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EXPLORING MARINE MAMMAL-FISHERY INTERACTIONS USING 'ECOPATH WITH ECOSIM': MODELLING THE BARENTS SEA ECOSYSTEM

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1. ABSTRACT

Ecopath with Ecosim has been proposed as a useful tool for exploring interactions between marine-mammals, their prey and fisheries. We have developed models for the Barents Sea ecosystem for future evaluation of the utility of this approach. The purpose of the present technical report is to document model construction, the sources and ranges of data utilised, model balancing, assumptions and limitations of the models. We considered two documented ecosystem states for the Barents Sea, namely years in which capelin (*Mallotus villosus*) are very abundant and years when capelin populations are much reduced. Our initial model consisted of 41 functional groups including 5 marine mammal/bird groups, 19 fish groups, 12 invertebrate groups, 2 primary producers and 3 categories of detritus.

The most important differences between the two models (1990 versus 1995) were associated with the biomass and production/biomass estimates of several major fish groups and the diets of three of the top predators (minke whales, harp seals, and cod). Ecopath outputs indicated that in terms of system functioning the two models were very similar. A comparison of direct and indirect trophic impacts revealed that when capelin abundance was greatly reduced, there was a shift in the reliance of top predators (minke whales, harp seals, and cod) from pelagic species towards predatory demersal fishes. The 1995 model was further parameterised for use with the Ecosim dynamic modelling package and the stability of our model was evaluated given different vulnerability and life-history settings. We found that the model was particularly sensitive to different vulnerability settings.

The models presented in this report will be used to test model stability, complexity, structure and sensitivity. We welcome others to make refinements to these models if they are to be explicitly used for questions pertaining to the Barents Sea ecosystem.

2. INTRODUCTION

2.1 IFAW - CEFAS Project

In the year 2000, IFAW (The International Fund for Animal Welfare), commissioned staff at the CEFAS Lowestoft laboratory, to begin a project focused on the potential competition between cetaceans and fisheries. Although this was not a particularly new issue, demands for management action to address problems of actual or perceived competition were thought likely to increase, yet the science underpinning advice remained poorly developed. IFAW contracted CEFAS to establish the extent to which models such as Ecopath and Ecosim were appropriate and/or useful for exploring interactions between marine-mammal predators, their prey and fisheries.

The Barents Sea was chosen for modelling purposes since it was perceived as a relatively simple system, but with potentially interesting temporal dynamics. Furthermore, reasonably complete data were known to exist for the majority of ecosystem components, substantial fisheries operated in the region and there existed substantial marine mammal populations.

The objectives of this report are to:

- Document the parameterisation of the Ecopath models for the Barents Sea in years when capelin abundance is high (1990) and low (1995)
- Compare Ecopath outputs and results for high and low capelin years
- Document Ecosim parameterisation for the low capelin (1995) model
- Evaluate stability and sensitivities to simulation settings of the low capelin (1995) model within Ecosim

2.2 Ecopath modelling approach

The Barents Sea ecosystem was modelled using the alpha-version of the Ecopath 4.1 (Ecopath with Ecosim) software (downloaded from http://www.Ecopath.org/). Ecopath is a programme for balancing steady-state ecosystem models and calculating network characteristics. Originally proposed by Polovina (1984), Ecopath is a program for balancing steady-state ecosystem models and has been combined with routines for network analysis based on the approach of Ulanowicz (1986). Trophic interactions among the functional groups of the ecosystem can be described by a set of linear equations, the equation for each group (*i*) being:

production by (*i*) - predation on (*i*) -
non-predation losses of (*i*) - export of (*i*) = 0

which may also be written as:

$$P_i = Y_i + B_i \cdot M2_i + E_i + P_i \cdot (1-EE_i) \qquad \text{[Equation 1]},$$

where P_i is the total proportion of *i*; *Y* is the total catch of *i*; $M2_i$ is the predation mortality rate for group *i*; *B* is the biomass of the group; *E* is the net migration rate (emigration-immigration) and EE_i is the ecotrophic efficiency of *i*, (the fraction of the production of *i* that is consumed within the system, exported or harvested). Equation 1, can also be expressed as:

$$B_i \cdot (P/B)_i \cdot EE_i - \sum_{j=1}^{n} B_j \cdot (Q/B)_j \cdot DC_{ji} - Y_i - E_i = 0 \qquad \text{[Equation 2]},$$

where P/B_i is the production/biomass ratio; Q/B_i is the consumption/biomass ratio and DC_{ji} the fraction of the prey (i) in the average diet of predator j (Christensen and Pauly, 1992).

The system of linear equations can be solved using standard matrix algebra (Christensen and Pauly, 1992), and although DC_{ji} and E_i must always be entered, entry is optional for any one of the other four parameters (B_i, P/B_i, Q/B_i, EE_i).

2.3 Characteristics of the Barents Sea ecosystem

2.3.1 Defining the System

The Barents Sea is a high latitude, shallow continental shelf covering approximately 1.4 million km^2 (Sakshaug, 1997). It is bounded by the archipelagos of Spitsbergen and Franz Josef Land in the northwest, the island of Novaya Zemyla to the east, and by the coasts of northern Norway and Russia in the south (approx. 68°N) (Figure 1). The western boundary between the Barents and Norwegian Seas is usually drawn along the edge of the continental slope at approximately 10° to 15°E (Gjøsæter, 1998). For fisheries management purposes the Barents Sea consists of ICES Area I, and a small part of ICES Areas IIa and IIb. The southwestern region is permanently ice-free whereas the remaining region is seasonally covered in ice.

Horizontal gradients and year-to year variation in polar water flux (due to supply of meltwater from sea-ice) cause pronounced variations in the biomass distributions and productivity of the pelagic Barents Sea ecosystem (Sakshaug, 1997). Sætersdal and Loeng (1987) demonstrated that good recruitment in the stocks of cod, haddock and herring in particular, have been associated with increased inflow of Atlantic water to the Barents Sea.

One of the most intriguing aspects of the Barents Sea ecosystem is the apparent cyclical fluctuation of capelin abundance (see Figure 2). Capelin are an important prey item in the diets of marine mammals, many fish and seabirds. Their dynamics are recognised to be influential in the Barents Sea as well as other ecosystems (Dolgov, 2002; Ushakov and Prozorkevich, 2002; Carscadden *et al.*, 2001 and 2002) The availability of published diet data for ‘low’ and ‘high’ capelin years provided us with the opportunity to compare these two distinct ecosystem states. We constructed Ecopath models for 1995 (low capelin abundance) and 1990 (high capelin abundance). The only differences between the two models were the biomass parameters of fish groups for which a time series of abundance estimates was available, the diets of three top predators (minke, whale, harp seal, and cod) and the fisheries landings.

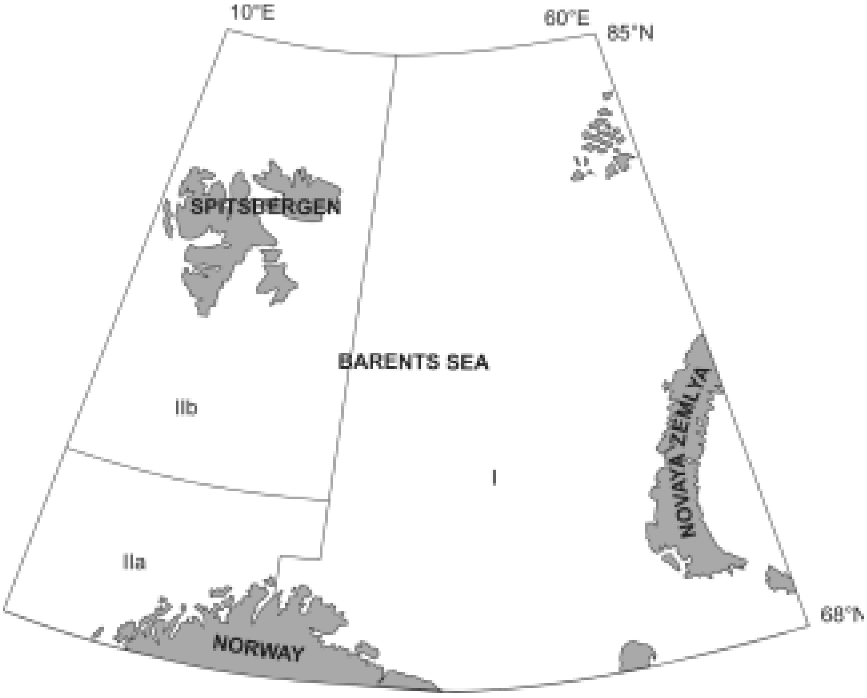


Figure 1. Map of the Barents Sea model area

2.3.2 Causes and consequences of changes in capelin abundance

Capelin, juvenile herring and polar cod are the most important plankton-eating fishes in the Barents Sea (Hamre, 1994, See Figure 2). The cyclical population dynamics of capelin are thought to be linked to a combination of factors including environmental variation (i.e. alternation of periods of cold and warm waters) and interactions with other species in the system. Recruitment of spring-spawning herring is also highly variable. Strong year classes have generally emerged at 10-year intervals (Hamre, 1988), followed by periods of poor recruitment. When the Norwegian spring-spawning herring stock collapsed in the late 1960s due to heavy fishing, the inflow of juvenile herring to the Barents Sea ceased. The Barents Sea capelin increased markedly and became the target of a directed fishery. Capelin biomass remained high in the 1970s despite heavy fishing. However, when recruitment to the Norwegian spring spawning herring stock improved, the influx of juvenile herring increased again. The increased predation pressure from herring together with heavy fishing are thought to have contributed to the collapse in the capelin stock in the mid-1980s (Gjøsæter, 1998). In particular, juvenile herring has been hypothesised to be a major predator of larval and juvenile capelin (Huse and Toresen, 1995), though recent studies have shown that predation by juvenile herring alone is not enough to drive capelin recruitment dynamics (Huse and Toresen, 2000).

Many other species were affected by the decline in capelin in the Barents Sea. Northeast Arctic cod, the most important predator on adult capelin in the region, experienced a decrease in growth and fecundity and an increase in cannibalism (Bogstad and Mehl, 1997; Bogstad and Gjøsæter, 2001). Seabirds and marine mammals feeding on capelin were also strongly affected. Harp seals migrated down the coast of Norway in 1987 in search of food and more than 100,000 seals were drowned in fishing nets (Haug and Nilssen, 1995). In the Barents Sea, guillemots suffered winter kills of thousands of individuals (Livingston and Tjelmeland, 2000; Anker-Nilssen *et al.* 1997). The capelin stock recovered as a result of the large 1989 year class, only to collapse again when the large 1991 and 1992 year classes of herring entered the area.

Changes in the state of the capelin stock are also thought to have influenced the biomass of zooplankton in the Barents Sea (Gjøsæter, 1998). Dalpadado and Skjoldal (1996) found that there was an increase in the abundance and biomass of euphausiid species following the capelin collapse (1984-1987). By contrast, a decrease in euphausiid abundance was observed to follow the recovery of the capelin stock in 1991. This suggests a predator-prey interrelationship between capelin and euphausiids (Gjøsæter, 1998). There is also believed be an important relationship between amphipod and capelin abundance (Dalpadado *et al.*, 2001).

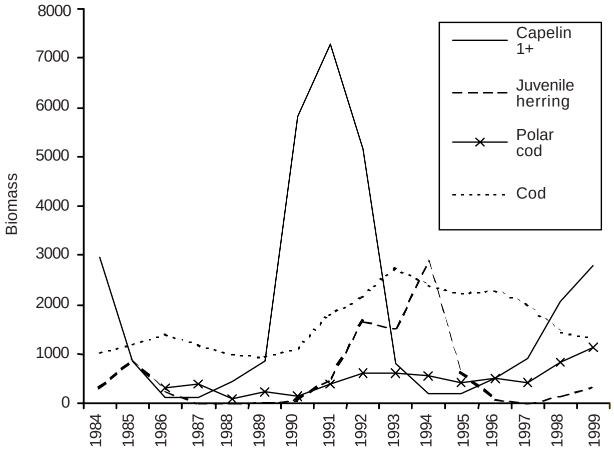


Figure 2.** **Biomass (000s tonnes) from acoustic estimates and VPA for several species of commercial fish in the Barents Sea, source: Bogstad et al., 2000

Competition for food is thought to take place between capelin and polar cod (*Boreogadus saida*), since both feed on pelagic zooplankton and there is considerable overlap in their distributions, especially in the spring (Panasenko and Soboleva, 1980). Recruitment to the polar cod stock was enhanced during the period of the first capelin stock collapse in 1985-1989 (ICES, 1996). Competition between capelin and juvenile herring has also been reported (Huse and Toresen, 1996), thus complicating the interactions between those species even further.

2.3.3 Fishing in the Barents Sea

Responsibility for fisheries management in the Barents Sea lies with the bilateral Norwegian-Russian Fisheries Commission, which meets every autumn to establish *total allowable catches* under the auspices of the International Council for the Exploration of the Sea (ICES). Historically fish resources in the region have been exploited by a number of nations, although mostly by Norwegian and Russian/USSR vessels (Figure 3).

The main commercial fish species caught in the Barents Sea are cod (*Gadus morhua*), capelin (*Mallotus villosus*), haddock (*Melanogrammus aeglefinus*), saithe (*Pollachius virens*), Greenland halibut (*Reinhardtius hippoglossoides*) and redfish (*Sebastes marinus* and *S. mentella*), all of which are managed based on ICES advice. Other commercial species include polar cod (*Boreogadus saida*), wolffish (*Anarhichas* spp.),

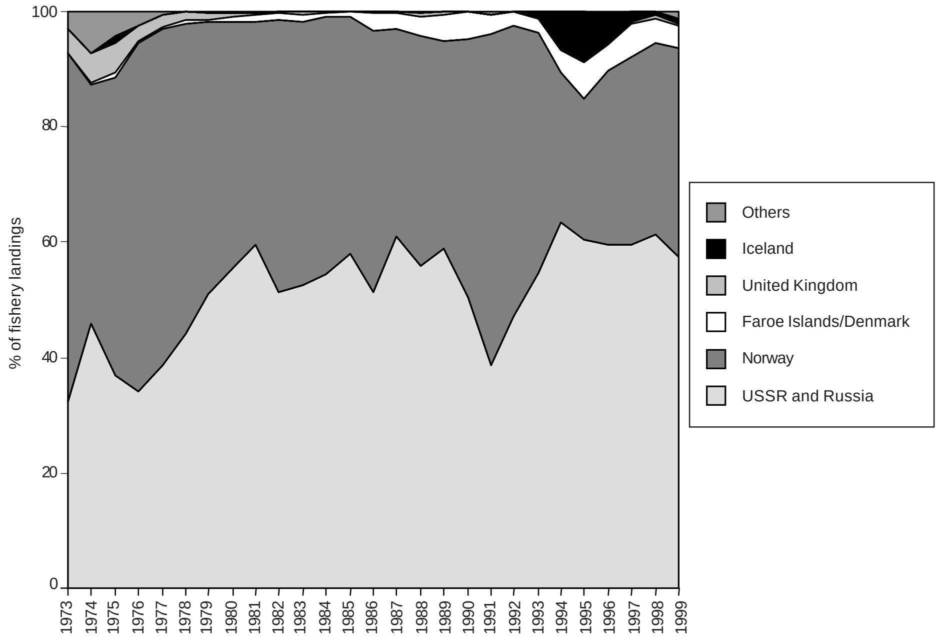


Figure 3. Percentage of fishery landings taken by vessels from different countries. Based on data compiled by ICES

lumpsucker (*Cyclopterus lumpus*), plaice (*Pleuronectes platessa*) and long rough dab (*Hippoglossoides platessoides*). The Barents Sea is a nursery area for Norwegian spring spawning herring (*Clupea harengus*) which is generally not exploited, except for occasional catches of adult herring in coastal waters (Jakobsen, 1999).

Total catches of fish from the Barents Sea increased markedly until the late 1960s (Nakken, 1998), but experienced a dramatic decline (Figure 4) during the late 1970s. Between 1977 and 1990 annual landings were reduced from nearly 3 million tonnes to 0.2 million tonnes, and much of this was related to the decline and eventual closure of the fishery for capelin.

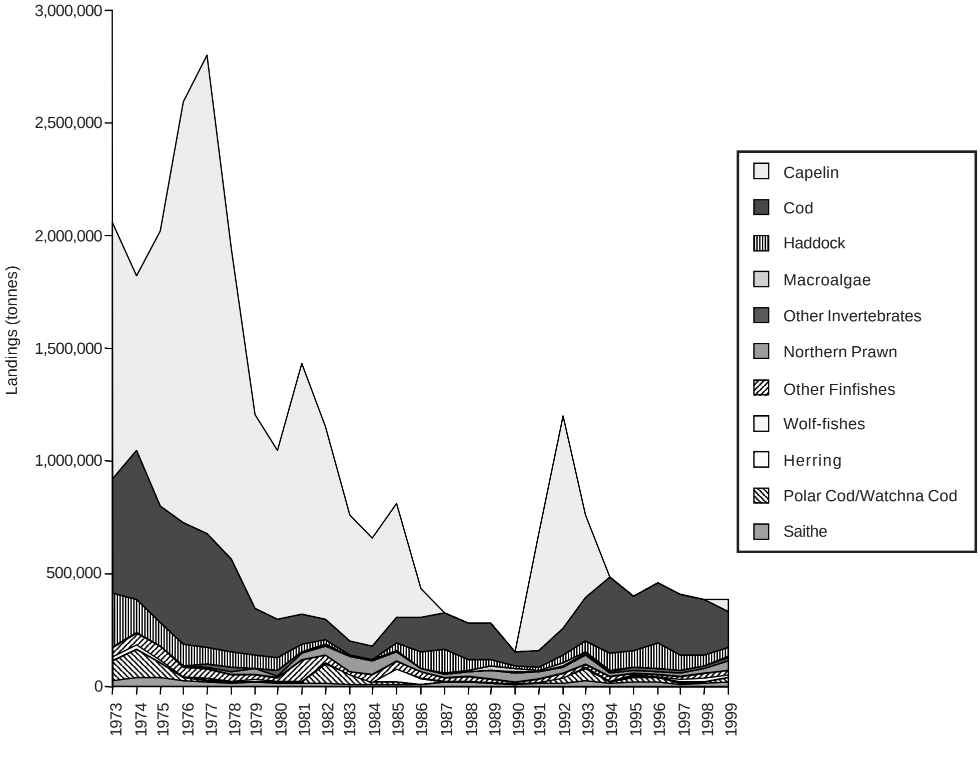


Figure 4. Barents Sea fishery landings between 1973 and 1999, based on data compiled by ICES

The Barents Sea capelin (*Mallotus villosus*) stock was probably the largest capelin stock in the world, its biomass on occasions reaching 6-8 million tonnes and supporting a fishery harvest in excess of 2 million tonnes (Gjøsæter, 1998) during the 1970s. By 1984, capelin catches decreased, partly because of quota restrictions but primarily because the stock had begun to collapse. The fishery closed from autumn 1986 until 1990, during which time the stock recovered somewhat. Fishing resumed between 1991 and 1993, albeit at a much lower level. The fishery was closed again in spring 1994, when a new stock collapse became evident (Gjøsæter, 1998).

2.3.4 Whaling and Seal Hunting

Marine mammals have been hunted in the Barents Sea for many centuries (Nakken, 1998), particularly off northern Norway and in the region of the Svalbard archipelago. Dutch and British vessels hunted right whales but also seals, and established processing stations as far north as Spitsbergen. Russian and Norwegian hunters caught walrus, polar bear and seals along the eastern side of the Svalbard Islands. By about 1800-1850 stocks of right whales and walrus were reduced to such low levels that the hunt for these species became unprofitable (Nakken, 1998).

A new era in the exploitation of marine mammals began in the Barents Sea around 1860-1870 (Nakken, 1998). With the advent of the grenade harpoon, hunting for large baleen and sperm whales became viable for the first time. Small vessels were also developed, which could penetrate far into the drift-ice, allowing harp and hooded seals to be targeted by Norwegian hunters. Between 1850 and 1900, the Norwegian offshore catch of both whales and seals increased considerably, while vessels from other nations gradually left the area. Catches of large whales (blue, fin, sei, sperm and humpback whale) levelled off during the first two decades of the twentieth century (Figure 5). Subsequently, management measures were introduced in order to limit catches, but the abundance of these large species was by then so low that hunting was unprofitable. An offshore hunt for small whales began in the 1930s, with minke whale as the main target. After World War II, annual catches reached 2300 animals but the harvest of both seals and whales has greatly decreased in recent years (Figure 5, Nakken, 1998).

2.4 Structure of the Barents Sea ecosystem model

Thousands of plant and animal species have been recorded in the Barents Sea ranging from microscopic phytoplankton, through invertebrates, fish, birds and mammals. Some species inhabit the Barents Sea all year, whereas others are present only seasonally.

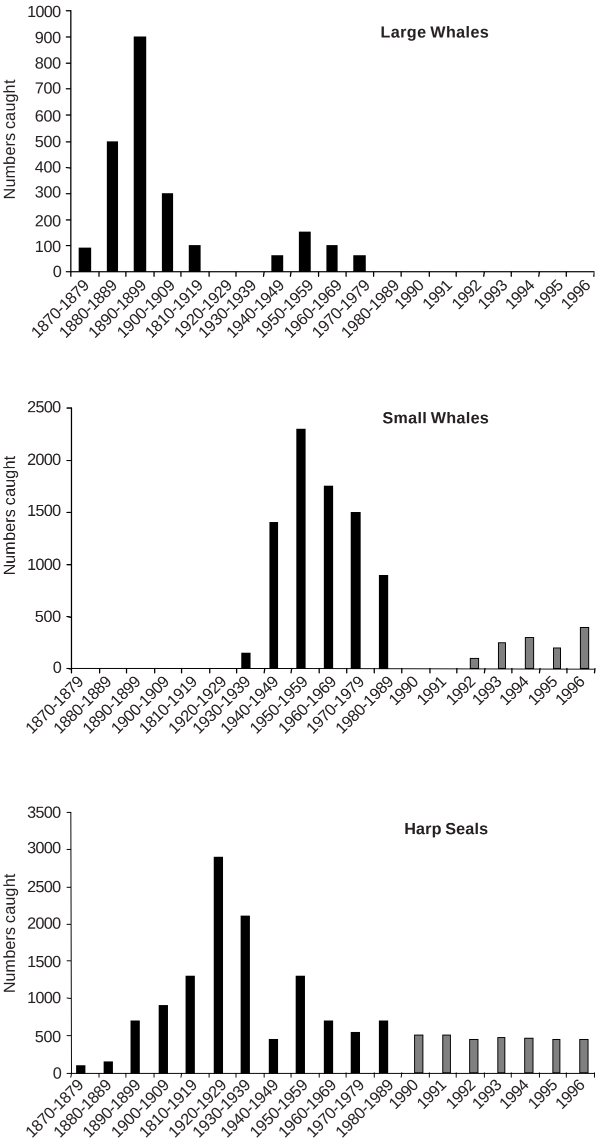


Figure 5. Catches of marine mammals in the Barents Sea (after Nakken, 1998). For 1870-1989, mean values of ten year periods are given and for 1990 onwards annual catches are given. 'Large whales' include blue whale, fin whale, sei whale, sperm whale and humpback; 'Small whales' include minke and bottlenose whales

Representing each of these species as a separate compartment in our model would require an enormous amount of information, most of which is not readily available. We began by considering 41 groupings of species in the model ecosystem. Some of these groups consisted of one species (such as minke whale, cod, herring), whereas others consisted of several species called functional groups. For some of these functional groups, species were amalgamated into widely used trophic guilds (i.e. 'Pelagic planktivorous fish' based on Dolgov, 1992) while other groups were formed on the basis of general taxonomic similarities (i.e. 'Lobsters and crabs'). The structure of the 41 box Barents Sea models is outlined overleaf.

Structure of 41 box Ecopath Model

Marine mammals and birds

1. Minke whales
2. Other baleen whales - *fin and humpback whales*
3. Toothed whales - *harbour porpoise,white-beaked dolphin and killer whales*
4. Birds - *21 species including: guillemots, kittiwakes, fulmars and gulls*
5. Seals - *harp, hooded, harbour, grey, ringed and bearded seals*

Fish Groups

6. Sharks - *porbeagle shark, Greenland shark and spiny dogfish*
7. Herring
8. Juvenile herring (1-3)
9. Adult capelin (2+)
10. Juvenile capelin (1)
11. Polar cod (1+)
12. Pelagic planktivorous fish - *blue whiting, sandeels, Norway pout, and others*
13. Mackerel
14. Redfishes - *deep sea and golden redfish*
15. Benthic Invertebrate Feeders - *flatfish (plaice, sole) and sculpins*
16. Adult haddock (4+)
17. Juvenile haddock (1-3)
18. Wolfishes - *common, spotted, and northern*
19. Adult cod (4+)
20. Juvenile cod (1-3)
21. Adult saithe
22. Juvenile saithe
23. Benthic piscivores - *Greenland halibut, thorny skate, long rough dab and monkfish*
24. Salmon and Seatrout

Invertebrates

25. Squid
26. Lobsters and crabs
27. Prawns and shrimps
28. Other crustaceans - *hermit crabs, gammarids, isopods, etc*
29. Epifaunal filter feeders - *sealilies,crinoids,urchins, etc.*
30. Infaunal filter feeders - *mostly bivalves,detritophages, and sediment feeders(polychaetes)*
31. Other macrobenthos - *predators,omnivores and carrion eaters, plant eaters and scrapers*
32. Meiofauna
33. Carnivorous zooplankton - *Euphausiids, amphipods, mysids,fish larvae and nauplii*
34. Herbivorous zooplankton - *Copepods, cladocerans, ostracods, etc.*
35. Planktonic micro-organisms
36. Benthic micro-organisms

Primary producers

37. Phytoplankton
38. Seaweeds

Detritus

39. Carcasses
40. Water column detritus
41. Benthic detritus

3. MODEL INPUTS

3.1 Details of species groups and parameters

For each group, three out of four of the basic parameters (B, Q/B, P/B, EE) were required to construct the mass-balance model. Usually biomass (B), per capita production (P/B) and per capita consumption (Q/B) were input and the program was allowed to estimate the linear equations for ecotrophic efficiency (EE). If one of the other parameters (for example, biomass for an entire group) was missing, it was necessary to enter a value (between 0 and 1) for EE. Ecotrophic efficiency is the most difficult of the parameters to measure (Van Rooij *et al*., 1998). Previous modelling has lead to generalisations about what values for EE are reasonable. A whole range exists in nature and a value close to one indicates that a group is being heavily predated or grazed upon and/or fishing pressure is high such that few individuals die of old age. One of the few directly measured EEs that exists is in a study by Van Rooij *et al.* (1998) who reported an EE for Caribbean parrotfish of 100%. Conversely, a value close to zero means that any other group does not consume the group within the system. Therefore, for groups that are heavily exploited or predated upon EEs should generally be close to one, whereas top predators (such as many cetaceans) and phytoplankton typically have lower EEs (Christensen *et al*., 2000).

3.1.1 Marine Mammals and Seabirds

Marine mammal biomass in the Barents Sea is dominated by harp seals and minke whales. Knowledge of marine mammal diets and population abundance for species other than minke whales and harp seal is at best incomplete and for some species non-existent (Bogstad *et al*., 2000). Along with minke whales, several other species of whale are known to be piscivores in the Barents Sea; these include humpback and fin whales (Christensen *et al*.,1992, cited in Bogstad *et al*., 2000). Other species, known to be largely planktivores, include blue whales and sei whales but their population sizes are not known (Christensen *et al*., 1992(a) from Bogstad *et al*., 2000). The most numerous toothed whales in the Barents Sea are thought to be white-beaked dolphins and harbour porpoises. A third toothed whale that may spend at least part of the year in the Barents Sea region is the killer whale, which is known to feed on herring in the coastal waters of North Norway (Christensen, 1982, Similä *et al*., 1996). Beluga whales are also known to occur seasonally in both the northernmost and south-eastern parts of the Barents Sea (Gurevich, 1980) but data concerning their abundance is lacking (Bogstad *et al*., 2000). Arctic seal species that are known to inhabit the Barents Sea include ringed seals, bearded seals and walruses. There is some information on the feeding biology of these species (Belikov and Boltunov, 1998; Lyderson, 1998; Wathne *et al.,* 2000; Timenshenko and Popov, 1990; Gertz and Wiig, 1992; Hjelset *et al*., 1999 references cited in Bogstad *et al*., 2000), but their abundance has not been quantified. Coastal pinniped species include harbour seals and grey seals.

Many species of seabirds inhabit the Barents Sea region. The most common species of these are Brünnich's guillemot, fulmars, kittiwakes and little auks (ICES, 2000(a)).

Abundance
Sightings-survey data were available for several of the marine mammal species. When abundance data were not available for all species within a group, the data that were available were used and assumed to be a minimum estimate.

Body weights
Average marine mammal body weights were used to estimate biomass. For the whale species these were obtained form Sigurjónsson and Víkingsson (1997). Body weight for harp seals were taken from Nilssen (1997) though more precise, weight-at-length estimates are given in Nilssen (2000). Bonner (1994) gave average body weight estimates for harbour and grey seals.

Q/B estimates
Q/B estimates were either based on those reported in the literature (total consumption estimates/biomass) or calculated for each species based on their average body weight and yearly ration (according to the method used in Trites *et al*., 1999). Individual ration (R, in percent of body weight per day) was estimated for each sex and species using: $R = 0.1W^{0.8}$, where W is the mean body weight in kg, 0.8 is from equation 23 in Innes et al (1987), and 0.1 is a downward adjusted value (from 0.123 in Innes *et al*., 1987), which accounts for the difference between ingestion for growth and ingestion for maintenance. A weighted average Q/B was used for some of the marine mammal groups.

P/B estimates
If there were no published local estimates of population growth rate (P/B), the values used by Trites *et al.* (1999) for the Bering Sea were used. Their values were based on half of the maximum rate of population growth rate for northern fur seals and other pinnipeds (12% from Small and DeMaster, 1995) and were approximately 6% per year. The exception for this was harp seal for which a P/B of 4% was used in Trites *et al.* (1999). The

maximum rate of population increase for large whales is assumed to be 4% (Reilly and Barlow, 1986) and the P/B ratio was estimated to be 2% (half of r_{max}).

1. Minke Whales (*Balaenoptera acutorostrata*)

Minke whales are currently harvested by Norwegian whalers at a much lower level than in the past (Figure 5) (Bogstad *et al*., 2000; Nakken, 1998). Minkes usually spend around 6 months (May - Oct) feeding in the Barents Sea but the rest of the year elsewhere. Table 3.1 shows the stock-size of Northeast Atlantic minke whale and the distribution within subareas from the NILS-95 sightings- survey (Schweder *et al.,* 1996). The total abundance used in our calculations was 84,761 individuals.

Table 1. Northeast Atlantic minke whale stock size and distribution within subareas from the results of NILS-95 sightings survey (Schweder et al 1996). Subareas are: ES= Spitsbergen and Bear Island, EB= Barents Sea and coastal areas of Finnmark and Kola, EC= Vesteralen and Lofoten. Standard deviations (s.d.) and coefficients of variation (c.v.) for each subarea are also shown

Subarea	Abundance	s.d.	c.v.
ES	25969	2908	0.112
EB	56330	7651	0.136
EC	2462	562	0.228
Total	84761		

Sigurjónsson and Víkingsson (1997) reported an average body weight of minke whales of 5.2 t. The average body weight was multiplied by the numbers of individuals and then divided by 2 (since the minke whales only spend half of the year in the Barents Sea). The resulting biomass estimate was 223168 t giving a biomass density of 0.159 t km^{-2}. Bogstad *et al.* (2000) reported the total consumption of minke whales when capelin abundance was both high and low. We calculated a Q/B value of 9.90 using estimates of yearly ration and body weight (Trites *et al*., 1999).

A P/B value of 0.035 was given for "whales" in the Barents Sea by Sakshaug *et al.* (1997) and this was the value we used in our model. However the values used by Trites *et al.* (1999) for whales was 0.02 which gives a range of P/B values from 0.02 - 0.035.

Diet composition was based on the extensive field-based diet study of Folkow *et al.* (1997). The average over three seasons and three areas was taken to be representative for the entire Barents Sea minke whale diet. A small portion (0.1 %) of the diet could not be allocated to a group as it consisted of unknown "other prey". The diet composition was therefore re-scaled to add up to one. Since the diet study spanned both high and low capelin years (1992 -1995), the diet for the high capelin year was based on the 1992 samples and for the low capelin years it was based on the average diet during 1993-1995.

2. Other baleen whales

Since abundance data were not available for blue (*Balaenoptera musculus*) and sei (*B. borealis*) whales, these species were not included in the model. Recent estimates of fin (*B. physalus*) and humpback (*Megaptera novaeangliae*) whale abundance have been reported as approximately 3000 and 1000 individuals respectively (NAMMCO, 1998, Christensen *et al*., 1992). Krill has been reported to be the main prey for fin whales (Johnsgåd, 1966). However, they have also been reported to eat capelin and, to a lesser extent, herring in the early spring (Sigurjósson and Víkingsson, 1997). Humpbacks feed primarily on capelin from September to February and then switch to krill in the spring and summer (Ingesbrigsten, 1929; Bogstad *et al*., 2000).

Average body weight for both species was estimated by Sigurjónsson and Víkingsson (1997) to be 42 t for fin whales and 32 t for humpback whales, yielding a total biomass of 0.112 t km^{-2} yr^{-1}. Q/B and P/B estimates were calculated according to the methods of Trites *et al.* (1999). The Q/B estimate for fin whales was 14.6. For humpback whales, Q/B estimates of 9.3 and 4.6 were calculated for May-Oct and Nov-Apr respectively. The weighted-average Q/B for this group was 13.11. P/B was set at 0.02, based on Trites *et al.* (1999).

3. Toothed whales

White-beaked dolphins (*Lagenorhynchus albirostris*) are thought to be fairly abundant in the Barents Sea. Between 60-70,000 individuals were sighted in 1989 (Bogstad *et al*., 2000), though information on feeding habits in the Barents Seas was not available. Information on feeding by white-beaked dolphin came from three individuals stranded in Scottish waters (Santos *et al*., 1995).

The approximate population size of Harbour porpoise (*Phocoena phocoena*) was 11,000 individuals (Bjorge and Øien 1995). Aarefjord and Bjørge (1995) reported that capelin and herring dominated the diet of harbour porpoises in coastal areas of Norway (20.5 and 25% respectively), but saithe and whiting were also important (18 and 13%).

Killer whales (*Orcinus orca*) occur seasonally in the coastal areas of Northern Norway, where they feed on the over-wintering population of adult herring (Christensen, 1982; Similä *et al*., 1996). Abundance of killer whales has been estimated as 7000 individuals

(NAMMCO, 1993). The diet of killer whales in the model was assumed to comprise 100% adult herring (Similä *et al.*, 1996).

The weighted Q/B and P/B estimates for Toothed whales were calculated using the method in Trites *et al.* (1999) and were 12.75 and 0.02, respectively.

4. Seals

The total population size of harp seals (*Phoca groenlandica*) in the Barents Sea has been estimated as 2.22 million individuals based on a mean production of 301,000 pups and current catch levels (ICES, 1999). The average body size of males and females has been reported as 0.1 t (Nilssen *et al.*, 1997). This yields a biomass density of 0.1588 t km^{-2} yr^{1}. Initially we used the estimate reported in ICES (1999). However, a more recent estimate has reported 1,676,300 individuals and during the balancing procedure it was necessary to use this mean value (ICES, 2001(c)). The 95% confidence interval reported for this recent estimate is 1,500,000 – 1,910,000 (ICES, 2001(c)).

Other pinniped species in the Barents Sea include approximately 2500 harbour seals (*Phoca vitulina*) and 440 grey seals (*Halichoerus grypus*) (Bogstad *et al.*, 2000). The mean body weights for each species are 59 kg (harbour seal) and 134 kg (grey seal) (Bonner, 1994). This yields a biomass of 737.1 tonnes (0.0005 t km^{-2} yr^{1}) for the two species combined.

Field studies of the feeding ecology of harp seals in the Barents Sea over 1990-1995 included the collection of stomachs during both high and low capelin years (Nilssen et al, 1995; Nilssen et al 1997; Nilssen et al . 2000). Spatio-temporal variation in the diets are thought to reflect changes in prey abundance (Nilssen et al, 2000). Estimating weighted Q/Bs for all seals in the model using Trites et al. method resulted in a Q/B = 15.59.

Bonner (1994) has suggested a P/B value for seals of 0.04 yr^{1}. However we calculated a P/B of 0.056 yr^{1}, using the method in Trites *et al.* (1999), and this was used in the model input.

Harp seals are by far the dominant species of the seal group (99% of total biomass) and their diet alone was used to represent the group. Nilssen *et al.* (1997) reported diet composition for harp seals when capelin was both abundant and depleted and this enabled us to use corresponding diets for the two models (1995 and 1990, low and high capelin years).

5. Seabirds

According to the ICES Working Group on Seabird Ecology (ICES 2000(a)) the total number of seabirds in the Barents Sea (Areas I, and parts of areas II a,b) was 16,924,030 in 1999. Total consumption of 'fatty fish', 'other fish' and 'invertebrates' was estimated for each species of seabird recorded in the study area. The overall total consumption for birds was estimated as 1,008,128 t yr^{1}. Brünnich's guillemot (*Uria lomvia*), the most abundant bird species in the Barents Sea, was responsible for half of the total consumption (55.3 % of total biomass and 35.1% of total numbers). The estimated diet composition was based on Table 4.9 in ICES (2000(a)).

Multiplying body weight by number for each species yielded a total biomass density for all species combined of 0.00766 t km^{-2}. The overall Q/B value 93.99 was calculated by dividing estimated total consumption by biomass. The P/B value used for birds was 1.0, as given by Sakshaug (1997).

3.1.2 Fish Groups

There are thought to be few species of fish in the Barents Sea that exist in great numbers (Dolgov, 2000). The most important commercial species are cod, herring and capelin and the population dynamics and interactions of these species have been studied in detail (Bogstad and Tjelmeland, 1992).

There are many other, less abundant fish species in the Barents Sea. Dolgov (2000) reported a total of 203 fish species based on catches from surveys and stomach contents. No abundance estimates were available for many of these fish, and there was little or no commercial catch. Dolgov (1992) divided fish species into trophic guilds based on data from the IMR (Norway)-PINRO (Russia) stomach contents database. We based our functional groups on a combination of these trophic guilds and additional trophic and ecological knowledge of species that occurred in ICES catch data but were not listed within Dolgov's (1992) trophic guilds.

Abundance
ICES VPA (survey-based) and acoustic estimates were the primary source of abundance values for the fish species. Time series of biomass for several commercial fish species in the Barents Sea are shown in Figure 2.

Body weights
Bogstad *et al.* (2000) reported biomass values (in tonnes) for several commercial fish species. In addition, weight-at-age estimates were used to estimate biomass for groups that were split into adult and juvenile components. To ensure the appropriate age-at-maturity was used for each juvenile-adult split, the estimates were compared with maturity data from ICES Working Group reports, when these were available.

Q/B and P/B estimates
Consumption/biomass (Q/B) ratios were calculated according to the empirical model of Pauly *et al.* (1990)

and Christensen and Pauly (1992):

$$Q/B = 10^{6.37} \cdot 0.0313^{Tk} \cdot W_\infty^{-0.168} \cdot 1.38^{Pf} \cdot 1.89^{Hd}$$ [Equation 5],

where W_∞ is the asymptotic weight of the fish; Tk is the mean annual temperature expressed as 1000/(T°C + 273.1); Pf is one for apex predators, pelagic predators and zooplankton feeders and zero for all other feeding types. Hd characterises the food type and is set at one for herbivores and zero for carnivores. Usually, W_∞ was calculated from L_∞ , using published values for the length/weight parameters *a* and *b*. Natural annual mortality (M) was estimated for each species from the empirical model of Pauly (1980):

$$\log_{10}M = -0.2107 - 0.0824 \log_{10} W_\infty + 0.6757 \log_{10} k + 0.4687 \log_{10}T$$ [Equation 6],

where k is the curvature parameter of the von Bertalanffy growth function and T is the mean environmental temperature in °C. A mean annual temperature of 4.6 °C was used for the Barents Sea (ICES, 1996).

It was assumed that under steady state conditions:

$$P/B = Z \quad \text{and} \quad Z = M + F$$ [Equations 7 and 8],

i.e. that instantaneous total mortality (Z) equals total production over mean biomass (Allen, 1971), and that total mortality (Z) comprises natural mortality (M) and fishing mortality (F). Where possible, fishing mortalities were taken directly from ICES reports (VPA tables). Fishing mortality can also be estimated directly from:

Fishing mortality (F) = catch / biomass [Equation 9]

Detailed information regarding each of the fish groups (6 - 24) are given in the following sections.

6. Sharks

There were no readily available estimates for shark biomass in the Barents Sea even though Greenland (*Somniosus microcephalus*), porbeagle (*Lamna nasus*) shark and spiny dogfish (*Squalus acanthius*) are reported in the ICES Area I catch statistics. Since sharks comprised a group on its own, it was possible to allow Ecopath to estimate biomass of the group by setting the ecotrophic efficiency of the group to 0.75. Due to lack of local data, we also assumed that estimates of Q/B, P/B and diets were the same as those previously used for sharks the North Sea (Mackinson, 2002).

7,8 Adult herring and Juvenile herring

The majority of herring (*Clupea harengus*) in the Barents Sea are juvenile fish. Herring enter the Barents Sea as juveniles (ages 1-3) (Devold, 1963; Dragesund *et al*., 1980) but after maturation (ca. age 4) they migrate west into the Norwegian Sea where they feed from April to Sept. The adult feeding migration was different over the period 1970-1990, when the stock was small and adults fed along Norwegian coast (Vilhjálmsson *et al*., 1997; Holst *et al*., 1998 and 1999). After feeding in the Norwegian Sea, the adults spend October-January in the more protected coastal area of northern Norway. Since 1987, most herring have wintered in Tysfjord and Ofotfjord (Dommasnes *et al*., 1993). However, the over-wintering area has changed throughout the stock's history (Dommasnes et al. 1993). Norwegian Spring Spawning herring spawn from Feb-April on the shelf along the Norwegian coast, from Lindesnes in the south to Vesterålen in the north, and then return to feed in the Norwegian Sea.

Biomass density was calculated from biomass-at-age data obtained from the Report of the ICES Northern Pelagic and Blue Whiting Working Group (ICES, 2001, Table 3.5.6.3). The biomass of juveniles was 2,683,670 tonnes, equivalent to 1.917 t km^{-2} yr^{-1}, in 1995 and 838,950 tonnes, 0.599 t km^{-2} yr^{-1}, in 1990. The migration patterns of adult herring were accounted for by assuming the biomass within our model area was equal to approximately one quarter of the total Norwegian Spring Spawning herring stock. The resulting biomass of adult herring was 1,983,375 tonnes or 1.416 t km^{-2} yr^{-1} , in 1995, and 1,042,150 tonnes, 0.744 t km^{-2} yr^{-1}, in 1990.

Q/B values were obtained from equation 5 using a mean annual temperature at 200 m depth of 4.6°C (3.6 (K) (ICES, 1996). The Q/B value for adult herring was 4.84. To estimate Q/B for the juvenile group we multiplied the Q/B of the adult group by a factor of 2, as in Mackinson (2002). P/B was calculated using a value for M of 0.244, calculated from equation 6, and a value for F obtained from the ICES, 2001 assessment report. F was 0.578 in 1995 and 0.282 in 1990 (ICES 2001(b)). This gave P/B estimates of 0.8229 in 1995 and 0.489 in 1990. Diet composition for juvenile herring was taken from Huse and Toresen (1996), for adult herring it was based on Dalpadado *et al.* (2000).

9,10 Adult and juvenile capelin

Capelin (*Mallotus villosus*) spend the entire year in the Barents Sea (for distribution see Gjoester *et al*., 1998). The biomass of capelin reported by ICES (2000(b)) was based on acoustic estimates performed yearly in Sept-Oct (see Table 4.3.22 of ICES, 2000(b)). Age at maturity of capelin was reported as 1.7 (Fishbase 2001) and therefore capelin of age 1 were assumed to be juveniles and 2+ represented adults. In 1995, juvenile biomass density was 0.0536 t km^{-2} yr^{-1} and adult biomass was 0.0843 t km^{-2} yr^{-1} . In 1990, the equivalent densities were 2.296 t km^{-2} yr^{-1} and 1.869 t km^{-2} yr^{-1}.

Q/B for adult capelin was calculated as 4.7 using equation 5 with Barents Sea growth and mortality data and a mean annual temperature of 4.6°C (ICES, 1996). Using the same rationale described for herring, juvenile Q/B was calculated as 2 times adult Q/B. P/B for adult capelin was assumed to be equal to their natural mortality M (0.63) as there was no fishing mortality in 1995 and 1990. This assumes that there was no bycatch or discards, although information on these are lacking. M for juveniles was 1.26.

Diets were based on stomach contents data from Aijad and Pushcheva (1991).

11. Polar cod (1+)

Polar cod (*Boreogadus saida*) remain in the model area for the whole year. Biomass estimates for polar cod were available from Bogstad *et al.* (2000) and are based on acoustic abundance estimates from ICES. The biomass of polar cod (1+) was 0.304 t km^{-2} yr^{-1} in 1995 and 0.91 t km^{-2} yr^{-1} in 1990. Q/B for polar cod in the Barents Sea was assumed to be equal to the value of 2.633 reported for polar cod in the Ecopath model for the Newfoundland and Labrador Shelf (Bundy *et al.*, 1999). P/B could not be calculated for this group, instead an ecotrophic efficiency of 0.99 was assumed.

Diet composition of polar cod was available from a study carried out during 1986-1988 in the northeastern part of the Barents Sea by Ajiad and Gjøsæter (1990).

12. Pelagic planktivorous fish

Species in this group were aggregated according to Dolgov's trophic guilds for the Barent's Sea (Dolgov, 1989). They included sandeels (Ammodytidae), Norway pout (*Trisopterus esmarkii*), blue whiting (*Micromesistius poutassou*), argentines (*Argentine spp.*) Atlantic spiny lumpsucker (*Cyclopterus lumpus*), sprat (*Sprattus sprattus*), smelts (Osmeridae), and clupeiods (Clupeidae). This group also included any additional planktivorous fish species that represented more than 0.001% of ICES reported landings for Area I, but were not included in Dolgov's guilds.

The primary representatives of this group were believed to be to be sand eels, blue whiting and Norway pout, although there were no biomass or abundance estimates for most of these species. Blue whiting had a biomass density of 0.364 t km^{-2} yr^{-1} in 1995 and 0.301 t km^{-2} yr^{-1} in 1990 (ICES, 2000(b)). We considered this a substantial underestimate for the whole group, and therefore allowed Ecopath to calculate a value of the biomass density of this group using equation 3 and an ecotrophic efficiency of 0.99. The Q/B for pelagic planktivores, calculated using the Pauly equations, was the average for these three species. We used P/B for blue whiting (based on $Z = F + M$) as an estimate of P/B for the entire group. In 1995 the P/B was 0.657 and in 1990 it was 0.857.

Due to the lack of local diet information for species in this group, diet composition was based on the average for this group from the North Sea model of Christensen (1995).

13. Mackerel

Based on landings data, mackerel do not appear to be abundant in the Barents Sea (landings <0.001% of total). However, part of Western Mackerel (*Scomber scombrus*) stock is known to feed in the Norwegian Sea. Dommasnes *et al.* (2002) used a density of 0.180 t km^{-2} yr^{-1} for both the Norwegian and Barents Sea, and we assumed that the value for the Barents Sea was similar. Equation 5 was used to calculate the Q/B value for *Scomber scombrus.* There is no evidence of Horse mackerel occurring in the Barents Sea (see Dolgov, 2000). Due to lack of available data, mackerel in the Barents Sea were assumed to have the same diet as North Sea mackerel (Christensen, 1995).

14. Redfishes

This group included deep-water redfish (*Sebastes mentella*) and golden redfish (*Sebastes marinus*). Biomass estimates for *S. mentella* were based on VPA estimates for ages 6+ redfish (Bogstad *et al.*, 2000) and therefore represented an underestimate for the entire population. Since there is no VPA-based assessment in place for *Sebastes marinus*, the biomass estimate was derived from Dommasnes *et al.* (2002). The total biomass density for this group was 0.207 t km^{-2} yr^{-1}. However, this was believed to be a substantial underestimate; and Ecopath was allowed to estimate the biomass under the assumptions of mass-balance and an ecotrophic efficiency of 0.99. Q/B was calculated as 2.59 using equation 5. The diet was based on stomach contents data for both *S. marinus* and *S. mentella* obtained from Dolgov (2000).

15. Benthic Invertebrate Feeders

This group was based on Dolgov's (1992) trophic guild structure and included flatfish (such as *Pleuronectes platessa* and *Limanda* spp.), scuplins (Cottidae), eelpouts (Zoarcidae), lumpfish (Cyclopteridae) and Wachna cod (*Eleginus navaga*). Since no biomass estimates were available for any of these species an ecotrophic efficiency of 0.99 was assumed and biomass estimated by assuming mass-balance. Data from *Pleuronectes platessa* and *Limanda limanda* were used in equation 5 to estimate Q/B. P/B was estimated by assuming F was 0.1 and M was 0.21. As there were no detailed stomach contents data for the species in this group, we used an average of the plaice and sole diets from Christensen's (1995) North Sea model.

16, 17. Adult and juvenile haddock

Haddock (*Melanogrammus aeglefinus*) is one of the main commercial species inhabiting the Barents Sea. Biomass for the adult (4+) and juvenile (1-3) components was calculated using weight at age estimates reported in ICES (2001(a)). Biomass density for juveniles was 0.103 t km^{-2} yr^{-1} in 1995 and 0.308 t km^{-2} yr^{-1} in 1990. Biomass density of adults was 0.367 t km^{-2} yr^{-1} in 1995 and 0.086 t km^{-2} yr^{-1} in 1990. Q/B was estimated to be 2.31 for adults and was assumed to be double this for juveniles. P/B values were calculated by assuming P/B = Z and using natural mortality estimates from equations 6-8 and fishing mortality estimates reported in the ICES assessment report (ICES, 2001(a)). P/B for adults was 0.670 in 1995 and 0.616 in 1990. Juvenile haddock P/Bs were 0.597 in 1995 and 0.591 in 1990. The haddock diets were based on Burgos and Mehl (1987), who gave detailed diet composition by length and season in the Barents Sea. This enabled us to use yearly averages of stomach contents data for both adults (30 cm +) and juvenile groups (< 30 cm). More recent data are available in Jiang and Jorgensen (1996), but this was not on a length-specific basis, and we concluded that Burgos and Mehl's (1987) data were more appropriate for our split into adult and juvenile groups.

18. Wolfishes

This group consists of common (*Anarhicus lupus*), spotted (*A. minor*) and northern wolfishes (*A. denticulatus*). Due to the lack of information on biomass, this group was given an ecotrophic efficiency of 0.99 and biomass density was estimated using the Ecopath mass-balance equations. Q/B was calculated using equation 5. P/B was calculated by assuming a fishing mortality of 0.1 and a natural mortality of 0.35. Local information on the diet of wolfishes was not available and the diet was therefore based on the average input diet for Atlantic, spotted, and northern wolfish in the Newfoundland and Labrador Shelf Ecopath model (Bundy *et al.*, 2000).

19, 20. Adult and juvenile cod

Cod (*Gadus morhua*) is thought to be one of the most important top predators in the Barents Sea ecosystem (Bogstad *et al.*, 2000). Cod were split into two groups: adults (age 4+), and juveniles (1-3). The biomass of each group was calculated from weights-at-age obtained from ICES VPA tables (2001(a)). Biomass density was estimated to be 1.213 t km^{-2} yr^{-1} in 1995 and 0.626 t km^{-2} yr^{-1} in 1990 for adults and 0.389 t km^{-2} yr^{-1} in 1995 and 0.154 t km^{-2} yr^{-1} in 1990 for juveniles. Q/B for adults was calculated using equation 5 (2.35), although estimates of total consumption for Barents Sea cod have been given in Bogstad *et al.* (2000). The Q/B estimate for juveniles was assumed to be double that of the adults.

P/Bs were calculated using estimates of natural mortality (0.213) and estimates of fishing mortality in ICES (2001(a)) and equations 6-8. The P/Bs for the adult group were 0.1 in 1995 and 0.49 in 1990, for juveniles they were 0.471 in 1995 and 0.469 in 1990.

Bogstad *et al.* (2000) provide information of the diet of cod in low and high capelin years during the period 1992-1995.

21, 22. Adult saithe and juvenile saithe

Saithe (*Pollachius virens*) are known to occur on the North Norwegian coast, we assumed that they also occur in the model area for the entire year. Biomass estimates for both adult and juvenile groups were determined from weight-at-age VPA tables (ICES, 2001). Biomass densities were 0. 321 t km^{-2} yr^{-1} in 1995 and 0.138 in 1990 for adults (4+), and 0.174 t km^{-2} yr^{-1} in 1995 and 0.146 in 1990 for juveniles (1-3). Equation 5 was used to calculate Q/B (1.47) for adults, and this was doubled for juveniles. Diets for both groups were based on stomach contents data for Barents Sea saithe given in Dolgov (2000).

23. Benthic Piscivores

This group included thorny skate (*Raja radiata*), Greenland halibut (*Reinhardtius hippoglossoides*), Atlantic halibut (*Hippoglossus hippoglossus*), long rough dab (*Hippoglossoides platessoides*) and monkfish (*Lophius piscatorius*) and was assembled according to Dolgov's trophic guilds (Dolgov, 1992). Ling (*Molva molva*), tusk (*Brosme brosme*), whiting (*Merlangius merlangius*), pollack (*Pollachius pollachius*), hake (*Merluccius merluccius*) and megrim (*Lepidorhombus boscii*) were added to the group due to the presence in landings data, though they amounted to less than 0.1 % of catch. Biomass estimates for Greenland halibut, thorny skate, and long rough dab (Table 2) were taken from Bogstad (2000) and ICES (2001(a)).

Table 2. Biomass densities for representative species in the 'Benthic piscivores' trophic guild

Representative spp.	Biomass density (t km^{-2} yr^{-1}) for 1995 (1990 in brackets)
Greenland halibut	0.035 (0.06571)
Thorny skate(ray)	0.02428 (0.0293)
Long rough dab	0.05214 (0.0321)
Total	0.111 (0.122)

The Q/B value estimated using equation 5 was 2.65 (average for thorny skate and long rough dab). P/B was calculated under the assumption that P/B = Z and using the natural mortality calculated for Greenland halibut, because fishing mortality estimates were available for this species only. Barents Sea thorny skate stomach contents data from Dolgov (1997) were used to represent the whole group. Stomach contents data for Greenland halibut (Shvagzhdis, 1990) and long rough dab (Simacheva and Glukhov, 1985) were expressed as frequency of occurrence, and were not used.

24. Salmon and Seatrout

Although salmon (*Salmo salar*) and sea trout (*Salmo trutta trutta*) are caught in relatively large numbers in the Barents Sea region (usually in coastal areas), no useable data could be found on this group. Diet, Q/B and P/B were all taken from an Ecopath model for the North Sea (Mackinson, 2002).

3.1.3 Invertebrates

Estimating parameter values for the groups of invertebrate species existing in the Barents Sea was challenging due to a pronounced lack of available information. However, some data were available for plankton and benthic species (see Kupriyanova *et al.*, 1999) from the extensive Russian research programmes conducted over the past century. Where possible, P/B and Q/B estimates were taken from the literature, otherwise they were 'borrowed' from other published Ecopath models.

25. Squid

Gonatus fabricii is the most abundant cephalopod species in arctic waters and is distributed throughout the Barents Sea (Nesis, 2001). However, there is a lack of reliable biomass estimates for this species. Dalpadado *et al.* (1998) estimated the distribution and ranges in the Nordic Sea (Norwegian, Iceland and Greenland Seas) and reported a total biomass in summer of 1994 of 4.1 million tonnes. Dommasnes *et al.* (2002) constructed an Ecopath model that encompassed both the Barents and Norwegian Seas. The authors used a biomass density of 2.63 t km^{-2} yr^{-1} for squid, based on data in Bjørke and Gjøsæter (1998) for the Norwegian Sea. Although this is outside of our model area, we assumed that the density of squid in the Barents Sea was the same as that in the Norwegian Sea. Diet composition for *Gonatus spp.* is based on stomach contents data from Sennikov *et al.* (1989). Values for P/B (3.0) and Q/B (15.0) for the Alaska Gyre Ecopath model (Pauly and Christensen, 1996) were used.

26. Lobster and crabs

A small catch for lobsters and crabs (Crustacea, Decapoda) was reported in ICES statistics for the Barents Sea. However, there is very little scientific information on these animals. Red king crab (*Paralithodes camtschaticus*) is known to have become abundant after it was introduced into the area in the 1950s (Kuzmin and Olsen, 1994). There are no published abundance estimates, although it is thought that there will be enough Red king crab to sustain a fishery in near future (Gerasimova, 1997). A Q/B estimate of 5.85 from the Newfoundland Shelf model (Bundy, 2000), based on consumption studies by Reddin (1973), was used. P/B was reported to be 2.5 for lobsters and crabs in the North Sea model (Mackinson, 2002) whereas Bundy (2000) gave a range of estimates (0.182 - 0.382). We used a value of 2.5, because the higher value was considered to be more appropriate for crabs, which we believe to be the dominant members of the group in the Barents Sea. Diet composition was assumed to be the same as in the North Sea (Mackinson, 2002).

27. Prawns and Shrimp

Abundance estimates were available for deep-water shrimp (*Pandalus borealis*), although these are thought to be an underestimate according to Bogstad et al. (2000) because they were obtained by the swept area method and only reflect what was available to the bottom trawl. Bogstad *et al.* (2000) gave biomass estimates for the period 1984-1999. These are probably minimum estimates of shrimp biomass in the Barents Sea. We used a P/B value of 1.7, based on Hopkins' (1988) study of shrimp off northern Norway.

28. Other crustaceans

This group comprised hermit crabs (*Lobochona limnoriae*), benthic amphipods (Suborder:Gammaridea) and isopods (Suborder:Asellota). No biomass estimates were available, an ecotrophic efficiency of 0.99 was assumed and the Ecopath mass-balance equations were solved to obtain an estimate of biomass density. Published Q/B estimates for this group are 3.0 (Mackinson, 2002) and 1.480 (Trites *et al.*, 1999). The latter was used for an initial input. We used a P/B value of 7.69 (Trites *et al.*, 1999), based on data from the Bering Sea.

29, 30, 31. Epifaunal filter feeders, Infaunal filter feeders, Other macrobenthos

Estimates of biomass for many benthic invertebrates in the Barents Sea were available from a study made using nearly 1000 Petersen grabs during the 1930s, the end of the late 1940s and beginning of the 1950s (Zatsepin and Rittikh, 1968). An even earlier work described detailed spatial distributions of bottom fauna in the Barents Sea in the 1930s (Brotskaya and Zenkevich, 1939). Recent published work on the benthic fauna of the Pechora Sea (located in the southeastern Barents Sea) was also available (Dahle *et al.*, 1998), but this covers only a small portion of our study area.

Zatsepin and Rittikh (1968) distinguished seven principal trophic guilds: i) filter feeders from the epi-fauna, ii) filter-feeders from the infauna, iii) detritophages, iv) bottom sediment feeders, v) predators, vi) omnivores and carrion-eaters and vii) plant-eaters and scrapers. The principle food of bottom invertebrates (except for predators) was thought to consist of detritus, bacteria, small bottom animals (microbenthos and meiobenthos), and dead organic matter present in the bottom material itself (Zatsepin and Rittikh, 1968). We combined the seven trophic groups proposed by Zatsepin and Rittikh (1968) into three groups: 'Epifauna' (epifaunal filter feeders sealilies, crinoids, urchins), 'Infauna' (infaunal filter feeders, mostly bivalves, detritivores and polychaetes), and 'Other macrobenthos' (omnivores and carrion eaters, plant eaters and scrapers, such as gastropods). The biomass density of the 'Epifauna' was calculated to be 20.098 t km^{-2} yr^{-1} , for 'Infauna' it was 65.196 t km^{-2} yr^{-1}, and for 'Other benthos' 13.235 t km^{-2} yr^{-1} .

We used Trites *et al.*'s (1999) estimates of Q/B from the Bering Sea: for 'Infauna' this was 12.0 and for 'Epifauna' it was 5.77.

Several P/B estimates were available for these groups from other published models. Mackinson (2002) used 1.9 for both infauna and epifauna. Other possible P/B estimates included those in Trites *et al.* (1999) where a P/B value of 1.578 was used for 'Epifauna' and 1.373 for 'Infauna'. In Bundy's (2000) Newfoundland and Labrador Shelf model a P/B of 2.00 was used for polycheates, 0.57 for molluscs, 0.60 for echinoderms and 2.50 for other benthic invertebrates. We used the P/Bs given for the Bering Sea by Trites *et al.* (1999).

The diet composition for each of these groups was based on descriptions in Zatsepin and Rittikh (1968) and the models mentioned above.

32. Meiofauna

There were no readily available biomass estimates of meiofauna in the Barents Sea. Biomass and P/B estimates were taken from the North Sea model of Mackinson (2002). Q/B was estimated within Ecopath by assuming an ecotrophic efficiency of 0.99.

33, 34. Carnivorous zooplankton and herbivorous zooplankton

Biomass estimates for carnivorous and herbivorous zooplankton were available from ICES (1998). The time series of mean annual zooplankton abundance monitored during annual 0-group and capelin surveys in Aug - Sept in the Barents Sea (ICES, 1998) is shown in Figure 6. Mean annual amphipod (*Themisto spp.*) abundance has also been estimated since 1985 (Dalpadado *et al.*, 2001). Dalpadado *et al.* (2001) have shown that there appear to be strong predator-prey interactions between macrozooplankton (such as *Themisto spp.*), capelin and cod in the Barents Sea. We assumed that 'zooplankton > 2000 µm' in ICES (1998) were equivalent to 'carnivorous zooplankton' (which consist of euphausiids, amphipods, jellyfish, arrow-worms, mysids, fish larvae and nauplii stages). Similarly, we assumed that 'zooplankton from 180-2000 µm' represented 'herbivorous zooplankton' (such as copepods, cladocerans and ostracods). These values were converted from g of carbon to wet weight using the formula: wet weight =10·Carbon weight (Matthews and Heimdal, 1980). The biomass density of carnivorous zooplankton was 38 t km^{-2} yr^{-1}, for herbivorous zooplankton it was 58 t km^{-2} yr^{-1}.

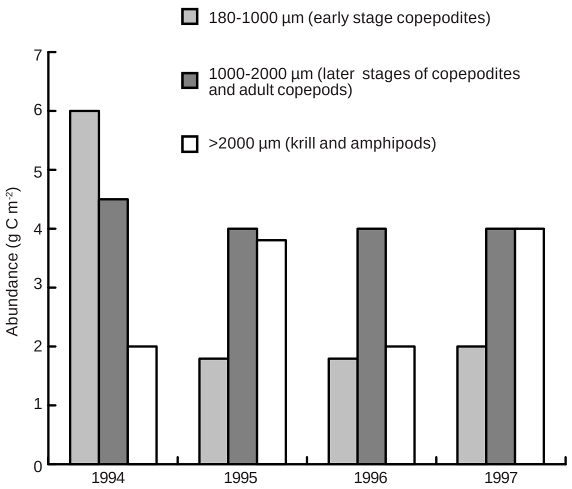


Figure 6. Mean annual zooplankton abundance monitored during annual 0-group and capelin surveys in August and September. After ICES (1998)

Q/B values for both groups were assumed to be the same as in the Bering Sea model, i.e. 22 yr^{-1}. Locally derived P/B values of 1.5 for carnivorous zooplankton and 4 for herbivorous zooplankton were available from Sakshaug (1997), i.e.. P/B values in the range 1.6 - 11.6 have been used for cold water zooplankton in other models (Trites *et al.*, 1999; Bundy *et al.*, 2000 and Okey and Pauly, 1999). Diet composition for zooplankton groups were based on Mackinson (2002).

3.1.4 Primary Producers and Bacteria

35, 36. Planktonic micro-organisms and benthic micro-organisms

Micro-organisms such as protozoa and bacteria were divided into planktonic micro-organisms and benthic micro-organisms. There were no available data on biomass or P/B for these two groups in the Barents Sea. We therefore used values from Mackinson (2002) of 3.038 t km^{-2} yr^{1} and 653 for the biomass and P/B of planktonic micro-organisms, and 0.48 t km^{-2} yr^{1} and 15625 for benthic micro-organisms. Sakshaug (1997) gives a broad estimates of the average biomass of 'bacteria' over the whole of the Barents Sea during 1984-1989 of 400 kg C m^{-2} (approx. 4 t km^{-2} yr^{1} wet weight) and a P/B of 200 (based on a productivity of 800 g m^{-2} in wet weight).

37. Phytoplankton

The phytoplankton community in the Barents Sea has been intensively investigated since the beginning of the last century, in particular by Russian scientists (e.g. Linko, 1907; Kiselev, 1928; Manteifel,1938). Over the last 30 years hydrodynamic, primary productivity, and taxonomic studies have been carried out (Bobrov, 1985; Larionov, 1997; Druzhkov and Makarevich, 1999; Makarevich and Larionov, 1992) and bibliographic information as well as a very detailed database of research survey results are available from the Biological Atlas of the Arctic Sea 2000: Plankton of the Barents and Kara Sea (See website: http://www.nodc.noaa.gov/OC5/BARPLANK/WWW/HTML/bioatlas.html).

Sakshaug (1997, and references therein) has contributed extensively to work on primary productivity and physical factors affecting this in the Barents Sea, and has also compiled overall biomass and P/B estimates for broad groups of organisms. There is a high degree of spatial, seasonal and inter-annual variation in primary productivity in the region, due in part to variation in the amount of melt-water from sea-ice (Loeng, 1991). Productivity (P) of phytoplankton ranges from 90 to 120 g C m^{-2} yr^{1} in the south of the Barents Sea, and from 20 to 50 g C m^{-2} yr^{1} in the north (Sakshaug, 1997). Total annual production increased by 30% over the 1981 - 1984 period. Sakshaug (1997) characterised the Barents Sea as being less productive (in terms of primary production) than the Bering Sea. Average biomass and P/B ratio for the whole sea were 20 t km^{-2} yr^{1} and 55 yr^{1}, respectively (Sakshaug, 1997).

38.Seaweeds

There were no recent biomass estimates for seaweeds in the Barents Sea. However, Brotsskaja and Zenkevivich (1939) suggested that macroalgal biomass in coastal areas of the Barents Sea was 24-28 kg m^{-2} (*Laminaria*, *Ascophyllum*, *Fucus*), and that biomass decreased rapidly with depth. P/B ratios were estimated to be approximately 2 yr^{1} for coastal vegetation. Therefore a minimum estimate of seaweed biomass density of 0.019 t km^{-2} yr^{1} for the entire Barents Sea can be calculated on the assumption that seaweed occurs only in coastal waters.

We assumed a P/B of 2 yr^{1} in order to use locally derived estimates although Lüning (1990) gave a P/B of approximately 4 yr^{1} for seaweeds and this was used in the Prince William Sound model of Okey and Pauly (1999).

3.1.5 Detritus Groups

39. Dead carcasses

The main source of dead carcasses was assumed to be fisheries discards. Very few data exist for discarding of target or by-caught fish in the Barents Sea. Mcbride and Fotland (1996) estimated that 6.9% of the total catch in the commercial trawl fishery is discarded or not reported, including 2% of all cod caught. In addition, we specified 1% of unused production of each group to the dead carcasses component of 'Detritus'.

40,41. Water column detritus and benthic detritus

Water column detritus and benthic detritus biomass estimates were not available for the Barents Sea. We used a value of 4.3 g C m^{-2} (50 g WW m^{-2}) for detritus biomass density for the southern North Sea from Hannon and Joires (1989) for both of these groups. It should also be noted that Sakshaug (1997) reported that the productivity of dissolved organic carbon released by phytoplankton in the Barents Sea was approximately 15 g C m^{-2} yr^{1}, however this was not incorporated into our model.

3.2 Unassimilated Food

The assimilation efficiency (*AE*) of consumers is highly variable, depending on factors such as food quality, amount of food consumed and the age of the consumer (Valiela, 1984). In Ecopath, the proportion of the food that is not assimilated (1-*AE*) must be entered if the currency of the model is energy or mass (Christensen and Pauly, 1992). Here we assumed an *AE* value of 88.8% for marine mammals, all carnivorous fish groups, cephalopods and seabirds, based on Pandian and Marian (1985); An *AE* of 80% was assumed for planktivorous fish groups and crustaceans, based on values reported in Arias-Gonzalez *et al.* (1997), Winberg (1956) and Daborn (1975). *AE* was assumed to be 65% for benthic invertebrates (Lawrence, 1987; Cammen, 1987; Carefoot, 1987). Meoifauna, zooplankton and microorganisms were all assumed to have an *AE* of 82% (Fenchel, 1982; Lasenby and Langford, 1973; Gaudy *et al.*, 1991; Bochdansky *et al.*, 1999; Dilling *et al.*, 1998, Vernberg, 1987; Conover, 1966).

3.3 Fishery parameters

Nominal landings of fish and shellfish are officially submitted to ICES by each member country on an annual basis. ICES has published these data in *Bulletin Statistique des Pêches Maritimes* from 1903 to 1987, and from 1988 onwards in *ICES Fisheries Statistics.* In the present study, aggregated data for ICES Division I were downloaded from the website www.ices.dk. Landings were expressed in tonnes live weight equivalent and divided by the total Barents Sea shelf area (1.4 million km^{2}) (Jakobsen, 1999) in order to calculate catch per m^{-2} yr^{-1}. There were no reported catches of capelin in either 1990 or 1995 (Figure 7).

Whaling data were available from IWC catch statistics, and sealing data from Nakken, 1998. An annual minke whale harvest of 87 individuals and a catch of 500 seals were used for both models based on catch in the Barents Sea only. Given an average body mass of 5.25 t for minke and 0.1 t for harp seals (Nilssen *et al.*, 1997), this equated to 3.26×10^{-4} t km^{-2} yr^{-1} of whales and 3.57×10^{-5} t km^{-2} yr^{-1} of seals.

All fishery landings were allocated to four gear types or 'fleets', in general accordance with those given in Nakken (1998). Catches of pelagic schooling species including capelin, herring, mackerel and blue whiting were allocated to the 'pelagic gear' category (purse seines and pelagic trawls). Landings of demersal fish (most fin-fishes), including cod, haddock, saithe, polar cod, redfishes and wolffishes, were allocated to the 'demersal-trawl' category. Northern shrimp (*Pandulus borealis*) was allocated to the 'shrimp-trawl' gear-type and all other invertebrates (e.g. crabs, lobsters and scallops) were grouped as 'other-gears', along with the collection of macroalgae. This last group included pots, handlines and shore-based collection methods. 'Whalers' and 'Seal hunters' were also included in the gear types.

As described in Section 3.1 above, estimates for discarded biomass from McBride and Fotland (1996) were directed within the Ecopath model towards the 'dead-carcasses' group. Discards of target species were assumed to be juvenile individuals. Elsewhere in the world, the bycatch of juvenile fish can be a major problem in fisheries with small meshed trawls, such as those used to catch shrimp (Alverson *et al.,* 1994). This is likely to be true for the Barents Sea shrimp fishery (Veim *et al.,* 1994) and estimates were available from Hylen and Jacobsen (1987) and Albert *et al*., (1994). The total amount of discards was estimated to be 0.0198 t km^{-2} yr^{-1}.

4. MODEL BALANCING

4.1 General approach and strategy to model balancing

If the total demand placed on a particular group by predation or fishing exceeds the production of that group, the group is commonly said to be out of balance. The degree of energy 'imbalance' of each functional group is usually determined in Ecopath by examining the ecotrophic efficiency (EE). The EE is calculated by Ecopath mass-balance equation 4 after initial input parameters have been entered. A value of EE greater than one indicates that total energy demand exceeds total production. Therefore, EE is used as the basis for model balancing; changes in EE values being monitored as adjustments are made to input parameters. Since balancing an Ecopath model requires that the user manually changes input values, it is necessary to employ a strategy and establish ground rules before balancing.

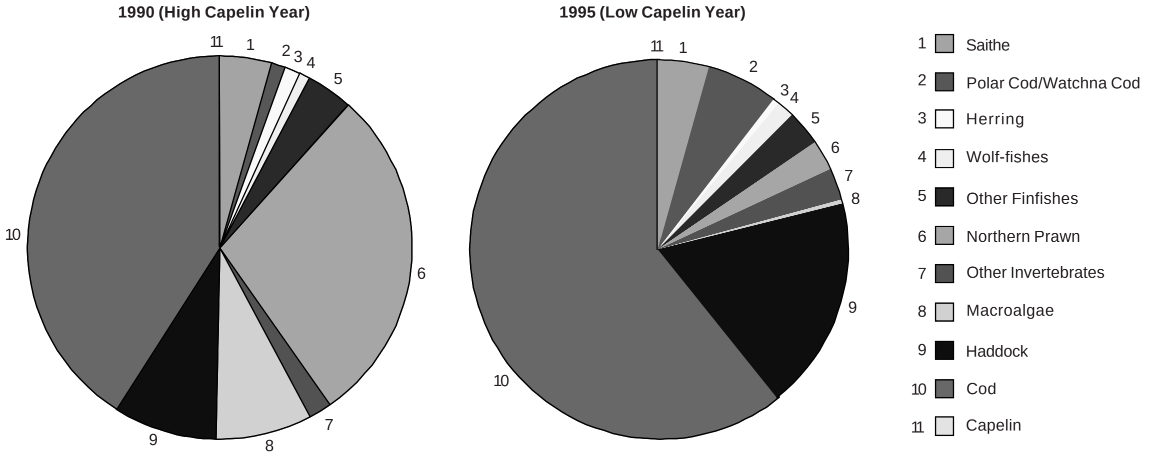


Figure 7. Composition of fishery landings in 1990 and 1995, based on data compiled by ICES

To help prevent unnecessary and unrealistic adjustments being made, the following strategic approach was developed:

(1) Adjustments to parameters should generally begin with those groups with the highest EEs
(2) Parameters to be targeted for adjustment should be prioritised according to assessment of the data quality and reliability.
(3) Diets are targeted first, because diet composition data tends have high low reliability relative to other parameters, but this should be assessed on a case-specific basis. If changes to the diets composition have only small effects, it is necessary to adjust P/B, Q/B, and/or B.

During the balancing of any Ecopath model, there is a danger of employing an overly 'top-down' strategy. Total biomasses of all groups can become unrealistically inflated if prey biomasses or production are increased in an attempt to meet the demands of higher predators. Ecopath users must make a conscious effort to apply an even-handed approach during balancing. Not only should the accounts tally but, more importantly, biological rates should stay within reasonable bounds and known ecological relationships should be preserved.

4.2 Balancing the low capelin (1995) model

The initial estimate of 'missing' parameters by Ecopath indicated a number of groups for which 'demand' exceeded 'supply' (i.e. EE >1). During the balancing process *ecological 'anchor' groups* were established. These were groups, positioned at different trophic levels, that were considered to have ecological importance and whose parameter estimates were believed to be of good quality. Our main anchor groups were cod, haddock, capelin, herring and phytoplankton. The strategy was to hold constant the parameter estimates for each of these anchor groups, while adjusting values for other groups. The capelin and herring components were considered to be particularly important anchors, as they formed a crucial link between top predators and primary production. Also they had a substantial estimated biomass, which was likely to have important impacts on other components of the system. In trying to avoid bias, we made adjustments in both 'top down' and 'bottom up' directions, such that predator demands were met by realistic productivity of prey. The sensitivities of changing input values on the estimated parameters within and among the groups in the model is detailed in Section 5.4.

The main problems and adjustments were:

- *Too much consumption of capelin.* Small changes were made to diets and Q/B for the main predators of capelin (whales, juvenile cod and haddock, saithe and squid). Finally, Ecopath was allowed to estimate the biomass of adult and juvenile capelin.
- *Too little production by juvenile groups.* P/B was increased to approximately double that of adults.
- *Too much consumption of benthic piscivores by seals and cod.* Biomass of seals was reduced to the most recent mean estimate from ICES 2001 report. Seal and cod Q/Bs were reduced and Ecopath was allowed to estimate the biomass of benthic piscivores.
- *Cannibalism* in cod was reduced to 1%. Diet was compensated through re-allocation to squid.
- *Too few prawns and shrimp.* Biomass was increased slightly because it was believed to be underestimated (Bogstad *et al.*, 2000).

The second balancing round focussed on resolving positive feedback loops relating to the diets of groups at lower trophic levels. These loops result in prey groups having very large estimated biomass; in order to sustain the high consumption of the predators higher up in the system. Small alterations to input parameters cascade down through the food web, resulting in the biomasses at lower trophic levels 'exploding' to ridiculous values. Meiofauna were found to be particularly affected by positive feedback loops. We used phytoplankton as an 'anchor group' in helping to resolve the issue of cascading excessive consumption in lower trophic levels. Furthermore, we made adjustments (to diets, Q/B, P/Q and biomass) to 5 dominant linkages: (i) benthic detritus consumption by meiofauna and benthic micro-organisms, (ii) water column detritus consumption by infaunal filter feeders and planktonic micro-organisms, (iii) herbivorous zooplankton consumption by carnivorous zooplankton (iv) phytoplankton consumption by herbivorous zooplankton and planktonic micro-organisms, (v) dead carcasses consumption by meiofauna and benthic micro-organisms.

Table 3 summarises the changes made during parameterisation by comparing the original input parameters with balanced model parameters and Table 4 summarises the input and balanced parameters used in the diet matrix during parameterisation.

Internal consistency checks

A parallel goal of our final balancing procedure was to ensure that the model parameters complied with physiological and thermodynamic constraints. Three important diagnostic indices were considered. *Gross food conversion efficiency* (production/consumption) typically ranges from 0.1 to 0.3, but can be higher for groups such as bacteria, fish larvae and other small, fast growing organisms. *Respiration/Biomass ratio*, should generally be in the range 1-10 year^{-1} for fish, but higher values are expected for faster turnover organisms such as zooplankton. *Respiration/Production ratio* can take any positive value, but thermodynamic constraints limit the realised range to 0-1 (see Table 5).

Table 3. Comparison of input and balanced model parameters for 1995 ‘low’ capelin model. Initial and (balanced) input data (where different from initial input). Asterisk values are estimated within Ecopath

Group name	Trophic level	Biomass in hab. Area (t km^{-2})	Production/ biomass (/year)	Consumption/ biomass (/year)	Ecotrophic efficiency	Production/ consumption	Unassimil./ consumption
Minke	4.3	0.159	0.035	8.14	0.058	0.004	0.112
Other baleen whales	4.3	0.112	0.02	13.11 (12.89)	0	0.002	0.112
Toothed whales	4.8	0.018	0.02	12.748	0	0.002	0.112
Birds	4.7	0.008	1	93.99 (80)	0	0.013	0.112
Seals	4.7	0.159 (0.111)	0.056	15.59 (13)	0.157	0.004	0.112
Sharks	4.7	0.020*	0.15	4.77	0.75	0.031	0.112
Adult herring (4+)	3.4	1.471 (1.000)	0.823 (0.70)	4.84	0.933	0.145	0.2
Juvenile herring (1-3)	3.2	1.917	0.489 (1.5)	9.684	0.402	0.155	0.2
Adult capelin (2+)	3.7	0.084 (0.574*)	0.63 (1)	4.7	0.99	0.213	0.2
Juvenile capelin (1)	3.2	0.054 (0.496*)	1.26 (2)	9.4	0.99	0.213	0.2
Polar cod (1+)	3.8	0.304 (0.597*)	(0.7)	2.633	0.99	0.266	0.2
Pelagic planktivorous fish	3.4	1.205*	0.657	5.465	0.99	0.12	0.2
Mackerel	4.1	0.18	0.624	2.27	0.926	0.275	0.2
Redfishes	3.8	0.207 (0.435*)	(0.5)	2.59 (2)	0.99	0.25	0.112
Benthic Invert. Feeders	3.7	0.968*	0.31	3.214	0.95	0.096	0.112
Adult haddock (4+)	3.9	0.367	0.67 (0.60)	2.315	0.905	0.259	0.112
Juvenile haddock (1-3)	3.9	0.103 (0.177*)	0.598 (1.5)	4.63 (3.5)	0.99	0.429	0.112
Wolfishes	4	0.036*	0.45	0.45 (1.77)	0.95	0.254	0.112
Adult cod (4+)	4.3	1.213 (1.000)	1 (0.60)	1 (2)	0.874	0.300	0.112
Juvenile cod (1-3)	4.0	0.389 (0.310*)	0.47 (1.5)	4.714 (3.5)	0.99	0.429	0.112
Adult saithe	4.5	0.321 (0.300)	0.85 (0.70)	1.469 (2)	0.996	0.35	0.112
Juvenile saithe	4.2	0.174	0.93 (1.306*)	0.174 (2.938)	0.99	0.445	0.112
Benthic piscivores	4.3	0.111 (0.546*)	0.54	2.654	0.99	0.204	0.112
Salmon and Seatrout	4.1	0.084*	0.4 (0.6)	7.14 (4)	0.99	0.15	0.112
Squid	3.7	2.632 (0.284*)	3 (1.4)	15 (10)	0.99	0.14	0.112
Lobsters crabs	3.4	0.100*	2.5 (2.0)	5.85 (6)	0.95	0.333	0.2
Prawns and shrimps	2.6	0.138 (0.307*)	1.7	9.67	0.99	0.176	0.2
Other crustaceans	2.7	1.143*	1.48	7.69	0.95	0.192	0.2
Epifaunal filter feeders	2.9	20	1.58	5.77	0.309	0.274	0.35
Infaunal filter feeders	2.6	65 (20)	1.37	12 (11)	0.717	0.125	0.35
Other macrobenthos	3	13.235	2.5	12.5	0.560	0.2	0.35
Meiofauna	2.4	34 (9.745*)	19	47.5*	0.99	0.4	0.18
Carnivorous zooplankton	2.9	38 (6)	4 (8)	22 (20)	0.453	0.4	0.18
Herbivorous zooplankton	2.2	58 (15)	6 (9)	22 (25)	0.680	0.36	0.18
Planktonic micro-organisms	2	3.038 (1.198*)	653 (150)	375*	0.99	0.4	0.18
Benthic micro-organisms	2	0.48 (1.127*)	15625 (150)	375*	0.99	0.4	0.18
Phytoplankton	1	20	55	-	0.290		
Seaweeds	1	0.019	2	-	0.233		
Dead carcasses	1	-		-	0.980		
Water column detritus	1	50		-	0.670		
Benthic detritus	1	50		-	0.957		

Table 4. Diet matrix for 1995 model showing input values (and final balanced values in brackets where changes were made during balancing)

	Prey\Predator	1	2	3	4	5	6	7	8	9	10	11
1	Minke											
2	Other baleen whales											
3	Toothed whales											
4	Birds											
5	Seals						0.001 (0.01)					
6	Sharks						0.001 (0.005)					
7	Adult herring (4+)		(0.184)	0.417	0.04	0.1	0.05					
8	Juvenile herring (1-3)	0.384 (0.361)	(0.2)		0.03	0.073 (0.07)	0.05					
9	Adult capelin (2+)	0.047 (0.025)	0.215 (0.025)	0.048		0.01	0.05 (0.01)					
10	Juvenile capelin (1)	0.02 (0.15)	0.1 (0.15)	0.02 (0.01)			0.07 (0.01)		(0.015)			
11	Polar cod (1+)					0.228 (0.075)	0.04					
12	Pelagic planktivorous fish	0.028 (0.072)	0.072	0.026	0.465		0.105 (0.106)					
13	Mackerel					(0.025)	0.041					
15	Benthic Invert. Feeders				0.165	(0.05)	0.05					
16	Adult haddock (4+)			0.019 (0.029)	0.002	(0.075)	0.005 (0.06)					
17	Juvenile haddock (1-3)	0.094 (0.05)	0.04		0.051	0.025 (0.012)	0.005					
18	Wolfishes					0.001	0.05					
19	Adult cod (4+)			0.091	0.032	0.05 (0.11)	0.025 (0.051)					
20	Juvenile cod (1-3)	0.121 (0.1)	0.05		0.051	0.085 (0.039)	0.025 (0)					
21	Adult saithe			0.06	0.014	(0.12)	0.025 (0.01)					
22	Juvenile saithe	0.029 (0.02)	(0.029)		0.051	0.012	0.025 (0.02)					
23	Benthic piscivores			0.257	0.096	0.165 (0.024)	0.057					
24	Salmon and Seatrout			0.06		(0.025)						
25	Squid			0.002			0.126					
26	Lobsters crabs						0.1					
27	Prawns and shrimps						0.01 (0)					0.008
28	Other crustaceans											
29	Epifaunal filter feeders											
30	Infaunal filter feeders											
31	Other macrobenthos						0.04 (0.097)					
32	Meiofauna											
33	Carnivorous zooplankton	0.277 (0.357)	0.685 (0.385)			0.253 (0.251)		0.35	0.10 (0.130)	0.751	0.059	0.889
34	Herbivorous zooplankton							0.55	0.67 (0.655)	0.249	0.941	0.103
35	Plank. Micro-organisms							0.05	0.1			
36	Benthic micro-organisms											
37	Phytoplankton							0.05	0.1			
38	Seaweeds											
39	Dead carcasses				0.002							
40	Water column detritus											
41	Benthic detritus											
	Import											
	Sum	1	1	1	1	1	1	1	1	1	1	1

Table 4. continued

	Prey\Predator	12	13	14	15	16	17	18	19	20	21	22	23	24
1	Minke													
2	Other baleen whales													
3	Toothed whales													
5	Seals													
7	Adult herring (4+)								0.013		0.1			0.1
9	Adult capelin (2+)					0.057	0.028		0.072	0.079	0.409 (0.17)		0.033 (0.03)	0.1
10	Juvenile capelin (1)		0.15	0.05					0.072	0.05	0.2 (0.14)	0.609 (0.43)		0.075
11	Polar cod (1+)								0.057	0.05	0.05	0.05	0.022	
13	Mackerel		0.01								(0.1)			
14	Redfishes			0.002		0.04	0.052	0.049	0.044	0.061 (0.01)			0.027	
15	Benthic Invert Feeders					0.008	0.003	0.004	0.021	0.008			(0.03)	
17	Juvenile haddock (1-3)		0.05				0.003		0.013			(0.01)		
18	Wolfishes											(0.01)		
19	Adult cod (4+)												0.1	
20	Juvenile cod (1-3)		0.05					0.005	0.088 (0.01)	0.009	0.009	0.009	0.129 (0.05)	
21	Adult saithe													
22	Juvenile saithe		0.04									(0.02)		
23	Benthic piscivores								0.056 (0.026)	0.049 (0.048)			0.055	
24	Salmon and Seatrout													
25	Squid								0.006 (0.115)	0.001	(0.1)		0.035 (0.062)	
26	Lobsters crabs							0.075					(0.1)	
27	Prawns and shrimps			0.224 (0.15)		0.06	0.052	0.012	0.082 (0.05)	0.263 (0.1)	0.002	0.002	0.177 (0.05)	
28	Other crustaceans			0.1 (0.174)		0.054	0.053 (0.063)		0.028 (0.029)	0.032 (0.251)			0.07 (0.05)	
29	Epifaunal filter feeders				0.25	0.382	0.235	0.549	0.008	0.013 (0.008)			(0.05)	
30	Infaunal filter feeders				0.65	0.084	0.071 (0.07)	0.008	0.01	0.011			0.131	
31	Other macrobenthos				0.1	0.04 (0.266)	0.046	0.273	(0.342)				(0.05)	
32	Meiofauna													
33	Carnivorous zooplankton	0.388	0.4	0.624		0.267 (0.04)	0.45 (0.44)	0.025	0.341 (0.03)	0.327	0.183	0.183 (0.292)	0.188	0.55
34	Herbivorous zooplankton	0.512	0.1						0.011	0.007				
35	Plank. Microorganisms	0.05												
36	Benthic micro-organisms													
37	Phytoplankton	0.05												
38	Seaweeds					0.005	0.007							
39	Dead carcasses													
40	Water column detritus													
41	Benthic detritus													
	Import													
	Sum	1	1	1	1	1	1	1	1	1	1	1	1	1

Table 4. continued

	Prey\Predator	25	26	27	28	29	30	31	32	33	34	35	36
1	Minke												
2	Other baleen whales												
3	Toothed whales												
4	Birds												
5	Seals												
6	Sharks												
7	Adult herring (4+)												
8	Juvenile herring (1-3)	0.05 (0.01)											
9	Adult capelin (2+)	0.025 (0)											
10	Juvenile capelin (1)	0.025 (0.01)											
11	Polar cod (1+)	0.05 (0.01)											
12	Pelagic planktivorous fish	0.05 (0.01)											
13	Mackerel												
14	Redfishes												
15	Benthic Invert Feeders												
16	Adult haddock (4+)												
17	Juvenile haddock (1-3)	(0.01)											
18	Wolfishes												
19	Adult cod (4+)												
20	Juvenile cod (1-3)	(0.01)											
21	Adult saithe												
22	Juvenile saithe	(0.01)											
23	Benthic piscivores												
24	Salmon and Seatrout												
25	Squid												
26	Lobsters crabs		0.05										
27	Prawns and shrimps												
28	Other crustaceans		0.15		0.1								
29	Epifaunal filter feeders		0.2					0.05					
30	Infaunal filter feeders		0.1	0.015	0.02			0.1	0.001				
31	Other macrobenthos		0.2	0.015				0.1	0.001				
32	Meiofauna		0.05		0.2	0.4	0.4	0.25		0.05			
33	Carnivorous zooplankton	0.4 (0.53)		0.12						0.05			
34	Herbivorous zooplankton	0.4		0.24	0.05					0.55			
35	Plank. Micro-organisms				0.05			0.1	0.15	0.1	0.2	0.05 (0.005)	
36	Benthic micro-organisms		0.05		0.08	0.3		0.1	0.25				
37	Phytoplankton			0.085	0.05					0.1	0.75	0.2 (0.05)	
38	Seaweeds												
39	Dead carcasses		0.1	0.05	0.05				0.05 (0.015)				0.05 (0.15)
40	Water column detritus			0.213	0.05	0.15	0.4		0.1	0.05	0.01	0.75 (0.85)	0.15 (0.055)
41	Benthic detritus		0.1	0.262	0.35	0.15	0.2	0.3	0.449 (0.484)	0.1	0.04	(0.095)	0.8 (0.93)
	Import												
	Sum	1	1	1	1	1	1	1	1	1	1	1	1

Table 5. Output parameters for key diagnostic indices used in model checking

Group name	Production / Consumption	Respiration/ Biomass (/year)	Production/ Respiration
Minke	0.004	7.193	0.005
Other baleen whales	0.002	11.426	0.002
Toothed whales	0.002	11.3	0.002
Birds	0.013	74.92	0.013
Seals	0.004	11.488	0.005
Sharks	0.031	4.086	0.037
Adult herring (4+)	0.145	3.172	0.221
Juvenile herring (1-3)	0.155	6.247	0.24
Adult capelin (2+)	0.213	2.76	0.362
Juvenile capelin (1)	0.213	5.52	0.362
Polar cod (1+)	0.266	1.406	0.498
Pelagic planktivorous fish	0.12	3.715	0.177
Mackerel	0.275	1.192	0.523
Redfishes	0.25	1.276	0.392
Benthic Invertebrate Feeders 1 (BIF1)	0.096	2.544	0.122
Adult haddock (4+)	0.259	1.456	0.412
Juvenile haddock (1-3)	0.429	1.608	0.933
Wolfishes	0.254	1.122	0.401
Adult cod (4+)	0.3	1.176	0.51
Juvenile cod (1-3)	0.429	1.608	0.933
Adult saithe	0.35	1.076	0.651
Juvenile saithe	0.445	1.303	1.003
Benthic piscivores	0.204	1.816	0.298
Salmon and Seatrout	0.15	2.952	0.203
Squid	0.14	7.480	0.187
Lobsters crabs	0.333	2.8	0.714
Prawns and shrimps	0.176	6.036	0.282
Other crustaceans	0.192	4.672	0.317
Epifaunal filter feeders	0.274	2.17	0.728
Infaunal filter feeders	0.125	5.78	0.237
Other macrobenthos	0.2	5.625	0.444
Meiofauna	0.4	19.95	0.952
Carnivorous zooplankton	0.4	8.4	0.952
Herbivorous zooplankton	0.36	11.5	0.783
Planktonic micro-organisms	0.4	157.5	0.952
Benthic micro-organisms	0.4	157.5	0.952

4.3 Differences between high (1990) and low (1995) capelin years

Three tables below (Tables 6, 7 and 8) summarise the differences between original input parameters for the two models.

4.4 Balancing the high capelin (1990) model

We employed the following criteria to help guide balancing the high capelin year model:

- Q/Bs were fixed at the same value as that of the low capelin model, based on the assumption that the required daily ration of groups would be stable over this short period of time. Differences in ration are more influenced by temperature (latitudinal) than time.
- Diet information for minke whales, seals and adult cod from this year was not to be changed during balancing.
- New biomass data for capelin and other fish species was to remain fixed.

The first attempt at Ecopath mass-balance showed that our new biomass estimates for polar cod, juvenile haddock, benthic piscivores and herring were too low to sustain the reported fishing catches. We refrained from manually modifying biomass data, opting rather to make small adjustments to diet compositions (including cannibalism). To alleviate excessive predation of herring, we reduced the proportion of herring in the diet of its predators. The predators short-fall was compensated by increasing the proportion of capelin in their diets. We considered this to be a reasonable assumption given the changes in relative abundance of capelin and herring. Seal predation, and cannibalism in benthic piscivores were also reduced. Minor diet adjustments were not sufficient to balance polar cod, juvenile haddock and benthic piscivore groups. Accordingly, we assigned ecotrophic efficiency values of 0.99 and allowed Ecopath to estimate biomass. Table 9 summarises the changes made during parameterisation by comparing the original input parameters with balanced model parameters. Comparison of differences in balanced model parameter for high and low capelin models is provided in Table 10 and Figure 8.

Table 6. Basic inputs comparison of differences bewteen high (1990) and low capelin year models

Group	Biomass (t km^{-2})		P/B (yr^{-1})	
	High capelin 1990	Low capelin 1995	High capelin 1990	Low capelin 1995
Herring	0.7444	1.417	0.53	0.82
Juvenile herring (1-3)	0.599	1.9169	0.49	0.49
Adult capelin (2+)	1.869	0.08428		0.63
Juvenile capelin (1)	2.296	0.05357		1.26
Polar cod (1+)	0.0907	0.3048		
Pelagic planktivorous fish				0.66
Mackerel		0.18	0.52	0.62
Redfishes		0.201		
Benthic Invertebrate Feeders 1 (BIF1)				0.31
Adult haddock (4+)	0.08598	0.367	0.62	0.67
Juvenile haddock (1-3)	0.0308	0.103	0.59	0.6
Benthic Invertebrate Feeders 2 (BIF2)				0.45
Adult cod (4+)	0.6263	1.213	0.49	1
Juvenile cod (1-3)	0.1536	0.389	0.47	0.47
Adult saithe	0.1377	0.321	0.95	0.85
Juvenile saithe	0.1456	0.174	0.97	0.93
Benthic carnivores	0.122	0.111	0.93	0.54
Prawns and shrimps	0.1871	0.138		1.7

Table 7. Fisheries catch data inputs comparison of differences between high (1990) and low capelin year models

Gear type	Functional group	Catch (t)	
		High capelin 1990	Low capelin 1995
Demersal trawl	Benthic piscivores	3055	4688
Demersal trawl	Sharks	98	124
Pelagic gear	Planktivores	277	
Demersal trawl	BIF 1	2678	5434
Demersal trawl	Wolfish	1661	5534
Demersal trawl	Haddock	13236	71992
Demersal trawl	Cod	62735	245184
Pelagic gear	Herring (juv)	1758	2604
Demersal trawl	Redfish	1926	2374
Invert	Sea weeds	5103	351
Invert	Lobster and Crabs	0	32
Invert	Infauna	0	55
Shrimp trawl	Shrimps	43673	9682
Demersal trawl	Polar cod	63	24030
Demersal trawl	Saithe	6593	17549
Demersal trawl	Other Macrobenthos	3105	8372
Pelagic gear	Capelin	0	0

Table 8. Diet composition inputs comparison of differences between high (1990) and low capelin year models

Prey\Predator	Minke		Seals		Adult Cod	
	High capelin 1990	Low capelin 1995	High capelin 1990	Low capelin 1995	High capelin 1990	Low capelin 1995
Adult herring (4+)				0.1	0.0009	0.013
Juvenile herring (1-3)	0.3990	0.384	0.1017	0.073	0.0009	0.013
Adult capelin (2+)	0.1487	0.047	0.3300	0.01	0.2071	0.072
Juvenile capelin (1)	0.0633	0.02			0.2071	0.072
Polar cod (1+)			0.1667	0.228	0.0016	0.057
Pelagic planktivorous fish	0.0226	0.028			0.1092	0.052
Redfishes					0.0617	0.044
Benthic Invertebrate Feeders 1 (BIF1)					0.0433	0.021
Adult haddock (4+)					0.0021	0.013
Juvenile haddock (1-3)	0.0760	0.094		0.025	0.0021	0.013
Adult cod (4+)				0.05		
Juvenile cod (1-3)	0.0430	0.121	0.0508	0.085	0.0052	0.088
Juvenile saithe	0.0234	0.029		0.012		
Benthic piscivores			0.0850	0.165	0.1171	0.056
Squid					0.0125	0.006
Prawns and shrimps					0.0495	0.082
Other crustaceans					0.0597	0.028
Epifaunal filter feeders					0.0158	0.008
Infaunal filter feeders					0.0211	0.01
Other macrobenthos					0.0005	0
Carnivorous zooplankton	0.22393	0.277	0.2658	0.253	0.0603	0.341
Herbivorous zooplankton					0.0224	0.011

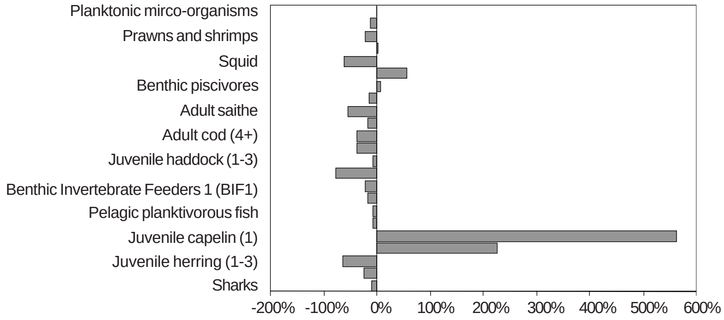
Table 9. ***Comparison of input versus balanced model parameters. Initial and (balanced) input data (where different from initial input). Asterisk values are estimated within Ecopath. Shaded areas are values which are different from the low capelin model (see Table 3 for detailed comparison). Note that departures of final input parameters from the best estimates are reasonably small.***

Group name	Trophic level	Biomass in hab. Area (t km^{-2})	Production/ biomass (/year)	Consump./ biomass (/year)	Ecotrophic efficiency	Production/ consumption	Unassimil./ consumption
Minke	4.3	0.159	0.035	8.14	0.058	0.004	0.112
Other baleen whales	4.3	0.112	0.02	12.89	0	0.002	0.112
Toothed whales	4.9	0.018	0.02	12.748	0	0.002	0.112
Birds	4.7	0.008	1	80	0	0.013	0.112
Seals	4.5	0.111	0.056	13	0.146	0.004	0.112
Sharks	4.7	0.018*	0.15	4.77	0.75	0.031	0.112
Adult herring (4+)	3.4	0.744	0.53	4.84	0.729	0.11	0.2
Juvenile herring (1-3)	3.2	0.599 (0.669)*	0.49 (1.5)	9.684	0.99	0.155	0.2
Adult capelin (2+)	3.7	1.869	1	4.7	0.794	0.213	0.2
Juvenile capelin (1)	3.2	2.296	2	9.4	0.252	0.213	0.2
Polar cod (1+)	3.8	0.0907 (0.534)*	0.7	2.633	0.99	0.266	0.2
Pelagic planktivorous fish	3.4	1.098*	0.657	5.465	0.99	0.12	0.2
Mackerel	4.2	0.18	0.52	2.27	0.376	0.229	0.2
Redfishes	3.8	0.352*	0.5	2	0.99	0.25	0.112
Benthic Invertebrate Feeders 1 (BIF1)	3.7	0.743*	0.31	3.214	0.95	0.096	0.112
Adult haddock (4+)	3.9	0.086	0.62	2.315	0.472	0.268	0.112
Juvenile haddock (1-3)	3.9	0.0308 (0.160)*	0.59 (1.5)	3.5	0.99	0.429	0.112
Wolfishes	4	0.023*	0.45	1.77	0.95	0.254	0.112
Adult cod (4+)	4.4	0.626	0.49	2	0.793	0.245	0.112
Juvenile cod (1-3)	4.1	0.154 (0.254)*	0.47 (1.5)	3.5	0.99	0.429	0.112
Adult saithe	4.5	0.138	0.95 (0.7)	2	0.288	0.35	0.112
Juvenile saithe	4.3	0.146	0.97 (1.274)*	2.938	0.99	0.434	0.112
Benthic piscivores	4.3	0.122 (0.579)*	0.93 (0.62)	2.654	0.99	0.234	0.112
Salmon and Seatrout	4.1	0.132*	0.6	4	0.99	0.15	0.112
Squid	3.7	0.109*	1.4	10	0.99	0.14	0.112
Lobsters crabs	3.4	0.103*	2	6	0.95	0.333	0.2
Prawns and shrimps	2.6	0.1871 (0.234)*	1.7	9.67	0.99	0.176	0.2
Other crustaceans	2.7	0.999*	1.48	7.69	0.95	0.192	0.2
Epifaunal filter feeders	2.9	20	1.58	5.77	0.295	0.274	0.35
Infaunal filter feeders	2.6	20	1.37	11	0.697	0.125	0.35
Other macrobenthos	3	13.235	2.5	12.5	0.531	0.2	0.35
Meiofauna	2.4	9.734*	19	47.5	0.99	0.4	0.18
Carnivorous zooplankton	2.9	6	8	20	0.492	0.4	0.18
Herbivorous zooplankton	2.2	15	9	25	0.735	0.36	0.18
Planktonic micro-organisms	2	1.189*	150	375	0.99	0.4	0.18
Benthic micro-organisms	2	1.126*	150	375	0.99	0.4	0.18
Phytoplankton	1	20	55	-	0.288		
Seaweeds	1	0.019	2	-	0.228		
Dead carcasses	1	-		-	0.975		
Water column detritus	1	50		-	0.669		
Benthic detritus	1	50		-	0.955		

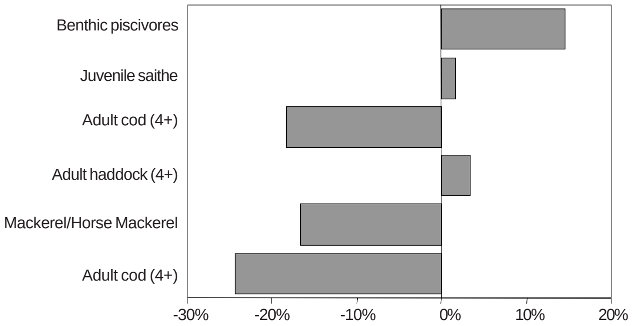
Table 10. Comparison of balanced parameters between Low capelin (High Capelin) years

Group name	Trophic level	Biomass (t km^{-2})	Production/biomass (/year)	Ecotrophic efficiency	Production/ consumption
Minke	4.3	0.159	0.035	0.058	0.004
Other baleen whales	4.3	0.112	0.02	0	0.002
Toothed whales	4.8 (4.9)	0.018	0.02	0	0.002
Birds	4.7	0.008	1	0	0.013
Seals	4.7 (4.5)	0.111	0.056	0.157 (0.146)	0.004
Sharks	4.7	0.02 (0.018)	0.15	0.75	0.031
Adult herring (4+)	3.4	1 (0.744)	0.7 (0.53)	0.933 (0.729)	0.145 (0.110)
Juvenile herring (1-3)	3.2	1.917 (0.669)	1.5	0.402 (0.99)	0.155
Adult capelin (2+)	3.7	0.57 (1.869)	1	0.99 (0.794)	0.213
Juvenile capelin (1)	3.2	0.496 (2.296)	2	0.99 (0.252)	0.213
Polar cod (1+)	3.8	0.572 (0.534)	0.7	0.99	0.266
Pelagic planktivorous fish	3.4	1.205 (1.098)	0.657	0.99	0.12
Mackerel	4.1 (4.2)	0.18	0.624 (0.52)	0.926 (0.376)	0.275 (0.229)
Redfishes	3.8	0.435 (0.352)	0.5	0.99	0.25
Benthic Invert. Feeders	3.7	0.968 (0.743)	0.31	0.95	0.096
Adult haddock (4+)	3.9	0.367 (0.086)	0.6 (0.62)	0.905 (0.472)	0.259 (0.268)
Juvenile haddock (1-3)	3.9	0.177 (0.160)	1.5	0.99	0.429
Wolfishes	4	0.036 (0.023)	0.45	0.95	0.254
Adult cod (4+)	4.3 (4.4)	1 (0.626)	0.6 (0.49)	0.874 (0.793)	0.3 (0.245)
Juvenile cod (1-3)	4 (4.1)	0.310 (0.254)	1.5	0.99	0.429
Adult saithe	4.5	0.3 (0.138)	0.7	0.996 (0.288)	0.35
Juvenile saithe	4.2 (4.3)	0.174 (0.146)	1.306 (1.274)	0.99	0.445 (0.434)
Benthic piscivores	4.3	0.546 (0.579)	0.541 (0.62)	0.99	0.204 (0.234)
Salmon and Seatrout	4.1	0.084 (0.132)	0.6	0.99	0.15
Squid	3.7	0.284 (0.109)	1.4	0.99	0.14
Lobsters crabs	3.4	0.1 (0.103)	2	0.95	0.333
Prawns and shrimps	2.6	0.307 (0.234)	1.7	0.99	0.176
Other crustaceans	2.7	1.143 (0.999)	1.48	0.95	0.192
Epifaunal filter feeders	2.9	20	1.58	0.309 (0.295)	0.274
Infaunal filter feeders	2.6	20	1.37	0.717 (0.697)	0.125
Other macrobenthos	3	13.235	2.5	0.56 (0.531)	0.2
Meiofauna	2.4	9.745 (9.734)	19	0.99	0.4
Carnivorous zooplankton	2.9	6	8	0.453 (0.492)	0.4
Herbivorous zooplankton	2.2	15	9	0.680 (0.735)	0.36
Planktonic micro-orgs	2	1.198 (1.189)	150	0.99	0.4
Benthic micro-organisms	2	1.127 (1.126)	150	0.99	0.4
Phytoplankton	1	20	55	0.29	-
Seaweeds	1	0.019	2	0.226	-
Dead carcasses	1	-	-	0.978 (0.974)	-
Water column detritus	1	50	-	0.668	-
Benthic detritus	1	50	-	0.954	-

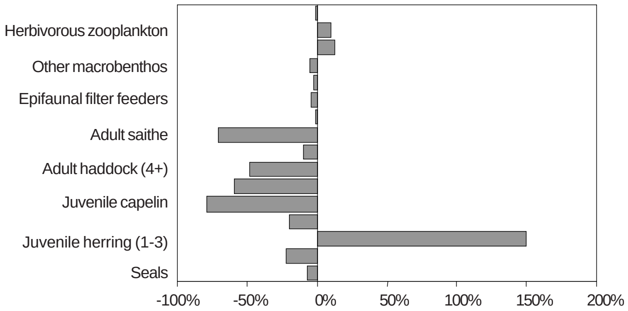
(a) Biomass (t km^{-2})



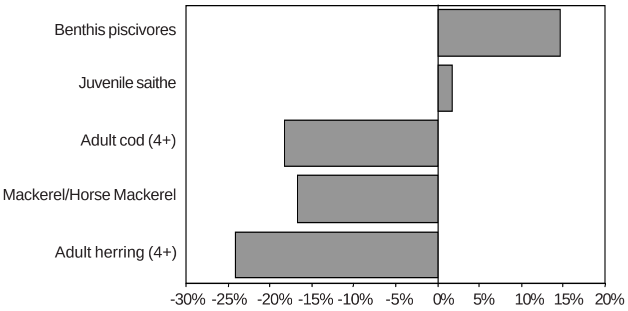
(b) Production/Biomass (/year)



(c) Ecotrophic efficiency



(d) Production/consumption



(e) Trophic level

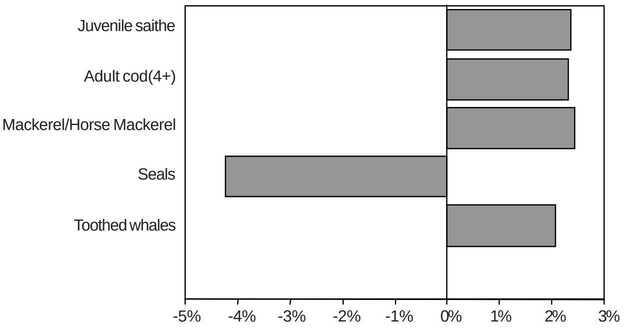


Figure 8. Differences in balanced parameters of 'High' compared to 'Low' capelin model. Differences expressed as percentage change in High model values relative to Low model

5. ECOPATH RESULTS

5.1 Mixed Trophic Impact Analysis

Leontief (1951) developed a method to reveal the direct and indirect interactions in the economy of the USA. Hannon (1973) and Hannon and Joiris (1989) introduced this method to ecology. It can be used to assess the impacts of increased biomass of a particular group on the biomass of other groups in the system. Ulanowicz and Puccia (1990) developed this approach further and a similar routine has now been incorporated into Ecopath (Christensen and Pauly 1992).

The 'mixed trophic impact' (MTI) routine (Majkowski, 1982) was used to evaluate the importance of minke whales, seals, capelin, herring and cod in the two Barents Sea models, both as predators and as prey (see Figure 9). Notable differences included the much greater negative impact of seals on adult saithe and haddock in the 1995 (low capelin) model, compared

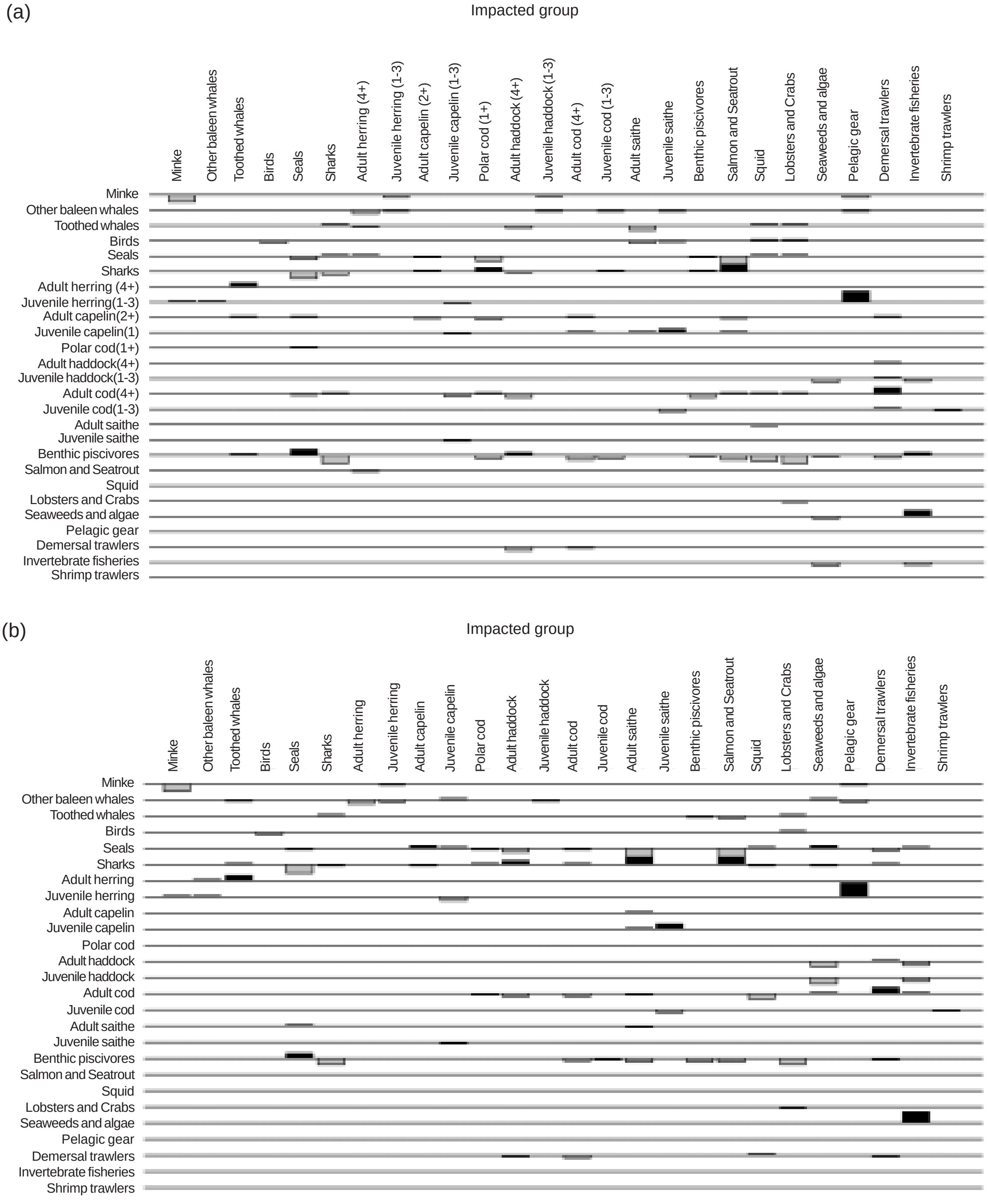


Figure 9. Mixed trophic impact plots for both Barents Sea Ecopath models. (a) 1990 - high capelin model and (b) 1995 - low capelin model. Darker shaded bars represent a positive impact whereas lighter shaded bars indicate a negative impact

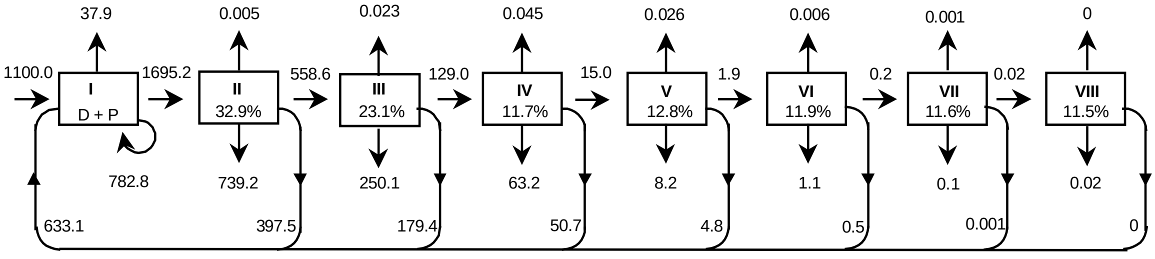
with their negative impact on polar cod, adult capelin and adult herring in the 1990 model. Indeed, seals had a negative impact on adult capelin in the 1990 model, but a positive impact on capelin in the 1995 model. Adult cod had positive impacts on sharks, polar cod, salmon/seatrout, squid and lobsters/crabs in the 1990 model, but a negative impact on polar cod, adult saithe, adult haddock, adult cod and squid in the 1995 model. Both adult and juvenile capelin had a greater impact on adult and juvenile saithe in the 1995 model compared to the 1990 model. Herring appeared to have a greater positive impact on minke, 'other baleen' and toothed whales in the 1995 model. Benthic piscivores (including thorny skate, Greenland halibut, Atlantic halibut, long rough dab and monkfish) appeared to have a positive impact on toothed whales, seals and adult haddock in the 1990 (high capelin) model, but the only positive impact was on seals in the 1995 model. Negative impacts on sharks, salmon, squid and lobsters/crabs were more pronounced in the 1990 model. Juvenile and adult haddock appeared to have a negative impact on seaweed in the 1995 model, as well as a slightly positive impact on the catch of demersal trawlers.

Overall, it was clear that when capelin numbers were reduced (the 1995 model) there was a shift towards the demersal species (saithe, cod, haddock squid, lobsters and crabs) compared to when capelin was abundant (1990 model) and pelagic species (capelin, polar cod and herring) dominated the diets of these predators. The greater reliance of predatory species on other groups in the system once capelin are not available fits well with observed patterns from the field (see Section 2.3). Specifically, it is in agreement with the observation of harp seal feeding migrations extending further down the Norwegian coast, the increase in cod cannibalism and the decline in growth and fecundity of cod during such periods. Capelin and herring are high-energy foods that generally occur in high-density shoals; it is probably difficult for predators to obtain sufficient energy when these small pelagic species are not available.

5.2 Lindeman Spine Analysis

The 'Lindeman spine' analysis, originally developed by Ulanowicz (1995), reduces complex reticulated food webs into a simple chain of trophic interactions. The food-chain that results from these procedures (e.g., Figure 10) can be compared with 'spines' from other systems.

1990 High- Capelin Year



1995 Low- Capelin Year

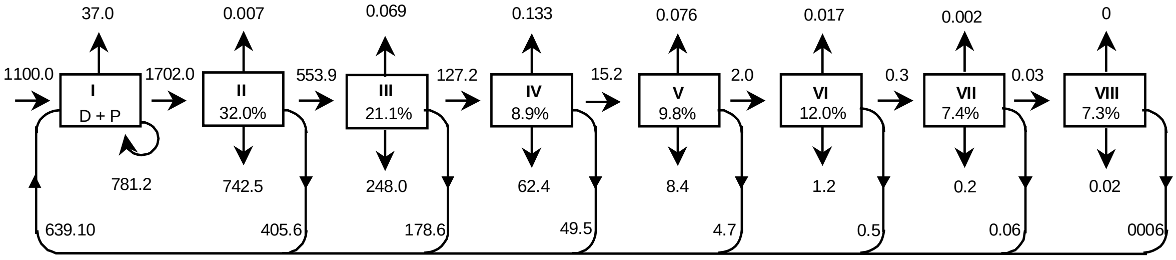


Figure 10. The aggregation of the flow (t/ km^2 y) web into a concatenated chain of transfers through eight trophic levels (after Ulanowicz, 1995). Flows out of the tops of compartment boxes represent export, and flows out of the bottom represent respiration. Recycling of non living material is through compartment D (detritus). The percentages in the boxes represent the annual trophic efficiencies

Table 11. Transfer efficiencies (% of ingested food) between trophic levels and biomass (tonnes wet weight/ km^{-2}) of each trophic category, based on the 'Lindeman spine' analysis

	I	II	III	IV	V	VI	VII	VIII	Average per trophic step
1990 Model									
Producers		27.1	17.2	14.9	12.3	11.2	11.1	11.7	19.1
Detritus		34.3	24.2	11.2	12.9	12.0	11.7	11.5	21.0
All Flows		32.9	23.1	11.7	12.8	11.9	11.6	11.5	20.7
Biomass	20.018	45.058	37.958	13.876	1.696	0.175	0.018	0.002	
1995 Model									
Producers		27.7	14.6	14.5	14.0	7.8	7.7		17.4
Detritus		33.7	22.2	8.3	9.0	13.2	7.3	7.6	18.4
All Flows		32.0	21.1	8.9	9.8	12.0	7.4	7.3	18.2
Biomass	20.019	45.345	37.560	13.822	1.842	0.206	0.018	0.001	

This method can also be used to calculate transfer efficiencies between trophic levels. Using Ulanowicz's method, it is possible to apportion the total amount of food consumed by a particular predator to each of the discrete trophic levels of the 'Lindeman Spine' (Figure 10). Our analysis suggests that, for the 1990 model, 10% of the consumption by minke whales (0.127 g m^{-2} y^{-1}) could be characterised as operating at trophic level III, 55% at level IV, 28% at level V and 6% at levels VI (0.717, 0.367, 0.078 g m^{-2} y^{-1} respectively). Results for the 1995 model were very similar.

The 'Lindeman spine' analysis, revealed trophic pathways of up to 8 links within both of the Barents Sea models. However, the biomass values associated with trophic levels VII and VIII were very small. Trophic flow from primary producers was 1520.622 g m^{-2} yr^{-1} for the 1990 model, and 1514.782 g m^{-2} yr^{-1} for the 1995 model. Trophic flow from detritus was 3674.556 g m^{-2} yr^{-1} for the 1990 model and 3686.665 g m^{-2} yr^{-1} for the 1995 model. This gave herbivory/detritivory ratios of 0.414 and 0.411, highlighting the relative importance of secondary production from the detritus.

Transfer efficiencies between trophic levels are presented in Table 11. The average transfer efficiency was 20.7% in the 1990 model and 18.2% in the 1995 model. The programme estimated high efficiencies at trophic levels II and III. Those originating from detritus were generally higher than those originating from primary producers, 71% of all flows originated from detritus in both the 1990 and 1995 models. Efficiencies at higher trophic levels were considerably lower.

5.3 Ecosystem properties

Odum (1971) described how the ratio between total primary productivity and total system respiration (P_p/R) would develop as systems become 'mature'. He predicted that for 'immature' systems primary production would exceed total respiration, whereas for 'mature' systems the ratio would move towards unity (i.e. $P_p/R = 1$). Christensen and Pauly (1993(a)) examined this relationship in 41 aquatic systems and found that in most communities P_p/R ratios fell within the range 0.8-3.3. For the Barents Sea we obtained a P_p/R value of ~1.035, indicating that respiration almost equals production and that recycling of biomass/ energy is important within this particular system. The inclusion of bacteria in our model, but not those considered by Christensen and Pauly (1993(a)) may be important because 'Ecopath type' models that exclude bacterial activity are likely to over-estimate P_p/R ratios (Christensen and Pauly, 1993(a)).

P_p/B has also been used as an indicator of system maturity (Odum, 1971; Christensen, 1995). 'Developing' systems tend to possess high P_p/B ratios, while 'developed' systems tend to have lower P_p/B ratios, associated with high biomasses and lower production rates (Christensen and Pauly, 1993(a)). The P_p/B ratio of our model (9.259) was relatively high, higher than the value of 4.94 reported for the Bering Sea, another high latitude shelf system (Trites *et al.*, 1999).

According to Odum (1969), the capacity of an ecosystem to entrap, withhold and cycle nutrients increases with maturity. The degree of recycling in a system can be measured with Finn's Cycling Index (*FCI*) which expresses the fraction of the total system throughput that is recycled (Finn, 1976; Christensen and Pauly, 1992; Christensen and Pauly, 1993a). Christensen and Pauly (1993(a)) found a strong correlation between the *FCI* and the maturity rankings described in Christensen (1995). The value for our models (~13.5%) was relatively high. Christensen and Pauly (1993(a)), Dalsgaard (1995) and Eppley (1981) reported that systems with low P_p/R ratios generally display a high degree of recycling (i.e. a high *FCI*). Christensen and Pauly (1993(a)) further demonstrated that the average path length, i.e. the average number of groups that a flow passes through (Finn, 1980) is strongly correlated with the *FCI*. Here a value of 4.7

Table 12. Summary statistics for the 1990 and 1995 Barents Sea models computed by Ecopath

Parameter	Value (1990)	Value (1995)	Units
Sum of all consumption	2399.850	2400.641	t km^{-2} y^{-1}
Sum of exports	38.026	37.288	t km^{-2} y^{-1}
Sum of respiratory flows	1062.029	1062.769	t km^{-2} y^{-1}
Sum of all flows into detritus	1695.290	1700.768	t km^{-2} y^{-1}
Total system throughput	5195.000	5201.000	t km^{-2} y^{-1}
Sum of all production	1917.000	1920.000	t km^{-2} y^{-1}
Mean Trophic level of catch	3.98	4.11	
Total catch	0.109	0.305	t km^{-2} y^{-1}
Calculated total net primary production	1100.037	1100.037	t km^{-2} y^{-1}
Total primary production/total respiration	1.036	1.035	
Total primary production/total biomass	9.259	9.259	
Total biomass/total throughput	0.023	0.023	
Total biomass (excluding detritus)	118.802	118.811	t km^{-2}
System Omnivory Index	0.225	0.228	
Finn's mean path length	4.723	4.728	
Finn's cycling index	13.53	13.56	% total throughput

was calculated (Table 12) and this is again high. High values are typically associated with estuarine and shelf-systems, whilst oceanic, upwelling and reef systems generally possess shorter path lengths (Baird *et al.*, 1991; Christensen and Pauly, 1993(a)). Vasconcellos *et al.* (1997) showed that recycling plays an important role in the maintenance of ecosystem stability as does path length. We can infer that the Barents Sea ecosystem is a relatively 'mature' one, according to the terminology of Odum (1971).

5.4 Sensitivity analysis

A simple routine for sensitivity analysis (*sensu* Majkowski 1982) is included within Ecopath. This routine varies all basic input parameters (*P/B, B, EE, Q/B*) in steps from -50% to +50% to check what the effect of altering each of these would be on the 'missing' parameters (i.e. those calculated via mass-balance). This routine was run for the 1995 Barents Sea model and in most cases (e.g. minke whales, seals, herring, mackerel, haddock and cod) a 30% increase in *B* was found to result in a 43% change in the estimated *EE* for that group (if *EE* was the missing parameter). A 30% decrease in *B* resulted in a 23% change in *EE*. The mean sensitivity of *EE* in relation to changes in the *Q/B* ratio and *P/B* was apparently similar in magnitude and direction to changes in biomass (*B). In fact, responses to changes in *EE, P/B, Q/B* and *B* were of similar magnitude irrespective of the missing parameter (*B, EE, Q/B, P/B*) for that particular group.

Estimates for the 'missing' parameters were also shown to be sensitive to changes in biomass, *P/B* ratio, *Q/B* ratio and *EE* of other groups within the system, although the effects were usually smaller. For example, a 30% increase in the biomass of minke whales resulted in a 12.3% reduction in juvenile herring, a 3.2% reduction in the biomass of adult capelin and an 8.6% reduction in the biomass of juvenile cod. Identical (in terms of magnitude and direction) indirect responses were also predicted to follow from a 30% increase in the *Q/B* ratio of minke whales.

The sensitivity of estimated parameters to changes in the input parameters of different groups depended on the degree of trophic connection between those groups. Some of the largest and most far-reaching effects were predicted to follow from changes to the input parameters of seals, sharks and 'benthic piscivores' (Figure 11). These three functional groups seemed to have a strong effect on one another, with a 30% decrease in the *P/B* ratio of 'benthic piscivores' resulting in a 58% increase in the *EE* of seals and a 61% increase in the biomass of sharks (Figure 11, c and d). A 30% increase in the *Q/B* ratio of 'benthic piscivores' resulted in a 30% increase in the *EE* of seals and a 31% increase in the biomass of sharks (Figure 11, g). Changes in the input parameters for minke whales were shown to affect the 'missing' parameters of nine other groups in the system: juvenile herring, adult capelin, pelagic planktivorous fish, juvenile haddock, juvenile cod, juvenile saithe, prawns and shrimps, 'other' crustaceans, and seaweeds. Changing the P/B, Q/B or EE of adult capelin impacted only the EE of carnivorous zooplankton.

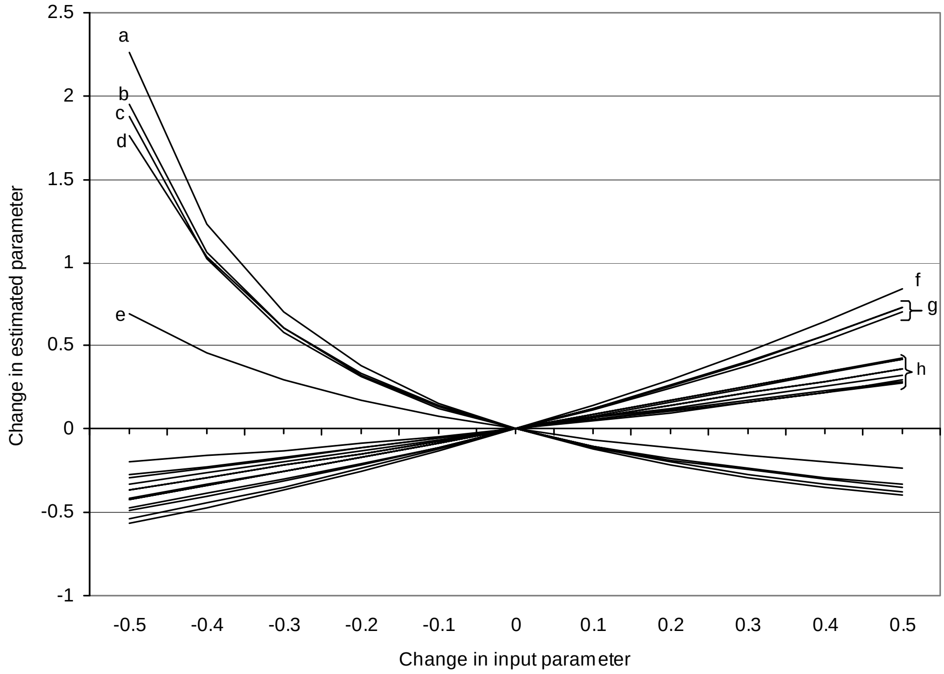


Figure 11. Sensitivity plot of indirect effects. Shown are sensitivities that were greater than 30% when input parameter was changed by 50%. (a) Benthic piscivores (P/B) on Lobsters and crabs (Biomass), (b) Benthic piscivores (P/B) on Sharks (Biomass), (c) Benthic Piscivores (P/B) on Seals (EE), (d) Sharks (P/B) on Seals (EE), (e) Meiofauna (EE) on Benthic microorganisms (Biomass), (f) Benthic Piscivores (Q/B) on Lobsters and crabs (Biomass), (g) from top to bottom: Benthic Piscivores (Q/B) on Sharks (Biomass), Sharks (Q/B) on Seals (EE), Benthic Piscivores (Q/B) on Seals (EE), (h) from top to bottom: Other macrobenthos (Biomass) on Infauna (EE), Other macrobenthos (Biomass) on Epifauna (EE), Seals (Biomass) on Adult Saithe (EE), Carnivorous Zoop. (Biomass) on Herbivorous Zoop. (EE), Adult cod (Biomass) on Squid (Biomass), Benthic Piscivores (Q/B) on Other Crusts. (Biomass), Adult Saithe (Biomass) on Mackerel (EE)

6. ECOSIM PARAMETERISATION AND EVALUATION OF DYNAMICS

6.1 Parameterisation

Ecosim is a dynamic simulation tool for ecosystem modelling that uses parameter values derived from the balanced Ecopath model (Walters *et al*., 1997). However, Ecosim requires additional parameters to define linkages between adults and their respective juvenile groups (Table 13). During simulations, account is kept of the numbers that recruit from the juvenile to the adult stages and the number at age/size in the adult group. A recruitment function is provided to relate recruitment to adult numbers, biomass and food consumption.

Ecosim also requires input of the vulnerability (*v*) of each prey species to its predators. Additional parameters are used to represent hypotheses about changes in growth rates with food availability, and to mimic the feeding ecology of predators. Model simulations are particularly sensitive to the value assigned to the prey vulnerability parameter. This represents the rate of exchange of biomass between two prey behavioral states: a state vulnerable to predation, and a state invulnerable to predation. This is largely a theoretical concept, and direct estimates of this parameter are not available from the literature (Walters *et al*., 1997).

Ecosim offers several approaches for trying to estimate vulnerability. One method requires time series data for the different ecosystem components in contrasting situations, in terms of both fisheries exploitation and environmental conditions. Vulnerabilities are then tuned to fit the observed data. The same approach can be used if two models of the same system are available for different time periods; a routine searches for vulnerability settings that will make it possible to move from the first to the second model state, given the exploitation rates. This procedure was not however used for our Barents Sea models.

6.2 Evaluation

The stability of the Barents Sea 1995 model was evaluated by examining its behaviour when the system was disturbed from Ecopath mass-balance. Adjustments

Table 13. Parameters linking adult and juvenile groups in Ecosim. Values in bold are those used as input to Ecosim

	Capelin	Herring[a]	Cod	Saithe	Haddock
Min time as Juvenile	1	2^{b}	3^{c}	3^{de}	2^{d}
Max time as Juvenile	2.5	5^{b}	8^{c}	9^{de}	6^{d}
Min time as Juv. (rel. to age at transition)	**0.57**	**0.69**	**0.91**	**0.83**	**0.74**
Max time as Juv. (rel. to age at transition)	**1.43**	**1.72**	**2.42**	**2.50**	**2.22**
Recruitment power parameter	**1**	**1**	**1**	**1**	**1**
Age at first maturity	2.4^{f}	2.9^{g}	3.3^{h}	3.6^{f}	2.7^{f}
Age at transition to adult group	**1.75**	**2.9**	**3.3**	**3.6**	**2.7**
K of the VBGF (based on L_{inf} below)	**0.3565^{j}**	**0.26^{k}**	**0.1^{m}**	**0.19^{n}**	**0.234^{p}**
L_{inf} (cm)	23.8^{j}	37^{k}	134^{m}	107^{n}	75.7^{p}
Average adult weight (kg)[q]	0.0154	0.3135	1.2769	1.2820	0.7582
Weight at transition (kg)[q]	0.01	0.066	0.49	0.56	0.215
Average adult weight/ weight at transition	**1.538**	**4.750**	**2.606**	**2.289**	**3.526**
Base fraction of food intake used for reproduction	**0.3**	**0.3**	**0.3**	**0.3**	**0.3**
Fraction of increase in food intake used for growth	**0.8**	**0.8**	**0.8**	**0.8**	**0.8**

[a] *data for Norwegian Spring Spawning herring;*
[b] *Chugonava, 1959 says 2 to 4 for USSR herring;*
[c] *Muus and Neilson, 1999 say 6 as minimum and 15 as maximum - but this does not tally with data on weights at age or age at first maturity. Used 3 and 8 for input;*
[d] *Cohen et al., 1990;*
[e] *Cohen et al., 1990 suggest min 5 and max 10, but this does not tally with age at first maturity. Used 3 and 9 for input;*
[f] *estimated in Fishbase;*
[g] *Jennings and Beverton, 1991;*
[h] *based on guess from juvenile age range,*
[j] *Dragesund et al., 1973;*
[k] *Toresen, 1988;*
[m] *Beverton and Holt, 1959;*
[n] *Gottlieb, 1957;*
[p] *Blacker, 1971;*
[q] *from ICES, 2001(a),(b).*

had to be made to adult-juvenile linkages, feeding time factors, and prey vulnerabilities in order to eliminate instabilities in the model. Three types of instabilities commonly found in Ecosim are: 1) predator-prey cycles and related multi-trophic level patterns; 2) system simplification (loss of biomass pools due to competition/predation effects); 3) stock-recruitment instabilities (cyclic or erratic changes in recruitment and stock size for split pool groups).

To examine the persistence of functional groups, we disturbed the system by applying an increase in fishing effort of all gears combined (Figure 12(c)) and evaluated how fast the system returned to an equilibrium state. Wolfishes and sharks responded very quickly to small changes, and were not able to recover (Figure 12(a)). Too simplistic feeding relationships combined with a predator-prey cycle between sharks and wolfish were identified as problematic for these groups. To help constrain these volatile responses we assumed that both seals and benthic piscivores consumed small amounts of juvenile sharks and wolfish and made changes to the diets accordingly. Given that both wolfish and sharks have a high proportion of unexplained mortality, an additional mechanism was used to control these responses: setting a non-zero feeding time adjustment and a high value for 'the fraction of other mortality sensitive to changes in feeding time' (see Christensen *et al.*, 2000). In addition to this ecotrophic efficiency (EE) for sharks was increased from 0.5 to 0.75. The changes resulted in less dramatic responses to the fishing scenario (Figure 12(b)).

The apparent cyclical and rather erratic changes in biomass of some groups in Figure 12 are indicative of stock-recruitment instabilities. The inclusion of age structure dynamics in Ecosim requires users to think carefully about compensatory processes relating to the 'stock-recruitment' concept. Adult-juvenile linkage parameters need to be set so as to produce an 'emergent' stock-recruitment (SR) relationship that is at least qualitatively similar to one of the many relationships for which there is now empirical data (see data summary in www.mscs.dal.ca/~myers/data.html). In most cases, these relationships are 'flat' over a wide range of spawning stock sizes, implying that in general there must be strong compensatory increase in juvenile survival rate as spawning stock declines (Christensen *et al.*, 2000).

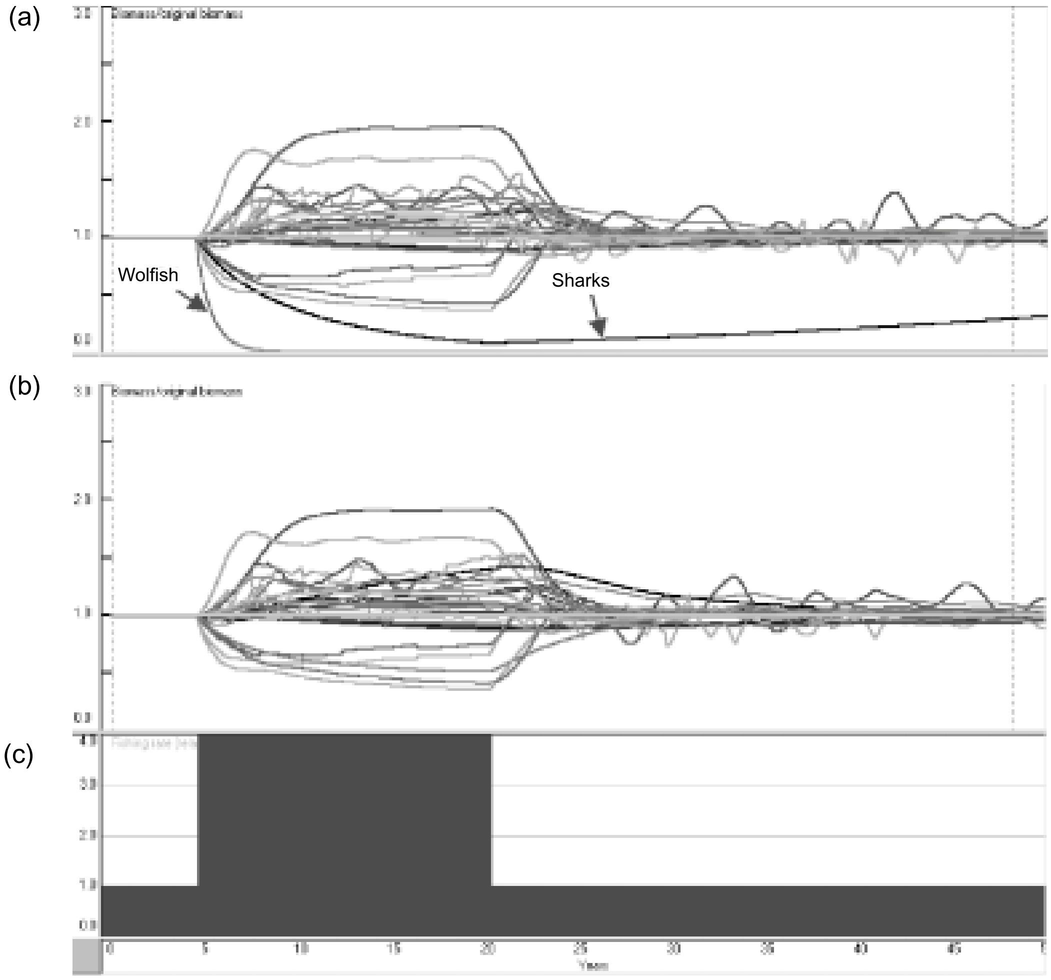


Figure 12. Testing model stability and persistence of functional groups. Bottom panel (c) shows fishing effort implemented across all gears. Panel (a) shows responses of groups before changes, and panel (b), after changes to wolfish and sharks groups

To eliminate stock-recruitment instabilities and implement compensatory changes in the mortality of juveniles, it was necessary to re-consider adult-juvenile parameters for the split pool groups. Christensen *et al*. (2000), detail that at least two initial conditions are needed. The juvenile group must have a relatively high P/B rate (total mortality rate) or a relatively high EE (so that most mortality is accounted for as predation effects within the model), otherwise the user must specify a high (near 1.0) value in the Ecosim 'Group Info' Tab entry for the juvenile group's 'prop. of other mortality sensitive to changes in feeding time' column. These conditions were implemented in the Barents Sea model.

Christensen *et al*. (2000) state: "Given these Ecopath conditions, Ecosim can then generate direct (as opposed to just predator-prey) compensatory changes in juvenile recruitment via at least three alternative mechanisms or hypotheses:

(1) simple density-dependence in juvenile production rate by adults, due to changes in adult feeding rates and fecundity (not a likely mechanism);

(2) changes in duration of the juvenile stage and hence in total time exposed to relatively high predation risk, implemented by setting (a) feeding time adjustment rate in Ecosim Group Info tab to 0.0; (b) setting a low value for 'min time juv' and a high value for 'max time juv' in Ecosim Stage tab, adult/juvenile group parameters button;

(3) changes in juvenile foraging time (and hence exposure to predation risk) with changes in juvenile feeding rates, implemented (as default) by (a) setting high (0.5 to 1.0) value for time adjust rate in Ecosim Group Info tab, and (b) setting min and max time as juveniles in Stage tab, group parameters button both to 1.0."

We examined the effects on stock-recruitment instabilities and general model dynamics, using methods 2 and 3 above. We focused the simulations on cod since this group appeared to have the most volatile dynamics.

Our results show that having a variable time in the juvenile stage, combined with a zero feeding time adjustment rate for juveniles (method 2), still resulted in instabilities, resulting in erratic biomass dynamics for adult and juveniles (Figure 13(a)). The effects were dampened, but not removed, when the vulnerability parameters setting was increased (Figures 13(b) and 14). Dynamic simulations and plots of emergent stock-recruitment curves further highlighted the stock-recruitment instability (Figures 14 and 15). Reducing the "min time in juvenile stage" and increasing the "maximum time in juvenile stage" had little effect.

Assigning juveniles a non-zero feeding time adjustment (tested at 0.5 and 1) further dampened the erratic changes in biomass dynamics and stock-recruitment peculiarities (Figures 16(a) and (b), Figure 17, Figure 18), but again, did not remove them.

Next we tried representing compensation of juvenile mortality by changing juvenile foraging time (and hence exposure to predation risk) with changes in juvenile feeding rates (method 3). We then set "min" and "max time as juveniles" to 1 and tried feeding time adjustment factors of 0 and 0.5. Instabilities in the stock-recruitment and biomass dynamics were no longer apparent (Figures 19, 20(a) and (b)). We opted to use a feeding time factor of 0.5, because it provided better representation of compensation in juvenile mortality (Figure 21).

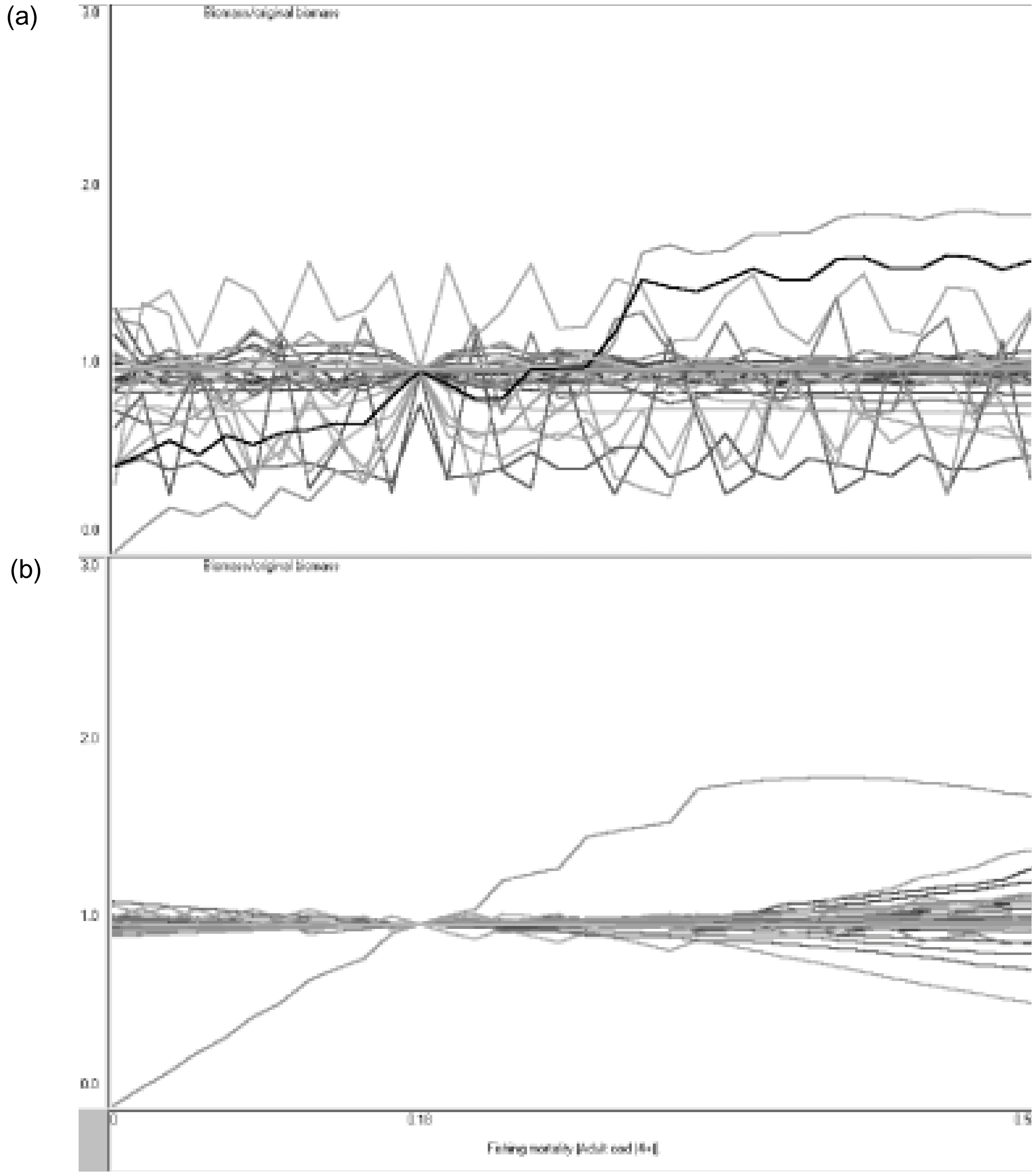


Figure 13. Equilibrium simulations of changing fishing mortality on adult cod.
(a) with zero feeding time adjustment, variable time juvenile stage, vulnerability setting=0.1.
(b) with zero feeding time adjustment, variable time juvenile stage, vulnerability setting=0.4.

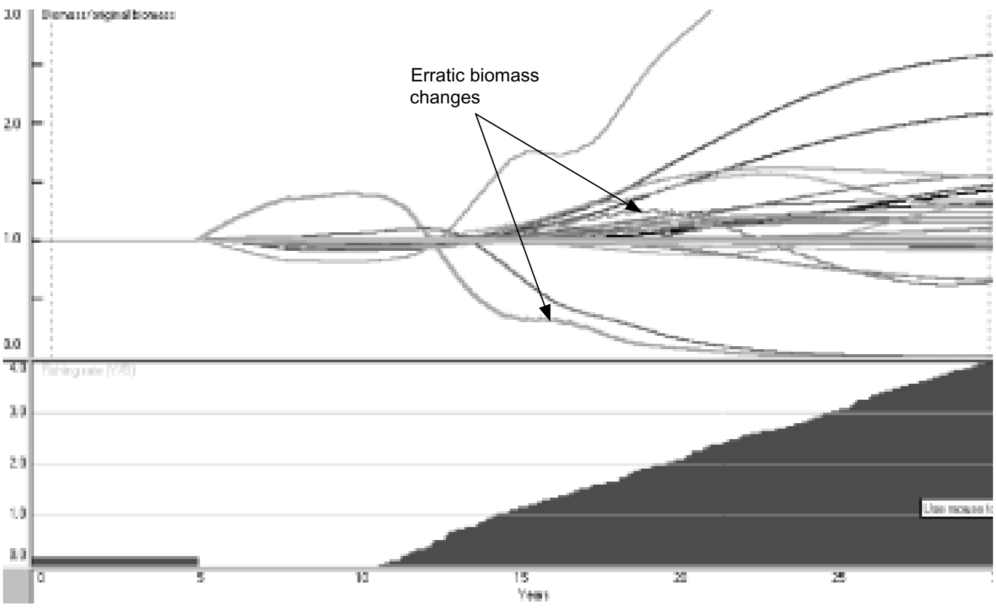


Figure 14. Dynamic run with increasing fishing mortality imposed on adult cod after a period of fishery closure. Settings are, v=0.4, zero feeding time adjustment and variable time in juvenile stage. Marked on the figure are erratic changes in the biomass dynamics

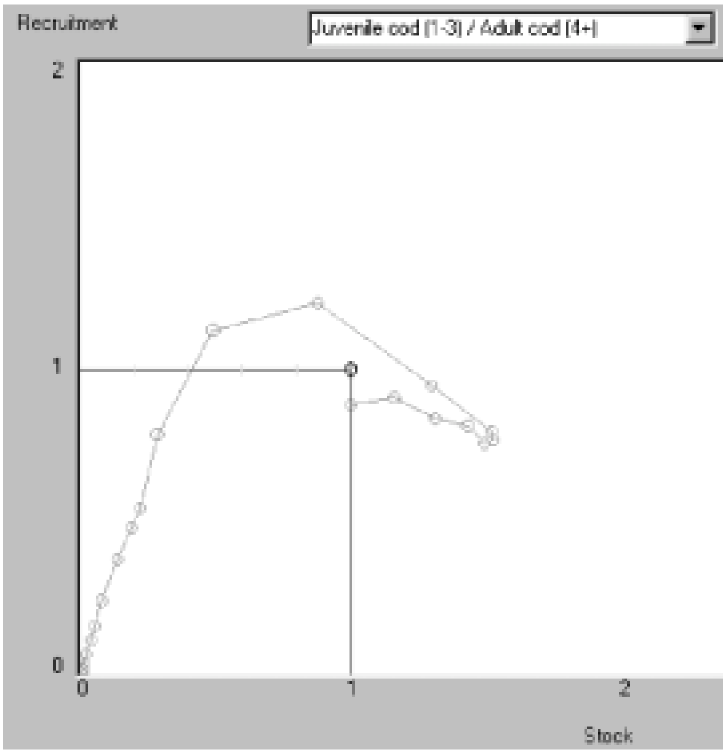


Figure 15. Cod stock-recruitment curve. Notice the spurious dome shape and linear (non-compensatory) change in recruitment as stock decline. v=0.4, zero feeding time adjustment and variable time juvenile stage.

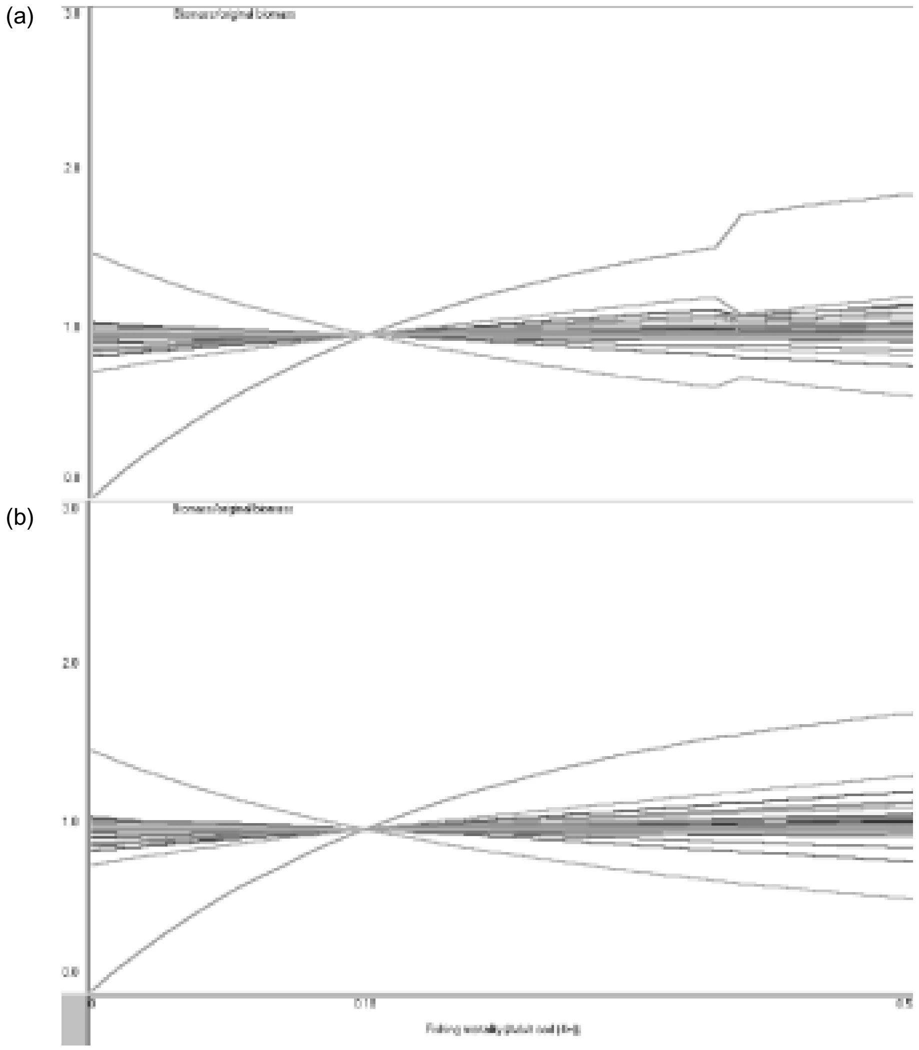


***Figure 16.** Equilibrium simulation of changing fishing mortality on adult cod. (a) with feeding time adjustment=0.5, variable time juvenile stage, v=0.4. (b) with feeding time adjustment=1, variable time juvenile stage, v=0.4*

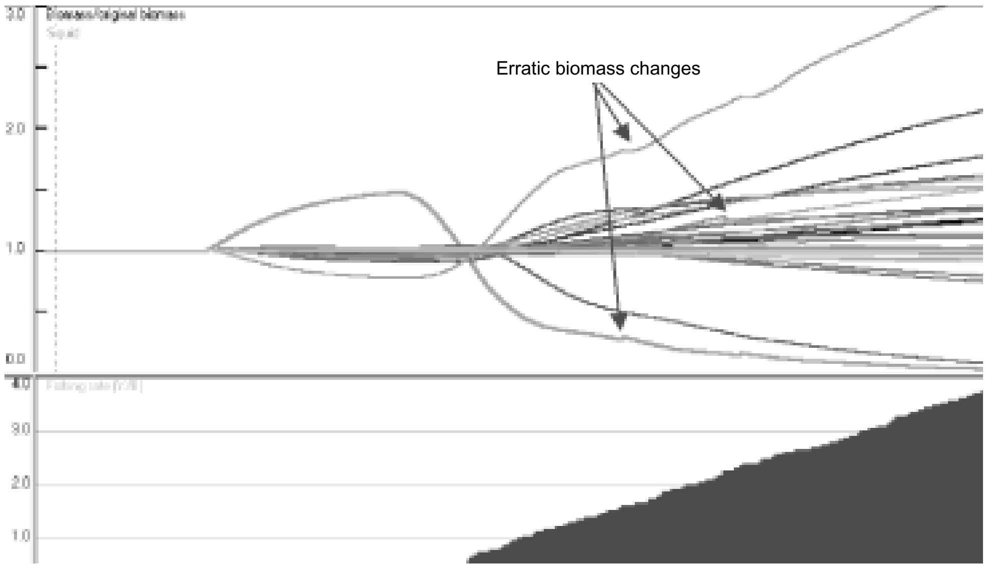


***Figure 17.** Dynamic run with increasing fishing mortality imposed on adult cod after a period of fishery closure. Settings are v=0.4, feeding time adjustment=1 and variable time in juvenile stage. Notice that erratic biomass dynamics are still evident*

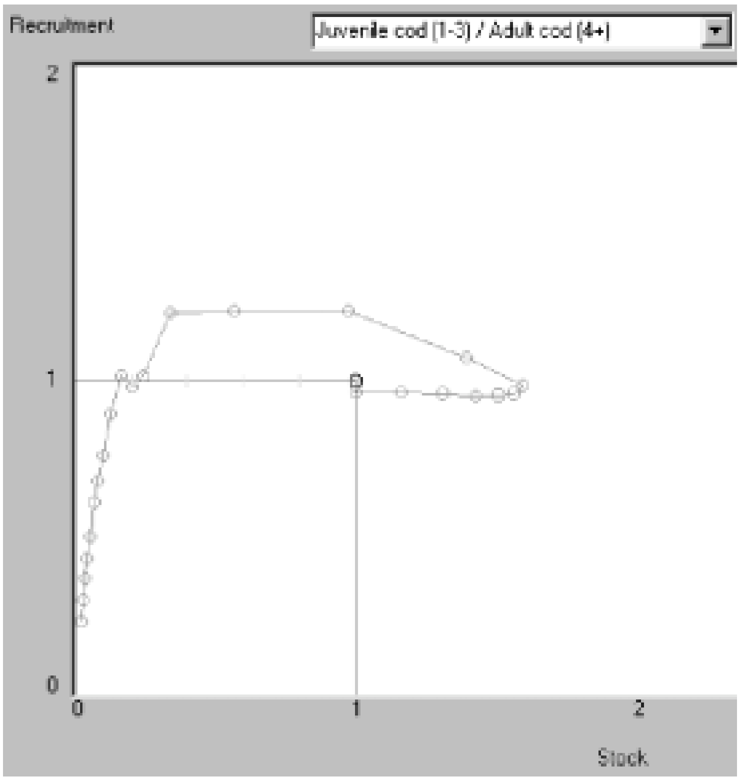


Figure 18. ***Cod stock-recruitment curve. v=0.4, feeding time adjustment=1 and variable time juvenile stage. Notice that recruitment is flatter over a wider range of stock sizes, indicating a compensatory response. Erratic changes are also still present***

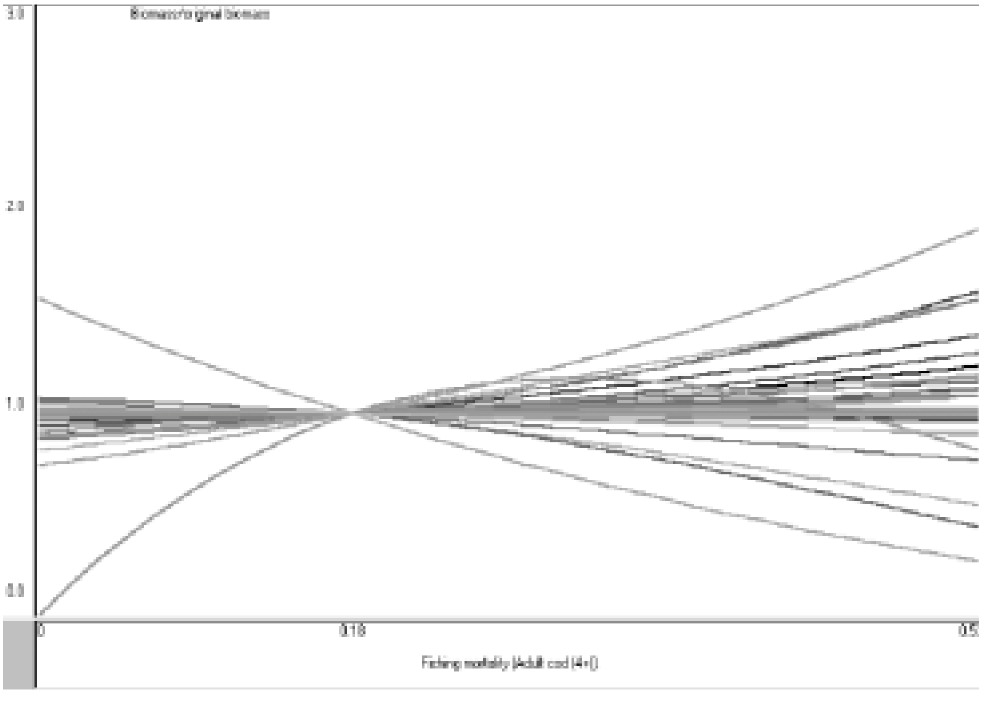


Figure 19. ***Equilibrium simulation of changing fishing mortality on adult cod. Settings, fixed time in juvenile stage (=1), feeding time adjustment=0, v=0.4***

Our test simulations (detailed above) identified a potential parameterisation problem with the squid group. Notice in Figure 20 that the biomass of squid reacts strongly to the decline of cod. There are two potential reasons for this. First, squid is a main prey item of cod, second, our P/B value of 3 was considered to be too high, resulting in high resilience. A revised estimate of P/B (from total mortality estimate used in stock assessments) of 1.4 per year for *Loligo* species (B. Roel-Olive, CEFAS, pers. comm.) was used in the model. The change resulted in juvenile cod and prawns going slightly out of balance. We opted to let Ecopath balance these groups by assigning an EE=0.99 for both groups. The result was an increase in juvenile cod from 0.30 to 0.31, and in prawns from 0.300 to 0.307. To compare the effects of the changes, we ran the same simulation as that in Figure 20(b) (Figure 22). Only minor changes were apparent, indicating that the strong predator-prey linkage between cod and squid was primarily responsible for the strong reaction exhibited by squid, and not the P/B value.

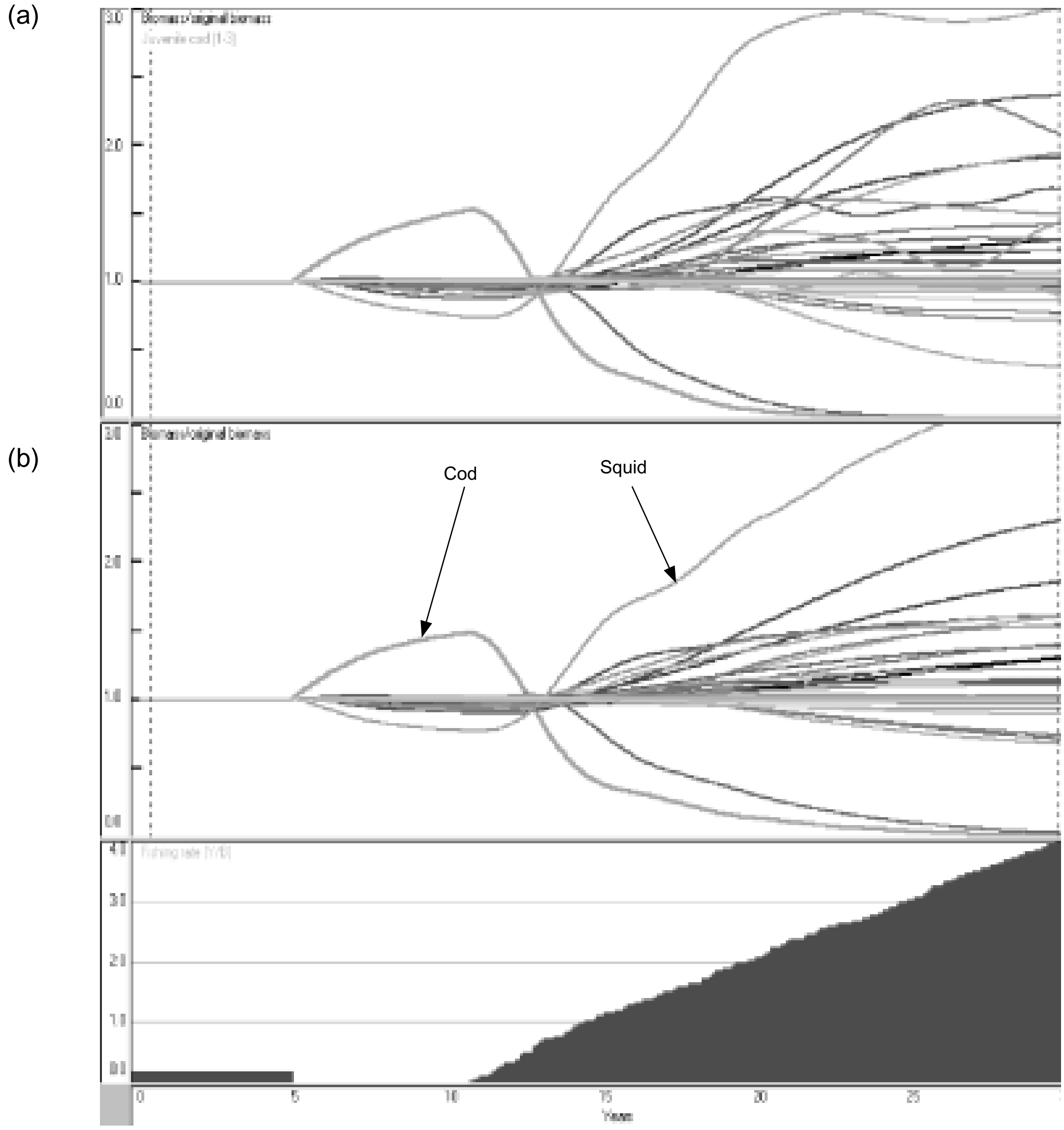


Figure 20. Dynamic run with increasing fishing mortality imposed on adult cod after a period of fishery closure.
(a) Settings, fixed time in juvenile stage (=1), feeding time adjustment=0, v=0.4.
(b) Settings, fixed time in juvenile stage (=1), feeding time adjustment=0.5, v=0.4

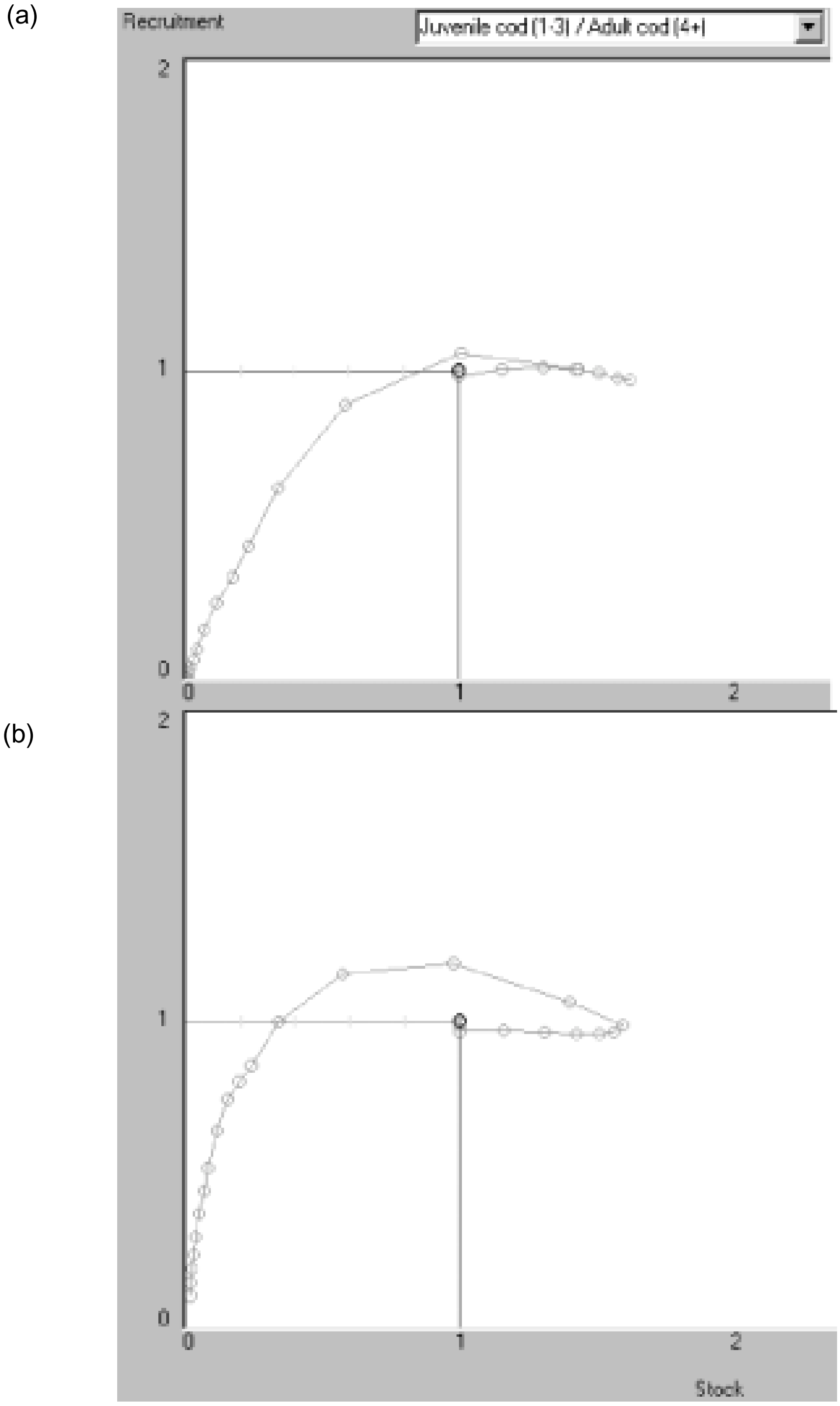


Figure 21. Cod stock-recruitment curve.
(a) v=0.4, Settings, fixed time in juvenile stage (=1), feeding time adjustment=0, v=0.4
(b) Settings, fixed time in juvenile stage (=1), feeding time adjustment=0.5, v=0.4

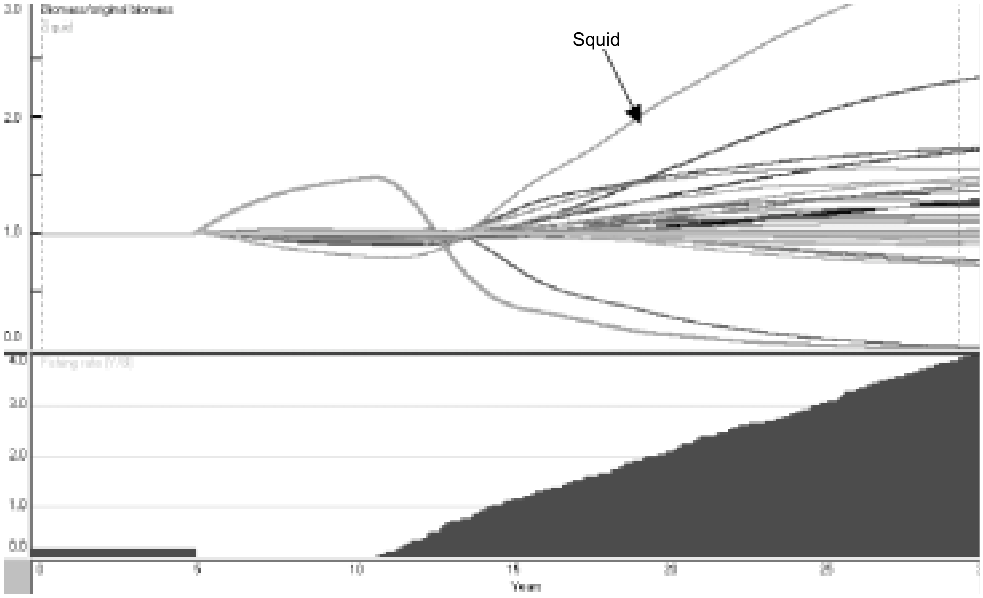


Figure 22. Dynamic run with increasing fishing mortality imposed on adult cod after a period of fishery closure. Simulation run to compare effects of reducing input P/B for squid. Settings, fixed time in juvenile stage (=1), feeding time adjustment=0.5, v=0.4

Finally, we examined the effects of the vulnerability parameter values on model behaviour by simulating an increase in fishing by all gears for a period of 10 years, followed by a reduction back to the baseline fishing mortality (Figure 23) (*sensu* Vasconcellos *et al.*, 1997). Simulations were run for 50 years. The model exhibited extreme erratic behaviour with a vulnerability setting of 0.1. For vulnerabilities in the range 0.2-0.4 the simulations exhibited persistence of all groups and relative stability. Increasing vulnerabilities to 0.5 and higher led to dramatic decreases in biomass. If v was increased beyond 0.6, extinction of groups occurred. It was possible to force the system to maintain all groups by applying different vulnerability values across the food web, for instance by setting lower vulnerabilities (v ≤ 0.2) for prey groups while keeping predators with v's higher than 0.5, or by scaling v's to be proportional to trophic level. In the absence of data to support a particular combination of vulnerabilities, it is difficult to justify any set of v values. Ideally simulations should be carried out under a range of settings for all predator-prey pairs. But in the absence of formal sensitivity testing, the tests performed here indicated that vulnerability setting of 0.4 provides reasonable dynamics and stability.

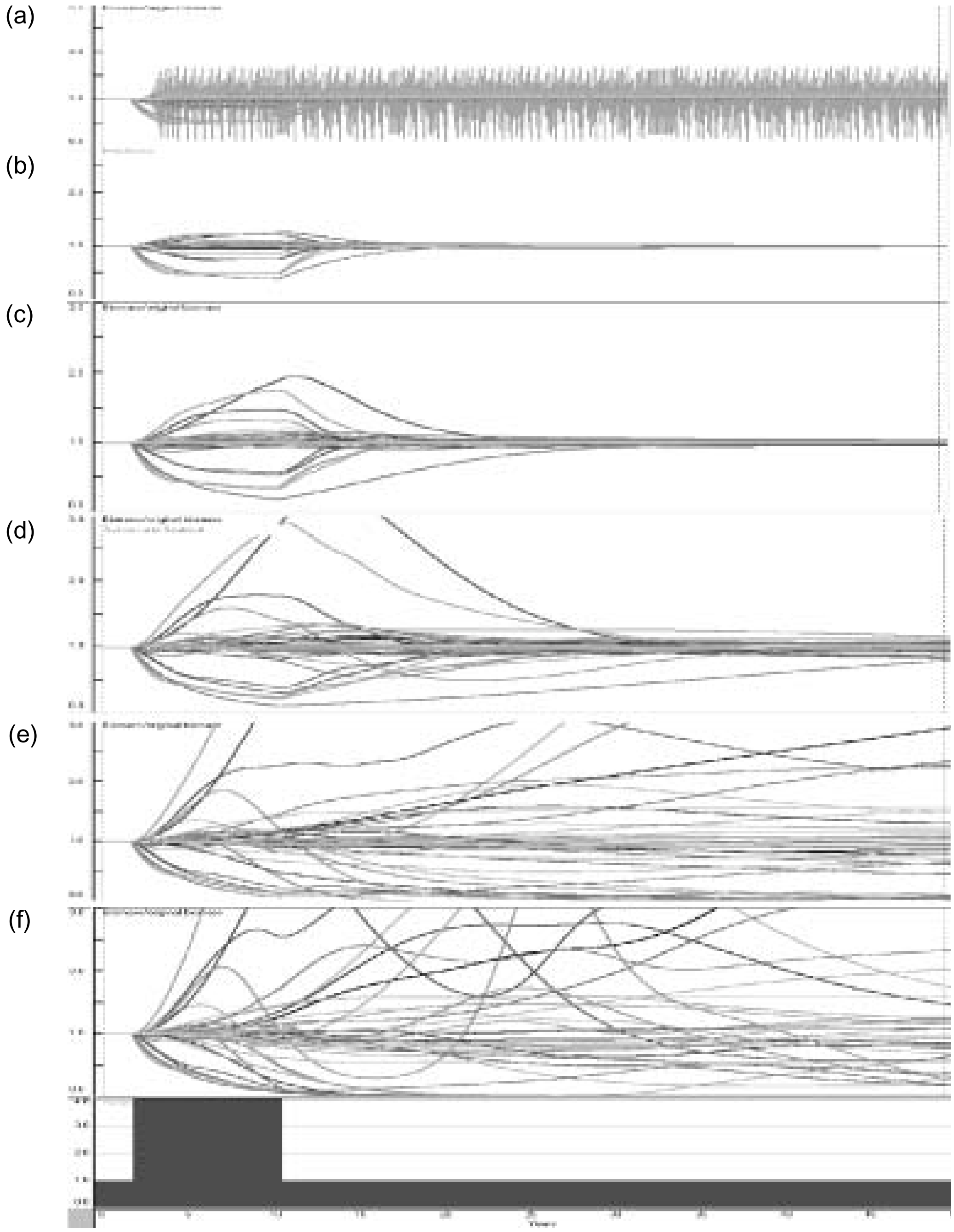


Figure 23. Effects on changes in vulnerability parameter setting on persistence of functional groups. (a) v=0.1 (b) v=0.2, (c) v=0.4, (d) v=0.6, (e) v=0.8 (f) v=0.99

7. CONCLUSIONS

There were very few system-level differences between the two modelled ecosystem states. This is somewhat expected considering the 1990 model shares many of the same input parameters as the 1995 model. However, the mixed trophic impact analysis indicated changing the diets of the top predators, the biomass of several commercial fish species and fisheries yields, resulted in different direct and indirect effects throughout the food web in the two years compared (1990 and 1995).

Our results from parameterisation and evaluation of model stability within Ecosim for the 1995 model clearly showed that the simulation outputs are sensitive to the vulnerability parameter (v). This aspect of Ecosim has been recognised by other researchers but there has been no systematic or formal analysis of the sensitivity of all of the parameters within Ecosim to date.

The models documented in this paper will be used for future sensitivity testing of Ecopath and Ecosim, evaluation of the effects of model structure and complexity necessary for the critical evaluation of this modelling approach. Our primary goal was not to construct a suite of definitive Barents Sea Ecopath models, we welcome refinements by others who may wish to use it for testing specific hypotheses regarding the Barents Sea ecosystem. A proposed next-step would be to link the two models using time series fitting of available environmental, biological and fisheries data.

8. ACKNOWLEDGEMENTS

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