FISKEN OG HAVET
nr. 7/2016

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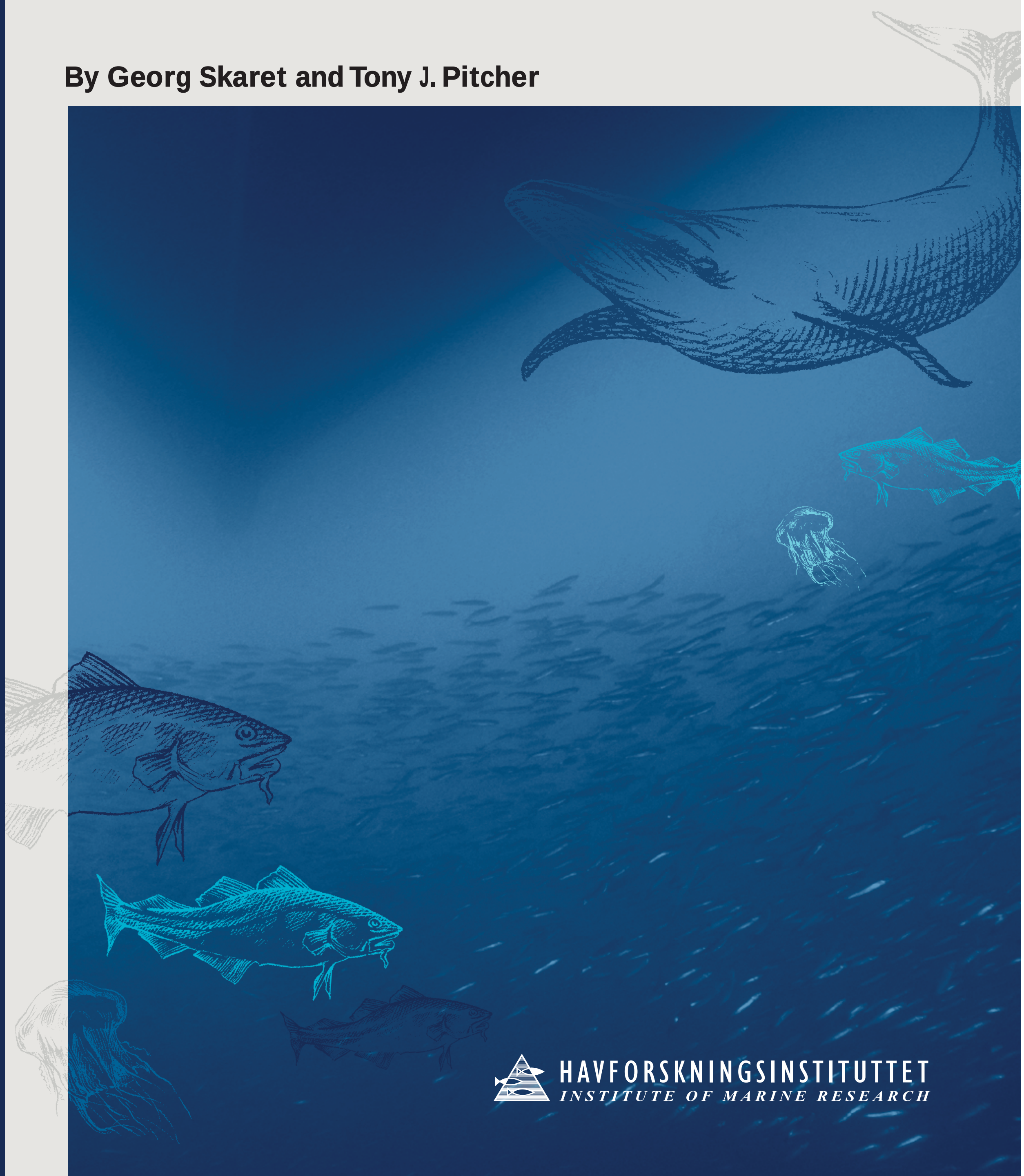
By Georg Skaret and Tony J. Pitcher



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PROSJEKTRAPPORT

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Flødevigen 4817 HIS

Distribusjon: Åpen

Prosjektnr.: 14482

Oppdragsgiver(e):

Oppdragsgivers referanse:

Rapport: Fisken og havet

Nr. - År 7-2016

Dato: 17/6 2016

Tittel (norsk/engelsk):
An Ecopath with Ecosim model of the Norwegian Sea and Barents Sea validated against time series of abundance.

Program:

Faggruppe: 433 Pelagisk Fisk

Forfatter(e):
Georg Skaret and Tony J. Pitcher

Antall sider totalt: 33

Sammendrag (norsk):

Her presenterer me ein Ecopath med Ecosim økosystemmodell for Norskehavet og Barentshavet som til dels er validert mot mengdemålingstidsseriar. Ecopath modellparametre på norskehavs- og barentshavsorganismar er henta frå litteraturen eller frå tilnærmingar viss ikkje annan informasjon er tilgjengeleg. Sårbarhetsparameteren som beskriv kor sårbart eit gitt bytte er for ein gitt predator, og som modellen er svært sensitiv ovafor, blei tilpassa ved å kjøra ein historisk modell balansert for året 1950 til 2000 og modellerte mengdemålingstidsseriar mot tidsseriar frå akustiske tokt eller VPA-kjøringar.

Estimert fiskedødelighet eller rapportert fangst blei trekt frå biomassen for kvar modellert organismegruppe gjennom 50-årsperioden. Sårbarhetsparameteren blei ekstarhert ut frå den balanserte 1950-modellen, og blei deretter brukt inn i ein modell for det same området og med identiske organismegrupper, men balansert for året 2000. Samsvaret mellom den modellerte biomassen og den observerte var rimeleg god og blei forbedra ved å inkludera fluktuasjon i årleg planteplanktonproduksjon. Særleg den fluktuerande biomassen som er karakteristisk for fleire av dei pelagiske bestandane blei meir realistisk gjenskapt ved å inkludera primærproduksjonen, noko som indikerer at botn-opp kontroll er viktig i dette marine systemet. Den sensitive sårbarhetsparameteren blei delvis evaluert gjennom ein samanlikning mellom modellert og observert diettsamansetting hos torsk og hyse. Dietten til torsk blei rimeleg godt gjenskapt i modellen, men dietten for hyse i mindre grad.

Optimalt fisketrykk ved langtidshausting som blei modellert med modellen balansert for år 2000, var konsistent med rådet frå det internasjonale råd for havforsking (ICES) for dei bestandane kor referansepunkt blir estimert.

Summary (English):

We here present a fitted and partly validated Ecopath with Ecosim model for the Norwegian Sea and Barents Sea. Ecopath mass-balance model parameters were obtained from the literature on Norwegian and Barents Sea organisms and from approximations. Predator-prey vulnerability parameters for Ecosim were fitted by driving a past state model balanced for the year 1950 from 1950 to 2000 and comparing the modelled biomass time series with series from VPA and acoustic surveys.

Estimated fishing mortalities or reported catch were used to drive the modelled biomass through the 50-year period. The vulnerability parameters from the fitted 1950 model were then used as input for a simulation model balanced for the year 2000. The fits were reasonably good, and were improved after including fluctuation in the yearly phytoplankton production through a primary production forcing function. The fluctuating biomass trends characteristic for many of the short-lived groups in the model were better reproduced when including the primary production forcing function, suggesting that bottom-up control is important in this marine system. When evaluating the vulnerability parameters through a comparison between modelled and observed diet compositions, the parameter settings seemed reasonable for cod as a predator, but less so for haddock.

The optimal long-term fishing pressure modelled in the model was consistent with advice from the International Council for the Exploration of the Sea (ICES) for the stocks for which values of target reference points are estimated.

Emneord (norsk):	**Subject heading (English):**
1. Ecopath med Ecosim modell	1. Ecopath with Ecosim model
2. Barentshavet og Norskehavet	2. Barents sea and Norwegian sea
3. Botn-opp prosess	3. Bottom-up forcing

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Prosjektleder	Faggruppeleder

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Abstract

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The optimal long-term fishing pressure modelled in the model was consistent with advice from the International Council for the Exploration of the Sea (ICES) for the stocks for which values of target reference points are estimated.

Introduction and aims of the study

The aim of this work was to build two ecosystem models for the Barents Sea and Norwegian Sea, one reflecting the 1950 situation (past state) and one reflecting the 2000 situation (recent state), and fit the historic model to the best obtainable biomass time series for the modelled area. We further aimed at comparing the overall fits when modelling the biomass with and without environmental influence included as a primary production forcing function. Lastly, we wanted to compare the model performance indirectly with the ICES single stock models through evaluating the long term optimal catch curves for selected stocks.

Background: the Barents Sea and Norwegian Sea ecosystems

The Norwegian Sea and Barents Sea are often treated as two discrete ecosystems (Skjoldal, 2004) separated by the continental shelf stretching from the western coast of Spitzbergen to the north Norwegian coast. The Norwegian Sea is a deep-water area with depths exceeding 2000 m in most of the area it covers, whereas the Barents Sea is a shelf area hardly exceeding 500 m in depth (Dommasnes et al., 2001). The Barents Sea is also more of an arctic system than the Norwegian Sea, where the ice is highly influential on the ecosystem dynamics.

Having mentioned the main differences, there is a range of ecological reasons for treating the Norwegian Sea and Barents Sea as one ecosystem in a modelling context. Hydrographically, the areas are tightly linked through the Atlantic and coastal currents running northwards along the

Norwegian coast (Helland-Hansen and Nansen, 1909). Currents transport larvae of key species such as cod, herring, haddock, saithe and redfish from the spawning areas in the Norwegian Sea to the nursery areas in the Barents Sea. As a consequence of the wide geographical distribution, none of the commercial fish stocks dealt with by the ICES are confined to single geographical sub areas within our modelled area. Also, the most important mammal predators, such as minke whale and harp seal use both the Barents Sea and Norwegian Sea as feeding areas and their spatial distribution varies a lot from year to year (Skaug et al., 2004). Our modelled area is similar to the one in the Ecopath model of Dommasnes *et al.* (2001) covering 3,116,000 km^2. It also largely corresponds to the ICES areas I, IIa and IIb (Figure 1).

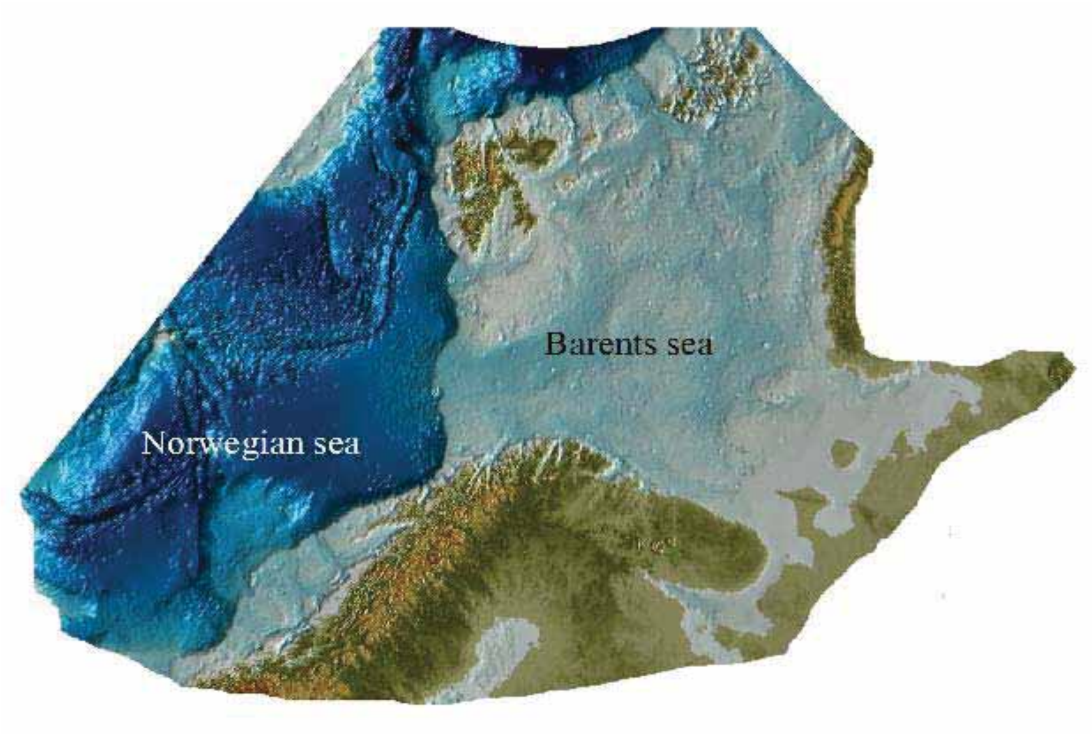


Figure 1. Map of the area included in the model.

Model construction and parameters

Group assemblages

Table 1. Overview of all functional groups (FG) included in the model. In multi-species groups, the species are ranked according to decreasing estimated biomass. P/B, Q/B, Ct and Dt refer to Production/Biomass ratio, Consumption/Biomass ratio, estimated catch and estimated diet respectively. 'X' indicates that the given species contributes in the calculation of that specific parameter value. Note that this is only relevant and listed for functional groups containing more than one species.

FG	Common name *Latin name*	P/B	Q/B	Ct	Dt
1	Minke whale *Balaenoptera acutorostrata*				
2	Sperm whale *Physeter macrocephalus*				
3	Killer whale *Orcinus orca*				
4	Other toothed whales				
	Northern bottlenose whale *Hyperoodon ampullatus*	X	X		X
	White beaked dolphin *Lagenorhynchus albirostri*	X	X		X
	Harbour porpoise *Phocoena phocoena*	X	X		X
5	Other baleen whales				
	Fin whale *Balaenoptera physalus*	X	X		X
	Humpback whale *Megaptera novaengliae*	X	X		X
	Blue whale *Balaenoptera musculus*	X	X		X
6	Harp seal (0) *Phoca groenlandica*				
7	Harp seal (1+) *Phoca groenlandica*				
8	Other seals (0)				
9	Other seals (1+)				
	HarbourSeals *Phoca vitulina*	X	X		X
	GreySeals *Halichoerus grypus*	X	X		X
	HoodedSeals *Cystophora cristata*	X	X		X
10	Atlantic puffin *Fratercula arctica*				
11	Other seabirds[a]				
	Brünnich's guillemot *Uria lomvia*	X	X		X
	Northern fulmar *Fulmarus glacialis*	X	X		X
	Black-legged kittiwake *Rissa tridactyla*	X	X		X
12	NE Arctic cod (0-2) *Gadus morhua*				
13	NE Arctic cod (3+) *Gadus morhua*				
14	Coastal cod (0-2) *Gadus morhua*				
15	Coastal cod (3+) *Gadus morhua*				
16	Haddock (0-2) *Melanogrammus aeglefinus*				
17	Haddock (3+) *Melanogrammus aeglefinus*				
18	Saithe (3+) *Pollachius virens*				
19	Saithe (0-2) *Pollachius virens*				
20	Flatfishes and rays				
	European plaice *Pleuronectes platessa*	X	X	X	
	Long rough dab *Hippoglossoides platessoides*			X	X
	Thornback ray *Raja clavata*	X	X	X[b]	X
	European flounder *Platichthys flesus*			X[c]	
	Common dab *Limanda limanda*			X	
	Brill *Scophthalmus rhombus*			X	
21	Other benthic fish				
	Cusk *Brosme brosme*	X	X	X	X
	Ling *Molva molva*	X	X	X	X
	Pollack *Pollachius pollachius*	X	X	X	
	Monkfish *Lophius piscatorius*	X	X	X	
	Whiting *Merlangius merlangus*			X	
	Eel *Anguilla anguilla*			X	
	European hake *Merluccius merluccius*			X	
	Atlantic halibut *Hippoglossus hippoglossus*			X	
	Blue ling *Molva dypterygia*			X	
22	Greenland halibut (0-4) *Reinhardtius hippoglossoides*				
23	Greenland halibut (5+) *Reinhardtius hippoglossoides*				
24	Deep-sea redfish (0-4) *Sebastes mentella*				
25	Deep-sea redfish (5+) *Sebastes mentella*				
26	Golden redfish (0-4) *Sebastes marinus*				
27	Golden redfish (5+) *Sebastes marinus*				

FG	Common name *Latin name*	P/B	Q/B	Ct	Dt
28	Blue whiting (0-1) *Micromesistius poutassou*				
29	Blue whiting (2+) *Micromesistius poutassou*				
30	Mackerel *Scomber scombrus*				
31	Herring (0) *Clupea harengus*				
32	Herring (1-2) *Clupea harengus*				
33	Herring (3+) *Clupea harengus*				
34	Polar cod *Boreogadus saida*				
35	Capelin (0) *Mallotus villosus*				
36	Capelin (1) *Mallotus villosus*				
37	Capelin (2+) *Mallotus villosus*				
38	Basking shark *Cetorhinus maximus*				
39	Other sharks				
	Spiny dogfish *Squalus acanthias*		X	X	X
	Porbeagle *Lamna nasus*	X		X	X
40	Atlantic salmon *Salmo salar*				
41	Lumpsucker *Cyclopterus lumpus*				
42	Small pelagic fish				
	Greater silver smelt *Argentina silus*	X	X	X	X
	Horse mackerel *Trachurus trachurus*	X	X	X	X
	Norway pout *Trisopterus esmarkii*	X	X	X	X
	Sprat *Sprattus sprattus*			X	
43	Mesopelagic fish				
	Pearlside *Maurolicus muelleri*	X	X		X
	Glacier lanternfish *Benthosema glaciale*	X	X		X
	Arctozenus risso	X	X		X
44	Squid *Gonatus fabricii*				
45	Edible crabs and lobster				
	Edible crab *Cancer pagurus*	X	X	X	X
	European lobster *Homarus gamarus*			X	
	Red king crab *Paralithodes camtschaticus*			X	
46	Corals *Lophelia pertusa*				
47	Other macrobenthos				
48	Prawns *Pandalus borealis*				
49	Krill				
	Meganyctiphanes norvegica	X	X	X	X
	Thysanoessa inermis	X	X	X	X
	Thysanoessa longicaudata	X	X	X	X
50	Pelagic amphipods				
	Themisto libellula	X	X	X	X
	Themisto abyssorum	X	X	X	X
	Themisto compressa	X	X	X	X
51	Calanus				
	Calanus finmarchicus	X	X	X	X
	Calanus hyperboreus	X	X	X	X
52	Zooplankton 2mm+				
53	Zooplankton 0-2mm				
54	Jellyfish *Periphylla periphylla*				
55	Seaweeds				
56	Wolffishes				
	Common *Anarhicus lupus*	X	X	X	X
	Spotted *Anarhicus minor*	X	X	X	X
	Northern *Anarhicus denticulatus*	X	X	X	X
57	Phytoplankton				
58	Detritus				

[a] Only the three most important consumers of a total of 18 species making up the functional group are listed
[b] Listed as 'Rays' in the ICES Catch Statistics Database
[c] Listed as 'Flatfishes' in the ICES Catch Statistics Database

We built two models, one ‘past state’, balanced for the year 1950 and one ‘recent state’ balanced for the year 2000. The models have identical functional groups, but the past state model was used for fitting the observed time series data. The vulnerability parameter settings from the fitted past state model were then applied in the recent state model, and the recent state model was used to compare the catch curves.

Altogether 58 groups were included in the models as listed in Table 1, some consisting of a single species or just a specific age group of a single species, others of many species combined having similar ecological niches.

Ten of the fish species were split into separate juvenile and adult groups, or stanzas (Table 3). Juveniles usually have a different mortality and consumption rate than adults, and for most of the split groups in our models both geographical distribution and overlap with potential predators differ markedly between the juveniles and the adults. More detailed information about the ecology of the important species inhabiting these systems can be found in Dommasnes *et al.* (2001) and Blanchard *et al.* (2002) in their model descriptions of the Norwegian Sea/Barents Sea and the Barents Sea, respectively, with functional groups similar to those presented here.

Biomass estimates, production, consumption and growth

The estimated biomass per unit area was based on five-year averaged biomass estimates whenever available from 1950-54 in the past state model and 1997-2001 in the recent state model (Table 2). In a few cases the value of biomass per area had to be reduced because the given species is not present in the model area during an entire year.

The minke whale, blue whale, bottlenose whale, hooded seal and harp seal were all assumed to spend half of the year within the model area (Dommasnes et al., 2001) and the Atlantic puffin two-thirds of the year (Barrett et al., 2002). The main spawning area of the blue whiting is west of the British Isles and we assumed the stock to be present for two-thirds of the year within our model area. We further assumed that half of the mackerel stock stays in the model area for a quarter of the year (Dommasnes et al., 2001). Average body weights used when calculating biomass of the whales were taken from Sigurjonsson and Vikingsson (1997). For a few fish groups biomass estimates were lacking, but catches were known and major declining trends in the stocks were known to be a result of high exploitation rates. This was true for the lumpsucker, basking shark, other sharks and other benthic fish. In each of these cases ‘sensitivity analyses’ were done, by keeping the Production/Biomass (P/B) and Consumption/Biomass (Q/B) ratios and diet matrix constant and changing the initial biomass until the fish reacted to the fishing pressure in an adequate way.

Most of the Q/B and P/B ratios were derived from the literature (Table 2), and the Q/B ratio for North East Arctic cod was based on mean consumption from 1984 to 1999 calculated in Bogstad *et al*. (2000). In a few cases the parameter values were calculated based on the equations below:

Consumption/Biomass (Q/B):

$$Q/B = 10^{6.37} \cdot 0.0313^{Tk} \cdot W_{\infty}^{-0.168} \cdot 1.38^{Pf} \cdot 1.89^{Hd} \qquad [1]$$

where W_∞ is the asymptotic weight (g) of the fish, *Tk* is the mean annual water temperature (=1000/Kelvin), *Pf* is one for apex predators, pelagic predators and zooplankton feeders and zero for all other groups while *Hd* is set at one for herbivores and zero for carnivores (Christensen and Pauly, 1992).

Table 2. Basic parameter values. P/B_{mod} and Q/B_{mod} are the final values of Production/Biomass and Consumption/ Biomass ratios used in the model after completing mass-balancing and time series fitting. P/B_{ref} and Q/B_{ref} are the reference parameter values as they are given in the literature. In cases where no change was done from the original reference value only P/B_{mod} and Q/B_{mod} are listed. Left and right columns show values used in the past state model and the r-model respectively. The 2000-values are only listed when different from the 1950-values. Values in italics are calculated in Ecopath and values in bold are modified during the balancing and fitting process.

	FG	Biomass/Area (t/km^2)		P/B_{mod}		P/B_{ref}	Q/B_{mod}	Q/B_{ref}	Reference
1	**Minke whale**	0.0589[1]	(0.0550)	0.07[16b]	(0.04)		8.14[23]		1 (Skaug et al., 2004)
2	**Sperm whale**	0.0455[2]		0.02[16]			4.55[16]		2 (Christensen et al., 1992)
3	**Killer whale**	0.0037[3]		0.02[16]			12.75[16]		3 (NAMMCO, 1998)
4	**Other toothed whales**	0.0202[4,5,6]		0.02[16]			12.75[16]		4 (Øien, 1993)
5	**Other baleen whales**	0.0605[3]		0.02[16]			14.6[16]		5 (Bjørge and Øien, 1995)
6	**Harp seal (0)**	*0.0053*	*(0.0035)*	**0.5**	**(0.3)**		*16.49*		6 (Skjoldal, 2004)
7	**Harp seal (1+)**	0.0668[7]	(0.0800)	0.1[16b]	(0.06)		15[7]		7 (Dommasnes et al., 2001)
8	**Other seals (0)**	*0.0018*	*(0.0018)*	**0.6**	**(0.35)**		*14.68*		8 (Barrett et al., 2002)
9	**Other seals (1+)**	0.022[7]		0.15[16b]	(0.11)		13.33[7]		9 (ICES, 2004a)
10	**Atlantic puffin**	0.0007[8]		1[17]			160[8]		10 (ICES, 2002)
11	**Other seabirds**	0.0042[8]		1[17]			112.32[8]		11 (ICES, 2004b)
12	**NE Arctic cod (0-2)**	*0.3015*	*(0.1640)*	**1.4**			*8*		12 (Michalsen, 2004)
13	**NE Arctic cod (3+)**	1.1[9]	(0.4150)	**0.5**	(0.6)	0.6[17c]	2.82[23]		13 (Sakshaug, 1997)
14	**Coastal cod (0-2)**	*0.0439*	*(0.0150)*	**1.4**			*8*		14 (Mortensen, P.B. pers. comm.)
15	**Coastal cod (3+)**	0.16[9]	(0.0530)	**0.5**	(0.6)	0.6[17c]	2.82[23]		15 (Dalpadado et al., 1998)
16	**Haddock (0-2)**	*0.0531*	*(0.0300)*	**1.5**			*7.95*		16 (Trites et al., 1999)
17	**Haddock (3+)**	0.153[9]	(0.0700)	**0.5**	**(0.65)**	0.6[17c]	2.82[7]		17 (Blanchard et al., 2002)
18	**Saithe (3+)**	**0.2778[9]**	**(0.2600)**	**0.45**		0.467[7]	4.88[7,24]		18 (Howell and Nedreås, 2005)
19	**Saithe (0-2)**	*0.0642*	*(0.0650)*	**1**			*11.95*		19 (Dommasnes, 2002)
20	**Flatfishes and rays**	*0.1132*	*(0.0772)*	**0.5**		0.27[17]	2.9[7,25,26]		20 (Mackinson, 2002)
21	**Other benthic fish**	0.08[a]	(0.0400)	**0.6**		0.25[17]	1.74[Eq1,Eq2]		21 (Hopkins, 1988)
22	**Greenland halibut (0-4)**	*0.0184*	*(0.0070)*	**0.9**			*6.77*		22 (Pauly and Christensen, 1996)
23	**Greenland halibut (5+)**	0.0629[9]	(0.0230)	**0.25**	**(0.3)**	0.42[Eq3]	2.03[Eq1,Eq2]		23 (Bogstad et al., 2000)
24	**Deep-sea redfish (0-4)**	*0.1567*	*(0.0150)*	**1.9**	**(1.8)**		*11.52*		24 (Pauly, 1978)
25	**Deep-sea redfish (5+)**	0.257[10]	(0.0470)	0.1[10]	**(0.18)**		2[Eq2]		25 (Palomares and Pauly, 1989)
26	**Golden redfish (0-4)**	*0.0513*	*(0.0540)*	**1.3**	**(1.7)**		*7.27*		26 (Holden, 1972)
27	**Golden redfish (5+)**	0.128[9]	(0.0550)	**0.2**		0.1[18]	2[Eq2]		27 (Cubillos and Arancibia, 1995)
28	**Blue whiting (0-1)**	*0.0738*	*(0.1720)*	**2.5**			*26.3*		28 (Gjøsæter, 1973)
29	**Blue whiting (2+)**	0.58[11]	(0.9300)	**0.5**	**(0.55)**	0.6[7]	7.53[7,24]		29 (Gjøsæter and Kawaguchi, 1980)
30	**Mackerel**	0.252[11]	(0.1690)	0.6[7]	**(0.7)**		5.2[7,24]		30 (Muus and Nielsen, 1999)
31	**Herring (0)**	*1.18*	*(0.5580)*	**8**			*39.92*		
32	**Herring (1-2)**	*2.93*	*(1.4050)*	1.52[19]			*9.83*		
33	**Herring (3+)**	5.5[11]	(2.7460)	0.49[19]			4.47[7]		
34	**Polar cod**	0.32[7]	(0.2550)	1.5[7]			5[7]		
35	**Capelin (0)**	*0.2164*	*(0.3670)*	**6**			*21.34*		
36	**Capelin (1)**	*0.5892*	*(0.6740)*	**1.2**			*7.83*		
37	**Capelin (2+)**	1.5[12]	(0.6500)	**1.3**	**(1.6)**	1.0[7]	4.7[17]		
38	**Basking shark**	0.05[a]	(0.0039)	**0.08**		0.16[Eq3]	3.7[24]		
39	**Other sharks**	0.03[a]		0.2[20]			2.80[Eq1]		
40	**Atlantic salmon**	0.0048[6]	(0.0020)	0.6[17c]	**(0.68)**		7.14[17]		

Table 2 cont.

41	**Lumpsucker**	0.075[a]	(0.0140)	**0.3**	**(0.35)**	0.26[Eq3]	1.7[24]		
42	**Small pelagic fish**	*0.2198*	*(0.2000)*	**1**	**(1.1)**	0.7[Eq3]	5.43[Eq1,7,24,27]		
43	**Mesopelagic fish**	1.84[13]		**1.35**	**(1.5)**	1.27[Eq3,7]	8.7[Eq1,28,29,30]		
44	**Squid**	2.63[7]		2.44[7]			10[17c]		
45	**Edible crabs and lobster**	*0.1651*	*(0.1486)*	2.5[20]			5.85[24]		
46	**Corals**	0.0024[14a]		1			12[14]		
47	**Other macrobenthos**	66[7]		1.5[7]			9.75[7]		
48	**Prawns**	0.3[7]	(0.2780)	1.7[21]			5[7]		
49	**Krill**	30.455[15]		1.6[6]			9[6]	8.2	
50	**Pelagic amphipods**	16[7]		**2**		1.3[6]	6.5[6]		
51	**Calanus**	45.45[6]		**7.1**		5.8[6]	22[6]	30	
52	**Zooplankton 2mm+**	13.63[6]		4[7]			17[7]	15	
53	**Zooplankton 0-2mm**	21.45[6]		10[7]			25[7]		
54	**Jellyfish**	4[7]		**4.2**		3[22]	10[22]		
55	**Seaweeds**	4.4[7]		0.65[7]					
56	**Wolffishes**	*0.1128*	*(0.1601)*	0.35[17]			1.77[17]		
57	**Phytoplankton**	15[7]		117.7[7]					
58	**Detritus**	100							

[a] Biomass value from 'sensitivity analyses' (see comments in the text)

[b] Fishing mortality added to the reference value

[c] Value based on their balanced model

We also estimated Q/B from

$$\log_{10}(Q/B) = 7.964 - 0.204 \cdot \log_{10} W_\infty - 1.965 \cdot Tk + 0.083 \cdot A + 0.532 \cdot h + 0.398 \cdot d \qquad [2]$$

where A is the aspect ratio of the caudal fin of the fish, h is a dummy variable (1 for herbivores and 0 for detrivores and carnivores) and d is a dummy variable expressing food type (1 for detrivores, and 0 for herbivores and carnivores) (Palomares and Pauly, 1998).

Table 3. Main parameters used when splitting functional groups into multi-stanzas. K is the curvature parameter in the von Bertalanffy's growth function. Wt_{mat}/Wt_{inf} is the ratio between weight at maturity and asymptotic weight. Age at transition is the age in months for the transition from one stanza to the next.

FG		K	Wt_{mat}/Wt_{inf}	Age at transition	Reference
6,7	Harp seal	6*	0.09*	12	1 (Pauly, 1978)
8,9	Other seals	6*	0.09*	12	2 (Beverton and Holt, 1959)
12,13	NE Arctic cod	0.15[1]	0.27[2]	32	3 (Nedreås, K., IMR, pers. comm.)
14,15	Coastal cod	0.15[1]	0.27[2]	32	4 (Howell and Nedreås, 2005)
16,17	Haddock	0.15[1]	0.29[1,6]	32	5 (Raitt, 1966)
18,19	Saithe	0.19[2]	0.29[2]	32	6 (ICES, 2004a)
22,23	Greenland halibut	0.056[1]	0.1[7*]	56	7 (Muus and Nielsen, 1999)
24,25	Deep-sea redfish	0.13[3]	0.37[6]	56	8 (Jennings et al., 1998)
26,27	Golden redfish	0.11[4]	0.37[6]	56	9 (Gjøsæter, 1998)
28,29	Blue whiting	0.23[5]	0.31[8]	20	
31-33	Herring	0.23[2]	0.5[2,6]	9,33	
35-37	Capelin	0.45[1]	0.9[9]	9,21	

Production/Biomass (P/B):

The natural mortality (M) can be calculated according to Pauly (1980) as:

$$\log_{10} M = -0.2107 - 0.0824 \log_{10} W_\infty + 0.6757 \log_{10} k + 0.4687 \log_{10} Tk \qquad [3]$$

where k is the curvature parameter of the von Bertalanffy's growth function. We found total instantaneous mortality (Z) by assuming that

$$P/B = Z \qquad [4]$$

and

$$Z = M + F \quad [5]$$

where F is fishing mortality (Table 3) (Allen, 1971).

Time series of biomass and catch

An overview of the groups for which there are time series data is given in Table 4. A few of the time series need a little further explanation. There is relatively little knowledge about the species in the group ‘other benthic fish’, not even enough to identify the stocks (Michalsen, 2004). However, CPUE indexes from Iceland show a 70 % reduction of tusk, ling and blue ling over the last 20 years, and we estimated that the 2000-biomass of the group ‘other benthic fish’ had been reduced to half of what it was in 1950. For deep-sea redfish, the fishery within the model area before 1965 was marginal (ICES, 2004), and we assumed an unexploited biomass of 800,000 tons for this stock from 1950 to 1965 (Nedreås, K., IMR, pers. comm.). The fishery for golden redfish has been continuous and unregulated since the start of the century (ICES, 2004a). The 1950-biomass is therefore not the unexploited biomass, but assumed to be 400,000 tons and 270,000 tons in 1985 (Nedreås, K., IMR, pers. comm.). The working group report for Atlantic salmon presents return data on Multi Sea-Winter (MSW) salmon for Norway (ICES, 2004c) and these data were used here as indices of biomass for the period 1983-2001.

The main coral species in our modelled area and the only one included here is *Lophelia pertusa.* The extensions of all coral ‘areas’ along the Norwegian coast are given in Fosså *et al*. (2002). A more detailed description estimates that 35 km^2 of one particular part of this area is physically part of *Lophelia* reefs (Mortensen et al., 2001). This particular part covers half of the distribution within our model area, and the *Lophelia* amount in the other half is estimated to be 80 % of the amount from the first half (Fosså et al., 2002; Mortensen and Fosså, 2001). The ratio of living to total coral biomass in a reef is about 2 to 10 (Mortensen, P.B., IMR, pers. comm.). We subtracted the areas that are assumed destroyed by fishing (Fosså et al., 2002; Mortensen and Fosså, 2001) and assumed that 50 % of the areas referred to as ‘destroyed’ are completely gone. We used an average value of ash-free dry weight of living tropical corals on a reef from Fitt *et al*. (2000) of 50 tons/km^2, and a conversion factor of 15 from dry ash weight to wet weight (Skjoldal, 2004). In total this added up to 7,460 tons wet weight or 0.0024 tons per km^2 within the model area.

Only the biomass time series considered to be the most reliable were used in the fitting process (Table 4). Time series of fishing mortality were taken from working group reports whenever available. For other groups targeted by fishery we used catch data from the ICES Fisheries Statistics Database for the ICES areas I, IIa and IIb available at http://www.ices.dk/products/fishstats.asp.

The time series on fishing mortalities and catch were used to drive the 1950-model from 1950 to 2000. Separate fishing mortalities are given for each age group in the reports and we used a mean value weighted according to the biomass at age from the VPA runs.

The coastal cod makes up a separate stock that differ genetically from the North East Arctic cod (ICES, 2004a). In fact there are probably several distinct stocks of coastal cod, but treated as one group here. The distribution of coastal cod overlaps with that of NE Arctic cod and the traditional fishery for spawning NE Arctic cod has been targeting the coastal cod as well. Investigations of otoliths from the last 15 years show that the fishing pressure on coastal cod is highly related to that on NE Arctic cod (ICES, 2004a), and we assume the fishing mortality for coastal cod and NE Arctic cod to be the same in the modelled years before separate time series for the two stocks were available (i.e. prior to 1984).

The time series of capelin biomass was based on acoustic biomass estimates for the years 1973 to the present. Before 1973 the biomass values were adapted from Marshall *et al*. (2000) also used in Gjøsæter (1998). The authors used the frequency of occurrence of capelin in cod stomachs to estimate capelin abundance. This method is not accurate, but the fluctuations correspond well with scattered CPUE data from the period and low periods of capelin documented by fishermen (Gjøsæter, 1998).

Biomass accumulation

A biomass accumulation of zero for all the groups in the Ecopath model is the same as assuming steady-state with the same biomass at the start and at the end of the modelled year. In this study, biomass accumulation values were calculated as the biomass in one year less biomass previous year averaged over 5 years; the sources used were the same as for the biomass time series given in Table 4. The values of biomass accumulation are given in Table 5.

Table 4. Overview of the biomass time series applied. The time series are listed with the time span for which there are data including reference and source of the time series, and the column to the right contains an ‘x’ if the time series was used in the fitting of the vulnerability parameter.

FG		Time span	Source	Used in fitting	Reference	
1	Minke whale	50-01[1]	Modelled		1	(Bjørndal and Conrad, 1998)
7	Harp seal (1+)	50-01[2]	Modelled		2	(ICES, 2005)
12	NE Arctic cod (0-2)	50-01[3]	0-group index		3	(Anon., 2002)
13	NE Arctic cod (3+)	50-01[4]	VPA	X	4	(ICES, 2004a)
15	Coastal cod (3+)	84-01[4]	VPA	X	5	(Michalsen, 2004)
16	Haddock (0-2)	50-01[3]	0-group index		6	(ICES, 2002)
17	Haddock (3+)	50-01[4]	VPA	X	7	(Howell and Nedreås, 2005)
18	Saithe (3+)	64-01[4]	VPA	X	8	(ICES, 2004b)
19	Saithe (0-2)	60-01[4]	VPA		9	(ICES, 2004c)
21	Other benthic fish	Endpoints[5]	CPUE		10	(Bjelland, O. IMR, unpublished results)
22	Greenland halibut (0-4)	70-01[3]	0-group index		11	(Ponomarenko and Yaragina, 1979)
23	Greenland halibut (5+)	64-01[4]	VPA	X		
24	Deep-sea redfish (0-4)	65-01[3]	0-group index			
25	Deep-sea redfish (5+)	91-01[6]	VPA	X		
27	Golden redfish (5+)	90-01[7]	VPA	X		
29	Blue whiting (2+)	81-01[8]	VPA	X		
30	Mackerel	72-01[8]	VPA	X		
31	Herring (0)	50-01[8]	VPA			
32	Herring (1-2)	50-01[8]	VPA			
33	Herring (3+)	50-01[8]	VPA	X		
34	Polar cod	86-01[5]	Acoustic survey	X		
35	Capelin (0)	65-01[3]	0-group index			
36	Capelin (1)	73-01[5]	Acoustic survey			
37	Capelin (2+)	50-00[5*]	Acoustic survey	X		
40	Atlantic salmon	83-01[9]	Recaptured 2SW	X		
41	Lumpsucker	88-01[5]	CPUE	X		
43	Mesopelagic fish	90-99[10]	MOCNESS survey			
48	Prawns	82-01[5]	Trawl survey	X		
49	Krill	50-76[11]	Trawl survey			

Diets

The diets for the functional groups were derived from the literature and are given in Annex Tables 1a-c. The diet for NE Arctic cod was based on mean consumption from 1984 to 1999 given in Bogstad *et al*. (2000). Similarly, the haddock diet is an average over the years 1984-1999 weighted after the number of stomachs sampled (Dolgov, 2000). The diet of saithe was also derived from Dolgov (2000) for the Barents Sea, but we allowed the contribution from herring in the diet to be higher as saithe in the Norwegian Sea are known to feed extensively on herring and even migrate along with herring schools (Pitcher et al., 1996). Dolgov (2000) also gives the diet of long rough dab from 89-99 and thornback ray from 94-99; we used an average weighted after number of stomachs and estimated biomass of each of the species as diet input for the ‘Flatfishes and rays’ group (Table 1). The diet of the white beaked dolphin is unknown (Dommasnes et al., 2001), but according to stable isotope measurements, they have a similar trophic level to that of gadoids (Das et al., 2003), and we have assumed the same diet as for cod.

Table 5. Functional groups where biomass accumulation values differ from zero in either the 1950- or the 2000-model. Values in italic are calculated in Ecopath, and blank boxes indicate a biomass accumulation of zero.

FG		Biomass accumulation	
		1950	2000
1	Minke whale	0.00100	
3	Killer whale	0.00005	
8	Other seals (0)	*-0.00009*	
9	Other seals (1+)	-0.00110	
12	NE Arctic cod (0-2)		*0.00131*
13	NE Arctic cod (3+)		0.00332
14	Coastal cod (0-2)		*-0.00168*
15	Coastal cod (3+)		-0.00583
16	Haddock (0-2)	*0.00159*	*-0.00052*
17	Haddock (3+)	0.00459	-0.00119
18	Saithe (3+)	0.01111	0.01482
19	Saithe (0-2)	*0.00257*	*0.00369*
21	Other benthic fish		-0.00300
22	Greenland halibut (0-4)	*0.00092*	*0.00015*
23	Greenland halibut (5+)	0.00314	0.00046
24	Golden redfish (0-4)	*-0.00103*	*-0.00152*
25	Golden redfish (5+)	-0.00256	-0.00469
26	Deep-sea redfish (0-4)		*-0.00107*
27	Deep-sea redfish (5+)		-0.00109
28	Blue whiting (0-1)		*0.00862*
29	Blue whiting (2+)		0.04650
30	Mackerel		0.00400
31	Herring (0)		*-0.00558*
32	Herring (1-2)		*-0.01405*
33	Herring (3+)		-0.02746
34	Polar cod		-0.02500
35	Capelin (0)	*-0.04328*	*0.10283*
36	Capelin (1)	*-0.11785*	*0.18861*
37	Capelin (2+)	-0.30000	0.18200
39	Other sharks	-0.00100	
40	Atlantic salmon		0.00040
41	Lumpsucker		-0.00200
48	Prawns		-0.02900

Fitting modelled biomass to observation time series

Ecosim produces a goodness-of-fit measure as a weighted sum of squared deviations (SS) of log observed biomasses from log predicted biomasses, and a lower SS implies a better overall fit to the data. The 15 observed reference biomass time series we included when fitting the modelled time series are given in Table 4.

Our fitting of modelled to observed biomass time series for the groups was done in two steps:

1) Adjusting the P/B and Q/B ratios and diet matrix for the functional group to respond adequately to historic fishing pressure.

For several functional groups in our modelled ecosystem, mortality due to fishing is known to be a main cause of specific historic decreasing trends in biomass (Michalsen, 2004). In such cases the fishing mortality should constitute a large proportion of the total mortality for the given group. The natural mortality of a functional group is normally a poorly-known parameter, and if it is put too high the effect of the fisheries will be underestimated or masked. We altered the relative proportion of the fishing mortality to the total mortality by changing predation mortality either through modifying the proportion of the target species in the diet of the main predators or through altering the Q/B of the main predators. Alternatively we modified the P/B, which will change the ratio

between fishing mortality and other mortality. The groups for which initial values of P/B or Q/B were changed are marked with bold font in Table 2.

2) Searching for the set of vulnerabilities for the modelled predator-to-prey interactions giving the best fit to data.

The consumption of a given prey by a given predator in Ecosim simulations is a function of the biomass of both groups and a theoretical flow rate at which the prey moves from an invulnerable to a vulnerable state. The value of the flow rate is commonly termed the vulnerability of the prey to a predator and given as:

$$v_{ij} = v'_{ij} . Q_{ij} / B_i, \quad [6]$$

where Q_{ij} is the Ecopath baseline estimate of the consumption of the species i by species j and B_i is the biomass of i. The vulnerabilities can be given values from 1 to infinity, with low values generating bottom-up and high values top-down control. A lower SS implies a better overall fit to the data. The default value in Ecosim is 2. The first step of the fitting procedure, namely adjusting P/B and Q/B ratios and diet matrix mentioned in the previous section, was done with all vulnerabilities set at 2 (default setting), creating a mixed control between predator and prey.

The second step included a search for the set of vulnerabilities giving the best fit to observed data measured as the lowest overall sum-of-squares with reference to the 15 observed time series listed in Table 4. The output value is given as SS1 in Table 6. The robustness of this vulnerability setting was then evaluated using the same vulnerability values but with reference to all the 29 biomass time series given in Table 4. The second output value is referred to as SS2 in Table 7. Note that the 14 new biomass time series added the SS2 were only used to evaluate the parameter settings, and not used in the search procedure to improve the goodness-of-fit.

A Marquardt non-linear search algorithm is applied in Ecosim to find the set of vulnerabilities giving the best fit to data. The search space is defined by the user, and all from one to all single predator-prey interactions in the model may be included. The number of possible combinations of parameter values will increase exponentially with increasing search space and we wanted to keep the search relatively simple by investigating three limited spaces as shown in Table 6.

Table 6. Overview of sum of squared deviations (SS) from the fitting of the model using different search spaces to find optimal vulnerability settings. PP anomaly is a primary production driver generated by the model. \`Fitting\` indicates the specific search space applied. \`SS1\` marks the SS-value obtained during fitting to the 15 functional reference groups while\`SS2\` is calculated using the same set of vulnerabilities but with all the time series given in Table 4 included (N=29). NI is indicated when no improvement was obtained during the fitting procedure.

PP anomaly	Fitting	SS1	SS2
No	None*	274	1443
No	15 cells	245	1455
No	By rows	177	970
No	By columns	NI	
Yes	By rows	156	948

* The default vulnerability value of 2 applied for all interactions

The first included the 15 cells most sensitive to a change in value, i.e., the 15 specific predator-prey interactions for which a change in the vulnerability parameter will improve the overall sum-of-squares the most. The second search space assigns one specific vulnerability value to each of the 45 prey groups in the model and the third assigns one specific value to each of the 56 predator groups, both searching for the combination of vulnerabilities giving best overall fit to observed biomass time series.

In addition to fitting the past state model to time series through altered vulnerabilities, we wanted to add an environmental variable. Ecosim provides the opportunity to add forcing functions that drive the biomass of functional groups. The phytoplankton group is likely to be extremely important and we wanted to drive the model with a primary production forcing function determining the yearly biomass of phytoplankton for the years 1950 to 2000.

There are no phytoplankton time series for this whole period from our model area, so we used an Ecosim search routine to find the primary production forcing function giving the best fit to observed data for the 15 reference biomass time series. Hence, the forcing function was generated through the fitting process, and is not a real environmental anomaly.

Results of the fitting process

When using 15 cells in the search space the SS1 decreased by about 10 % from the default vulnerability setting (Table 6). When searching by prey (rows) the SS1 decreased by about 35 %, and no improvement was obtained when searching by predators (columns). We therefore used the vulnerability parameter values from the fitting by rows as input for the 2000-model. When including the primary production anomaly to the model fitted by rows, the fit was further improved to a SS 43 % lower than with the default setting.

The generated primary production anomaly was significantly positively correlated with the NAO winter index, the temperature of the Kola section and the average sea surface temperature in the Barents Sea (Figure 2).

Overall, the modelled biomass time series fluctuated more with the primary production driver than without it (Figures 3 and 4). This was particularly pronounced for the short-lived groups like the plankton and the capelin, shrimp and polar cod. Through mere fitting of the vulnerability parameter we were not able to recreate biomass fluctuations similar to the ones present in the observed biomass time series.

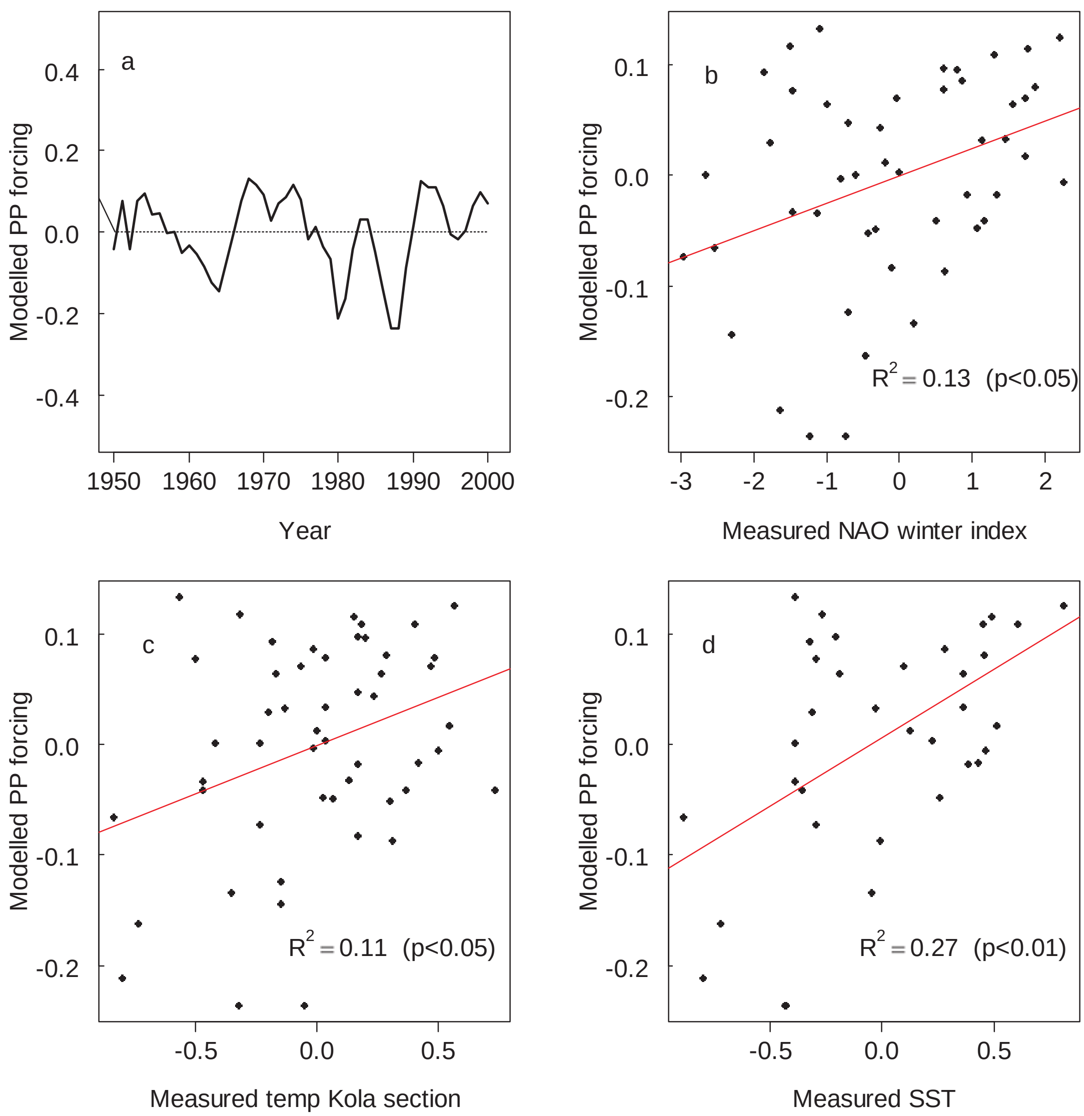


Figure 2. The primary production forcing function smoothed over three years generated by Ecosim using the past state model (balanced for the year 1950) is shown in Fig 2a. The modelled primary production is plotted against b) A 3-year smoothed time series of mean winter North Atlantic Oscillation (NAO) index values from the months December-March. c) A 3-year smoothed time series of annual mean temperatures at the Kola section. d) Average sea surface temperatures from the 0-group survey in the Barents Sea for 1965-2000. The fitted line from a linear least square regression is shown in red on figs. b-d with associated R^2 and p-values denoted in each panel.

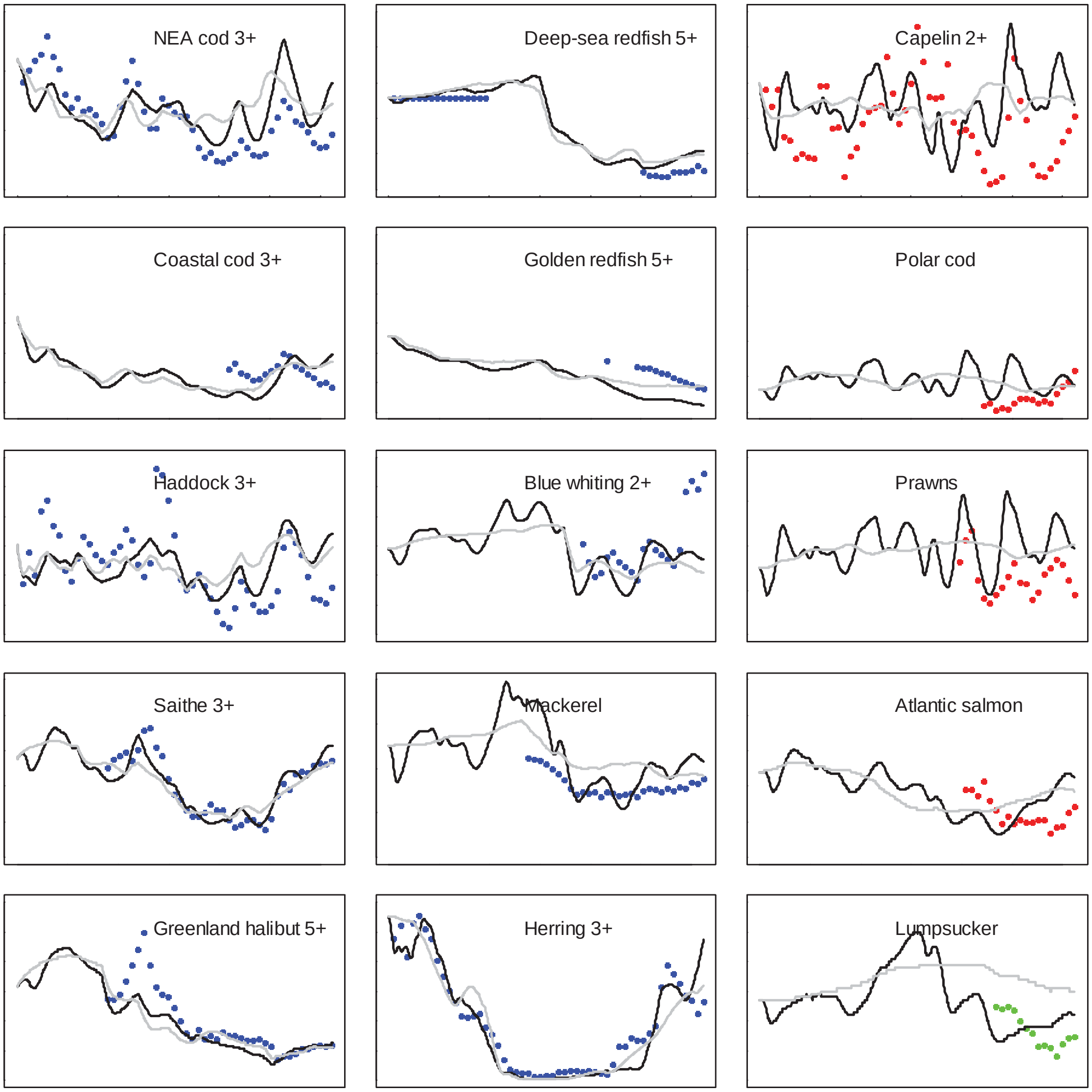
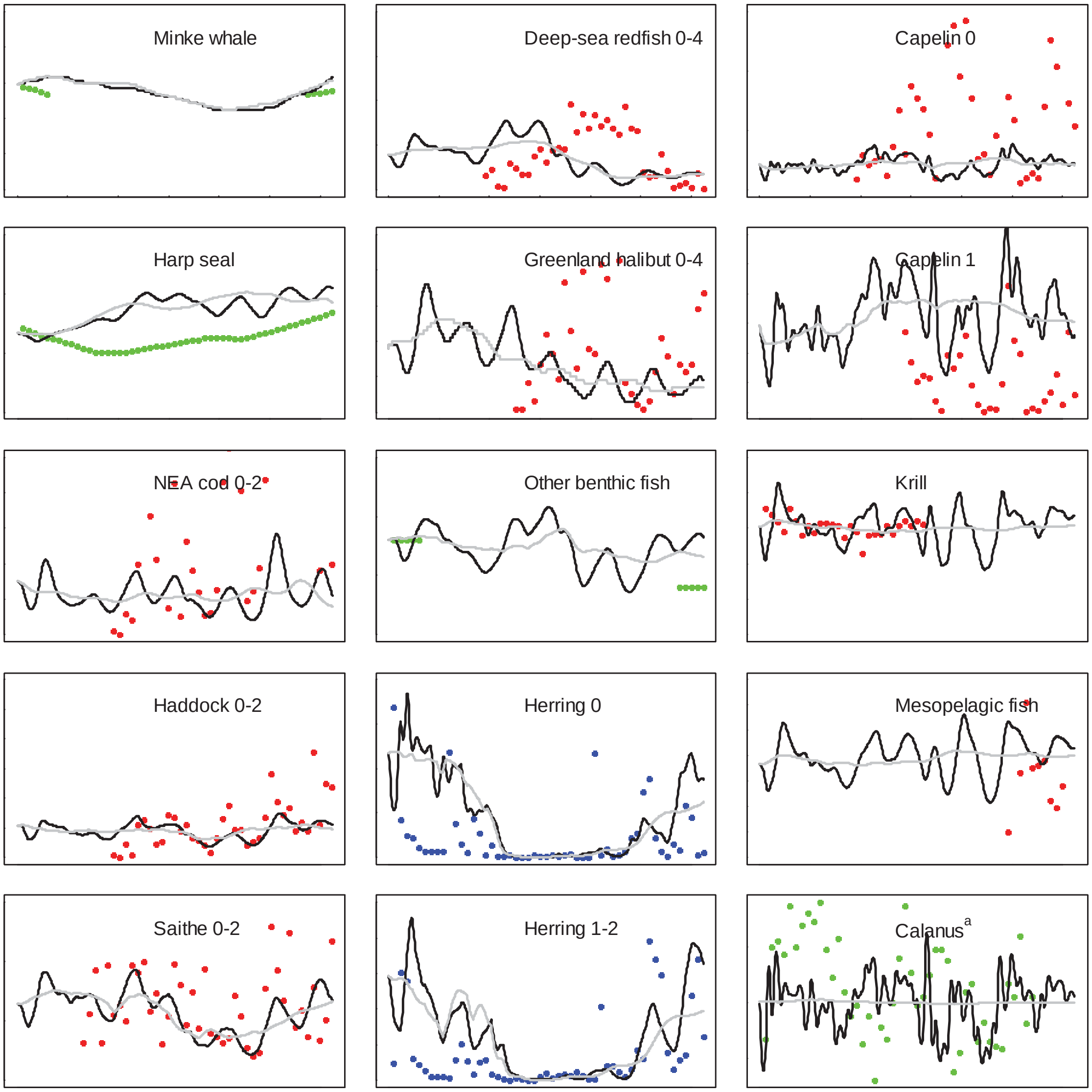


Figure 3. Time series fit for the past state model for the period 1950-2001 for the 15 functional groups included in the fitting of the vulnerability parameter. The past state model (balanced for the year 1950) was used in the fitting process. Dotted line marks the modelled biomass without production anomaly. Black line marks modelled biomass including production anomaly. The dots mark observed biomass with blue dots indicating estimated biomass time series from VPA, red dots from surveys and green dots from CPUE data.



[a]Biomass time series not included when calculating SS2

Figure 4. Modelled versus observed abundance for the period 1950-2000 for the extra abundance time series included to calculate the SS2 (see text for details). Grey line marks the modelled biomass without production anomaly. Black line marks modelled biomass with production anomaly. The dots mark observed biomass with blue dots indicating biomass time series from VPA, red dots from surveys and green dots modelled biomass in the case of the whales, CPUE data in the case of benthic fish and relative abundance index from historical data on herring condition in the case of *Calanus*.

Validation of the vulnerability parameters for some predator-prey interactions

There are time series of stomach content from 1984-1999 for both NE Arctic cod and haddock. They show that the diets are dominated by capelin, herring and large plankton such as krill and amphipods (Fig 5). For cod, the proportion of capelin is high in years with high capelin abundance, and they alter the diet to constitute more of plankton when the abundance of fish prey is low. This trend was also reflected in our modelled cod diet even though the variation in the observed diet was higher (Fig 5). The coherence between modelled and observed data is a good indication that the vulnerability settings for the interactions between cod and capelin, herring, amphipods and krill, respectively, are reasonable. The exclusion of plankton in the diet in capelin and herring rich years is less pronounced in haddock suggesting that this is a more selective feeder or it feeds on alternative prey in years with low abundance of fish prey. Our modelled haddock diet, however, is fairly similar to the modelled cod diet and does not reflect well the yearly changes in diet.

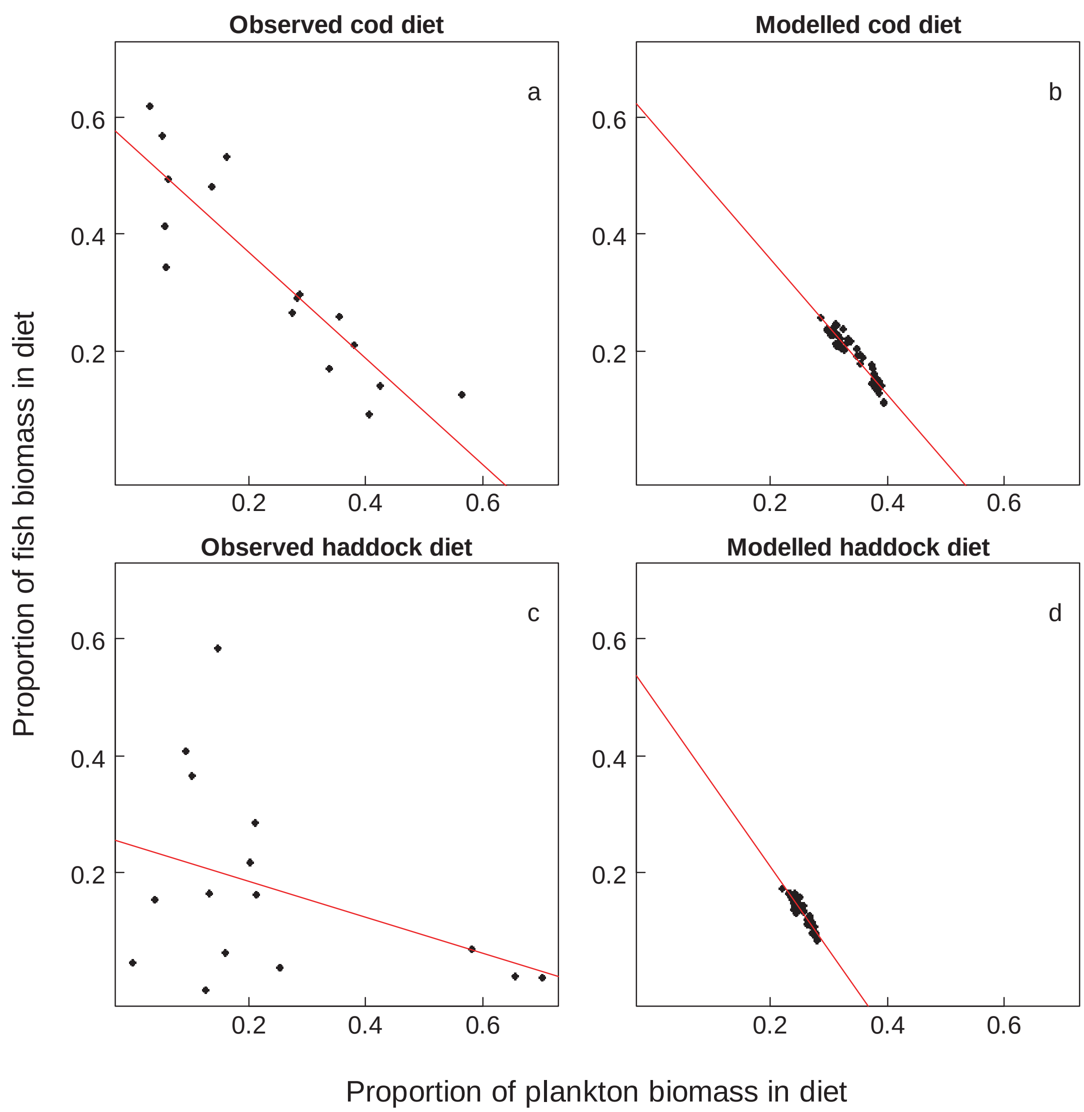


Figure 5. Observed and modelled diets of cod and haddock. The regression line is indicated.

Comparison of catch curves

A rough, partial validation of our model performance in comparison with the single stock models applied by the ICES working groups could be made through a comparison between our modelled single species catch curves and the ICES target reference level F_{lim}. This reference level is defined as the catch level above which long-term recruitment is believed to be impaired (Fig 6). The recent state model was applied and there seemed to be a fairly good consistency between the models for the six fish stocks for which the F_{lim} is provided. In general our model seemed to be a little bit more generous towards high fishing pressures than the ICES models from which the F_{lim} values were derived.

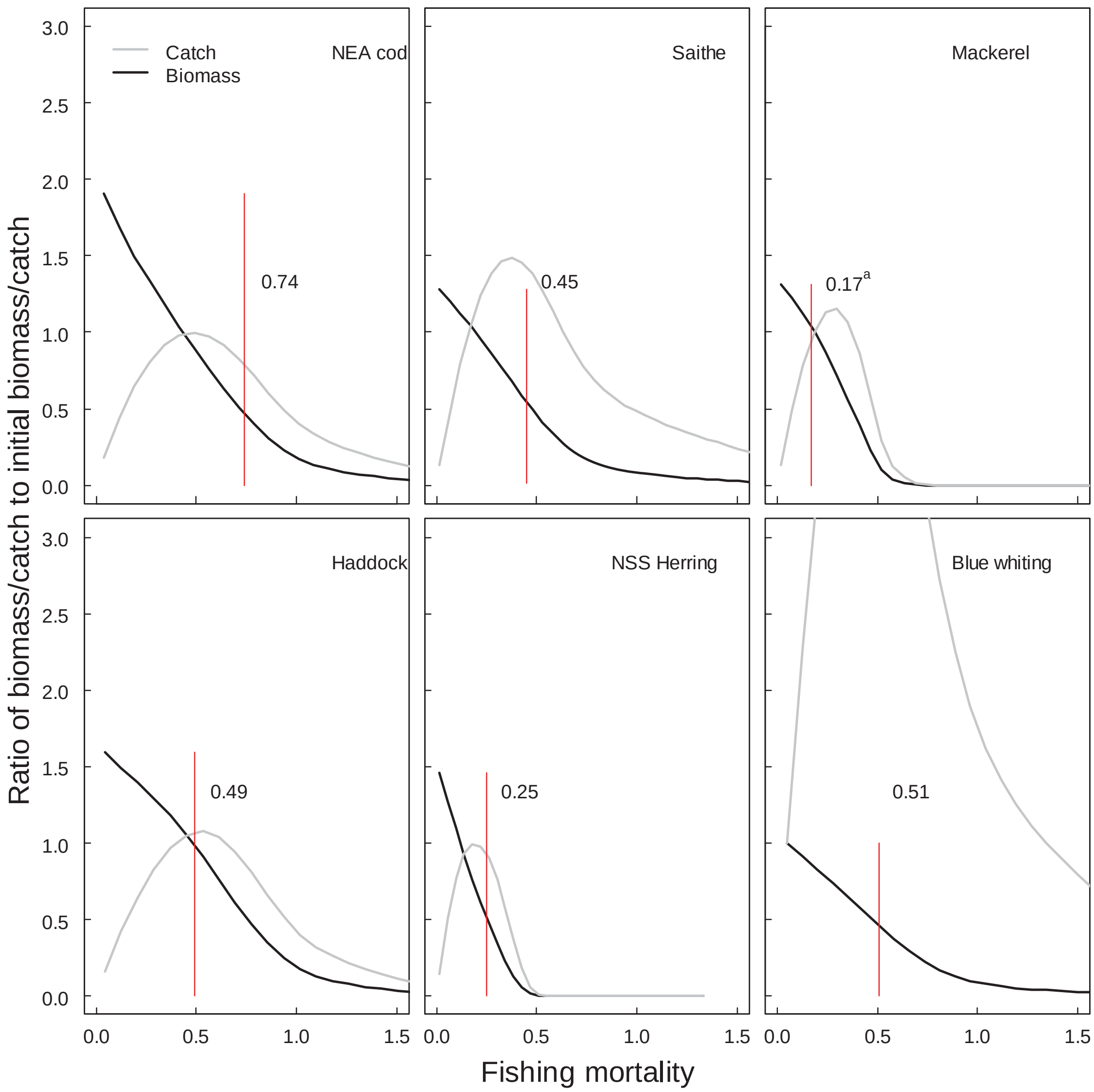


Figure 6. Modelled catch curves of six main commercial species. The grey line indicates catch and the black line biomass. The crossing point between the two lines marks initial state, the input biomass and fishing pressure in the year 2000 (the reference year for balancing the recent state model). The value on the y-axis is a multiplier of biomass/catch to biomass/catch in the initial state; a value of 2 thus represents a doubling of the biomass or catch from the initial state. The vertical red line marks the F_{lim} value given by ICES for that particular species above which long-term recruitment is believed to be impaired.

Conclusions

We fitted an historical ecosystem model to observed time series of abundance and got a reasonably good fit, which was further improved when adding environmental forcing through a primary production anomaly. In particular, some of the short-lived groups in our model system whose abundances are characterised by large fluctuations were better captured when applying the primary production anomaly. This is an indication that bottom-up mechanisms are important in the system. Our recent state (balanced for the year 2000) model for the same area seemed to be relatively consistent with the single stock models reference limits of the ICES when comparing the catch curves for single groups. A natural next step in the work would be to use the recent-state model to compare different fishing pressures, fleet structures and assessment strategies to see how they affect the groups in the modelled system.

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Appendix

Table 1. Diet matrices for all functional groups included in the two models including a) mammals and birds, b) fish and c) invertebrates. The values are from past state model (balanced for the year 1950), with values from the recent state model (balanced for the year 2000) in parentheses if they differ from the 1950-model values. Numbers in superscript refer to references which are given in Table 1c.

Table 1a. Diet matrix for mammals and birds.

FG	Minke whale[1,2]	Sperm whale[3]	Killer whale[4]	Other toothed whales[3,5,6]	Other baleen whales[1,5]	Harp seal (0)[1]	Harp seal (1+)[1]	Other seals (0)[1]	Other seals (1+)[1]	Atlantic puffin[7]	Other seabirds[7]
12 NE Arctic cod (0-2)	0.02				0.02	0.02	0.02	0.006	0.006	0.02	0.002
13 NE Arctic cod (3+)	0.2					0.04 (0.015)	0.04 (0.015)	0.006 (0,002)	0.006 (0.002)		
14 Coastal cod (0-2)	0.005						0.0006			0.02	0.002
15 Coastal cod (3+)	0.01 (0.004)	0.002			0.002 (0)	0.005	0.002				
16 Haddock (0-2)	0.02 (0.015)							0.006	0.006	0.1	0.01
17 Haddock (3+)	0.005 (0.0025)	0.0005				0.005 (0.0025)	0.001 (0.0005)				
18 Saithe (3+)	0.002					0.01	0.002	0.01	0.01		
19 Saithe (0-2)	0.001					0.01	0.01	0.007	0.007	0.17	0.01
21 Other benthic fish		0.0015						0.01 (0,005)	0.01 (0.005)		
23 Greenland halibut (5+)							0.001 (0.0004)		0.001 (0.0004)		
24 Deep-sea redfish (0-4)							0.011	0.03	0.03	0.01	
25 Deep-sea redfish (5+)						0.004 (0)	0.001 (0.0005)	0.005 (0)	0.004		
26 Golden redfish (0-4)									0.01 (0.005)		
27 Golden redfish (5+)							(0.0005)		(0.002)		
28 Blue whiting (0-1)		0.015		0.03				0.12	0.12		0.03
29 Blue whiting (2+)		0.06		0.05				0.12	0.12		
30 Mackerel			0.01	0.01							
31 Herring (0)	0.02				0.006	0.01	0.01 (0.015)			0.29	0.02
32 Herring (1-2)	0.31		0.28	0.03	0.11 (0.03)	0.1	0.1 (0.14)			0.03	0.02
33 Herring (3+)	0.05		0.7	0.1	0.02						
34 Polar cod						0.16	0.16 (0.12)	0.16	0.16		0.08
35 Capelin (0)										0.03	0.05
36 Capelin (1)	0.015			0.01	0.03					0.11	0.16
37 Capelin (2+)	0.07			0.05	0.11 (0.02)	0.17 (0.1)	0.17 (0.1)				
40 Atlantic salmon							0.0001 (0.00004)		0.001 (0.0004)		0.0002 (0.0001)
41 Lumpsucker		0.02 (0.01)									
42 Small pelagic fish	0.03				0.01	0.05	0.05	0.01	0.01	0.22	0.01
43 Mesopelagic fish						0.05	0.05				
44 Squid		0.89 (0.9005)		0.7		0.01	0.01	0.418 (0.432)	0.404 (0.4172)		0.05
47 Other macrobenthos						0.04	0.04				0.3558 (0.3559)
48 Prawns		0.011		0.01		0.05	0.05				
49 Krill	0.242 (0.3555)			0.01	0.632 (0.804)	0.166 (0.23)	0.1683 (0.23)	0.002	0.002		0.09
50 Pelagic amphipods					0.06	0.1 (0.1375)	0.1 (0.12946)	0.09	0.09		0.1
54 Jellyfish			0.01								
56 Wolffishes							0.003		0.003		
58 Detritus											(0.01)

Table 1b. Diet matrix for fish.

	FG	NE Arctic cod (0-3)[1]	NE Arctic cod (3+)[1]	Coastal cod (0-2)[1,8]	Coastal cod (3+)[1,8]	Haddock (0-2)[9]	Haddock (3+)[9]	Saithe (0-2)[9]	Saithe (3+)[9]	Flatfishes and rays[9]	Other benthic fish[10,11]	G halibut (0-4)[12]	G halibut (5+)[13]	Deep-sea red-fish (0-4)[9,11]
12	NE Arctic cod (0-2)	0.01	0.03					0.05 (0.035)		0.14 (0.1)	0.008	0.55 (0.455)	0.08	
13	NE Arctic cod (3+)													
14	Coastal cod (0-2)		0.001					0.01 (0.007)		0.04 (0.03)		0.01	0.01	
15	Coastal cod (3+)													
16	Haddock (0-2)		0.01 (0.008)			0.003	0.0003		0.002	0.008	0.005		0.07 (0.05)	
17	Haddock (3+)		0.0005 (0.00025)					0.001 (0.0005)					0.02 (0.01)	
18	Saithe (3+)						0.0001	0.001		0.03	0.001			
19	Saithe (0-2)		0.002								0.005			
20	Flatfishes and rays		0.005 (0.01)		0.01	0.003	0.01	0.005			0.01	0.04	0.004	
21	Other benthic fish						0.01 (0.005)			0.003		0.01 (0.005)	0.003	
22	Greenland halibut (0-4)		0.0005 (0.0002)							0.02 (0.01)				
23	Greenland halibut (5+)		0.001 (0.0004)											
24	Deep-sea redfish (0-4)	0.01	0.025		0.01	0.01	0.02			0.02	0.001	0.06	0.03	
25	Deep-sea redfish (5+)		0.001 (0.0005)											
26	Golden redfish (0-4)		0.015		0.002 (0)	0.002 (0)	0.005 (0)			0.005		0.02	0.01	
27	Golden redfish (5+)		0.001											
28	Blue whiting (0-1)									0.02 (0.03)	0.05			
29	Blue whiting (2+)	0.005 (0.01)	0.0005 (0.005)					0.015	0.015	0.05 (0.06)	0.2		0.03	
30	Mackerel				0.005		0.005	0.005						
31	Herring (0)	0.01	0.03	0.001	0.001		0.005	0.02	0.01		0.002			
32	Herring (1-2)	0.02 (0.06)	0.04 (0,09)		0.01	0.01	0.01	0.02	0.02	0.004	0.01		0.02	
33	Herring (3+)		0.04 (0.02)		0.06		0.06	0.2 (0.1)			0.02		0.18	
34	Polar cod	0.02	0.04 (0.03)	0.01	0.01					0.015		0.16 (0.21)		
35	Capelin (0)													
36	Capelin (1)	0.015	0.06			0.02	0.01							0.01
37	Capelin (2+)	0.14 (0.1)	0.25 (0.15)	0.02	0.15		0.19 (0.15)	0.14 (0.07)	0.02	0.1	0.01		0.04	0.05
40	Atlantic salmon		0.00004 (0.00002)				0.0001 (0.00005)	0.0001 (0.00005)						
41	Lumpsucker		0.0001											
42	Small pelagic fish			0.01	0.01		0.01	0.05	0.02		0.05			
43	Mesopelagic fish				0.01			0.02	0.02		0.11			
44	Squid							0.02	0.02		0.01		0.313 (0.338)	
45	Ed. crabs and lobster		0.01		0.04			0.005	0.005	0.01	0.05			
47	Other macrobenthos	0.1	0.11 (0.13)	0.659	0.482 (0.484)	0.5	0.4245 (0.47455)	0.06	0.05	0.325 (0.365)	0.418			
48	Prawns	0.05	0.06			0.02	0.02			0.08		0.15 (0.2)	0.01	
49	Krill	0.29	0.12 (0.19)	0.15	0.1	0.232 (0.234)	0.17	0.19 (0.28)	0.41	0.01	0.01			0.8
50	Pelagic amphipods	0.33 (0.325)	0.14536 (0.12953)	0.15	0.1	0.19	0.04	0.1879 (0.28645)	0.408	0.02				0.02
51	Calanus										0.01			0.1
52	Zooplankton 2mm+										0.01			0.02
53	Zooplankton 0-2mm										0.01			
54	Jellyfish													
56	Wolffishes		0.002											
58	Detritus					0.01	0.01			0.1			0.18 (0.185)	

Table 1b cont.

	FG	Deep-sea redfish (4+)[9,11]	Golden redfish (0-4)[9]	Golden redfish (5+)[9]	B whiting (0-1)[14]	B whiting (2+)[15]	Macke-rel[2]	Herring (0)[16]	Herring (1-2)[17]	Herring (3+)[17]	Polar cod[5]	Capelin (0)[18]	Capelin (1)[18]	Capelin (2+)[18]	Basking shark[19]	Other sharks[20]	Atlantic salmon[21]	Lump-sucker[22]	Small pelagics[5]	Meso-pelagics[2]	Wolf-fishes[26]
12	NE Arctic cod (0-2)															0.02					0.005
13	NE Arctic cod (3+)															0.02					
14	Coastal cod (0-2)															0.01					
15	Coastal cod (3+)															0.01					
16	Haddock (0-2)				0.0001	0.0001															
17	Haddock (3+)															0.07					
18	Saithe (3+)															0.01					0.005
19	Saithe (0-2)															0.001					
21	Other benthic fish															0.003					
24	Deep-sea redfish (0-4)	0.002 (0)		(0.002)																	0.05
26	Golden redfish (0-4)																				0.01 (0.005)
28	Blue whiting (0-1)					0.002										0.04					
29	Blue whiting (2+)					0.001										0.225	0.02				
30	Mackerel															0.06	0.03				
31	Herring (0)				0.05	0.05	0.01			0.01						0.01	0.1		0.002		
33	Herring (3+)															0.07	0.13				
35	Capelin (0)							0.001	0.01												
36	Capelin (1)		0.01																		
37	Capelin (2+)	0.01		0.14																	
39	Other sharks															0.001					
42	Small pelagic fish															0.01	0.01		0.01		
43	Mesopelagic fish				0.01	0.05	0.01									0.06	0.43		0.01	0.04	
44	Squid				0.01	0.01										0.23	0.02		0.01		
45	Ed. crabs and lobster															0.02					0.02
47	Other macrobenthos				0.01	0.01										0.13			0.1		0.87 (0.885)
48	Prawns	0.025	0.025 (0.05)																		0.01
49	Krill	0.423 (0.425)	0.465 (0.44)	0.8 (0.798)	0.05	0.5769	0.07	0.01	0.06	0.06	0.55	0.03	0.65	0.69			0.04		0.238	0.58	0.02 (0.01)
50	Pelagic amphipods	0.16	0.17	0.02	0.05	0.15	0.04	0.01	0.14	0.13	0.32	0.02	0.14	0.15			0.18	0.12	0.05	0.04	0.01
51	Calanus	0.18	0.15	0.02	0.7599	0.09	0.48	0.33	0.64	0.65	0.07	0.5	0.2	0.15	0.45				0.22	0.26	
52	Zooplankton 2mm+	0.15	0.13	0.02	0.01	0.01	0.38	0.01	0.13	0.13	0.03	0.05	0.005	0.005	0.33		0.04		0.17	0.04	
53	Zooplankton 0-2mm	0.05	0.05		0.05	0.05	0.01	0.639	0.02	0.02	0.03	0.4	0.005	0.005	0.22				0.1	0.04	
54	Jellyfish																	0.88	0.05		
58	Detritus																		0.04		

Table 1c. Invertebrates diet matrix

FG	Squid[23]	Edible crabs and lobster[20]	Corals[24]	Other macrobenthos[5]	Prawns[25]	Krill	Pelagic amphipods[2]	Calanus[5]	Zooplankton 0-2 mm[5]	Zooplankton 2mm+[5]	Jellyfish[5]		Reference		Reference
28 Blue whiting (0-1)	0.001											1	(Bogstad et al., 2000)	16	(Bjørke, 1978)
29 Blue whiting (2+)	0.003											2	(Skjoldal, 2004)	17	(Dommasnes et al., 2004)
43 Mesopelagic fish	0.016											3	(Bjørke, 2001)	18	(Gjøsæter, 1998)
44 Squid	0.04											4	(Simila et al., 1996)	19	(Cortes, 1999)
45 Edible crabs and lobster	0.05	0.05										5	(Dommasnes et al., 2001)	20	(Mackinson, 2002)
47 Other macrobenthos		0.75	0.05	0.1	0.1							6	(Das et al., 2003)	21	(Jacobsen and Hansen, 2001)
49 Krill	0.17		0.05		0.25		0.02				0.05	7	(Barrett et al., 2002)	22	(Haugland, 2001)
50 Pelagic amphipods	0.46		0.05				0.01				0.05	8	(Salvanes, 1995)	23	(Sennikov et al., 1989)
51 Calanus	0.2		0.39		0.25	0.05	0.47			0.23	0.46	9	(Dolgov, 2000)	24	(Mortensen, 2001)
52 Zooplankton 2mm+	0.02		0.05	0.01	0.1		0.05				0.1	10	(Bergstad, 1991)	25	(Blanchard et al., 2002)
53 Zooplankton 0-2mm	0.04		0.1	0.05	0.1	0.05	0.24			0.12	0.24	11	(Husebø et al., 2002)	26	(Bundy et al., 2000)
54 Jellyfish											0.1	12	(Vollen et al., 2004)		
55 Seaweeds			0.01									13	(Hovde et al., 2002)		
57 Phytoplankton				0.02		0.8		0.9	0.9	0.6		14	Bjelland in prep		
58 Detritus		0.2	0.3	0.82	0.2	0.1	0.21	0.1	0.1	0.05		15	(Bjelland and Monstad, 1997)		

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