1993) estimated the biomass of different plankton organisms in the Norwegian Sea for different months in 1959 and 1960. The average biomass of *Calanus finmarchicus* and *C. hyperboreus* over all months sampled was 8.49 and 5.17 $t{\cdot}km^{-2}$ for 1959 and 1960, respectively. This gave an average for the two years of 6.83 $t{\cdot}km^{-2}$. For other copepods (*Pseudocalanus elongatus*, *Metridia longa*, *M. lucens*, and others) the averages were 2.77 $t{\cdot}km^{-2}$ and 1.19 $t{\cdot}km^{-2}$ for 1959 and 1960, respectively, with an average of 1.98 $t{\cdot}km^{-2}$.

When comparing the biomass densities calculated by Timokhina (1964) for the Norwegian Sea and those calculated by Sakshaug *et al.* (1994) from the Barents Sea one has to keep in mind that the variation in plankton biomass between years can be very large (e.g., Pavshtiks and Timokhina, 1972). Still, the deep Norwegian Sea is considered to be the center of production of *Calanus finmarchicus* (Melle, 1998), and it seems unlikely that the standing stock of *C. finmarchicus* is less than in the Barents Sea. Possibly, the use of very different methods to calculate biomass by Timokhina (1964) as compared with Sakshaug *et al.* (1994) is the main reason for the higher biomass estimate in the Barents Sea compared to the Norwegian Sea.

The sum of the biomass in size fractions 180 and 1000 µm is termed 'small zooplankton'. The biomass sampled in June-July in ICES area II and in September-October in area I was considered representative for the whole area as described in the section above. The total biomass of small zooplankton in areas I and II was 103 million t, and the average biomass for the model region was 33 $t{\cdot}km^{-2}$.

Given that this value ignores the considerable component of very small zooplankton (less than 180 µm), we accounted for this by increasing the biomass to 50 $t{\cdot}km^{-2}$, and the P/B value to 10.0 $year^{-1}$ (Table 2). No value was available for consumption/biomass, but we estimated a value of 25.0 $year^{-1}$ (Table 2).

Jellyfish

Dalpadado *et al.* (1998) found that the total summer time biomass of the jellyfish *Periphylla periphylla* in the Norwegian Sea (1.7 million km^2) was 11.0 million tonnes, mainly in arctic and Atlantic waters. This corresponds to a density of 6.47 t·km^{-2}. This value is likely to vary greatly during the year, and a value of 4.0 t·km^{-2} was used for mean biomass during the year (Table 2).

In the workshop model for the Alaska gyre, Pauly and Christensen (1996) used the values 3.00 year^{-1} and 10.00 year^{-1} for production/biomass and consumption/biomass, respectively. In the absence of other data, we adopted these values (Table 2).

Seaweeds

The large brown algae of genera *Laminaria*, *Ascophyllum* and *Fucus* make up the bulk of macroalgae (kelp and seaweeds) along the coasts within the model area. Along the whole Norwegian coast the estimated area with macroalgae is approximately 8-10,000 km^2, and about half of this area is covered with *L. hyperborea*. The biomass of *L. hyperborea* alone is estimated to at least 10 million tonnes wet weight, averaging 2,000 t·km^{-2} in the areas where *L. hyperborea* actually grow (Sivertsen *et al.*, 1990).

In the littoral zone the genera *Ascophyllum* and *Fucus* dominate. The biomass of *Ascophyllum* alone along the Norwegian coast is estimated to 1.8 million tonnes wet weight (Baardseth 1970, Rueness 1980). The weight ratio of *Ascophyllum* to *Fucus vesiculosus* in the Møre region is found to be 100:30 (Baardseth and Grenager, 1961), further north along the west coast of Norway the weight ratio *Ascophyllum* to *F. vesiculosus* and *F. serratus* was found to be 100:39:41, indicating a total biomass of *Fucus* spp. to be 1.8 million tonnes * 0.8 = 1.4 million tonnes. From the Murman part of the Russian coast more than 0.5 million tonnes wet weight of rockweeds (*Ascophyllum* and *Fucus*) has been reported (Zenkevitch, 1963).

These macroalgae are scarce or absent in the Svalbard (Spitsbergen) area. As for *Ascophyllum,* the distribution stops at the eastern limit of the White Sea.

A minimum estimate of the biomass of macroalgae in the model area thus is 13.2 million tonnes kelp and rockweeds along the Norwegian coast and 0.5 million tonnes of rockweeds along the Murman coast, summing up to 13.7 million tonnes. If we assume that the total area with macroalgae along the Norwegian coast and the Murman coast is 10,000 km, this is 1,370 t·km^{-2} of macroalgae in the areas where they actually grow, or 4.4 t·km^{-2} as a mean for the total model area.

The annual biomass production of *L. hyperborea* in mid-Norway is approximately 1.5-2 kg·m^{-2} dry weight, and in northernmost Norway 0.8 kg·m^{-2} dry weight (Gunnarsson 1931, *in* Sjøtun *et al.*, 1995). The estimates of biomass production per m^2 of *L. hyperborea* found in different regions of Norway are within the same range as those reported from other studies in Europe, where the biomass production is between 0.8 and 3.9 kg·m^{-2} dry weight (Sjøtun *et al.*, op. cit.). In some areas of western Norway the annual production of *L. hyperborea* has been estimated to 2 kg·m^{-2} dry weight, the equivalent values for the Vega and Finnmark regions were 13 kg-1.3 kg and 8-0.8 kg, respectively (Sjøtun *et al.*, 1995). Dry weight of *L. hyperborea* is approximately 15% of the wet weight (Kain, 1977). It is not possible from these data to calculate an exact production of *L. hyperborea* that is valid for the whole coast, but if we assume a mean production of 2 kg·m^{-2} dry weight, this equals approximately 13 kg·m^{-2} or 1,300 t·km^{-2} wet weight. The P/B ratio for *L. hyperborea* alone is then approximately 0.65·year^{-1}.

Several studies have been made with regard to the *in situ* production of *A. nodosum*; in the White Sea Vozzinskaya (1970) estimated an annual production of 1.3 kg·m^{-2} dry weight; in New England Chock and Mathieson (1979) found 1.5 kg·m^{-2}; in northern Spain Soneira and Niell (1975) estimated 2.3 kg·m^{-2}; while Cousens (1984) found that annual production estimates from the coast of Nova Scotia ranged from 0.61 to 2.82 kg·m^{-2} depending upon the site, the method and the assumptions made. Baardseth (1970) reported that after harvesting it is possible to restore the original biomass of *A. nodosum* after 4-6 years, which means it is a rather slow growing and low productive species.

As mentioned above *L. hyperborea* makes up the bulk of the biomass of macroalgae. *A. nodosum* may have a somewhat lower P/B ratio than *L. hyperborea*, but we have no data for *Fucus* and other species of macroalgae. We have therefore adopted P/B = 0.65·year^{-1} as representative for all the macroalgae.

The time series for harvest of seaweeds comes from the ICES Fisheries Statistics database.

Phytoplankton

The phytoplankton consists partly of ice biota and partly of a true pelagic community. Sakshaug *et al.* (1994) estimated biomass density of phytoplankton in the Barents Sea to 2,000 kg C km^{-2}. Using their conversion factors this corresponds to 15 tonnes wet biomass·km^{-2} (Table 2). Using an ecotrophic efficiency of 0.95 leads to a P/B ratio of 117.7 $year^{-1}$ in the balanced model (Table 2). This indicates a required production of approximately 1,600 t·km^{-2}. This level of required production is supported by data of primary productivity from satellite imagery. The total primary productivity for the Norwegian-Barents Sea area for 1998 is estimated to 225 g C·m^{-2} , which (using a conversion factor of 1:9 for carbon to wet weight) corresponds to approximately 2000 t·km^{-2}·$year^{-1}$. This estimate is based on a model incorporating 'SeaWiFS' monthly Chlorophyll, photosynthetically active radiation and sea surface temperature, obtained through the Marine Environment Unit of the SAI, EC Joint Research Centre, Ispra, Italy (V. Christensen, pers. comm.).

Conclusions

The main purpose of this report was to document the basic input data used to generate the 1997 Ecopath model for the Norwegian Sea and Barents Sea as constructed during the workshop held at the Institute of Marine Research in Bergen, Norway, in November 2000. This model forms part of the ocean-wide assessment of ecosystem effects of fishing in the North Atlantic as conducted by the *Sea Around Us* project at the University of British Columbia. In the future, this model can be used as well to evaluate specific local and regional questions of interest to the Institute of Marine Research. It is anticipated that the model input data will change as better and more location specific data becomes available for various model parameters.

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References

Aarefjord, H. and Bjørge, A. J. 1995. Diet of the harbour porpoise (*Phocoena phocoena*) in Scandinavian waters. In Biology of the Phocoenids. Report of the International Whaling Commission, Special Issue 16, pp. 212-222. Ed. by A. Bjørge and G. P. Donovan. Cambridge.

Ajiad, A. M. and Gjøsæter, H. 1990. Diet of Polar Cod, *Boreogadus saida*, in the Barents Sea Related to Fish Size and Geographical Distribution. ICES CM 1990/G:48. 9 pp.

Anon. 1979. Ressursoversikt for 1979-1980. Fisken og Havet 1979, Særnummer 1.

Anon. 1982. Ressursoversikt for 1981-1982. Fisken og Havet 1982, Særnummer 1.

Anon. 1986. Ressursoversikt for 1986. Fisken og Havet 1986, Særnummer 1.

Anon. 1991. Ressursoversikt for 1991. Fisken og Havet 1991, Særnummer 1.

Anon. 1995a. Report on Surveys of the Distribution and Migrations of the Norwegian Spring Spawning Herring and the Environment of the Norwegian Sea and Adjacent Waters in the Spring and Summer of 1995. Reykjavik 11-13 September 1995. 51 pp.

Anon. 1995b. Report of the Atlanto-Scandian Herring, Capelin and Blue Whiting Assessment Working Group. ICES CM 1996/Assess:9. 150 pp.

Anon. 1996. Report on Surveys of the Distribution and Migrations of the Norwegian Spring Spawning Herring and the Environment of the Norwegian Sea and Adjacent Waters in Late Winter, Spring and Summer of 1996. Marine Research Institute, Reykjavik, Iceland, 24-26 Sept. 1996. 49 pp.

Anon. 1998. Report of the ICES Arctic Fisheries Working Group. ICES CM 1998/Assess:2. 366 pp.

Anon. 1999. Report of the Joint ICES/NAFO Working Group on Harp and Hooded Seals. ICES CM 1999/ACFM:7 :1-36.

Anon. 2000. Survey Report from the Joint Norwegian/Russian Acoustic Survey of Pelagic Fish in the Barents Sea, September-October 2000. IMR, PINRO Joint Report Series, Vol. 1. Murmansk. 30 pp.

Anon. 2000a. Report of the Working Group on Seabird Ecology. ICES CM 2000/C:4, 72. pp.

Anon. 2000b. Report of the Northern Pelagic and Blue Whiting Fisheries Working Group. ICES 2000/ACFM:16. 303 pp.

Anon. 2001a. Report of the Arctic Fisheries Working Group. ICES CM 2001/ACFM:02. 340 pp.

Anon. 2001b. Report of the Working Group on the Assessment of Mackerel, Horse Mackerel, Sardine and Anchovy. ICES CM 2001/ACFM:06. 456 pp.

Baardseth, E. 1970. Synopsis on Biological Data on Knobbed Wrack *Ascophyllum nodosum* (Linnaeus) Le Jolis. FAO Fisheries Synopsis, Vol. 38, no. 1. 48 pp.

Baardseth, E. and Grenager, B. 1961. A method of estimating seaweed quantities. Rep. Norw. Inst. Seaweed. Res., 25. 39 pp.

Bjørge, A. and Øien, N. 1995. Distribution and abundance of harbour porpoise, *Phocaena phocaena*, in Norwegian waters. In Biology of the Phocoenids. Report of the International Whaling Commission, Special Issue 16, pp 89-98. Ed. By A. Bjørge and G. P. Donovan. Cambridge.

Bjørke, H., Blindheim, J., and Melle, W. 1999. Hydrographic Conditions and Vertical Distribution of Plankton and Nekton in the Eastern Norwegian Sea. Fisken og Havet 2. Institute of Marine Research, Bergen, Norway. 30 pp.

Bjørke, H. and Gjøsæter, J. 1998. Who Eats the Larger *Gonatus fabricii* (Lichtenstein) in the Norwegian Sea? ICES CM M:10. 11 pp.

Bogstad, B., Haug, T., and Mehl, S. 2000. Who eats whom in the Barents Sea. North Atlantic Marine Mammals Commission Scientific Publications, 2: 98-119.

Bonner, N. 1993. Whales of the World. Blandford, London. 191 pp.

Bonner, N. 1994. Seals and Sea Lions of the World. Blandford A Cassel Imprint, London. 224 pp.

Chock, J. S. and Mathieson, A. C. 1979. Physiological ecology of *Ascophyllum nodosum* and its detached ecad *scorpioides* (Fucales, Phaeophyta). Botanica Marina, 22: 21-26.

Christensen, I. 1982. Killer whales in Norwegian coastal waters. Report of the International Whaling Commission, 32: 633-642.

Christensen, I., Haug, T., and Øien, N. 1992a. A review of feeding and reproduction in large baleen whales (Mysticeti) and sperm whales *Physeter macrocephalus* in Norwegian and adjacent waters. Fauna Norvegica, Series A, 13: 39-48.

Christensen, I., Haug, T. and Øien, N. 1992b. Seasonal distribution, exploitation and present abundance of stocks of large baleen whales (Mysticeti) and sperm whales (*Physeter macrocephalus*) in Norwegian and adjacent waters. ICES Journal of Marine Science, 49: 341-355.

Christensen, V. 1995. A model of trophic interactions in the North Sea in 1981, the year of the stomach. Dana, 11: 1-28.

Christensen, V. and Pauly, D. (Editors) 1993. Trophic Models of Aquatic Ecosystems. ICLARM Conference Proceedings, no. 26. 390 pp.

Christensen, V., Walters, C. J. and Pauly, D. 2000. Ecopath with Ecosim: A User's Guide. University of British Columbia, Fisheries Centre, Vancouver, Canada and ICLARM, Penang, Malaysia. 131 pp.

Cousens, R. 1984. Estimation of annual production by the intertidal brown alga *Ascophyllum nodosum* (L.) Le Jolis. Botanica Marina, 17: 217-227.

Dalpadado, P., Melle, W., Ellertsen, B. and Dommasnes, A. 2000. Food and feeding conditions of herring *Clupea harengus* through its feeding migrations. ICES Journal of Marine Science, 57: 843-857.

Dalpadado, P., Ellertsen, B., Melle, W. and Skjoldal, H. R. 1998. Summer distribution patterns and biomass estimates of macrozooplankton and micronekton in the nordic seas. Sarsia, 83: 103-116.

Devold, F. 1963. The life history of the Atlanto-Scandian herring. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 154: 98-108.

Dragesund, O., Hamre, J. and Ulltang, Ø. 1980. Biology and population dynamics of the Norwegian spring-spawning herring. In The Assessment and Management of Pelagic Fish Stocks, pp. 43-71. Ed. by A. Saville. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, Vol. 177.

Dommasnes, A., Rey, F. and Røttingen, I. 1994. Reduced oxygen concentrations in herring wintering areas. ICES Journal of Marine Science, 51: 63-69.

Folkow, L., Haug, T., Nilssen, K. T. and Nordøy, E. S. 2000. Estimated food consumption of minke whales *Balaenoptera acutorostrata* in Northeast Atlantic waters in 1992-1995. North Atlantic Marine Mammals Commission Scientific Publications, 2: 65-80.

Giske, J. *et al.* 1990. Vertical distribution and trophic interactions of zooplankton and fish in Masfjorden, Norway. Sarsia, 75: 65-81.

Gjøsæter, J. 1973. The food of the myctophid fish, *Benthosema glaciale* (Reinhardt), from western Norway. Sarsia, 52: 53-58.

Gjøsæter, J. 1981a. Life history and ecology of *Maurolicus muelleri* (Gonostomatidae) in Norwegian waters. Fiskeridirektoratets Skrifter Serie HavUndersøkelser, 17: 109-131.

Gjøsæter, J. 1981b. Life history and ecology of the myctophid fish *Notoscopelus elongatus kroeyeri* from the northeast Atlantic. Fiskeridirektoratets Skrifter Serie Havundersøkelser, 17: 133-152.

Gjøsæter, H. 1998. The population biology and exploitation of capelin (*Mallotus villosus*) in the Barents Sea. Sarsia, 83: 453-496.

Hassel, A. and Melle, W. 1999. Plankton som råstoffkilde for fremstilling av fôrmidler til bruk innen fiskeoppdrett. Et forprosjekt. Delprosjekt: Utredning av forekomster og tilgjengelighet av dyeareplankton. Institute of Marine Research, Bergen. Interne notat, no. 3.

Haug, T. *et al.* 1998. Sjøpattedyear-om hval og sel i norske farvann. Universitetsforlaget, Oslo. 239 pp.

Holst, J. C. *et al.* 1998. Report on Surveys of the Distribution, Abundance and Migrations of the Norwegian Spring-Spawning Herring, Other Pelagic Fish and the Environment of the Norwegian Sea and Adjacent Waters in Late Winter, Spring and Summer of 1998. ICES CM 1998/D:3. 67 pp.

Holst, J. C. *et al.* 1999. Report on Surveys of the Distribution, Abundance and Migrations of the Norwegian Spring-Spawning Herring, Other Pelagic Fish and the Environment of the Norwegian Sea and Adjacent Waters in Late Winter, Spring and Summer of 1999. ICES CM 1999/D:3. 50 pp.

Hureau, J. C. and Litvinenko, N. I. 1986. Scorpaenidae. In Fishes of the North-Eastern Atlantic and the Mediterranean, Vol. 3, pp. 1211-1229. Ed. by P. J. P. Whitehead, M. L. Bauchot, J. C. Hureau, J. Nielsen and E. Tortonese. UNESCO, Paris.

Huse, G. and Toresen, R. 1996. A comparative study of the feeding habits of herring (*Clupea harengus*, Clupeidae, L.) and capelin (*Mallotus villosus*, Osmeridae, Müller) in the Barents Sea. Sarsia, 81: 143-153.

Ingebrigtsen A. 1929. Whales Caught in the North Atlantic and Other Seas. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 56: 1-26.

Jiang, W. and Jørgensen, T. 1996. The diet of haddock (*Melanogrammus aeglefinus* L.) in the Barents Sea during the period 1984-1991. ICES Jounal of Marine Science, 53: 11-21.

Johnsgård, Å. 1966. Biology of the North Atlantic fin whale *Balaenoptera physalus* (L.). Taxonomy, distribution, migration and food. Hvalrådets Skrifter, 49: 1-62.

Kain, J. M. 1977. The biology of *Laminaria hyperborea* X. The effect of depth on some populations. Journal of the Marine Biological Association of the U. K., 57: 587-607.

Kawaguchi, K. and Mauchline, J. 1982. Biology of myctophid fishes (family Myctophidae) in the Rockall Through, northeastern Atlantic Ocean. Biological Oceanography, 1: 337-373.

Kawakami, T. 1980. A review of sperm whale food. Scientific Reports of the Whales Research Institute, 32: 199-218.

Kristensen, T. K. 1984. Biology of the squid *Gonatus fabricii* (Lichtenstein, 1818) from West Greenland waters. Meddelelser om Grønland, Bioscience, 13: 3-17.

Lindstrøm, U., Haug, T. and Røttingen, I. 1999. Consumption of herring *Clupea harengus* by minke whales *Balaenoptera acutorostrata* in the Barents Sea. Report of the International Whaling Commission, SC/51/E7: 1-19.

Lockyer, C. 1976. Body weights of some large whales. ICES Journal of Conservation, 36: 259-273.

Markussen, N. H., Bjørge, A. and Øritsland, N. A. 1989. Growth in harbour seals (*Phoca vitulina*) on the Norwegian coast. Journal of Zoology, 219: 433-440.

Martin, A. R. and Clarke, M. R. 1986. The diet of sperm whales (*Physeter macrocephalus*) captured between Iceland and Greenland. Journal of the Marine Biological Association of the U. K., 66: 779-790.

Mehlum, F. and Gabrielsen, G. W. 1995. Energy expenditure and food consumption by seabird populations in the Barents Sea region. In Ecology of Fjords and Coastal Waters, pp 457-470. Ed. by H. R. Skjoldal, C. C. E. Hopkins, K. E. Erikstad and H. P. Leinaas. Elsevier Science B. V., Amsterdam.

Melle, W. 1998. Reproduction, life cycles, and distributions of *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* in relation to environmental conditions in the Barents Sea. Ph. D. Thesis. Department of Fisheries and Marine Biology, University of Bergen, Norway. 164 pp.

Misund, O. A., Melle, W. and Fernø, A. 1997. Migration behaviour of Norwegian spring spawning herring when entering the cold front in the Norwegian Sea. Sarsia, 82: 107-112.

Mitchell, E. 1973. Draft report on humpback whales taken under special scientific permit by eastern Canadian land stations, 1969-1971. Report of the International Whaling Commission, 23: 138-154.

NAMMCO. 1998. Report of the Fifth Meeting of the Scientific Committee, Tromsø, Norway. 10-14 March 1997. North Atlantic Marine Mammal Commision Annual Report 1997: 85-202.

Nesis, K. N. 1971. Squid *Gonatus fabricii* (Lichtenstein) in the centre of the Arctic region. Hydrobiological Journal, 7: 93-96.

Nilssen, K. T., Pedersen, O.-P., Folkow, L. and Haug, T. 2000. Food consumption estimates of Barents Sea harp seals. North Atlantic Marine Mammals Commision Scientific Publications, 2: 9-27.

Nordøy, E. S., Folkow, L. P., Mårtensson, P. E. and Blix, A. S. 1995. Food requirements of Northeast Atlantic minke whales. In Whales, Seals, Fish and Man. Ed. by A. S. Blix, L. Walløe and Ø. Ulltang. Elsevier Science B. V., Amsterdam. 307 pp.

O´Dor, R. K. and Dawe, E. G. 1998. *Illex illecebrosus*. In Squid Recruitment Dynamics, pp. 77-104. Ed. by P. G. Rodhouse, E. G. Dawe and R. K. O´Dor. FAO Fisheries Technical Paper, 376.

Øien, N. 1993. A Note on *Lagenorhynchus* Species in Norwegian waters. ICES Study Group on Seals and Small Cetaceans in European Seas, Cambrigde, 31 March-2 April 1993. Working Paper. 9 pp.

Øien, N. 2000. Sel. In Havets Ressurser 2000. Særnummer 1-2000, pp. 35-40. Ed. by R. Toresen. Institute of Narine Research, Bergen.

Palomares, M. L. D. and Pauly, D. 1989. A multiple regression model for predicting the food consumption of marine fish populations. Austrailian Journal of Marine and Freshwater Research, 40: 259-273.

Pauly, D. 1989. Food consumption by tropical and temperate marine fishes: some generalizations. Journal of Fish Biology, 35 (Suppl. A): 11-20.

Pauly, D., Christensen, V. and Sambilay, V. 1990. Some Features of Fish Food Consumption Estimates Used by Ecosystem Modellers. ICES Council Meeting, 1990/G:17. 8 pp.

Pauly, D. and Christensen, V. (eds.) 1996. Mass-Balance Models of North-Eastern Pacific Ecosystems. Fisheries Centre Research Report 4(1), 131 pp.

Pauly, D., Trites, A. W., Capuli, E. and Christensen, V. 1998. Diet composition and trophic levels of marine mammals. ICES Journal of Marine Science, 55: 467-481.

Pavshtiks, E. A. and Timokhina, A. F. 1972. History of investigations on plankton in the Norwegian Sea and the main results of Soviet investigations. Proceedings of the Royal Society of Edinburgh (B), 73: 267-278.

Robb, A. P. 1981. Observations on the food and diel feeding behaviour of pelagic 0-group gadoids in the northern North Sea. Journal of Fish Biology, 18: 183-194.

Robb, A.P. and Hislop, J. R. G. 1980. The food of five gadoid species during the pelagic 0-group phase in the northern North Sea. Journal of Fish Biology, 16: 199-217.

Romero-Wetzel, M. 1989. Struktur und Bioturbation des Makrobenthos auf dem Vöring-Plateau (Norwegische See). Berichte aus dem Sonderforschungsbereich 313, no. 13. 204 pp.

Rueness, J. 1980. Praktisk betydning av marine makroalger. Naturen, 5: 196-210.

Soneira, A. and Niell, F. X. 1975. Sobre la biología de *Ascophyllum nodosum* en Galicia I. Distributión y abundancia en la ría de Vigo. Investigación Pesquera, 39: 43-59.

Sakshaug, E., Bjørge, A., Gulliksen, B., Loeng, H. and Mehlum, F. 1994. Structure, biomass distribution, and energetics of the pelagic ecosystem in the Barents Sea: A synopsis. Polar Biology, 14: 405-411.

Sameoto, D. D. 1988. Feeding of lantern fish *Benthosema glaciale* off the Nova Scotia Shelf. Marine Ecology Progress Series, 44: 113-129.

Sameoto, D. D. 1989. Feeding ecology of the lantern fish *Benthosema glaciale* in a subarctic region. Polar Biology, 9: 161-178.

Schweder, T., Skaug, H. J., Dimakos, X. K. and Langaas, M. 1996. Abundance of northeastern Atlantic minke whales, estimates for 1989 and 1995. Report of the International Whaling Commission, 47: 453-483.

Sennikov, A. M., Mukhin, S. G. and Bliznichenko, T. E. 1989. Distribution and trophic importance of juvenile squid (*Gonatus fabricii* Lichtenstein) in the Norwegian and Barents Seas in 1986-1988. ICES CM K:15.

Sigurjonsson, J. and Vikingsson, G. A. 1997. Seasonal abundance of and estimated food consumption by cetaceans in Icelandic and adjacent waters. Journal of Northwest Atlantic Fishery Science, 22: 271-287.

Similä, T., Holst, J. C. and Christensen, I. 1996. Occurence and diet of killer whales in northern Norway: seasonal patterns relative to the distribution and abundance of Norwegian spring spawning herring. Canadian Journal of Fisheries and Aquatic Sciences, 53: 769-779.

Sivertsen, A., Indergaard, M., Jensen, A. and Jørgensen, L. 1990. Høsting og økologisk betydning av stortare (*Laminaria hyperborea*) langs kysten av Sør-Trøndelag. SINTEF Rapport, 3 Sep 1990, no. 21. 37 pp.

Sjøtun, K., Fredriksen, S., Rueness, J. and Lein, T. E. 1995. Ecological studies of the kelp *Laminaria hyperborea* (Gunnerus) Foslie in Norway. In Ecology of Fjords and Coastal Waters, pp 525-536. Ed. by H. R. Skjoldal, C. C. E. Hopkins, K. E. Erikstad and H. P. Leinaas. Elsevier Science B. V., Amsterdam.

Skjoldal, H. R., Noji, T. T., Giske, J., Fosså, J. H., Blindheim, J. and Sundby, S. 1993. Mare Cognitum: Science Plan for Research on Marine Ecology of the Nordic Seas (Greenland, Norwegian, Iceland Seas), 1993-2000. Institute of Marine Research, Bergen, Norway. 162 pp.

Slotte, A. 1998. Spawning migration of Norwegian spring spawning herring (*Clupea harengus* L.) in relation to population structure. Ph. D. Thesis. Department of Fisheries and Marine Biology, University of Bergen, Norway. 180 pp.

Slotte, A. and Dommasnes, A. 1998. Distribution and Abundance of Norwegian Spring Spawning Herring During the Spawning Season in 1998. Fisken og Havet, no. 5.

Timokhina, A. F. 1964. On zooplankton production in different water masses of the Norwegian Sea. Trudy PINRO, 16: 165-182.

Timokhina, A. F. 1974. Feeding and daily food consumption of the Blue Whiting (*Micromesistius poutassou*) in the Norwegian Sea. Journal of Ichthyology, 14: 760-765.

Torsvik, N., Mortensen, S. and Nedreaas, K. H. (Editors) 1995. Fiskeribiologi. Landbruksforlaget, Oslo.

Vilhjalmsson, H. *et al.* 1997. Report on Surveys of the Distribution, Abundance and Migrations of the Norwegian Spring-Spawning Herring, Other Pelagic Fish and the Environment of the Norwegian Sea and Adjacent Waters in Late Winter, Spring and Summer of 1997. ICES CM 1997/Y:04. 32 pp.

Vozzhinskaya, V. B. 1970. Fucoids of the White Sea, Their Distribution, Developmental Biology and Production, pp. 170-182. Nauka, Moscow.

Wiebe, P. H. *et al.* 1985. New developments in the MOCNESS, an apparatus for sampling zooplankton and micronekton. Marine Biology, 87: 313-323.

Zatsepin V. I. and Rittikh, L. A. 1976. Quantitative distribution of macrobenthos in the Norwegian Sea and southern part of the Greenland Sea. Oceanology, 16: 397-400

Zenkevitch, L. 1963. Biology of the Seas of the U.S.S.R. George Allen & Unwin Ltd., London. 95 pp.