Direct and indirect effects of minke whale abundance on cod and herring fisheries: A scenario experiment for the Greater Barents Sea.

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ABSTRACT

To study the pattern of interaction between minke whale (*Balaenoptera acutorostrata*) abundance and the main fisheries in the Greater Barents Sea, a simulation experiment was carried out. The population model involves 4 species interconnected in a food web: cod (*Gadus morhua*), capelin (*Mallotus villosus*), herring (*Clupea harengus*) and minke whales. Minke whales are preying on cod, capelin and herring; cod are preying on (young) cod, capelin and herring; herring in the Barents Sea are preying on capelin; while capelin is a bottom prey in the model. The consumption function for minke whales is non-linear in available prey abundance, and is estimated from stomach content data and prey abundance data. The model is dynamic, with a time step of one month, and there are two areas: the Barents Sea and the Norwegian Sea. Minke whale abundances are kept on fixed levels, while recruitment in fish is stochastic.

Cod and herring fisheries are managed by quotas targeting fixed fishing mortalities, while capelin is managed with a view to allow the cod to have enough food and leaving a sufficient spawning stock of capelin. The model is simulated over a period of 100 years for a number of fixed levels of minke whale abundance, and simulated catches of cod, herring and capelin are recorded.

The experiment showed interactions between whale abundance and fish catches to be mainly linear. For cod catches, both the direct effect of whales consuming cod, and the indirect effect due to whales competing with cod for food and otherwise altering the ecosystem, are linear and of equal importance. The net effect on the herring fishery is of the same magnitude as the net effect on the cod fishery, with each extra whale reducing the catches of both species by some 5 tonnes. These conclusions are conditional on the model and its parameterisation.

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Introduction

Minke whale (*Balaenoptera acutorostrata*) abundance has been estimated at around 85,000 in the Greater Barents Sea and the Vestfjorden area in the eastern Atlantic north of 65° north in 1995 (Schweder *et al.* 1997). Their total consumption has been estimated to be around 1.8 million tonnes of biomass yearly (Folkow *et al.* 2000) (Fig. 1).

Will the fishermen be able to take more cod (*Gadus morhua*), capelin (*Mallotus villosus*) and herring (*Clupea harengus*) if the stocks of marine mammals are reduced? Will the fisheries respond linearly to changes in whale abundance, or are there perhaps levels of whale abundance where an increase can have a positive effect, at least on some fisheries? How much of the effect on the fisheries can be ascribed to minke whale predation on the fish stock in question, and how much is due to the indirect effect of minke whales being competitors of cod and herring and otherwise influencing the ecosystem?

We will investigate these questions by running a scenario experiment in a multi-species and multi-fleet model roughly tailored to the fisheries and ecosystem of the Barents and the Norwegian Sea. The multi-fleet aspect of the model is of no consequence in the present exercise other than to distribute the catches in time, space and over year classes.

The effect on the stocks of cod, herring and capelin by hypothetically removing the stock of minke whales was studied by Bogstad *et al.* (1997), in a simulation study using the MULTSPEC model, which also contained harp seals. They also ran experiments with varying predation models for minke whales, and with an increasing stock. For cod, they found the stock to be inversely correlated with minke whale abundance, but with a stronger negative association between cod and harp seals than between cod and minke whales. When minke whales were removed, the herring stock gained considerably with a consequential more extensive predation on young capelin in the Barents Sea. Since capelin are an important prey for cod, the herring-capelin-cod dynamics modified the direct positive effect on the cod stock by eliminating the natural mortality due to minke whale predation on cod when minke whales were removed from the system. Bogstad *et al.* (1997) included fisheries in their model, but with fishing mortalities constant, independent of the state of the stocks. Tjelmeland and Bogstad (1998) call for studies of the effects of varying minke whale abundance on fish stocks and catches, when fisheries are managed by adaptive strategies. Their tentative conclusion is that the effect of an increasing stock of minke whales on the important fish stocks is that the herring stock will be most heavily affected.

In the present study, a model with a much coarser spatial resolution than the MULTSPEC model is used. There are two areas: the Norwegian Sea and the Barents Sea proper. The time step is one month. The species in the model are minke whales, cod, herring and capelin, all distributed by area, time and age. Cod, herring and capelin are also length distributed. The food web of the model is as follows. Minke whales prey on cod, herring and capelin. Cod prey on herring and capelin, and also on young cod. Herring prey on

Fig. 1
Although minke whales feed mainly on invertebrates and small fish, they occasionally take larger items such as this cod.

Photo: Tore Haug

young capelin in years with herring in the Barents Sea proper. This predation is modelled as reduced recruitment. Minke whales, cod, herring and capelin also prey on food items not in the model.

As in Bogstad *et al.* (1997), the interesting herring-capelin-cod dynamics are included in our model, and our main concern is to see whether this is sufficiently strong to dampen or reverse the anticipated negative effect of an increasing stock of minke whales on the cod fishery, at least at some levels of minke whale abundance.

For cod and herring, recruitment is stochastic around a Beverton-Holt recruitment function, and is positively correlated between the two. Mortality in fish is mainly caused by fishing and modelled predation. No dynamics are modelled for minke whales, and the stock is kept at constant levels within runs.

In addition to the strength of the herring-capelin-cod dynamics, the structure of the minke whale predation will influence the various fisheries. Predation of minke whales on cod, herring and capelin (Appendix) is estimated from stomach data and abundance data. The variability in the abundance data is, unfortunately, poorly understood, and uncertainty in estimates of predation parameters could not be estimated. The predation function is assumed to be of modified logistic form, with diet composition depending on the availability of all the three fish species, see below. The modified logistic function can accommodate sharp (or slow) switching from one food item to the other as the vectors of abundance of fish species change. The function can thus have an arbitrary degree of non-linearity, and might be an alternative to the more popular class of functions, $c = rb^v/(s^v + b^v)$, where v, r and s are parameters and b is prey biomass and c is consumed quantity (Spencer and Collie, 1996). The pattern of cod predation is estimated from stomach data.

The cod fishery is managed using quotas targeting a fishing mortality rate of F=0.45, while management of the herring fishery uses a fixed fishing mortality rate of F=0.2. The capelin fishery is managed by an adaptive strategy. The model is basically the same as that in Schweder *et al.* (1998), and the present investigation is a parallel to that study. There, the effects on cod and herring fisheries of retuning the Revised Management Procedure (RMS) of the International Whaling Commission (IWC) when applied to minke whaling are studied. Schweder *et al.* (1998) found that retuning the RMS from a target final stock size at 72% of carrying capacity to 60% had a substantial effect on the cod stock and cod catches, while the effect on the herring stock and catch was more uncertain. The catch of cod was estimated to increase by some 6 tonnes when the mean whale stock was reduced by one animal. Our present concern is to see whether this pattern emerges also at whale abundances outside the range covered by tuning the RMS for minke whaling at various levels.

To simplify matters, the present scenario experiment is one-dimensional, with only whale abundance varied as an experimental factor. This is in contrast to the experiment in Schweder *et al.* (1998), which also contained a number of uncertainty factors in addition to the tuning factor. In such uncertainty experiments, uncertainty due to absent or imperfect knowledge is represented by uncertainty factors and their levels in an experimental design aimed at investigating the performance of a management scheme. The present experiment is not an uncertainty experiment, since we do not attempt any broad study of the uncertainty involved, but rather ask what would happen in the model when minke whale abundance is manipulated over a broad and perhaps unrealistic range.

MATERIALS AND METHODS

The only experimental factor in our computer simulation experiment is the abundance of minke whales. This abundance is kept constant in pairs of experimental runs, but is varied across pairs. All other parameters of the model were kept at fixed levels. This applies also to starting values for the abundance of fish stocks, which were taken to be current estimates.

For each level of minke whale abundance, the model was run for a period of 100 years. In order to investigate the equilibrium characteristics of the model, the first 10 years of output were discarded from each experimental run. The

Table 1. Recruitment parameters. Number of recruits in billions. Half value in million tonnes

Species	R_{normal}	$R_{extreme}$	β	σ
Cod	1.33	2.22	0.21	0.67
Herring	26.52	280.63	1.29	3.0
Capelin	1800	1800	0.20	200

response variables were various means calculated from the last 90 years of each run. The most important of these are mean catches of cod and herring. Mean stock abundance, fishing mortality rate and quantum consumed by minke whales were also recorded.

Due to the one-dimensional nature of the experiment, the conditional mean response for a given minke whale abundance is studied by simple scatter plots and simple regression.

The basic structure of the scenario model we will use is as follows. The ecological system consists of herring, capelin, cod and minke whales. There are two areas: the Barents Sea proper and the Norwegian Sea. The time step is one month. The model is briefly described in the following. For more information, see Schweder *et al.* (1998).

Stock size and distribution

The abundance of minke whales was assumed to be constant throughout each simulation. There is thus no population dynamics or catch management for minke whales. The whales were evenly distributed between the two areas of the model. Abundance was varied from 10,000 to 200,000 in steps of 10,000 across simulations. The minke whale stock was present in the two areas in the model, representing the feeding grounds north of 65 degrees north, in the 7 months April - October, and absent in the remaining 5 months. For cod, herring and capelin, the initial stock sizes were specified as the abundance for the year 1993 (Bjarte Bogstad, personal communication).

Recruitment in fish

Separate Beverton-Holt recruitment functions with additive normal variation were used for cod, herring and capelin. Good years are common to herring and cod, and were stochastically chosen. The mean lag between good years was about 10 years, and pairs of good years were separated by at least 5 years. Mean capelin recruitment was proportional to spawning stock, but with reduced recruitment in years with herring in the Barents Sea area, to account for predation of herring on young capelin (detailed under Fish predation).

More precisely, let be the number of recruits andthe spawning biomass of the particular stock. The recruitment function is

$$r = R \frac{B}{B + \beta} + \sigma Z$$

when the right hand side is positive and zero otherwise. Here, β is a half-value parameter, σ is a parameter governing the size of the additive noise, Z is a standard normally distributed random variable, and R is the median maximum number of recruits. For cod and herring, this maximum number varies between one value in normal years and another value in extreme years, which are common to both species. The numerical values are given in Table 1.

Mortality in excess of predation and fishing mortality

For cod and herring, we set the excess mortality rate at 0.05, while for non-spawning capelin there was no natural mortality in excess of that caused by minke whales, cod, herring and man.

The excess mortality we used might be on the low side. It was, however, necessary to limit the excess mortality in the model used in Schweder *et al.* (1998), since in several scenarios the minke whale stock grew to high levels and the mortality caused by these whales was substantial. In order to obtain comparability, the same model was used in the present experiment.

Minke whale predation

Minke whales prey on herring, capelin and cod. From energetic calculations, each whale on the feeding ground is assumed to have a daily consumption capacity of 90kg. The total daily consumption of fish is thus at most C_{max} = 0.09 tonnes (Haug *et al.* 1996).

The whale's diet is determined by availability of the three fish components. Due to migratory patterns and fish behavior, we assumed that there is a limited overlap between the prey species and the minke whale. If there are b fish in a prey component each with mass m, the biomass of this fish component available to the minke whales is assumed to be $B = \omega \cdot b \cdot m$. In the simulation experiment we used the overlap coefficients, ω, given in Table 2.

By comparing stomach contents in whales to local prey abundance, Skaug *et al.* (1997) found support for the view that minke whales are quite flexible in their choice of food, adapting well to local prey abundance situations with few, if any, strong preferences. They found, however, that whales may be more reluctant to feed upon plankton, mainly krill, than upon other prey items such as herring and capelin. This observation has lead us to a three-stage model for minke whale predation.

It is the total consumption of herring, capelin and cod, given the available abundance of these species in our two areas, that concerns us. Since capelin and cod have a relatively high spatial correlation, these two prey items were first grouped. At the first stage, the herring consumption was determined on the basis of the available biomass of herring, B_{her}, and on the basis of the combined available biomass of capelin and cod, $B_{cc} = B_{cap} + B_{cod}$. When the herring consumption had been decided, the combined consumption of capelin and cod was evaluated. This combined consumption was then, at the third stage, divided between the two food items. The remaining consumption was composed of food items outside our model: other fish species and plankton.

Denoting the potential daily consumption of herring, C'_{her}, and the potential daily combined consumption of capelin and cod C'_{cc}, the potential daily consumption function may be written

$$C'_{her} = C_{max} \cdot c_h(B_{her}, B_{cc}),$$
$$C'_{cc} = (C_{max} - C'_{her}) \cdot c_{cc}(B_{cc}).$$

Considering the apparent minke whale food preferences, we require the following properties of the proportion of herring in the daily consumption, c_h, and the proportion of cod and capelin combined in the remaining total consumption, c_{cc},

$$c_h^1 > 0,\ c_h^2 < 0,\ c_h(0, B_{cc}) = 0,\ 0 \leq c_h \leq 1,$$
$$c_{cc}^1 > 0,\ c_{cc}(0) = 0,\ 0 \leq c_{cc} \leq 1,$$

Table 2. Overlap coefficients

Species	ω
Cod	0.50
Capelin	0.67
Herring	0.65

where superscripts 1 and 2 denote the partial derivatives with respect to their respective arguments. There are many functions satisfying these requirements. We chose to use the modified logistic functions:

$$c_h = \frac{\exp(\kappa + \kappa_H B_{her} - \kappa_C B_{cc})}{1 + \exp(\kappa + \kappa_H B_{her} - \kappa_C B_{cc})} [1 - \exp(-\kappa_H B_{her})] \quad (1)$$

$$c_{cc} = \frac{\exp(\xi + \xi_C B_{cc})}{1 + \exp(\xi + \xi_C B_{cc})} [1 - \exp(-\xi_C B_{cc})], \quad (2)$$

with $\kappa_H > 0$, $\kappa_C > 0$, $\xi_C > 0$.

The combined potential capelin and cod consumption, was divided between capelin and cod according to the formula

$$C'_{cap} = C'_{cc} \frac{a_{cap} B_{cap}}{a_{cap} B_{cap} + (1 - a_{cap}) B_{cod}}. \quad (3)$$

We assumed $0.5 \leq a_{cap} \leq 1$ since capelin is a fatter fish than cod, and it is presumably no less attractive to the minke whale.

The consumption functions were scaled up to represent potential monthly consumption for all the whales in the area, w, rather than daily consumption for one whale. To prevent the predation of the minke whales from exhausting its prey stocks, or even from creating negative stocks during the time step of one month, we assume that the actual consumption during one month, C_{her} etc. is at most half the biomass of the food item. Generically

$$C_{her} = \min\,(30wC'_{her}, B_{her}/2),$$

while for cod a further restriction is imposed,

$$C_{cod} = \min\,(20, 30wC'_{cod}, B_{cod}/2).$$

Table 3: Predation parameter estimates found in the Appendix. Biomass is measured in million tonnes

Parameter	Estimate
κ	-2.75
κ_H	1.18
κ_C	0.24
ξ	-0.27
ξ_C	1.66
a_{cap}	0.50

The parameters were estimated from observed stomach content data and abundance data (see Appendix). The fitted values are given in Table 3.

This estimation should be regarded with some suspicion since the spatial distribution of the prey abundance data is somewhat questionable, and since standard errors are unavailable because the sampling variation in the prey abundance data is unknown.

Fish predation

The predation of cod on young cod, herring and capelin, was determined by empirical formulae estimated from stomach content data. Cod predation was differentiated by year class: age 1, age 2, and age 3+. These predators prey on three groups of capelin: immature <10cm, immature at least 10cm, and mature; on herring in the Barents Sea; and on young cod (cannibalism).

Define the following quantities:

H Indicator for period, H=1 for second half-year;

CAP_1 Number of immature capelin <10cm;

CAP_2 Number of immature capelin at least 10cm;

CAP_3 Number of mature capelin;

HER Number of herring in Barents Sea;

COD_1 Number of 1 year old cod;

COD_2 Number of 2 year old cod;

COD_3 Number of cod 3 years and older;

CY Indicator for 2 year old cod.

The cod predation was modelled in two steps. First we modelled the total stomach content as a linear function of the number of fish on log-scale. The response is the ratio between the weight of the stomach content and the total weight of the fish. The model for young cod (1-2 years old) and older cod differs, and the stomach content models are:

$$R_1 = \alpha_0 + \alpha_1 \cdot \log(CAP_1) + \alpha_2 \cdot CY \cdot \log(CAP_2) + \alpha_3 \cdot CY \cdot (1-H) \cdot \log(CAP_3) + \alpha_4 \cdot CY \cdot \log(HER) + \alpha_5 \cdot \log(COD_1) + \alpha_6 \cdot \log(COD_2) + \alpha_7 \cdot \log(COD_3),$$

for 1 and 2 year old cod, and for older cod,

$$R_3 = \beta_0 + \beta_1 \cdot \log(CAP_1) + \beta_2 \cdot \log(CAP_2) + \beta_3 \cdot (1-H) \cdot \log(CAP_3) + \beta_4 \cdot \log(HER) + (\beta_5 + \beta_6(1-H)) \cdot \log(COD_1) + \beta_7 \cdot \log(COD_2) + \beta_8 \cdot \log(COD_3).$$

These formulae show that one year old cod feed on small immature capelin, competing with the older cod. Two year old cod feed on capelin and herring, competing with both younger and older cod. The older cod feed on both capelin, herring and young cod, competing with the rest of the cod stock. The mature capelin is only preyed upon in first half of the year, while for the old cod the eventual cannibalism has a different pattern in first and second halves of the year. We distinguish between the two halves of the year due to the spawning migrations.

The above models were computed for each age group of cod, and the next step was to model the distribution of the different prey species. This was done separately for each group of prey species (immature capelin, mature capelin, herring, 1 and 2 year old cod), and the modelled value was the percentage of the actual prey specie for each predator group. The linear model was parallel to the stomach content models:

$$P = \gamma_0 + \gamma_1 \cdot \log(CAP_1) + \gamma_2 \cdot \log(CAP_2) + \gamma_3 \cdot (1-H) \cdot \log(CAP_3) + \gamma_4 \cdot \log(HER) + (\gamma_5 + \gamma_6(1-H)) \cdot \log(COD_1) + \gamma_7 \cdot \log(COD_2) + \gamma_8 \cdot \log(COD_3).$$

The left hand quantity, P, corresponds to the percentage of the total consumption, R, which is constituted by the actual prey species, e.g. CAP_1 etc., and the model is for each predator group estimated for every prey group. The model describes a mixture of availability (the prey species) and competition (the other predator groups).

All models were estimated separately (unpublished note: STAT/02/1995, Norwegian Computing Center). One is not assured that the percentages for one predator group will sum to 100. One is not even sure that the model will give only non-negative percentages. It was therefore necessary to do an adjustment. After computing the model percentages, all negative numbers were substituted with zeros and the remaining percentages were scaled to sum to 100.

Herring feed mostly outside of our modelled area or on food items outside of of our model. The only component of the herring predation that was included in the model was the predation on young capelin when there was herring in the Barents Sea. Let r_{pot} be the number of potential capelin recruits obtained from the Beverton-Holt equation and let r_{CAP} be the number of these that survive the herring predation. The two numbers (in billions) are related by a piecewise linear function similar to that used by Hamre and Hatlebakk (1998)

$$r_{CAP} = \begin{cases} r_{pot} & \text{if } r_{pot}<20 \text{ or } HER<2 \\ \min(r_{pot},20) & \text{if } HER \geq 3 \\ 20+(r_{pot}-20)\cdot(3-HER) & \text{if } 2 \leq HER < 3. \end{cases}$$

Observational and management regime

In the VPA assessments for cod, survey indices are used (Hagen *et al.* 1998). In the present study, we assumed that the indices are linear, unbiased and without error.

Cod is managed by yearly VPA-based quotas targeting the fixed fishing mortality rate F=0.45. Herring is managed by setting quotas targeting the fixed fishing mortality rate F=0.2. The herring stock is assumed known when the yearly quota is set. An upper limit of 1 million tonne of herring per year is, however, imposed. Capelin is managed by the strategy outlined in Tjelmeland and Bogstad (1998), targeting a spawning stock of capelin of 500,000 tonnes, and leaving sufficient capelin in the sea as prey for the estimated cod stock. The temporal and spatial distribution of the catches of cod, herring and capelin is similar to that for the current fisheries, and is described in Schweder *et al.* (1998).

RESULTS

Biomass of stocks, catch and consumption is reported in millions of tonnes throughout. We denote biomass by B, catch by C, whale abundance in number of individuals by W, fishing mortality rate by F and natural mortality rate by M. The mortality rates are probabilities of dying of a certain cause during the year. The regression equations given throughout are estimated conditional means in an equilibrium state for given abundance level for minke whales, W.

Cod

A scatter plot (not shown) indicated a near linear response on cod abundance, but with an increased variability at high levels of minke whale abundance (above 130,000). The fitted line is

$$B_{cod} = 3.17-8W10^{-6}.$$

The biomass of cod is thus, on average, reduced by 8 tonnes for each whale, and the yearly standing stock of cod is thus reduced from above 3 million tonnes at low whale abundance to below 2 million tonnes with 200,000 minke whales.

The mean yearly catch of cod is also linearly related to whale abundance (Fig. 2). The fitted line is

$$C_{cod} = 1.15-5W10^{-6}.$$

The fit is excellent. For each extra whale in the ocean, the yearly mean catch of cod is thus reduced by some 5 tonnes, this regardless of whale abundance provided $10{,}000 \leq W \leq 200{,}000$.

The direct impact of minke whale abundance on whale inflicted natural mortality rate for cod is proportional for $W \leq 130{,}000$, but then it seems to flatten out. In the proportionality range, each minke whale consumes some 2.5 tonnes of cod yearly. The net impact on the cod fisheries, as managed by the chosen VPA procedure, and with herring and capelin managed as specified, is a loss of some 5 tonnes per whale. This impact is thus the result of a direct effect from whales preying on cod, and an indirect effect by whales preying on herring and capelin. In the reasonable range of whale abundance, $W \leq 130{,}000$, the direct and the indirect effects are of equal importance.

Fishing mortality rate falls nearly linearly for $W \leq 130{,}000$ according to

$$F_{cod} = 0.47 - 1.4W10^{-6},$$

but falls faster at higher levels of minke whale abundance. With W=200,000, both runs gave $F_{cod} < 0.1$. The natural mortality rate has a quadratic pattern:

$$M_{cod} = 0.075 + 0.11W^2 10^{-10}.$$

At low and intermediate levels of whale abundance, the decrease in fishing mortality is nearly cancelled by the increase in natural mortality, and total mortality is almost flat for $W \leq 130{,}000$ at 0.52 (Fig. 3).

Finally, the mean yearly number of cod recruits is fairly independent of whale abundance, but with more variance at high abundance.

Herring

Biomass of herring falls linearly with increasing minke whale abundance for $W \leq 130{,}000$. The fitted line is $B_{her} = 17.9 - 85W10^{-6}$. With more minke whales in the system, the herring stock is also reduced, but more slowly, when whale abundance increases. At low and intermediate levels of minke whale abundance, each extra whale thus reduces the herring stock by 85 tonnes.

Herring catches respond differently from cod catches when whale abundance is increased. At low levels, $W \leq 60{,}000$, there is only a slight drop from a high of some 1 million tonnes, but at levels above this threshold, the response is linear (Fig. 4). The fitted line has a slope of -4.5 tonnes per whale. An increase in whale abundance by one whale thus causes a mean decrease of 4.5 tonnes in the herring fishery, when the stock of minke whales is at moderate or high level.

The mass of herring consumed by one minke whale is nearly constant for $W \leq 60{,}000$, but is reduced at higher levels of W. With whale abundance in the interval $60{,}000 \leq W \leq 120{,}000$ each whale consumes on the average some 5.4 tonnes of herring. Thus, the direct effect of increased minke whale abundance on the herring fishery is negative. The indirect effect is, however, positive, making the total effect of an extra whale causing a loss of some 4.5 tonnes in the herring fishery.

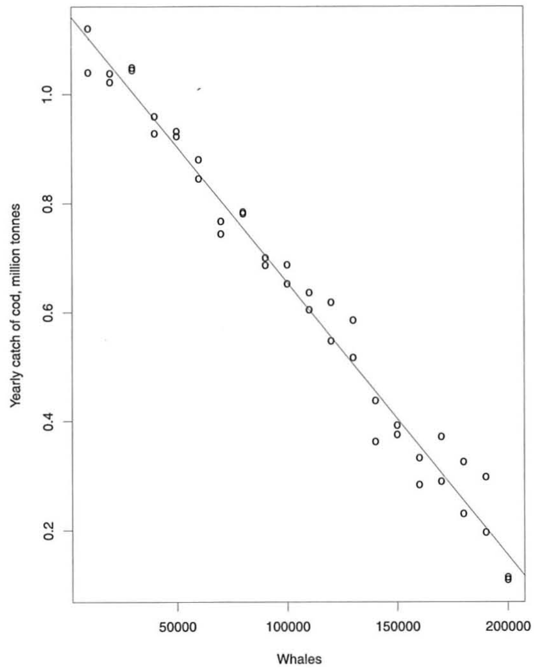


Fig. 2. *Mean yearly catch of cod (million tonnes) by minke whale abundance.*

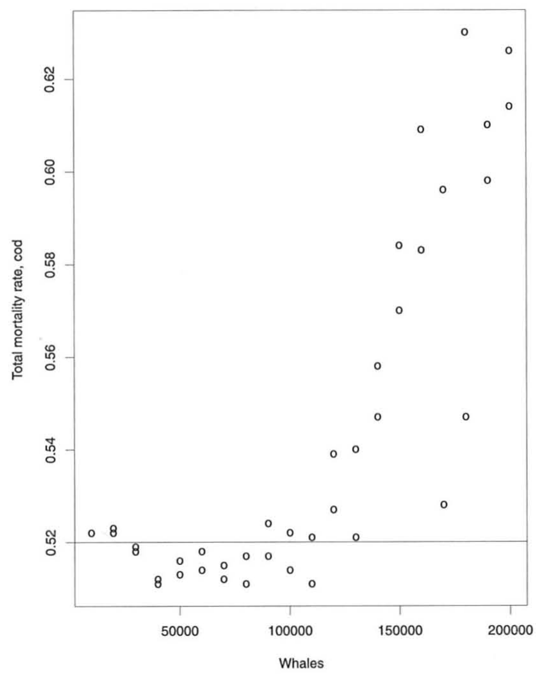


Fig. 3. *Total mortality rate for cod (yearly mean) by minke whale abundance.*

Fig. 4. *Yearly mean catch of herring (million tonnes) by minke whales abundance.*

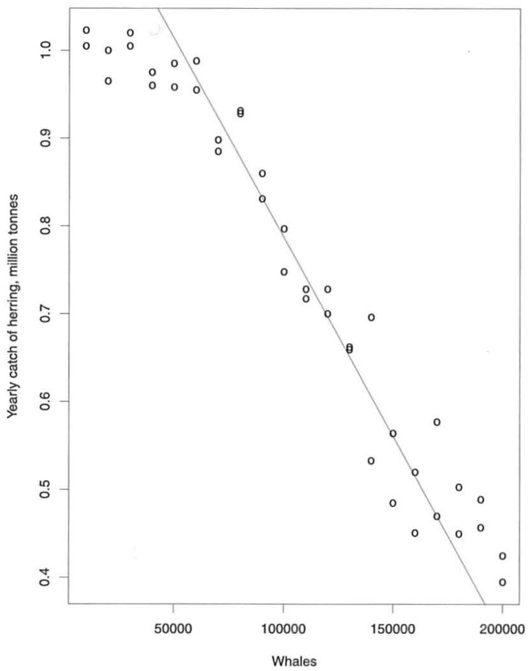
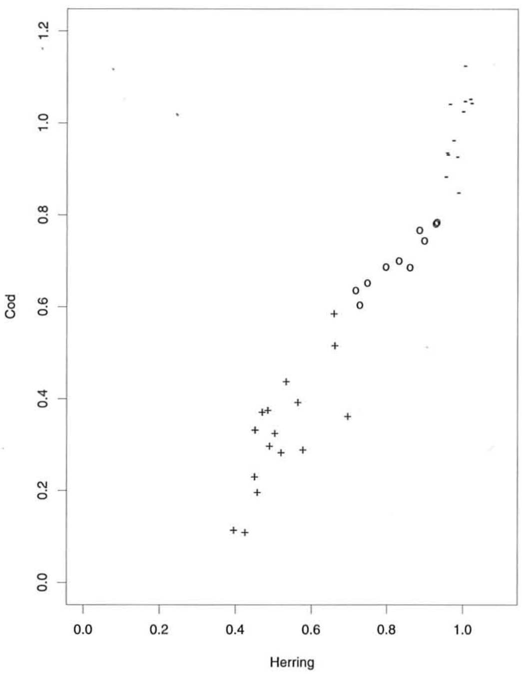


Fig. 5. *Mean yearly catch of cod versus herring (both in million of tonnes) by grouped whale abundance, W: + when W>120,000; 0 when 70,000≤W≤120,000; - when W<70,000.*



The fishing mortality rate increases nearly linearly to a peak of $F_{her} = 0.1$ at $W \leq 130,000$, but then it drops linearly. Note that the target fishing mortality rate is 0.2. This limit is not reached, since we have limited the herring fishery to 1 million tonnes.

Herring and cod

From the scatter plot in Fig. 5 of mean yearly catch of cod and herring, a strong positive correlation can be seen. Both herring and cod catches correlate negatively with minke whale abundance.

Capelin

Capelin catches varied considerably between runs, but declined roughly linearly with increasing minke whale abundance. The mean yearly loss in the catch of capelin for an extra minke whale in the system is some 2.8 tonnes.

DISCUSSION

The present experiment is a simple companion experiment to that reported by Schweder *et al* (1998). In contrast to that experiment, no systematic evaluation of the total uncertainty surrounding the model has been attempted. The only uncertainty that has been included in the model is the stochastic variability in the recruitment of cod, herring and capelin.

Our rationale for presenting the results from the present one-dimensional experiment is the following. To investigate direct and indirect effects of minke whale abundance on the fisheries, an experiment with sufficient contrast in minke whale abundance is called for. To see whether the effect is linear or even monotonic, it is important to keep other sources of variability at a minimum, at least in a first experiment. The stochastic element in the recruitment in cod, herring and capelin was kept in the model to mediate a potential resonance effect in the fish system at particular levels of minke whale abundance. If the deterministic version of the model, say with good recruitment in cod and herring every 10 year, and with recruitment following deterministic Beverton-Holt models, has resonance effects at some levels of W, this effect could be lost at nearby levels which are included in the design. With our stochastic element in recruitment, nearby values of W would possibly show such nonlinear effects in moderated form.

Since other important sources of variability and of uncertainty have been excluded from the present experiment, the conclusions from the experiment must be regarded as conditional on the model used and its parameterisation. The findings, as understood as statements about the Greater Barents Sea system, should therefore be regarded as tentative. The uncertainty associated with our numerical estimates is not quantified. We could, of course, have computed standard errors etc. for regression coefficients estimated from the scatter plots, but these standard errors would not fully represent the uncertainty associated with the estimates.

With these caveats, the findings are:

Generally, catches of cod, herring and capelin are reduced with an increased abundance of minke whales.

For cod, the direct effect on the catches of an extra minke whale in the system is a direct loss of some 2.5 tonnes due to minke whale consumption of cod, and an additional loss of some 2.5 tonnes due to predation on capelin and herring. These numbers are essentially independent of minke whale abundance within the range modelled.

For herring, the indirect effects seems to be positive, probably due to decreased predation on herring by cod. The direct negative effect from predation is, however, stronger. At intermediate levels of minke whale abundance, the net loss to the herring fishery is some 4.5 tonnes for each additional minke whale.

The experiment was expected to show non-linear indirect effects for cod. We hypothesised that at some levels of minke whale abundance, an increase in the whale stock would decrease the herring stock, with a consequential reduction in predation on young capelin (from herring), possibly causing a net positive effect on the cod fishery. Instead we found the effects of whale abundance on the cod to be linear. This cannot be due to an incorrect scaling factor in the predation function for minke whales, since the effect prevails over the range of minke whale abundance.

One reason for the effect of whale abundance on the cod fishery to be nearly linear in our model is the large amount of herring in the Barents Sea in years with herring in the area. In extreme recruitment years, the number of herring recruits is some 100 times larger than in ordinary years (Table 1). In the years following extreme herring recruitment, there is a large sub-stock of herring in the Barents Sea. With our predation model for minke whales, and with minke whale abundance below 200,000, there is herring enough in the Barents Sea in herring years to satisfy the whales. The surviving herring in the area are actually abundant enough, by our model for the herring-capelin interaction, to decimate the capelin stock by their predation on capelin fry.

Positive indirect effects on the cod fisheries have been reported (Bogstad et al. 1997). In previous studies, the impact of minke whales was found to be stronger on herring than on cod (Tjelmeland and Bogstad 1998). We found the net impact to be approximately of the same size in terms of catch in tonnes, but in value and in relative terms, the impact is stronger on cod. This difference in conclusion is likely due to differences in the models. There are two main differences. First, we let the fisheries be managed by an adaptive procedure instead of assuming fixed fishing mortalities. Secondly, we have modelled the food web differently. Instead of using suitability coefficients and predation functions of the Spencer-Collie form for minke whale predation, we have used modified logistic functions estimated from stomach data and prey abundance data. This has, we hope, been a realistic choice. There are also differences in the way the capelin-herring interaction is modelled, and in the consumption function for cod.

To identify a good and realistic model for the system we have studied is a huge project. We have not attempted to settle this difficult modelling problem, and we have refrained from attempting a complete discussion of the impact of minke whales on fisheries in the Norwegian Sea and the Barents Sea. The scenario model we have used could, in fact, be improved in several ways. The predation model for cod should, for example, be re-estimated using more extensive data. It should also be re-parameterised, probably with fewer parameters. The herring-capelin interaction is difficult to estimate, but with more data on capelin recruitment in years of herring in the Barents Sea, an improved model could presumably be identified. Even without these improvements, we regard our scenario model as a potentially useful supplement to the MULTSPEC model for uncertainty experiments to assess the collective uncertainties surrounding the management of fisheries in the Greater Barents Sea, and also for more specific experiments to compare management strategies or to investigate specific hypotheses like the one considered in the present paper.

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APPENDIX: FITTING THE WHALE-FISH PREDATION MODEL

Table 1: Definition of seasons	
Season	Month
Spring	1-5
Summer	6-7
Autumn	8-12

The year is divided in seasons according to Table 1.

From Haug (personal communication, see also Folkow *et al.* 2000, Table 3), we have obtained data given in Table 2 on relative stomach contents (biomass) in whales caught in three management areas.

Abundance of herring, capelin and cod on an aggregated level has been obtained from Institute of Marine Research, Bergen. We have disaggregated these. By furthermore assuming that there is no herring in the relevant part of the ES area and no capelin in the relevant part of the EB or EC areas, as was done in Haug *et al.* (1996), we obtain the temporal and spatial abundance of the various prey items for minke whales given in Table 3.

In the fish predation model specified in Section 2, minke whale prey on capelin, cod and herring according to the available biomass of each of these prey species. We assume that there is a limited overlap between the minke whales and the fish species, and that only the components of the fish stocks that overlap with the minke whales are available for predation. The overlap coefficients used for estimation are given in Table 4. Note that in the simulation, we used overlap coefficients without a seasonal structure (see Table 2 in text). The biomass of herring available to the minke whale in spring is, for example, 80% of the total herring biomass less than 4 years of age plus 10% of the 4+ component of the herring stock.

From Tables 3 and 4, the biomasses of available prey of herring, B_{her}, capelin, B_{cap}, and cod, B_{cod}, respectively are calculated. The parameters of the consumption function (1), (2) and (3) are estimated by minimizing the weighted sum of squares

$$\sum_{pas} \frac{\left[c_{pas} - \hat{c}_{pas}\right]^2}{\hat{c}_{pas}\left(1 - \hat{c}_{pas}\right)}$$

over prey item, *p*, area, *a* and season, *s*, with $c_{pas}(1-c_{pas}) > 0.01$. Here, c_{pas} is the relative stomach content in area *a* and season *s* that is constituted by prey item *p*, as given in Table 2, while c_{pas} is the corresponding modelled quantity obtained from the consumption function for given values of the parameters. The minimization is, of course, with respect to the parameters κ, κ_H, κ_C, ξ, ξ_C. The parameter a_{cap} was also taken as a free parameter, but the optimal value within the allowed interval [0.5, 1] was 0.5, which is taken as the estimate. The fit was not much better at the unconstrained optimum for this parameter. The point estimates of the other parameters are given in Table 3 of the text. We do not provide standard errors, since we do not fully understand the sampling variability in the prey abundance data.

Table 2: Relative content in minke whale stomachs (percent). ES denotes west Spitzbergen and Bjørnøya area, EB the management areas EB and EC, the Barents Sea and Coastal areas of the Norwegian Sea. Source: Tore Haug, personal communication

		Herring			Capelin			Cod			n		
Year	Season	ES	EB	EC	ES	EB	EC	ES	EB	EC	ES	EB	EC
1992	Summer	0.1	49.0	69.7	58.6	5.0	0.0	0.4	12.5	0.0	35	38	18
1993	Spring	0.0	1.5	11.3	5.3	0.0	0.0	94.5	83.7	4.6	1	1	2
	Summer	6.1	100.0	31.8	9.0	0.0	15.0	7.6	0.0	0.0	21	4	6
	Autumn	5.0	85.7	95.1	22.4	0.0	0.0	12.9	14.3	2.2	8	7	13
1994	Spring	0.1	69.5	24.5	0.1	0.0	0.0	20.0	13.8	27.7	5	7	6
	Summer	0.1	79.4	61.0	0.0	0.0	0.0	7.4	7.0	15.2	5	9	6
	Autumn	0.0	33.7	100.0	52.0	0.0	0.0	31.1	31.3	0.0	6	3	5
1995	Spring	0.0	24.2	-	0.0	19.4	-	0.0	12.7	-	16	19	0
1996	Spring	0.0	0.3	-	0.0	37.5	-	3.7	8.0	-	27	15	0
	Summer	-	1.4	-	-	37.4	-	-	5.2	-	0	19	0

Table 3: Abundance of prey for minke whales, in million of tonnes. Her. is herring, others as in Table 2.

		Her. (0-3)		Her. (4+)	Capelin	Cod		
Year	Season	EB	EC	EC	ES	ES	EB	EC
1992	Summer	3.13	.903	4.69	3.37	0.79	1.85	0
1993	Spring	3.30	.907	4.58	2.14	0.46	1.86	0.72
	Summer	3.42	.807	4.67	1.22	0.89	2.08	0
	Autumn	3.80	.707	4.75	0.84	1.29	1.94	0
1994	Spring	3.44	.992	4.98	0.37	0.41	1.64	0.61
	Summer	3.65	.874	4.99	0.23	0.78	1.83	0
	Autumn	3.89	.755	5.0	0.17	1.20	1.80	0
1995	Spring	2.10	-	-	0.12	0.37	1.47	-

Table 4: Overlapping coefficients used in the estimation.

Season	Herring (0-3)	Herring (4+)	Cod	Capelin
Spring	0.8	0.1	0.5	0.5
Summer	0.8	0.4	0.5	0.5
Autumn	0.8	0.8	0.5	1.0