PART III: NORTHEAST ATLANTIC

CONSTRUCTING AN ICELANDIC MARINE ECOSYSTEM MODEL FOR 1997 USING A MASS-BALANCE MODELLING APPROACH

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ABSTRACT

This paper, as part of the *Sea Around Us* project (SAUP), documents the construction of an ecosystem model for the Icelandic marine ecosystem comprising twenty-four functional groups and including fourteen fleets.

INTRODUCTION

Iceland (Figure 1) covers an area of 103,000 km² (*www.fao.org/fi/fcp/Icele.asp*). The surrounding continental shelf (0-200 m depth) has a total area of 111,000 km², while the 200 nm EEZ covers 750,000 km² (*www.fao.org/fi/fcp/Icele.asp;* Figure 2). ICES area Va and the EEZ overlap to a large extent, although 373,000 km² of the EEZ is outside of ICES area Va (Figure 3). The present model covers ICES fishing area Va (Figure 2, 3), an area of 376,766 km² (R. Watson, pers. comm.).

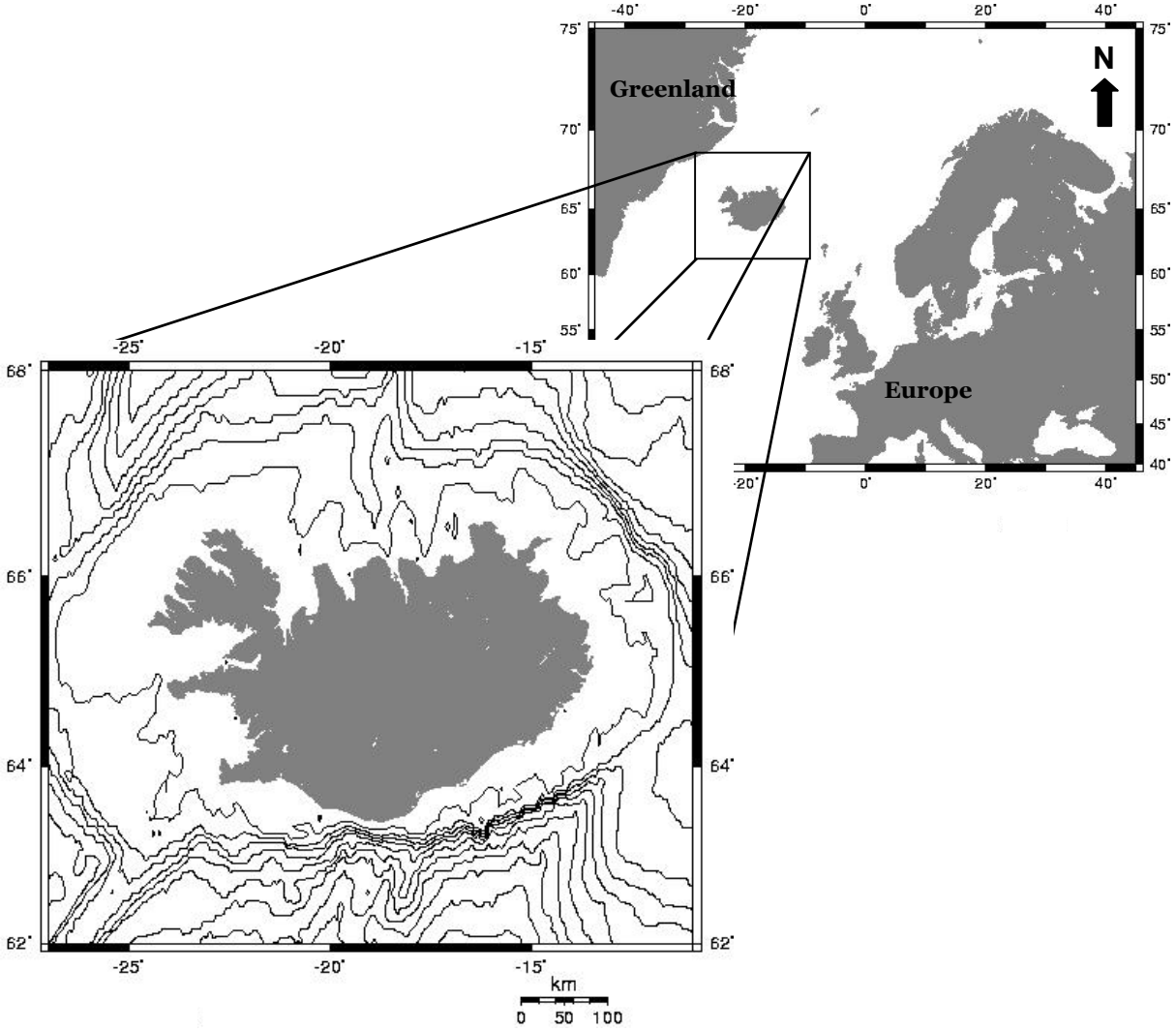

Figure 1: Location of Iceland and bathymetry in the surrounding waters.

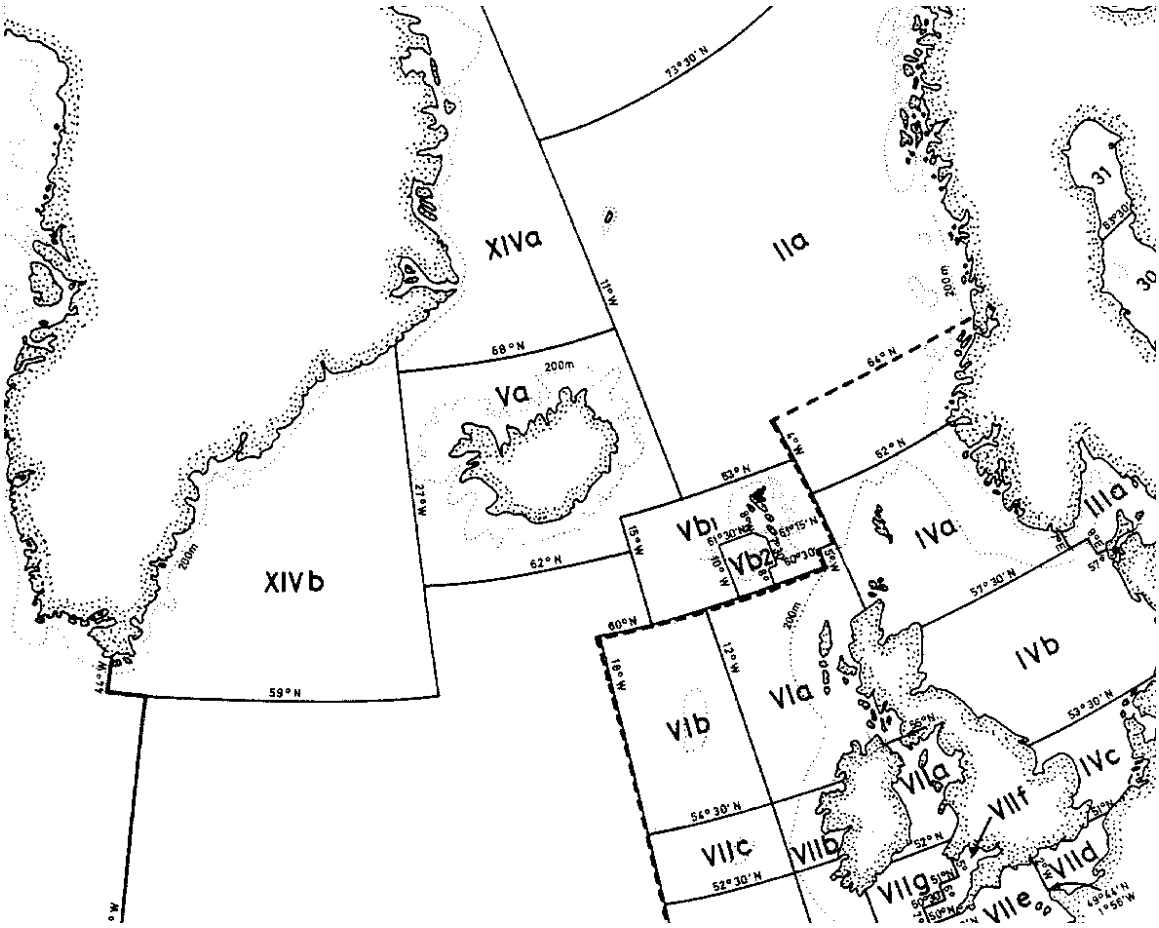

Figure 2: ICES Fisheries Statistical Areas, illustrating ICES area Va (11° - 27° W and 62° - 68° N), used here as the model area (376,766 km²).

The present model of Icelandic marine ecosystem covers the year 1997. Marine mammals are divided into three ecologically distinct groups, i.e., 'toothed whales', 'baleen whales' and 'pinnipeds'. 'Split groups' (Walters *et al*., 1997) were used only for cod, by splitting juvenile and adult biomass pools. The fisheries are represented by fourteen fleets: (1) foreign pelagic, (2) foreign demersal, (3) line and gillnet, (4) danish seines, (5) bottom trawls, (6) midwater trawls, (7) lobster trawls, (8) herring seines, (9) capelin seines, (10) capelin midwater trawls, (11) shrimp trawls, (12) dredge and traps, (13) seal guns, and (14) harpoons.

Harpoons were used in the 1950s to hunt toothed whales and baleen whales, but their use had stopped by 1997 (Valtýsson, 2001). In order to make comparison feasible between the past (1950; see Buchary, this volume) and the present-day (1997) models of Icelandic waters, 'harpoons' were included as a 'fleet' in the 1997 model. The 1997 catch proportion of harpoons was taken from the 1950 model, but the actual catches were $^{1}/_{100,000}{}^{th}$ of those in the 1950s – thus the 1997 catches were essentially zero.

Biomass data of most fished groups were taken from the single species stock assessment analyses undertaken by the Marine Research Institute using virtual population analysis (VPA) (Marine Research Institute, 2000). The production/biomass (P/B) ratios of these fished groups were estimated using the same single species VPA data. The consumption/biomass (Q/B) ratios were calculated using the empirical formula of Pauly *et al.* (1990), based on fish growth study information provided in FishBase (Froese and Pauly, 2001; *www.fishbase.org*). Unless the fish growth study cited in FishBase provided information on temperature, a median temperature of 4°C was assumed. Diet composition data for marine mammals were taken from Pauly *et al.* (1998). Biomass, P/B and Q/B data for the three marine mammal groups were derived from the Marine Mammals Database of the *Sea Around Us* project (Kaschner, 2001). In the case of certain functional groups, such as the seabirds, or groups that are not commercially fished, data from neighboring ecosystems were used. These include the Newfoundland-Labrador

Shelf model (Bundy *et al.*, 2000) and the North Sea model (Christensen, 1995).

Catch data were obtained from the official ICES fisheries statistics database (ICES STATLANT version 1999, *www.ices.dk/fish/statlant.htm*), except for catches of capelin and marine mammals, which were taken from the national fisheries statistics database of Iceland assembled by Valtýsson (2001). As ICES STATLANT database only provides total catches by species, country and area, the distribution of catches by gear type was derived from a cross-tabulation between the national fisheries statistics of Iceland (Valtýsson, 2001) and the ICES STATLANT database. In general, the 1997 statistics of Icelandic fisheries in the ICES STATLANT database were very similar to those in the national fisheries statistics of Iceland. Discard information was taken from a 1992 study on discarding practices by the Icelandic groundfish trawlers reported by Agnarsson (2000), and collated by Valtýsson (2001). In this model, the resulting estimates of discards were applied to trawlers that actually caught the species in question in 1997.

In 1997 three countries were fishing in area Va, Faroe Islands, Norway and Portugal. Since the level of foreign fishing was relatively low, foreign fleets were only divided into two fleets, foreign pelagic and foreign demersal.

All parameters were pedigreed (see Christensen *et al.*, 2000) and the resulting model (Tables 1-4) has 25 functional groups, comprising of two primary producer groups, six invertebrate groups, twelve fish groups, one seabirds group, three marine mammals groups and one detritus group.

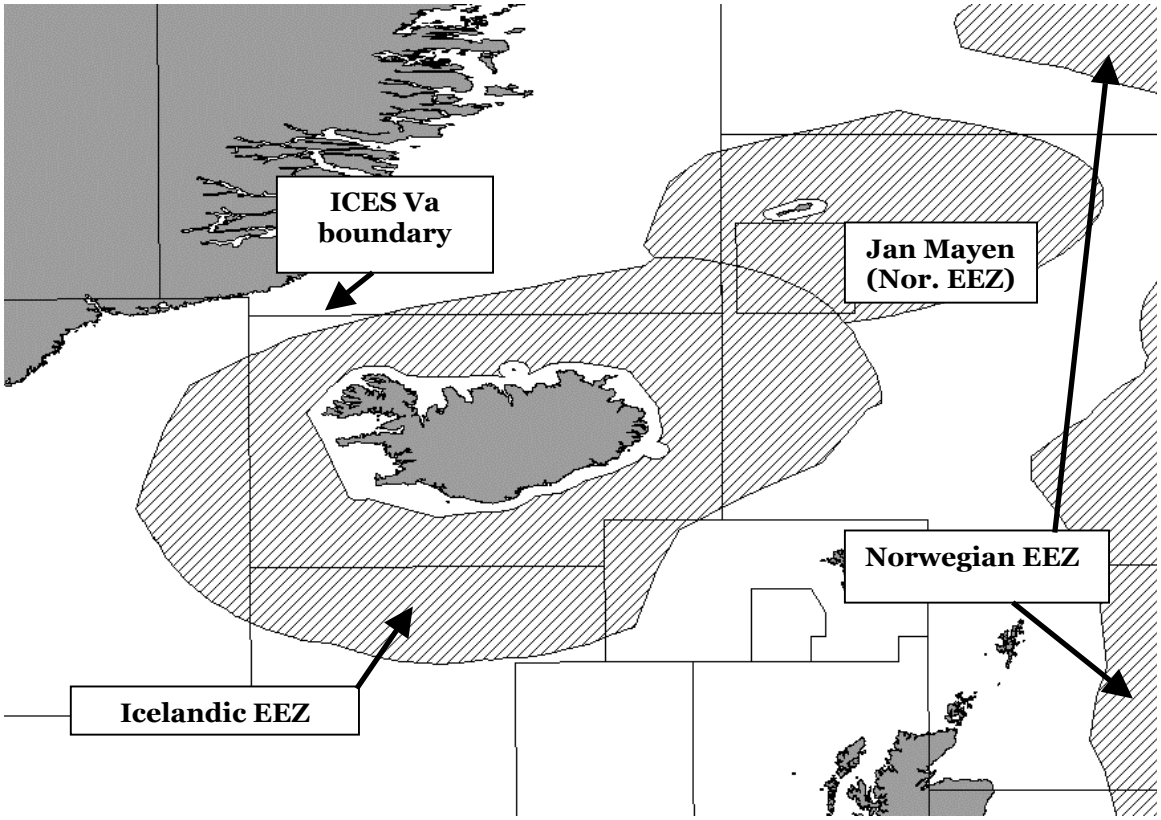

Figure 3: Overlap between ICES area Va and Icelandic 200 nm EEZ (hatched area). Parts of the Norwegian EEZ, including around Jan Mayen Island are also shown.

Table 1: Input (and output) parameters of the Ecopath model of Icelandic marine ecosystem in 1997. Values in brackets were estimated by the program.

No.	Group name	Trophic level	Biomass ($t \cdot km^{-2}$)	P/B ($year^{-1}$)	Q/B ($year^{-1}$)	EE	P/Q
1	Toothed whales	(4.3)	0.024	0.003	2.471	(0.755)	(0.001)
2	Baleen whales	(4.0)	0.068	0.009	4.275	(0.897)	(0.002)
3	Pinnipeds	(4.1)	0.057	0.023	11.184	(0.824)	(0.002)
4	Seabirds	(3.8)	0.012	0.250	54.750	(0.674)	(0.005)
5	Adult cod	(3.9)	2.643	0.475	2.454	(0.503)	(0.194)
6	Juvenile cod	(3.4)	0.213	(1.827)	6.090	(0.423)	0.300
7	Haddock	(3.5)	0.277	0.642	2.947	(0.964)	(0.218)
8	Saithe	(4.0)	0.428	0.496	2.327	(0.774)	(0.213)
9	Redfish	(3.9)	2.000	(0.400)	2.000	(0.743)	0.200
10	Greenland halibut	(4.3)	(0.347)	(0.488)	2.440	0.950	0.200
11	Other flatfish	(3.6)	(0.604)	(0.530)	2.649	0.950	0.200
12	Other dem. fish	(3.4)	(1.243)	(0.347)	2.312	0.950	0.150
13	Herring	(3.0)	1.555	(0.708)	4.723	(0.324)	0.150
14	Capelin	(2.9)	6.776	(1.327)	6.633	(0.792)	0.200
15	Other pelagics	(3.1)	(9.468)	0.290	(1.933)	0.950	0.150
16	*Nephrops*	(2.8)	0.037	0.310	(1.548)	(0.961)	0.200
17	Northern shrimp	(2.9)	(0.875)	1.830	(9.150)	0.950	0.200
18	Molluscs	(3.0)	(0.358)	(0.950)	6.330	0.750	0.150
19	Benthos	(2.0)	(39.152)	0.600	(6.667)	0.500	0.090
20	Other fish	(3.5)	(4.397)	(0.700)	3.500	0.950	0.200
21	Krill	(3.0)	(4.497)	3.000	15.000	0.950	0.200
22	Zooplankton	(2.0)	(24.949)	5.915	20.085	0.950	(0.294)
23	Benthic producers	(1.0)	3,685	4.430	-	(0.005)	-
24	Phytoplankton	(1.0)	(6.336)	200	-	0.400	-
25	Detritus	(1.0)	200	-	-	(0.011)	-

MODEL PARAMETERIZATION

Marine mammals: toothed whales, baleen whales and pinnipeds

The Marine Mammal Database of the SAUP (Kaschner, 2001) provides comprehensive ecosystem related data on marine mammals that have been collated from various sources (e.g., Trites *et al.*, 1997; Trites and Pauly, 1998; Pauly *et al.*, 1998). The information is arranged around three spatial classification systems: FAO areas, biogeochemical provinces (Longhurst, 1995; 1998) and ocean basins. For the purpose of the present model, Longhurst provinces were used to derive the relevant marine mammal data. The study area (ICES area Va) is located in the biogeochemical provincees ARCT (Atlantic Arctic, 2.1×10^6 km^2) and SARC (Atlantic Subarctic, 2.33×10^6 km^2). Therefore, biomass, production, consumption and diet information for marine mammals were derived from these two areas.

According to the database, there are fourteen species of toothed whales in ARCT and SARC: Atlantic white-sided dolphin (*Lagenorhynchus acutus*), bottlenose dolphin (*Tursiops truncatus*), common dolphin (*Delphinus delphis*), killer whale (*Orcinus orca*), long-finned pilot whale (*Globicephala melas*), white-beaked dolphin (*Lagenorhynchus albirostris*), beluga or white whale (*Delphinapterus leucas*), narwhal (*Monodon monoceros*), sperm whale (*Physeter catodon*), Blainville's beaked whale (*Mesoplodon densirostris*), Cuvier's beaked whale (*Ziphius cavirostris*), northern bottlenose whale (*Hyperoodon ampullatus*), harbor porpoise (*Phocoena phocoena*), and Sowerby's beaked whale (*Mesoplodon bidens*).

Estimation of toothed whale populations in ARCT and SARC areas from the database (Kaschner, 2001) resulted in a biomass of 0.024 $t \cdot km^{-2}$. P/B was indirectly estimated using the maximum population rate of increase (r_{max}) for toothed whales, i.e., 4% (Reilly and Barlow, 1986), while production was estimated to be half of r_{max},

Table 2: Catch data (t·km^{-2}·year^{-1}) for the model of Icelandic marine ecosystem in 1997 and the estimated mean trophic level (TL) of the catch for each fishing sector. Catches with very low values are represented by '0' in the matrix.

	Catch (t·km^{-2}·year^{-1})														
Group	**Foreign Pelagic**	**Foreign Demersal**	**Line & Gillnet**	**Danish Seine**	**Bottom Trawl**	**MW Trawl**	**Lobster Trawl**	**Herring Seine**	**Capelin Seine**	**Capelin MWT**	**Shrimp trawl**	**Dredge & Traps**	**Seal guns**	**Har-poons**	**Total**
Toothed whales														0	0
Baleen whales														0	0
Pinnipeds													0.0004		0
Adult cod		0.00108	0.27513	0.03936	0.2201		0.00339		0		0.00014				0.54
Haddock		0.0009	0.02653	0.01423	0.0731		0.00091		0		0.00002				0.12
Saithe		0.0019	0.02646	0.00451	0.0658		0.00028								0.1
Redfish		0.00064				0.19634									0.2
Greenland halibut		0.00007	0.00445		0.04						0				0.04
Other flatfish		0.0003	0.00349	0.05699	0.0098		0.00268				0				0.07
Other dem. fish		0.00303	0.05683	0.0072	0.0297	0.00001	0.0018				0				0.1
Herring			0		0			0.06488	0.0522	0.07157					0.19
Capelin	0.2557							0.03408	3.3683	0.08426					3.74
Other pelagics	0.0002		0.00001	0	0.00001					0.02767					0.03
Nephrops					0		0.00322								0
Northern shrimp											0.19126				0.19
Molluscs					0.00001							0.04234			0.04
Benthos		0										0.00005			0
Benthic producers												0.5177			0.52
Total catch	**0.256**	**0.00792**	**0.39291**	**0.12229**	**0.4386**	**0.19636**	**0.01228**	**0.09896**	**3.4204**	**0.1835**	**0.19143**	**0.56009**	**0.0004**	**0**	**5.88**
TL	**2.9**	**3.68**	**3.83**	**3.70**	**3.86**	**3.87**	**3.45**	**2.97**	**2.90**	**2.96**	**2.85**	**1.15**	**4.13**	**4.04**	**2.92**

Note: MW = mid-water; MWT = mid-water trawls

resulting in a generic P/B of 2% for toothed whales (Trites and Heise, 1996). When this generic P/B was weighted-averaged by the estimated total population biomass of toothed whales, P/B was then estimated to be 0.003 $year^{-1}$ for toothed whales population in both ARCT and SARC. The consumption/biomass (Q/B) ratio was derived using the mean body mass data (Trites and Pauly, 1998) for each identified toothed whales species and weighted-averaged by the estimated total population biomass of each identified toothed whale species in both ARCT and SARC areas, using the method described by Trites and Heise (1996). Q/B was estimated as 2.471 $year^{-1}$. Diet composition information for toothed whales (Table 3) was also extracted from the database (Kaschner, 2001; based on Pauly *et al.*, 1998) and reapportioned into appropriate functional groups.

Seven species of baleen whales were recorded in the ARCT and SARC areas: bowhead whale (*Balaena mysticetus*), northern right whale (*Eubalaena glacialis*), blue whale (*Balaenoptera musculus*), fin whale (*Balaenoptera physalus*), humpback whale (*Megaptera novaeangliae*), minke whale (*Balaenoptera acutorostrata*), and sei whale (*Balaenoptera borealis*).

The biomass estimated for the baleen whales population in ARCT and SARC areas is 0.068 $t \cdot km^{-2}$. Reilly and Barlow (1986) also estimated a maximum population rate of increase (r_{max}) of 4% for baleen whales, and production was estimated to be half of r_{max}, resulting in a generic P/B of 2% for baleen whales (Trites and Heise, 1996). When weighted-averaged by the estimated total population biomass, the P/B ratio for baleen whales population in ARCT and SARC became 0.009 $year^{-1}$. The Q/B ratio for the baleen whales population was estimated using the same approach as for the toothed whales, resulting in an estimate of 4.275 $year^{-1}$. Diet composition data for baleen whales (Table 3) were also extracted from the database (Kaschner, 2001; based on Pauly *et al.*, 1998) and reapportioned into appropriate functional groups.

The SAUP Marine Mammal Database (Kaschner, 2001) recorded seven species of pinnipeds in ARCT and SARC areas: walrus (*Odobenus rosmarus*), bearded seal (*Erignathus barbatus*), grey seal (*Halichoerus grypus*), harbor/common seal (*Phoca vitulina*), harp seal (*Phoca groenlandica*), hooded seal (*Cystophora cristata*), ringed seal (*Phoca hispida*).

Using the same biomass estimation approach applied to toothed and baleen whales, the estimated biomass for the total population of pinnipeds in ARCT and SARC is 0.057 $t \cdot km^{-2}$. Assuming a maximum population rate of increase (r_{max}) of 12% for northern fur seals and other pinnipeds (Small and DeMaster, 1995), the production was estimated to be half of r_{max}, resulting in a generic P/B of 6% for pinnipeds (Trites and Heise, 1996). When weighted-averaged by their total population biomass in ARCT and SARC, the estimated P/B for pinnipeds became 0.023 $year^{-1}$. Following the same Q/B estimation method described above, the weighted-averaged biomass Q/B for pinnipeds in ARCT and SARC areas was 11.184 $year^{-1}$. Diet composition information for pinnipeds were also extracted from the Marine Mammal Database (Kaschner, 2001; based on Pauly *et al.*, 1998) and reapportioned into appropriate functional groups (Table 3).

In terms of marine mammal catches, the Marine Research Institute (2000) indicated that there were 1,973 seals caught in 1997, consisting of 674 common seal pups, 356 grey seal pups, 16 adult common seals, 918 adult grey seals, and 9 other seals. These catches equal to 148 tonnes (Valtýsson, 2001), resulting in Ecopath catches of 0.000393 $t \cdot km^{-2} \cdot year^{-1}$ for pinnipeds (Table 2). Toothed whales and baleen whales were not caught in 1997, however, as explained in the Introduction section, very low catches by harpoons were assigned for these two groups. There were no known discards for pinnipeds in 1997.

Seabirds

Various studies indicate that seabirds migrate seasonally throughout the northern Atlantic ocean, but timing and routes are not well understood. The six most numerous seabird species found in Iceland are included here, and their diet composition was based on Lilliendahl and Solmundsson (1997; see Table 3). These six seabird species are common murres or common guillemots (*Uria aalge*), thicked-billed murres or Bruennich's guillemots (*Uria lomvia*), razorbills (*Alca torda*), puffins (*Fratercula arctica*), kittiwakes (*Rissa tridactyla*), and northern fulmars (*Fulmarus glacialis*).

The other input parameters were adapted from the same species from the Newfoundland-Labrador Shelf model of Bundy *et al.* (2000). Thus, biomass, P/B and Q/B were set at 0.012 $t \cdot km^{-2}$, 0.25 $year^{-1}$ and 54.75 $year^{-1}$, respectively. Diet composition date (Table 3) were taken from Lilliendahl and Solmundsson (1997). No landings nor discards were assigned to this group.

Table 3: Diet composition matrix for all functional groups of the Icelandic marine ecosystem model in 1997. Values represent the proportion (on a weight or volume basis) each prey contributes to the diet of a predator. All diet proportions sum to 1 for each predator. See text for sources.

Group no.	Prey	Predator group									
		1	2	3	4	5	6	7	8	9	10
1	Toothed whales	0.001									
2	Baleen whales	0.006		0.0003							
3	Pinnipeds	0.006		0.0005							
4	Seabirds	0.0072		0.0025							
5	Adult cod	0.0296	0.0072	0.0429							0.0541
6	Juvenile cod	0.0296	0.0072	0.0429		0.0053			0.001	0.005	0.0359
7	Haddock	0.0296	0.0072	0.0304		0.0035			0.01		
8	Saithe	0.0296	0.0072	0.0429		0.0053					
9	Redfish	0.0911	0.0144	0.007		0.0105		0.003	0.01		0.158
10	Greenland halibut	0.0296	0.0072	0.0429		0.0055					0.0585
11	Other flatfish	0.0296	0.0072	0.0429		0.0296		0.007	0.002		
12	Other dem. fish	0.0296	0.0072	0.0429		0.0219					0.1556
13	Herring	0.0354	0.0395	0.1124	0.0084	0.0055			0.001		
14	Capelin	0.0354	0.0395	0.1124	0.6767	0.2957		0.1	0.29	0.03	0.2854
15	Other pelagics	0.0299	0.0072	0.0433	0.024	0.057			0.001	0.02	0.0718
16	Nephrops	0.0209	0.005	0.002							
17	Northern shrimp	0.0209	0.0096	0.096		0.1217	0.15	0.035		0.013	0.0479
18	Molluscs	0.4846	0.0144	0.1194							0.0156
19	Benthos	0.0209	0.0096	0.096		0.1206	0.41	0.532	0.08	0.15	0.0204
20	Other fish	0.0295	0.0072	0.0429	0.0677	0.0931	0.07	0.013	0.26	0.04	0.0959
21	Krill	0.0041	0.8032	0.0773	0.1205	0.2249	0.27	0.31	0.344	0.742	0.001
22	Zooplankton										
23	Benthic producers										
24	Phytoplankton						0.1				
25	Detritus				0.1028				0.001		

Table 3: Continued.

Group no.	Prey	Predator group											
		11	12	13	14	15	16	17	18	19	20	21	22
1	Toothed whales												
2	Baleen whales												
3	Pinnipeds												
4	Seabirds												
5	Adult cod		0.0052										
6	Juvenile cod	0.0114	0.0102										
7	Haddock												
8	Saithe												
9	Redfish	0.0682	0.0209										
10	Greenland halibut												
11	Other flatfish												
12	Other dem. fish		0.0021										
13	Herring					0.001					0.0015		
14	Capelin	0.042	0.0387								0.001		
15	Other pelagics					0.0252					0.1014		
16	Nephrops		0.0005						0.001				
17	Northern shrimp	0.0375	0.0345										
18	Molluscs		0.0314										
19	Benthos	0.5685	0.4796			0.1893	0.3	0.3	0.2351		0.0345		
20	Other fish	0.2274	0.2094			0.0151			0.1763				
21	Krill	0.0450	0.042	0.1							0.3998		
22	Zooplankton			0.8	0.9	0.7693	0.5	0.55	0.3526		0.4618	1.0	
23	Benthic producers									0.3			
24	Phytoplankton			0.1	0.1		0.05	0.05					1.0
25	Detritus		0.1255				0.15	0.1	0.2351	0.7			

Table 4: Primary production required to sustain the fisheries (PPR, *sensu* Christensen and Pauly, 1993), calculated based on all food path ways in the modeled system.

Group Name	No. of paths	TL	PPR[a]	Catch[b]	PPR/catch	PPR/Tot PP (%)	PPR/unit of catch[c]
Toothed whales	22,634	4.25	0.01	0	757,460.40	0	21.89 [d]
Baleen whales	5,640	4.04	0.01	0	20,482.02	0	0.59[d]
Pinnipeds	1,1317	4.13	33.76	0	85,909.55	0.1	2.48
Adult cod	1,326	3.93	142.36	0.54	264.02	0.41	0.01
Haddock	202	3.47	13.07	0.12	112.99	0.04	0
Saithe	442	4.04	17.94	0.1	181.37	0.05	0.01
Redfish	64	3.87	23.51	0.2	119.33	0.07	0
Greenland halibut	2,214	4.34	29.23	0.04	655.75	0.08	0.02
Other flatfish	113	3.60	17.43	0.07	237.80	0.05	0.01
Other dem. fish	1,183	3.40	29.12	0.1	295.39	0.08	0.01
Herring	3	3.00	6.09	0.19	32.27	0.02	0
Capelin	2	2.90	62.06	3.74	16.58	0.18	0
Other pelagics	15	3.05	1.46	0.03	52.41	0	0
Nephrops	5	2.80	0.14	0	43.27	0	0
Northern shrimp	5	2.85	8.40	0.19	43.91	0.02	0
Molluscs	24	3.03	5.87	0.04	138.67	0.02	0
Benthos	2	2.00	0	0	11.11	0	0
Benthic producers	0	1.00	0	0.52	0	0	0
Total	**45,191**	**2.92**	**299.86**	**5.88**	**50.99**	**1.7**	**-**

[a]PPR, in t PP·km^{-2}·year^{-1}.
[b]Catch, in t·km^{-2}·year^{-1}.
[c]This is for a catch of 1 t·km^{-2}·year^{-1}.
[d]This is an artifact of the very low dummy catches of harpoons assigned in the model; see 'Introduction'.

Adult cod

This group consists only of adult stage *Gadus morhua*. We defined 'adult' here as post-recruit stage of ≥ 3 years. The biomass for this group was estimated using the 1997 single species VPA analysis of cod ages 3 - 14 in Iceland (Tables 3.1.2., and 3.1.6. in Marine Research Institute, 2000), and corresponds to 2.643 t·km^{-2}.

Assuming a natural mortality of 0.2 year^{-1} for cod (Table 3.1.9. in Marine Research Institute, 2000) and using fishing mortality of cod ages 3-14 from the VPA analysis (Table 3.1.7. in Marine Research Institute, 2000), P/B was estimated to be 0.475 year^{-1}. The Q/B ratio (2.454 year^{-1}) was estimated using an empirical formula in Christensen and Pauly (1992) and information from growth studies of cod in Iceland (Saemundsson, 1923; Jónsson, 1957, 1965; Schopka and Hempel, 1973; all as compiled in FishBase, Froese and Pauly, 2001). Diet composition for cod (Table 3) was modified from Pálsson (1983) and Gunnarson *et al.* (1998).

The Ecopath catch value for cod (Table 2) in 1997 equals to 0.539 t·km^{-2}·year^{-1} (ICES STATLANT version 1999) which can be broken down (Valtýsson, 2001) to 202,745 t for the Icelandic fleets (103,658 t by line & gillnet, 14,829 t by Danish seines, 82,927 t by bottom trawls, 1,278 t by lobster trawls, 2 t by capelin seines, and 52 t by shrimp trawls) and 408 t for Faroese fleets (which were assumed to be 'foreign demersal' fleets).

The reported cod discard rate of 0.4% (Agnarsson, 2000, cited in Valtýsson, 2001) was used in this model, and resulted in discards of 0.0009 t·km^{-2}·year^{-1} for bottom trawls, 0.000014 t·km^{-2}·year^{-1} for lobster trawls, and 0.000001 t·km^{-2}·year^{-1} for shrimp trawls. Consequently, by subtracting the discards from the catches, total cod landing became 0.538 t·km^{-2}·year^{-1} in 1997.

Juvenile cod

We defined 'juvenile cod' as pre-recruit *Gadus morhua*, and these include cod ages 0-2. This assumption is similar to the one used in the Newfoundland-Labrador Shelf model of Bundy *et al.* (2000).

Assuming that the natural mortality rate of juvenile cod is 0.6 $year^{-1}$ (Bundy *et al.*, 2000) and that catch of juvenile cod is negligible, the biomass of this group was calculated using the back estimation of the single species VPA abundance of cod age 3 in 2000, 1999 and 1998 in Iceland (Table 3.1.6 in Marine Research Institute, 2000) to obtain the 1997 cod biomass of ages 0, 1 and 2, respectively. Average body weight used are 0.0023 kg for age 0 (Thorisson, 1991), 0.0233 kg for age 1 and 0.231 kg for age 2 (Anon., 1997). The estimate gives average biomass of 80,234 t of age 0-2 cod in the study area, or 0.213 $t \cdot km^{-2}$.

Instead of calculating P/B ratio, the P/Q (gross food conversion efficiency ratio) was set to 0.3 following suggestions by Christensen *et al.* (2000) for juvenile groups. The Q/B (= 6.09 $year^{-1}$) was taken from the Q/B of cod ≤ 35 cm in the Newfoundland-Labrador Shelf model (Bundy *et al.* 2000). Diet composition for juvenile cod (Table 3) was taken from Pálsson (1983) and Gunnarson *et al.* (1998). No landings or discards were assigned to this group.

Haddock

The biomass of haddock (*Melanogrammus aeglefinus*) was estimated from the single species VPA of haddock ages 2-9 in Iceland (Tables 3.2.6 and 3.2.3 in Marine Research Institute, 2000), which equaled to 0.277 $t \cdot km^{-2}$.

Assuming a natural mortality rate of 0.2 $year^{-1}$ (Table 3.2.8 in Marine Research Institute, 2000) and using the VPA data (Marine Research Institute, 2000), the P/B ratio for haddock was estimated to be 0.642 $year^{-1}$. Q/B (= 2.947 $year^{-1}$) was derived using an empirical formula in Christensen and Pauly (1992) and information from a growth study of haddock in Iceland (Blacker, 1971; compiled in FishBase, Froese and Pauly, 2001). Diet composition for haddock (Table 3) was taken from Pálsson (1983) and Gunnarson *et al.* (1998).

The 1997 catches of haddock in Icelandic waters (ICES STATLANT 1999 version; Valtýsson, 2001) were comprised of 43,245 t caught by the Icelandic fleets (9,997 t by line & gill, 5,362 t by Danish seines, 27,535 t by bottom trawls, 0.01 t by midwater trawls, 342 t by lobster trawls, 1 t by capelin seines, and 8 t by shrimp trawls) and 340 t by the Faroe Islands (demersal) fleets. Thus, the haddock's Ecopath catch value equals to 0.115682 $t \cdot km^{-2} \cdot year^{-1}$ (Table 2).

In this model, a discard rate of 2.2% (Agnarsson, 2000, cited in Valtýsson, 2001) was used for haddock and was applied to bottom trawls (0.001608 $t \cdot km^{-2} \cdot year^{-1}$) and lobster trawls (0.00002 $t \cdot km^{-2} \cdot year^{-1}$), resulting in a total landing of 0.114053 $t \cdot km^{-2} \cdot year^{-1}$ for haddock in 1997.

Saithe

A biomass of 0.428 $t \cdot km^{-2}$ was estimated for saithe (*Pollachius virens*) based on a VPA for saithe ages 3-14 (Tables 3.3.5 and 3.3.2 in Marine Research Institute, 2000).

The P/B ratio (= 0.496 $year^{-1}$) was estimated using the same VPA (Tables 3.3.5 and 3.3.2 in Marine Research Institute, 2000) and by assuming a natural mortality rate of 0.2 $year^{-1}$ (Tables 3.3.7 in Marine Research Institute, 2000).

The consumption/biomass (Q/B) ratio was estimated at 2.327 $year^{-1}$ using an empirical formula (Christensen and Pauly, 1992) and a growth study of saithe in Iceland (Jones and Jónsson, 1971; compiled in FishBase, Froese and Pauly, 2001). Diet composition for saithe (Table 3) was taken from Pálsson (1983) and Gunnarson *et al.* (1998).

The total catches of saithe for 1997 (ICES STATLANT 1999 version; Valtýsson, 2001) comprised 36,548 t that were caught by the Icelandic fleets (9,971 t by line & gill, 1,700 t by Danish seines, 24,774 t by bottom trawls, 0.006 t by midwater trawls, 103 t by lobster trawls and 0.1 t by shrimp trawls) and 716 t by the Faroe Islands (demersal) fleets. In total, this was 0.098905 $t \cdot km^{-2} \cdot year^{-1}$ (Table 2).

Agnarsson (2000, cited in Valtýsson, 2001) reported that saithe has the lowest discard rate (0.2%) of all commercially fished finfish species caught by trawlers. Using this rate, discards for saithe were estimated as 0.000132 $t \cdot km^{-2} \cdot year^{-1}$ for bottom trawls and 0.000001 $t \cdot km^{-2} \cdot year^{-1}$ for lobster trawls. Therefore, by subtracting the discards from the catches, total saithe landing was 0.098773 $t \cdot km^{-2} \cdot year^{-1}$ in 1997.

Redfish

In this model, we only included two species/stocks of redfish, the golden redfish (*Sebastes marinus*) and the deep-sea redfish (*S. mentella*). Given biomasses observed elsewhere, the biomass of redfish was set at 2.0 $t \cdot km^{-2}$.

The Q/B ratio (= 2.00 $year^{-1}$) was taken from the Newfoundland-Labrador Shelf model (Bundy *et al.*, 2000), while the P/Q was assumed to be 0.2 as suggested by Christensen *et al.* (2000) for many fishes. Diet composition for redfish (Table 3) was taken from Pálsson (1983) and Gunnarson *et al.* (1998).

The total catches of redfish in 1997 (ICES STATLANT 1999 version; Valtýsson, 2001) was 73,976 t from Icelandic fleets and 242 t from Faroe Islands fleets (assumed to be 'foreign demersal' fleets), which equaled to 0.196987 $t \cdot km^{-2} \cdot year^{-1}$ (Table 2). The Icelandic catches of redfish were taken only by midwater trawls. According to Agnarsson (2000, cited in Valtýsson, 2001), the highest discard rate was for redfish at 12.9% and it was primarily small redfish that were targeted for discards. Using this discard rate, redfish discards in the model was 0.025328 $t \cdot km^{-2} \cdot year^{-1}$ for midwater trawls, resulting in a total redfish landing of 0.171658 $t \cdot km^{-2} \cdot year^{-1}$.

Greenland halibut

As there has been no VPA for Greenland halibut (*Reinhardtius hippoglossoides*) in Iceland (Marine Research Institute, 2000), the biomass and P/B for this group were not estimated. In the absence of a biomass input, Ecotrophic Efficiency (EE) was set at 0.95 and P/Q was fixed at 0.2 (Christensen *et al.*, 2000). Diet composition for Greenland halibut (Table 3) was modified from Gunnarson *et al.* (1998).

The Q/B ratio was derived as an average of the Q/B of Greenland halibut > 40 cm (1.478 $year^{-1}$) and Greenland halibut ≤ 40 cm (3.401 $year^{-1}$) in the Newfoundland-Labrador Shelf model (Bundy *et al.*, 2000), resulting in a Q/B of 2.440 $year^{-1}$.

The total catches of Greenland halibut in 1997 was 16,766 t from Icelandic fleets (1,678 t by line & gill, 15,087 t by bottom trawls, 0.003 t by lobster trawls and 1 t by shrimp trawls) and 26 t from Faroe Islands (demersal) fleets, which added up to a catch of 0.044568 $t \cdot km^{-2} \cdot year^{-1}$ (Table 2). Greenland halibut discard rate by the Icelandic groundfish trawlers was estimated to be 2.2% (Agnarsson, 2000, cited in Valtýsson, 2001). Therefore, discards were applied at 0.000881 $t \cdot km^{-2} \cdot year^{-1}$ for bottom trawls and 0.0000001 $t \cdot km^{-2} \cdot year^{-1}$ for shrimp trawls, resulting in a total landing of 0.043688 $t \cdot km^{-2} \cdot year^{-1}$.

Other flatfish

Based on species composition of catches in the ICES STATLANT database, the remaining flatfish species were pooled into this category. These include: witch flounder (*Glyptocephalus cynoglossus*), American plaice or long rough dab (*Hippoglossoides platessoides*), Atlantic halibut (*Hippoglossus hippoglossus*), megrim (*Lepidorhombus whiffiagonis*), common dab (*Limanda limanda*), lemon sole (*Microstomus kitt*), and European plaice (*Pleuronectes platessus*).

In the absence of stock assessments for any of these species in Icelandic waters, EE was assumed to be 0.95 and P/Q was set at 0.2 (Christensen *et al.*, 2000), and the biomass and P/B value left for Ecopath to estimate.

Valtýsson (2001) indicated that American plaice is probably the most abundant flatfish in Iceland, with European plaice also being very common. The 1997 landings of 'Other Flatfish' in ICES STATLANT was also dominated (=10,557 t) by the landing of European plaice (*Pleuronectes platessa*). Therefore, the Q/B ratio (=2.649 $year^{-1}$) for this group is represented by a Q/B value averaged from the Q/B values for American plaice (*Hippoglossoides platessoides*, > 35 cm (1.262 $year^{-1}$) and ≤ 35 cm (3.736 $year^{-1}$) in the Newfoundland-Labrador Shelf model, Bundy *et al.*, 2000) and European plaice (*Pleuronectes platessa* (2.8 $year^{-1}$) in the North Sea model, Christensen, 1995). Diet composition for this group (Table 3) was modified from Pálsson (1983) and Gunnarson *et al.* (1998).

The 1997 catches of this group (ICES STATLANT version 1999) was estimated as 27,505 t from the Icelandic fleets and 113 t from Faroe Islands (demersal) fleets. The Icelandic catch of this group was distributed (Valtýsson, 2001) into line & gill (1,317 t), Danish seines (21,470 t), bottom trawls (3,708 t), lobster trawls (1,010 t), shrimp trawls (0.3 t) and dredge & traps (0.2 t). This equals to a total Ecopath catch value of 0.073303 $t \cdot km^{-2} \cdot year^{-1}$ (Table 2).

The discard rate for this group was assumed to be similar to that of plaice, estimated at 2.4% (Agnarsson, 2000; cited in Valtýsson, 2001). Consequently, discards were applied at 0.000236 $t \cdot km^{-2} \cdot year^{-1}$ for bottom trawls and 0.000064 $t \cdot km^{-2} \cdot year^{-1}$ for lobster trawls. Thus, the resulted total landing for this group became 0.073002 $t \cdot km^{-2} \cdot year^{-1}$.

Other demersal fish

This functional group consists of several demersal fish species: Atlantic wolffish/catfish (*Anarhichas lupus*), spotted catfish (*Anarhichas minor*), argentines/silver smelts (*Argentina spp.*), tusk/cusk (*Brosme brosme*), roundnose grenadier (*Coryphaenoides rupestris*), lumpfish/lumpsucker (*Cyclopterus lumpus*), orange roughy (*Hoplostethus atlanticus*), angler/monk (*Lophius piscatorius*), roughhead grenadier (*Macrourus berglax*), whiting (*Merlangius merlangus*), blue ling (*Molva dypterygia*), ling (*Molva molva*), blue skate (*Raja batis*), shagreen ray (*Raja fullonica*), other skates (*Raja spp.*), Greenland shark (*Somniosus microcephalus*), and picked/spiny dogfish (*Squalus acanthias*).

In the absence of stock assessment analyses for these species in Iceland, biomass and P/B were not estimated. Therefore, EE was assumed to be 0.95 and P/Q was set at 0.15.

The consumption/biomass ratio was estimated as an average of the Q/B of skates (= 2.878 $year^{-1}$) and large demersal feeders (= 1.747 $year^{-1}$) in the Newfoundland-Labrador Shelf model (Bundy *et al.*, 2000), which resulted in a Q/B of 2.312 $year^{-1}$. Diet composition (Table 3) was modified from Pálsson (1983) and Gunnarson *et al.* (1998).

ICES STATLANT database (1999 release) and Valtýsson (2001) indicated that the 1997 catches for this group were estimated to be 36,000 t from the Icelandic fleets (21,411 t by line & gill, 2,712 t by Danish seines, 11, 194 t by bottom trawls, 4 t by midwater trawls, 677 t by lobster trawls, and 2 t by shrimp trawls), 931 t by Faroe Islands (demersal) fleets and 209 t by the Portuguese (demersal) fleets. In total, these catches amounted to 0.098576 $t \cdot km^{-2} \cdot year^{-1}$ (Table 2). No discards were assigned to this group.

Herring

The herring (*Clupea harengus*) modelled in this group is the Icelandic Summer Spawning stock, as described in Valtýsson (2001). The biomass of this group (1.555 $t \cdot km^{-2}$) was estimated using the VPA of herring ages 2-15 (Tables 3.18.5 and 3.18.2 in Marine Research Institute, 2000). P/B was not estimated; instead, P/Q was set at 0.15.

The Q/B ratio (= 4.723 $year^{-1}$) was estimated from the empirical relationship in Christensen and Pauly (1992) and the growth parameters of herrings in the Norwegian Sea (Beverton and Holt, 1959; compiled in FishBase, Froese and Pauly, 2001). The diet composition for herring (Table 3) was taken from Jakobsson *et al.* (1993).

In 1997, herring was caught only by the Icelandic fleets, totaling 71,076 t (ICES STATLANT). These catches were distributed (Valtýsson, 2001) into line & gill (0.32 t), Danish seines (0.02 t), bottom trawls (0.43 t), herring seines (24,446 t), capelin seines (19,663 t), and capelin midwater trawls (26,966 t). These equal to 0.18865 $t \cdot km^{-2} \cdot year^{-1}$ of catches (Table 2). No discards were allocated to herring.

Capelin

The biomass of capelin (*Mallotus villosus*) was estimated from the single species VPA of immature and mature capelin (Tables 3.19.5 in Marine Research Institute, 2000), resulting in a biomass of 6.776 $t \cdot km^{-2}$.

Capelin's Q/B (= 6.633 $year^{-1}$) was estimated using an empirical formula (Christensen and Pauly, 1992) and the growth study of capelin in the Labrador Sea (Templeman, 1948; in FishBase, Froese and Pauly, 2001).

As P/B was not estimated, but the gross food efficiency ratio or P/Q was set at 0.2 (Christensen *et al.*, 2000). The diet composition for capelin (Table 3) was taken from Vilhjalmsson (1994).

Examination of catches of capelin revealed an error in the ICES STATLANT database (1999 release). This provided an erroneous catch for capelin for 1997, reporting 11,620,280 t of capelin being caught by the Icelandic fleets alone. In contrast, the FAO catch data in 1997 recorded 1,319,191 t of capelin for Iceland. The Icelandic national fisheries statistic database recorded 1,313,624 t of capelin catch in 1997 by the Icelandic fleets, which is very similar to the FAO data. Therefore, for this group we decided to use the catch data from the Icelandic fisheries statistic database. ICES was informed of the erroneous data entry.

The 1997 total catch of capelin from the study area was 1,409,977 t. These catches were caught by the Icelandic fleets (1,313,624 t), Faroe Islands pelagic fleets (35,308 t) and Norwegian pelagic fleets (61,045 t). The catches that were caught by the Icelandic fleets were distributed (Valtýsson, 2001) into herring seines (12,839 t), capelin seines (1,269,041 t) and capelin midwater trawls (31,744 t). Overall, this resulted in a total Ecopath input catch of 3.7423 $t \cdot km^{-2} \cdot year^{-1}$ (Table 2). No discards were allocated to capelin.

Other pelagics

Similar to 'other demersal fish', this group was also comprised of several species, such as black scabbardfish (*Aphanopus carbo*), porbeagle (*Lamna nasus*), blue whiting/poutassou (*Micromesistius poutassou*), Atlantic mackerel (*Scomber scombrus*), sandeel (*Ammodytes* sp.) and northern bluefin tuna (*Thunnus thynnus*).

The biomass and the Q/B ratio were not estimated, but rather, EE was set at 0.95 and a value of 0.15 was entered for P/Q (Christensen *et al.*, 2000). P/B (= 0.29 $year^{-1}$) and diet composition for this group (Table 3) were adopted from the North Sea model (Christensen, 1995).

The ICES STATLANT database (1999 release) recorded a catch of 10,512 t for this group in 1997, which was distributed into 10,431 t caught by the Icelandic fleets (3 t by line & gill, 0.45 t by Danish seines, 2 t by bottom trawls, and 10,426 t by capelin midwater trawls) and 81 t caught by Faroe Islands pelagic fleets. These equal to 0.0279 $t \cdot km^{-2} \cdot year^{-1}$ (Table 2). No discards were allocated to this group.

Norway lobster (*Nephrops norvegicus*)

The biomass of Norway lobsters (*Nephrops norvegicus*) was estimated from the VPA of *Nephrops* ages 3-16 (Tables 3.22.4 and 3.22.6 in Marine Research Institute, 2000), resulting in a biomass of 0.037 $t \cdot km^{-2}$.

The P/B ratio was calculated using the VPA data (Tables 3.22.5 and 3.22.6 in Marine Research Institute 2000). Assuming a natural mortality of 0.2 $year^{-1}$, P/B was estimated to be 0.31 $year^{-1}$.

The Q/B ratio was not estimated. Therefore, P/Q was assumed to be 0.2 (Christensen *et al.*, 2000). The diet composition for this group (Table 3) originates from Unnur Skuladottir (pers. comm., 1998).

In 1997, there were 1,215 t of *Nephrops* caught from the study area by the Icelandic fleets (ICES STATLANT, 1999 release). The distribution of catches (Valtýsson, 2001) was 1,1215 t by lobster trawls and 0.31 t by bottom trawls, resulting in an Ecopath catches of 0.003225 $t \cdot km^{-2} \cdot year^{-1}$ (Table 2). Foreign catches and discards were non existent in 1997 for Norway lobsters (ICES STATLANT, version 1999; Valtýsson, 2001).

Northern shrimps

In the absence of biomass and Q/B data for northern shrimps (*Pandalus borealis*) in the study area, EE was assumed to be 0.95 and P/Q was set at 0.2 (Christensen *et al.*, 2000).

The production/biomass ratio was taken from the total mortality estimate for northern shrimp in northern Norway (1.83 $year^{-1}$, Hopkins and Nilssen, 1990). The diet composition for northern shrimps (Table 3) originates from Unnur Skuladottir (pers. comm., 1998).

In 1997, northern shrimps were only caught by the Icelandic shrimp trawls, with catches of 72,060 t (ICES STATLANT, version 1999) or 0.191259 $t \cdot km^{-2} \cdot year^{-1}$ (Table 2). Discards of northern shrimps were not recorded.

Molluscs

This group is comprised of whelks (*Buccinum undatum*), Icelandic scallops (*Chlamys islandica*), European flying squid (*Todarodes sagittatus*), and other molluscs.

In the absence of biomass and P/B data, EE was assumed to be 0.75 and P/Q was set at 0.15. The Q/B ratio was adopted from the Q/B of molluscs (= 6.33 $year^{-1}$) in the Newfoundland-Labrador Shelf model (Bundy *et al.* 2000). The diet composition for this group (Table 3) was modified from Gunnarson *et al.* (1998) and Unnur Skuladottir (pers. comm., 1998).

The total catch of molluscs in 1997 (ICES STATLANT, version 1999) from the study area was 15,958 t or 0.04236 $t \cdot km^{-2} \cdot year^{-1}$ (Table 2). These were mainly caught by dredge and traps (15,953 t), and about 5 t were caught by bottom trawls and 0.03 t by Danish seines (Valtýsson, 2001). No discards were recorded.

Benthos

This group is mainly comprised of sea urchins (Echinoidea) and marine crustaceans. The biomass and Q/B were not estimated, but rather, EE was assumed to be 0.5 since this group is not heavily fished (Christensen *et al.*, 2000). The P/Q ratio was assumed to be 0.09, based on the gross food conversion efficiency of sea urchins (Brey, 1995).

The P/B ratio (= 0.6 $year^{-1}$) was adopted from the P/B of echinoderms in the Newfoundland-Labrador Shelf model (Bundy *et al.*, 2000), while the diet information (Table 3) was modified from

Gunnarson *et al.* (1998) and Unnur Skuladottir (pers. comm., 1998).

The 1997 catches of benthos from the study area were recorded as 20 t by the Icelandic fleets (dredge and traps) and 1 t by the Portuguese demersal fleet (ICES STATLANT, version 1999; Valtýsson, 2001), totaling to 0.000056 $t \cdot km^{-2} \cdot year^{-1}$ (Table 2). No discards were recorded.

Other fish

We defined this group as fish that are not commercially important and are generally of small size. This includes both pelagic and demersal species (H. Valtýsson, pers. comm.).

The biomass and P/B were not estimated, the EE was assumed to be 0.95 and the P/Q was set to 0.2 (Christensen *et al.*, 2000). A Q/B ratio (= 3.5 $year^{-1}$) was assumed corresponding to the Q/B of other prey fish in the North Sea model (Christensen, 1995). The diet composition was constructed based on the general ecology of small fishes. No landings or discards were recorded for this group.

Krill

Parameter estimates for Krill at Iceland were not available, instead generic values were used (V. Christensen, pers. comm.).

Zooplankton

The biomass was not estimated and EE was set at 0.95. The P/B ratio (= 5.915 $year^{-1}$) as well as the Q/B ratio (= 20.085 $year^{-1}$) for this group was estimated from the averages of the respective ratios of large zooplankton (P/B = 3.43 $year^{-1}$, Q/B = 19.5 $year^{-1}$) and small zooplankton (P/B = 8.4 $year^{-1}$, Q/B = 20.67 $year^{-1}$) in the Newfoundland-Labrador Shelf model (Bundy *et al.*, 2000). Following suggestion by Christensen *et al.* (2000), the unassimilated food/consumption ratio was readjusted to 0.4. The diet composition (Table 3) was based on general knowledge about the biology of zooplankton.

Benthic producers

This group is mainly comprised of brown seaweeds (kelp, Phaeophyceae). The biomass (= 3,685 $t \cdot km^{-2}$) and P/B ratio (= 4.43 $year^{-1}$) was adopted from data on *Laminaria* spp. in the northwest Atlantic (Brady-Campbell *et al.*, 1984). Harvests (or landings) of this group in 1997 were recorded as 195,050 t (0.517695 $t \cdot km^{-2} \cdot year^{-1}$) by the dredges and traps of the Icelandic fleets (ICES STATLANT, version 1999; Valtýsson, 2001). No discards were recorded.

Phytoplankton

Phytoplankton biomass data was not available. The P/B ratio was adopted from the P/B of phytoplankton (= 200 $year^{-1}$) in the Strait of Georgia, north-east Pacific (Mackinson, 1996). The EE was assumed to be 0.4, reflecting the assumption that the bulk of the primary production is not utilized directly in the system, but cycled to the detritus (Christensen *et al.*, 2000).

Detritus

Detritus, which comprised of both dissolved and particulate organic matters, was guesstimated to have a biomass of 200 $t \cdot km^{-2}$.

RESULTS AND DISCUSSION

The Icelandic marine ecosystem in 1997 spans over approximately four trophic levels, with the toothed whales and the Greenland halibut as top predators, i.e., occupying the highest trophic level (Table 1).

The updated, balanced Ecopath model shows that, in 1997, the fisheries targeted intermediate trophic levels; the mean trophic level of the catch was 2.85 (Table 2).

All parameters entered have been pedigreed, resulting in a pedigree index of 0.2952 and a measure of fit (t*) of 1.42. However, these values cannot yet be compared with those of other models, as their computation is a novel feature of Ecopath/Ecosim.

The present Ecopath model of the Icelandic marine ecosystem represents a summary of our current knowledge of the biomass, consumption, production, food web structure and trophic flows in the ecosystem exploited by fourteen fishing fleets in ICES area Va.

The main uncertainties in our model lie in the diet composition information, potentially resulting in inappropriate trophic level estimates. Moreover, the annual averages used in Ecopath ignore competitive interactions in feeding and the fact that the prevalence of diet items may change on a seasonal basis. More information on

the invertebrate groups and the seabirds are also needed for future refinement of the model. Enhancement of the present model could include application of environmental and ecological variations, non-trophic relations, and spatial consideration.

One issue that needs to be addressed in the future revision of the model is the sandeel (*Ammodytes* sp.). At this moment, sandeels are included in the 'other pelagics' group. Although sandeels have not been harvested in significant amount, they play a vital ecological role in the ecosystem (H. Valtýsson, pers. comm.). Therefore, sandeels merit their own functional group.

Of great concern are the recently detected uncertainties in stock assessment results for cod, one of the major commercial species (H. Valtýsson, pers. comm.). If these uncertainties in assessment are borne out, then many, if not all, biomass estimates used here for commercial species will be overestimates.

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