Modelling diet composition dynamics among North Sea predatory fish using a length-structured partial ecosystem model.

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Abstract

Studies of the gut contents of fish stocks in the North Sea show decadal changes in diet composition, as might be expected when the relative abundances of prey species change. In this paper we explore the extent to which a simple model of prey consumption deployed within a dynamic multispecies population model is able to capture those changes. We make use of a length-structured partial-ecosystem model (FishSUMS) in which the relative diet preferences are set by a combination of species weightings and predator-to-prey length ratios. Eleven species were included in the model with full length structure, together with other trophic resources represented in less detail. By tuning to various sources of data we show that, despite the simplicity of the representation of the predation process, it is capable of capturing some of the large observed changes in the sampled diets of predator species. We also quantify the rate at which individuals are lost to three sources of mortality; fishing, predation and density-dependent mortality. Multispecies model, Population dynamics, Size-structured populations, Ecosystem-based fisheries management

Introduction

Fisheries management has a long history of using single species assessment methods to calculate maximum sustainable yields (MSY) and other such population references. In recent years there has been an increasing realisation that inter-specific competition and predator-prey interactions play an important role in marine ecosystems. This has led to the use of multispecies approaches to study commercially important species, and the species with which they interact, (Hollowed *et al.*, 2000; Plagányi, 2007) and these models must track multispecies trophic interactions within the ecosystem. Studying these interactions can give an insight into the relative importance of fishing and predation, and their associated contribution to overall mortality. For example, introducing predation into models can lower MSY, while raising the spawning stock biomass required to achieve MSY (Moustahfid *et al.*, 2009). Although predator-prey interactions can be found through stomach sampling it is important to note that the stomach contents data may have a "long tail", with many prey species each making up very small proportions of the predator diet, and it may not be possible to sample enough of the predators to see all of the predator-prey interactions (Goldwasser and Roughgarden, 1997).

These trophic interactions can be modelled in different ways: one approach makes use of predator-prey theory with a functional response describing the rate at which prey are consumed by predators. In such models the predator population is inhibited in some way by a shortage of prey (reduced growth or fecundity, or increased mortality), so that the predator population is controlled in a bottom-up way (Andersen and Ursin, 1977; Walters *et al.*, 1997).

Alternatively predators can be modelled as always consuming some ration that meets their trophic requirements in terms of metabolic cost, growth and fecundity (Datta *et al.*, 2010; Hall *et al.*, 2006). This approach leads to prey populations that are inhibited by an abundant predator, which we can think of as applying top-down control. Top-down and bottom-up control have been shown to affect species at different levels within an ecosystem's food web, with bottom-up controls affecting the lower trophic levels and top-down controls affecting the higher trophic levels (Brett and Goldman, 1997).

Speirs *et al.* (2010) describe a top-down model in which the main species of interest are modelled by a length-structure, covering the full lifespan from eggs to mature adults, with other trophic resources considered in less detail. This differs from other models which do not describe the full life cycle but instead have recruitment to the fishery modelled by some fixed stock recruitment term (Magnússon, 1995; Livingston and Jurado-Molina, 2000; Hall *et al.*, 2006). Discounting pre-settlement stages of the life cycle means that predation on eggs and larvae, which has been suggested as an important factor for cod and other species (Köster and Mölmann, 2000; Godiksen *et al.*, 2006; Segers *et al.*, 2007; Bakun *et al.*, 2009), does not feature

in the model.

Stomach sampling projects (Daan, 1989; Hislop, 1996) show decadal changes in the diets of predators as abundances of both predators and prey change. Capturing the mixed diet of a predator requires some suitability coefficient to describe the extent to which a prey is preferred by the predator, although some experimental results have suggested that the in some cases predators display negative switching whereby a predators preference for a particular prey drops as the prey becomes more abundant (Rindorf and Gislason, 2005; Rindorf *et al.*, 2006). The suitability takes account of the age or size (depending on the structure of the model) of both the predator and prey. Multispecies virtual population analysis (MSVPA), and the forecasting version MSFOR (Magnússon, 1995; Livingston and Jurado-Molina, 2000), calculates these coefficients by the same iterative process that calculates the other unknown parameters in the model. An alternative approach defines some function to capture the preference of a predator for its prey (Datta *et al.*, 2010; Hall *et al.*, 2006; Speirs *et al.*, 2010). The Stochastic Multi Species model (SMS) proposed by Lewy and Vinther (2004) reconciles these two approaches by using a size dependent suitability function that relies on the average lengths of both the predator and prey, with a vulnerability parameter that is tuned in the same way as the suitability coefficients in MSVPA.

In the work presented here we make use of FishSUMS, a modelling package based on the partial ecosystem model of Speirs *et al.* (2010), to study the diets of five important predators in the North Sea. The model developed by Speirs *et al.* provides a length structured, multispecies modelling framework that is used to study predator-prey interactions between fish, with other trophic resources represented in an unstructured manner. By analysing data from two stomach sampling projects (Daan, 1989; Hislop, 1996) we can find the proportions of the diets of our predators that are made up of the species in our model, and use this as novel tuning data, along with stock assessments (ICES, 2009a; 2009b).

With FishSUMS tuned to the data we study changes in the magnitude of mortality rates that come from three distinct sources – fishing, predation and density dependent mortality. We also investigate changes in the fluxes within our model, which are a result of changing populations, and study changes in the equilibrium biomass that are caused by changes in fishing mortality.

Methods

Model overview

The underlying model of FishSUMS is the length-structured partial ecosystem model developed by Speirs *et al.* (for full details see the appendix of Speirs *et al.*, 2010). The structured species are each represented

by a chain of length classes spanning the whole life history from egg to large adults. Sexual maturity is determined solely by length. For each length class there is a *per capita* fecundity, which starts at zero for the smallest immature fish and increases with body size for mature fish. Over a timestep the egg production of all of the surviving members of the population is added to the egg class. Progression between length classes is strictly one way and in each time step a fixed proportion of the surviving population in each length class progress to the next class. This growth implies a food consumption that meets the metabolic costs of all surviving fish and the increase in weight of the growing fraction of the population. The food requirements of each length class are taken from its prey length classes according to prey abundance and a length-based preference function (described in more detail below).

The model parameters for the length-structured species are given in Tables 1 – 3.

Species selection

We began our studies with the nine trophically linked species studied by Speirs *et al.* (2010): the piscivorous demersal gadoids cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and whiting (*Merlangius merlangus*), the zooplanktivorous gadoid Norway pout (*Trisopterus esmarkii*), the pelagic planktivores herring (*Clupea herengus*) and sandeel (*Ammodytes marinus*), the demersal benthivore common dab (*Limanda limanda*), the demersal piscivore grey gurnard (*Eutrigla gurnardus*) and the commercially important invertebrate Norway lobster (*Nephrops norvegicus*). To these we have added two species that also feature in the North Sea ecosystem; the pelagic piscivore saithe (*Pollachius virens*) and the demersal benthivore plaice (*Pleuronectes platessa*). These additional species are important in estimating the Large Fish Indicator, which describes the proportion (by weight) of the fish population that is larger than some length threshold and was developed as an indicator of the state of a fish community (Greenstreet *et al.*, 2011). In addition saithe is of particular interest to us since it is one of the piscivorous predators for which diet composition data is available (Daan, 1989; Hislop, 1996).

Trophic resources that do not feature within this cadre of structured species are included as generic size-spectra representing zooplankton, benthic invertebrates and other fish.

Length-structured growth

For the length-structured species in the model length follows a von Bertalanffy curve (von Bertalanffy, 1938), such that the mean length of a cohort of fish hatched at the same time is given by

$$\hat{L}(a) = L_\infty - (L_\infty - L_0)e^{-\gamma a} \tag{1}$$

where $\hat{L}(a)$ is the mean length at age a, L_0 is the mean length of a hatchling, L_∞ is the asymptotic length and γ is the von Bertalanffy growth rate. Von Bertalanffy growth has been widely used to describe growth in a population mean but in reality growth of individuals is highly variable, which leads to a high variability around the cohort mean length. Also growth is typically compensatory so that variability in length is not constant with age. To capture these aspects of growth Speirs $et\ al.$ (2010) combined methods developed by Andrews $et\ al.$ (2006) and Gurney $et\ al.$ (2007). For each species the population is divided into j_{max} length classes starting at the hatchling length L_0, and ending at the maximum modelled length L_{max}, which is typically $90 - 95\%$ of L_∞. In each model timestep , δt, a fixed fraction of the surviving number in each length class moves on to the next length class. The length classes are not of equal width, with small fish, whose rate of increase of length is largest, represented by wider length classes. For each species there is also a settlement length assumed (L_s), which represents the transition from a pelagic phase to a demersal one. The main reasons for this transition are the move from exclusively zooplanktonic food to the wider diets of demersal fish and to allow for different mortality rates for pelagic and settled fish. For species that do not settle L_s represents the transition between early-life-history mortality rates and adult ones.

Maturity and reproduction

For each species in the model there is a length dependent proportion of mature individuals. The probability density of an individual maturing is normally distributed with mean L_m and standard deviation L_s. Since the mortality rate is independent of maturity the fraction of mature individuals in each length class is obtained from the corresponding cumulative normal distribution. Weight is taken to be a power relation of length, with a the constant of proportionality and b the power, generally of order three. Egg production per mature female is proportional to body weight with constant of proportionality ρ, so that the annual egg output per gramme of mature fish biomass is $\rho/2$ with a one-to-one sex ratio.

Seasonality in reproduction is captured by having annual egg production occur over a spawning season where S_0 and S_1 are the species-specific start and end days of the spawning season. Egg production during the spawning season occurs at a constant rate so that the annual output per mature fish is distributed equally between the model timesteps during spawning. In each timestep the egg production from surviving mature fish is taken to be constant and continuous and is used in the calculation of the change in egg numbers.

Data

The model run is for the period from 1950 to 2008, but since there is very little data available before 1960 we focus our fitting effort on the period from 1960 and this is what we feature in our figures. In addition to this

time period for the main model run FishSUMS has two periods to allow the model population to settle to a steady state (one with no fishing and one with fishing at the level of the first year of the model run). Speirs *et al.* (2010) used 100 years for each of these, but found that in practice the model settled to equilibrium in a much shorter time. Since the North Sea experienced a period without fishing during World War II we use spin up periods to capture the reality of this change, namely a fishing free spinup of six years, to represent the years from 1939 to 1944, and a spinup with 1950 fishing mortalities of five years, to represent the period from 1945 to 1949.

Six aspects of the model output are tuned to data: species total stock biomass (TSB), spawning stock biomass (SSB), recruitment, landings, length distributions and diet, though these are not all available for all species. For the assessed species the data fitted to for TSB (Fig.), SSB (Fig.), recruitment (Fig.) and landings (Fig.) come from the ICES assessments (ICES, 2009a; 2009b). For the unassessed species (Norway lobster, common dab and grey gurnard) we have compared our model output only to data for TSB and landings. In the case of Norway lobster TSB we estimated abundance from the annual underwater television surveys of burrow density (millions of individuals) for all sub-stocks. For occasional years in which a sub-stock was not sampled we assumed that the missing value was in the same proportion to the observed stocks as in the mean of all the fully sampled years. We then applied a mean weight per individual for each year, which was available from one of the surveys. Finally this biomass estimate from the four TV survey areas was scaled up to the whole north sea by the proportion of landings coming from the assessed areas (which accounted for 75-85% of total north sea landings). For common dab and grey gurnard we estimate TSB from the International Bottom Trawl Survey (IBTS, http://datras.ices.dk/Home/default.aspx).

For landings, rather than model discards in detail the model defines an 'effective landing size' (L_l) below which any catch is discarded. For cod, haddock and whiting there have been changes in the legal minimum landing sizes, and these are reflected in the values of L_l for those species.

We output catchability adjusted length distributions for a single year (1991) for a subset of our species and these can be seen along with the length distributions from IBTS (http://datras.ices.dk/Home/default.aspx) in Fig. . The catchability, q, at length l is given by

$$q(l) = \frac{\gamma exp\left(\frac{l-l_h}{\omega}\right)}{1 + exp\left(\frac{l-l_h}{\omega}\right)}, \tag{2}$$

which gives a sigmoidal function where γ is the catchability of the longest fish, l_h is the length at which the catchability is $\gamma/2$ and ω governs the slope of the function. The value of γ was chosen as 1 for all species since this parameter does not affect the shape of the length distribution, which is rescaled to give a unitary

area under the curve.

The diet data fitted to for the five predator species in our model - cod, haddock, whiting, saithe, grey gurnard - come from the reports of the Year of the Stomach projects in 1981 and 1991 (Daan, 1989; Hislop 1996). The data give percentages of stomach contents that are made up of several taxa, all summing to 100% for each quarter and age of the predator. Further to that there are percentages of diet that are each of several commercially important species, including the structured fish species in our model. We calculated the portion of the diet that we describe as other fish by taking the percentage described as *gnathostomata* (jawed vertebrates) and subtracting the percentages that were attributed to each of the structured fish species in our model. Similarly the benthos percentages were calculated by taking everything that was not gnathostomata (since no zooplankton featured in the data) and subtracting the percentages that were attributed to Norway lobster (the only one of our structured species that would not be described as gnathostomata). The details of how we calculate the data points and error bars used in Figs. - can be found in the Appendix.

Mortality

Each of our structured species is subject to three distinct sources of mortality: predation, fishing and density dependent mortality. The density dependent mortality consists of a stage-dependent background mortality (with mortality rates m_e, m_p, and m_s for eggs, pre-settlement and post-settlement stages respectively) and a biomass-dependent mortality term (with *per capita* rates δ_p and δ_s for pre- and post-settlement stages). Background mortality represents sources of mortality whose effect is constant and not influenced by population levels such as parasites, pathogens and un-modelled predators including seals and sea birds. The biomass-dependent mortality imposes population control and represents processes that generate higher mortality at higher species abundance, such as limited resources or un-modelled predators that are not strongly coupled to the target species but switch to abundant prey.

For the species that undergo annual stock assessment by ICES (cod, haddock, herring, Norway pout, plaice, saithe, sandeel, and whiting) the annual fishing mortality rates (F's) in the model are the assessed values for each age class of fish (ICES, 2009a; 2009b). These age-dependent estimates of F are applied to the length structured model by making use of the von Bertalanffy relationship between age and length to give a nominal age for each of the model length classes. The assessment commenced in different years for different species (1957 for plaice; 1960 for herring; 1963 for cod and haddock; 1967 for saithe; 1980 for whiting; 1983 for Norway pout and sandeel) so it was necessary to infer F's for varying numbers of years for the different species. We use the methods described by Speirs *et al.* (2010) to derive age specific F's outside of the assessments (including the full model run for the unassessed species common dab, grey gurnard and Norway

lobster). These derived F's were treated as tunable to achieve the best fit to the data.

Predation in the model assumes that all surviving members of the population meet their food require-ments, for which wet weight is the 'energy' currency. The energy costs have three distinct sources. Firstly, all surviving members of the population meet a metabolic cost (η), which is expressed as a weight loss rate. Secondly, the growing fraction of the population must obtain the additional mass required to progress to the next length class, assuming a constant weight-length relationship applies to all individuals. Finally sexually mature individuals must meet the cost of reproduction, which is simply the weight of the eggs produced. The weight of the egg is taken to be the weight associated with the shortest hatch length. In order to convert these three costs into a food requirement there is an assumed assimilation efficiency (ϵ), which represents the fraction of the food consumption that is available for meeting the costs.

A preference function is defined that loads the food uptake among the prey species. This preference function provides the weighting used in assigning the food requirements of a given species and length class to the various prey species and length classes. There are two components to the preference function. Firstly a species-specific component that describes whether a prey species is in the diet of the predator and to what extent it is a favoured prey. This component of the preference function captures spatial domain overlap or other behavioural propensities of the predator. Secondly there is a length based component to the preference which depends on the ratio of prey to predator lengths. This is captured with a four parameter function in which there are minimum and maximum prey/predator length ratios (Φ_{min} and Φ_{max}), a preferred prey/predator ratio (Φ_{opt}) and a parameter (β) that determines tightness of the preference function around Φ_{opt}. The preference function parameters used by Speirs *et al.* (2010) were used as the starting point for parameter tuning aimed at obtaining good correspondence between modelled and observed diets.

When we study the changes in the three different mortalities we use the proportion that die within the first timestep of the year from each of the three sources. We study these mortality rates for immature fish (lengths from L_s to L_m) and mature fish (lengths over L_m) separately, by taking the arithmetic mean of each mortality over the relevant length classes. Due to the way in which growth is defined in the model fish spend an equal amount of time in each length class so that the calculated values represent the average mortality rates experienced by an individual fish while immature and mature.

Fluxes

We studied changes in the fluxes in our model over two periods: 1977–1985 and 1985–2005. The period from 1977 to 1985 was chosen because of the contrast in the system offered, with herring stocks low and cod stocks high in 1977 and herring having recovered and cod stocks reduced by 1985. The period from 1985 to 2005

was chosen to give insight into changes in the system towards the end of the period studied, with similar important changes in the system – by 2005 cod is further reduced, herring is near an all time high and grey gurnard is also at much higher stock abundance than in 1985. We calculated these fluxes across the full life cycle of both predators and prey, so that herring predation on eggs and larvae of other structured species is represented, as well as the fluxes from zooplankton to the larvae of all species. Since they are of different orders of magnitude we studied the fluxes from the unstructured and structured species separately.

Equilibrium biomass

An obvious approach to managing fish stocks would be to lower the total fishing mortality (for example by reducing the total allowable catch), with the expectation that this would increase the abundance of the stock. To investigate this approach we study the effects of changing the fishing mortalities on the demersal species in our model. We consider the fishing mortalities to have come from four distinct demersal fleets, or metiers (Laurec *et al.*, 1991): beam trawlers; otter trawlers targeting fish; otter trawlers targeting Norway lobster; and seine gear. We ran the model forward to 2050, to allow it to settle to equilibrium, with 2008 fishing mortalities and then repeated with reduced fishing mortalities post-2008 for each of the separate metiers in turn. We make use of data for the proportions of total landings of six of these species (cod, haddock, whiting, saithe, plaice, Norway lobster), between 1997 and 2004, that were made by each of the metiers (Greenstreet et al., 2007; personal communication with S. Greenstreet on 27/10/2011). In the absence of data on the other two demersal species we assume that grey gurnard is caught in the same proportions as whiting, since grey gurnard is an important predator of whiting, and dab is caught in the same proportions as cod, since cod is an important predator of dab. These assumptions are made on the basis that predator-prey relationships indicate a strong spatial overlap of the species, which would lead to similar proportions of catch from each of the metiers. The proportions of landings for our demersal species that are attributed to each of the demersal metiers are given in Table 5.

We investigate the effects on each of the structured species in our model of reducing the fishing mortality of each metier by 10%. All of the rows in Table 5 sum to 1, so by multiplying the column by 0.9 and summing each row we find the factors by which the fishing mortalities for each species must be multiplied to model a drop in the relevant fishing mortality of 10%.

Results

Tuned model run

The parameters in Tables 1 – 4, along with all unassessed fishing mortalities, were treated as tunable to our six datasets (TSB, SSB, recruitment, landings, diet and length distributions). The model was fitted to data by eye. This involved confronting the model simultaneously with all of the data and attempting to minimise the differences between the model run and the data, while generating a SMAPE error function (Flores 1986) to ensure quantitatively that chosen changes to the parameters were improving the fit.

Speirs *et al.* (2010) invoked temporal changes in parameters to capture apparent changes in the data, and some of these are maintained here. Firstly, haddock recruitment appears to be highly variable and in order to capture two of the largest recruitment spikes in the data the background mortality of pre-settlement haddock (m_e, m_p) is reduced for two single years: by 85% in 1967 and by 50% in 1974. Secondly, there is a discrete reduction in herring recruitment after 2001, with an attendant reduction in stock levels and landings. To capture this we employ an increase in the background mortality of pre-settlement herring (m_e, m_p) of 20% for all years after 2001.

We have additionally introduced temporal changes to the pre-settlement mortality of cod. Initial attempts to fit the model to data arrived at parameters that gave a very good fit for cod from 1970 onwards, but that gave biomass, recruitment and landings fits pre-1970 that greatly overestimated the data. To tackle this we increase all cod pre-1970 pre-settlement mortality parameters (m_e, m_p, δ_p) by 17%.

The fits for TSB, SSB, recruitment, landings and length distributions can be found in Figs. – and the fits for the predator diets are dealt with in the next section.

Predator diets

We fitted the model output of diet composition (percentages of total diet that are each of the model species) to the data points we found from the Years of the Stomach data (Daan, 1989; Hislop, 1996), as described in the Appendix. This involved tuning the diet preferences, and the mortality parameters since increasing, or decreasing, the predation upon a prey species can have a major effect on the total mortality of that species. The results of these fits are presented in Figs. – .

In many of the cases the plot of the model output lies close to the data points and in most the difference between the model output for 1981 and 1991 shows a change in the diet that is at least in the correct direction (e.g. both the model and data points show a decadal rise). However, one notable exception to this is the percentage of herring in the whiting diet. We know that the biomass of herring in the North Sea was close

to an historic low in 1981 and had recovered by 1991. As we would expect in this situation the model, which matches the data for herring TSB very well, shows the level of herring in the whiting diet rising between 1981 and 1991. The data, however, suggest that the percentage of herring in the whiting diet fell over this period. For all of the other predators of herring both the model output and data are as expected, with herring making up more of the diet in 1991 than in 1981.

This unexpected result may merely be a sampling error. It is not clear where the extra predation on whiting is assigned in the data for 1991: the groups that are consumed more in 1991 are cod, Norway pout and the generic other fish. One possible explanation for this discrepancy could be that some of the diet that was identified to only taxa level, as gnathostomata, was actually made up of whiting but could not be identified to species level. Alternatively the result could be due to changes in the spatial distribution of both whiting and herring between 1981 and 1991. For example, Corten (2001) found that over the period 1960-1990 the distribution of herring moved gradually north within the North Sea. Meanwhile Zheng *et al.* (2002) found that the area of peak whiting abundance moves year on year and is correlated, among other factors, to sea surface temperature. If changes such as these meant that the spatial overlap of whiting and herring was smaller in 1991 than 1981 it could explain the change we see in the whiting diet. Despite the fact that we know there was more herring in the North Sea in 1991, there may have been less herring in the regions where the sampled whiting were.

Having used the data to tune the diets of our predators we can study the model run. For instance in the immediate aftermath of the two haddock recruitment spikes cod, whiting, saithe and grey gurnard all have haddock as a greater fraction of their diet, though for grey gurnard it is still a small percentage of the diet. Obviously this means that other species have to make up smaller percentage of the diet: for cod we can see this effect most strongly in the percentages of the diet that are dab, Norway lobster, sandeel, Norway pout and the generic other fish; for whiting and saithe the effect is clearest for sandeel and Norway pout. These dips are not as clear cut as the spike in haddock predation since the abundance of these other species, as well as any alternative prey of the predators, are all changing during this period.

Since haddock is not cannibalistic we may expect that the diet percentages (Fig.) would not be affected by the short term super-abundance in the wake of the recruitment spikes. However, we see that the proportions of the diet that are sandeel and Norway pout (the two main fish prey of haddock) dip sharply. This effect is due to the drop in abundance due to increased predation by haddock (we see related dips in the TSB of these species in Fig.) but could also be partly due to haddock having to find more abundant prey than sandeel and Norway pout to meet its increased trophic requirements. The extra predation by haddock is taken up by benthos, which we see spiking sharply in Fig. as sandeel and Norway pout dip.

For grey gurnard, as it becomes more abundant (after 1990) wee see it become more piscivorous. Changes

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in the percentages of the grey gurnard diet (Fig.) that are each of our structured species are largely driven by changes in the abundance of the prey (comparing the shape of the graphs in Fig. to the relevant graphs in Fig.) and in absolute terms any changes are relatively small. However, after 1990 there is a reduction in the percentage of the diet that is benthos and a rise in the percentage that is other fish.

Mortality

As described above there are three distinct types of mortality in our model; predation, fishing and density dependent mortality, and we separately present the results of these for settled, immature fish (length classes from L_s to L_m, Fig.) and mature fish (length classes above L_m, Fig.) at the start of each year. The fishing mortalities in Figs. and are merely the values that we defined (including all of the assessed fishing mortalities that were available), taking the average across the relevant length classes.

The predation and density dependent mortality rates come about because of the interaction of the modelled species and their mortality and diet preference parameters. For example we can see for the immature fish (Fig.) that following the two haddock recruitment spikes, when the biomass of haddock also spikes, density dependent mortality of haddock spikes since the resulting increased biomass raises the density dependent component of mortality. In the absence of any sharp increase in the abundance of the predators of haddock at this time, the overall predation rate of haddock falls sharply as the overall increase in haddock means that an individual haddock is less likely to be predated upon. Similarly for cod, whiting, herring and Norway pout there is an immediate reduction in the predation mortality as predators switch to super-abundant haddock (as discussed in the previous section). For herring and Norway pout, both prey species of haddock, these reductions are very short lived: as the very large haddock cohorts grow, and become predators, there are very sharp increases in predation mortality for these species. The other prey of haddock, sandeel, experiences an increase in predation mortality immediately after the spike in haddock. Of these three prey species of haddock, sandeel and Norway pout show a dip in density dependent mortality to accompany the spike in predation, which occurs because density dependent mortality is reduced as the biomass is reduced by the increased predation.

For herring, in the wake of the recruitment failure at the start of this century the density dependent mortality rate is reduced as a result of the reduced biomass. Meanwhile for Norway lobster we see a peak in predation, with a small fall in density dependent mortality, during the 1970s when cod, the only predator of Norway lobster in our model, is at an historic peak. At the same time herring is depleted and it could be that this effect is in part also due to cod switching predation from herring to Norway lobster due to the relative scarcity of herring.

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The sharp rise in grey gurnard abundance from around 1990 onwards has an impact on the predation mortality of its prey. The effect is seen most strongly for sandeel, with the predation rate approximately doubling as grey gurnard becomes more abundant, but can also be seen in the predation rate for Norway pout.

In general we see in Fig. that predation is a greater source of mortality than fishing for immature fish. The species for which this is never true are plaice and saithe, which suffer no predation in our model; grey gurnard, which is only predated upon in pre-settlement stages by herring; dab, which is predated on by relatively few species; and cod, which is heavily fished throughout the study period with TSB greatly reduced. The other situations where fishing is greater than predation as a source of mortality coincide with reductions in the relevant stocks, which suggests that over-fishing contributed to the reduced stock. The most notable of these are for herring: in the 1970s when herring stocks were almost wiped out, requiring a sharp reduction in landings to allow the stock to recover; and also around 1990 when there was also a sharp reduction in the herring stock. The other case when fishing is a greater source of mortality than predation is for Norway lobster towards the end of the study period when landings are showing a sharp increase. Another factor for Norway lobster at this time is that cod, its only predator, is at historically low levels, which means that the predation upon Norway lobster is reduced.

For mature fish (Fig.) we see that in general predation is a much lesser source of mortality than for immature fish, with predation mortality being greatly reduced for all species. In particular there is no, or almost no, predation on mature cod, haddock, dab and herring. This difference between mature and immature fish happens because mature fish are larger and, therefore, there are very few fish of the predator species that are large enough to consume them. In contrast all of the fishing mortalities are significantly higher for mature fish than immature fish, which is due to larger fish being more sought after by the fishery as well as minimum landing sizes requiring mesh sizes that allow smaller fish to escape. The density dependent mortality of a particular length class is unaffected by length so the average rate is the same for immature and mature fish.

Modelled fluxes

Figs. – present changes in the modelled fluxes over two periods, 1977-1985 (Figs. and) and 1985–2005 (Figs. and). We use separate diagrams for the fluxes from unstructured (Figs. and) and structured species (Figs. and), with positive changes in black and negative changes in grey. Figs. and capture the changes in all of the fluxes from our structured species to predation by the structured species (including cannibalism), to fishing, and to density dependent mortality. In these graphs the thickness of the lines is proportional to

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$log(500 \times cf)$, where cf is the change in the flux and the units of flux are g m^{-2} y^{-1}. Figs. and feature the fluxes from the unstructured trophic resources to our eleven structured species and in these cases the width of the lines are directly proportional to $log(50 \times cf)$.

The most striking change in Fig, is for the flux from zooplankton to herring. As we might expect zooplankton, which is an important prey for herring throughout its life cycle, is taken much more in 1985 when herring is abundant than in 1977 when herring stocks are at an historic low within our time series. Similarly as we would expect the flux from zooplankton to cod larvae is among the largest negative changes since cod stocks are lower in 1985. We can see that saithe has changed its diet from Norway pout to herring over this period due to the increased availability of herring and a slight reduction in Norway pout abundance. In Fig, the fluxes from all three unstructured resources to grey gurnard have among the largest increases along with the flux from benthos to dab. These changes are to be expected as both grey gurnard and dab are more abundant in 2005 than in 1985.

Of the fluxes between the structured species in the first period (Fig.) the largest increases are in the fluxes from herring to saithe, whiting and cod, which is caused by the increased availability of herring. Even larger are the increase in the fluxes from herring to fishing and density dependent mortality as well as the flux from sandeel to density dependence. The greatest reductions in Fig. are in the fluxes from dab, grey gurnard, cod and Norway pout to density dependent mortality, which all arise because these species are less abundant in 1985 than in 1977. In 2005 grey gurnard and dab stocks are both greatly increased and as a result the largest increases captured in Fig. are in the fluxes from these two species to density dependence and the flux from sandeel to grey gurnard. In this second period the greatest reduction is the flux from sandeel to density dependence because of the lower level of the sandeel stock in 2005. Apart from a significant increase of the flux from dab and a small increase in the flux from Norway lobster the fluxes to the fishery all show a reduction, which are due to a combination of reduced stock levels as well as reduced fishing mortalities.

Equilibrium biomass

The results of reducing the fishing mortality of each of the four demersal metiers by 10% are given in Table 6. Here we can see that the greatest changes appear by reducing the fishing mortality of the otter trawl targeting fish, with cod equilibrium TSB raised by 30.8% and Norway pout, an important prey of cod, lowered by 71.4%. The only other changes that are greater than 10% are also for Norway pout, which is reduced by 19.6% by reducing the beam trawl F by 10% and reduced by 23.1% by reducing the seine gear F by 10%. The reduction of F for these two fisheries also leads to increases in cod biomass, which explains

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the reduction for Norway pout.

In Table 6 the species that are increased by reducing F for all four of the metiers are cod, saithe, grey gurnard, dab and plaice. Saithe and plaice do not feature as prey in our model, so no extra predation mortality is introduced by reducing the fishing mortality on any metier. Meanwhile cod and grey gurnard feature as predators to a much greater extent than as a prey, so that the increased predation mortality is small compared to the reduced fishing mortality. Dab equilibrium TSB is also raised by reducing the fishing mortality for all of the metiers. This happens because, although dab is an important prey of cod, predation is a lesser source of mortality for dab than fishing (Fig.). Also the increase in dab biomass across the board is always less than the increase for cod, which suggests that the increased predation mortality is having an effect although to a lesser extent than for the other prey only species.

Some of the results in Table 6 appear counter-intuitive at first, since although we are lowering fishing mortalities we see reduced equilibrium TSB for six species. For the pelagic species in our model – sandeel, herring and Norway pout – the fishing mortalities are not reduced since the demersal fleets would not be responsible for the fishing, but predation mortality is raised because the TSB of the predators cod, saithe and grey gurnard is increased. However, for haddock, whiting and Norway lobster we see that an reduction in fishing mortality leads to an reduction in the equilibrium biomass. Perhaps the most surprising of these results is that reducing the fishing mortality from the otter trawl targeting Norway lobster by 10% leads to a small reduction in the equilibrium biomass of Norway lobster, despite more than 70% of its fishing mortality coming from this metier. This is because of a relatively large increase in the cod biomass increasing predation upon Norway lobster. The same is true for the other results for Norway lobster and all the results for haddock and whiting: the reduced fishing mortality leads to an increase in the biomass of cod, and to a lesser extent grey gurnard, which increases the predation mortality, overcoming the reduced fishing mortality. These results demonstrate that merely changing fishing mortalities in order to manage stock levels is likely to fail if predator-prey interactions are not taken into account (since increasing $\overline{F}$ similarly leads to an increase in equilibrium TSB of prey).

Discussion

In the work described in this paper we have used FishSUMS, a package based on the 'partial ecosystem' model of Speirs *et al.* (2010), to study in detail the diets of five important piscivorous predators in the North Sea. The model developed by Speirs *et al.* facilitates such a study by having a versatile approach to defining diet. This approach allows us to study changes in diet, which are a consequence of the changing abundances of predator and prey species over time. By analysing data from the stomach sampling projects of 1981 and

1991 (Daan, 1989; Hislop, 1996) we can see decadal changes in the diets of cod, haddock, whiting and saithe and, novelly, use these as tuning data for our model.

FishSUMS considers three distinct types of mortality of the species in the model: fishing mortality, predation mortality, and density dependent mortality. By studying the mortality rates from these three sources we find that for many of the species in our modelled partial ecosystem predation is a greater source of mortality than fishing. The cases when this was not true were for species that are not heavily predated upon (plaice, saithe, grey gurnard, dab) or where stocks are in decline, suggesting fishing may be at unsustainably high levels (e.g. herring in the 1970s and cod since 1980). The fact that predation is often a greater source of mortality than the fishery means that fisheries management must take account of the trophic interactions within the ecosystem, since merely reducing fishing mortalities may not allow the stock levels to rise in the desired way.

Results of experiments changing fishing mortalities to investigate this question showed that reducing the fishing mortalities of each of the four main demersal fishing fleets actually led to a drop in the biomass of several species – with increased fishing mortality similarly raising the biomass. This happens because the reduced fishing mortality raises the biomass of predator species, in turn raising the predation mortality on prey species to a greater extent than the drop in fishing mortality so that the total mortality pressure on the species is increased. Perhaps most surprising of these results was that reducing the fishing mortality of the otter trawl targeting Norway lobster led to a small drop in the equilibrium TSB of Norway lobster, despite over 70% of the Norway lobster fishing mortality coming from this fleet. This highlights the fact that managing stock levels is not a simple linear trade-off between fishing and abundance and ecosystem approaches to testing management regimes are essential. FishSUMS lends itself to this sort of question by having a flexible method of defining trophic interactions based on prey/predator ratio and species specific preferences.

Another interesting result we can see from studying the mortality rates is that the predation mortality of several of our species rises after 1990: most strikingly whiting but also sandeel and Norway pout. These rises coincide with a sharp increase in grey gurnard abundance and illustrate the theory that grey gurnard is an important piscivorous predator, whose high abundance could be an important factor in falling fish populations (Floeter *et al.*, 2005), since all of the species mentioned show a falling TSB over this period to accompany the rising predation mortality.

We are able to study the fluxes, not just of predation between the structured species but also to the fishery and to density dependent mortality, as well as the fluxes from the unstructured trophic resources to the structured species. By studying changes in these fluxes we see important shifts in the fluxes to and from our key structured species. Although the fluxes between structured species, and therefore the changes

in these fluxes, are much smaller than for the fluxes to fishing and density dependent mortality, we can see important shifts. For instance, from 1977 to 1985 all of the fluxes to and from herring are increased due to the increased abundance of herring. Over both periods studied most of the fluxes to and from cod are reduced, due to an overall decrease in cod abundance, with a notable exception being the rise in the flux to grey gurnard between 1985 and 2005, which is caused by the dramatic rise in grey gurnard abundance. This rise in the grey gurnard stock, to become the most abundant of our predators by the turn of the century, means that all of the fluxes to grey gurnard rise from 1985 to 2005. FishSUMS allows us to study these changes in a way that has never been done before.

FishSUMS does not seek to model the entire food web and there are unmodelled aspects to both the bottom (where do the resources for unstructured species come from?) and top of the system (what happens to fish lost to density dependent mortality or discarded from the fishery?). In truth these two aspects will be linked with dead fish being scavenged at the bottom of the chain and the scavengers making up part of the unstructured resources in our model. However, by focussing our effort on key commercially important species, and the main species with which they interact, we can study the development of an important partial ecosystem.

In the work presented here we have used ICES assessments (ICES 2009a,2009b), along with stomach sampling projects (Daan, 1989; Hislop, 1996) and trawl survey data (http://datras.ices.dk/Home/default.aspx) to fit our model. Future work will confront FishSUMS with survey data and attempt to estimate fishing mortalities. In this way FishSUMS could provide an alternative assessment method for regions and species where there are currently no assessments.

Acknowledgements

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Appendix: Estimating annual diet percentages from the 1981 and 1991 stomach contents data

Annual mean diet percentages

For a given predator species we will assume that numbers and rates are constant on a quarterly timescale. We also assume that feeding and stomach evacuation are in balance over this same timescale, and that stomach residence time per unit weight of food depends on age (equivalent to size) and quarter (because of changes in temperature), but not on food type. These assumptions imply that the total biomass consumption rate $(U_{a,q})$ for fish of age a in quarter q is given by

$$U_{a,q} = \frac{f_{a,q} n_{a,q} W_{a,q}}{\tau_{a,q}}$$

where $f_{a,q}$ is the fraction of feeding fish, $n_{a,q}$ is the number of fish, $W_{a,q}$ is the mean weight of all prey in the stomachs of individual feeding fish, and $\tau_{a,q}$ the stomach residence time. Similarly, the biomass uptake of the ith prey taxa by fish of age a in quarter q is

$$u_{a,q,i} = \frac{f_{a,q} n_{a,q} w_{a,q,i}}{\tau_{a,q}}$$

where $w_{a,q,i}$ is the weight of prey of taxa i (in the stomachs of age a fish in quarter q).

Now the proportional contribution to the quarter-and-age-resolved diet made by taxa i is

$$\begin{aligned} \pi_{a,q,i} &= \frac{u_{a,q,i}}{U_{a,q}} \\ &= \frac{w_{a,q,i}}{W_{a,q}} \end{aligned}$$

and so

$$w_{a,q,i} = \pi_{a,q,i} W_{a,q}.$$

The proportional contribution to the diet made by taxa i over all quarters and ages is

$$\Pi_i = \frac{\sum_{a=0}^{N} \sum_{q=1}^{4} u_{a,q,i}}{\sum_{a=0}^{N} \sum_{q=1}^{4} U_{a,q}}$$

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which we can expand to give

$$\Pi_i = \frac{\sum_{a=0}^{N} \sum_{q=1}^{4} f_{a,q} n_{a,q} \pi_{a,q,i} W_{a,q}/\tau_{a,q}}{\sum_{a=0}^{N} \sum_{q=1}^{4} f_{a,q} n_{a,q} W_{a,q}/\tau_{a,q}}. \tag{1}$$

Stomach residence time

The following argument, apart from the effect of temperature, is adapted from Kooijman (1993, pp. 68–71). We assume that food intake is a saturating function of prey abundance with an asymptote that is proportional to the square of body length, and that stomach residence time is exponentially distributed. We have

$$\frac{dw_{a,q}}{dt} = \phi_q l_{a,q}^2 f_q(F) - w_{a,q}/\tau_{a,q}$$

where ϕ_q is a constant related to the search volume and which changes by quarter through the effect of temperature, $f_q(F)$ is the normalised functional response dependent on prey abundance F, and also changes with quarter through the effect of temperature on handling time, $l_{a,q}$ is the length of a fish of age a in quarter q.

If food is super-abundant $f_q(F) \to 1$ and the stomach will fill to its maximum volume, $max(v_a)$, containing a maximum weight of food, $max(w_{a,q})$, in it. This gives us a steady state at saturating prey abundance

$$\phi_q l_a^2 = max(w_{a,q})/\tau_{a,q}.$$

Adopting the standard assumption of isomorphism means that the stomach capacity, and hence $max(w_{a,q})$, will be proportional (with constant c) to the cube of the body length l_a^3. Thus we have

$$\phi_q l_{a,q}^2 = c l_{a,q}^3/\tau_{a,q}$$

and so

$$\tau_{a,q} = \Omega_q l_{a,q}$$

where $\Omega_q \equiv c/\phi_q$. In other words, for a given quarter (*i.e.* temperature) the stomach residence time is proportional to body length.

For the temperature dependence, we assume that stomach residence time changes exponentially with the

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mean quarterly temperature (T_q) so that

$$\Omega_q = \theta \exp(-T_q/T_c)$$

where θ is a constant and T_c is a characteristic temperature determining the sensitivity of the temperature response. So, we can now write

$$\tau_{a,q} = \theta l_{a,q} \exp(-T_q/T_c).$$

We note that the Q_{10} associated with the stomach residence time is by definition the ratio of the evacuation rates (*i.e.* $1/\tau_{a,q}$) $10°$ C apart. Thus

$$Q_{10} = \frac{e^{-(T_q+10)/T_c}/(\theta l_{a,q})}{e^{-T_q/T_c}/(\theta l_a)}$$

and so

$$Q_{10} = e^{10/T_c}.$$

So we can write the stomach residence time as

$$\tau_{a,q} = \theta l_{a,q} Q_{10}^{(-T_q/10)}.$$

Substituting for $\tau_{a,q}$ in equation 1 the parameter θ cancels out and we get

$$\Pi_i = \frac{\sum_{a=0}^{N} \sum_{q=1}^{4} f_{a,q} n_{a,q} \pi_{a,q,i} W_{a,q}/l_{a,q} Q_{10}^{(-T_q/10)}}{\sum_{a=0}^{N} \sum_{q=1}^{4} f_{a,q} n_{a,q} W_{a,q}/l_{a,q} Q_{10}^{(-T_q/10)}}. \tag{2}$$

So, to obtain this from data we need the fraction of feeding fish $(f_{a,q})$, the number of fish $(n_{a,q})$, the biomass fraction of prey taxon i in the diet $(\pi_{a,q,i})$, the mean length of fish (l_a), the Q_{10} for gut evacuation rate, the mean temperature in each quarter (T_q), and the mean total stomach content weight $(W_{a,q})$.

The 1991 stomach contents data

The report by Hislop *et al.* (1996) (*e.g.* Table 8-A-1, p.93) gives us, among other things, the "% empty stomachs", and the "Total weight all prey", and the "Weight % by major taxa" by quarter and age-class. Although not explicitly defined, it seems safe to assume, given the numerical values, that the "Total weight all prey" refers to a mean weight of the total stomach contents over all prey. This, however, could be a mean over all fish or a mean over feeding fish (*i.e.* non-empty stomachs). The former seems more likely given their

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equation 1 (page 5)

$$W_S = \frac{W_{TOT}}{N_F} \cdot \frac{N_F + N_{SR} + N_R}{N} \tag{3}$$

where

$$
\begin{aligned}
W_S \quad &= \quad \text{average weight of stomach contents} \\
&\qquad \text{in a haul (sample)} \\
W_{TOT} \quad &= \quad \text{weight of prey in all stomachs sampled} \\
N \quad &= \quad \text{number of stomachs sampled} \\
&\qquad (= \text{sample size}) \\
N_F \quad &= \quad \text{number of feeding (valid) stomachs} \\
N_{SR} \quad &= \quad \text{number of stomachs containing only} \\
&\qquad \text{skeletal remains} \\
N_R \quad &= \quad \text{number of feeding (regurgitated)} \\
&\qquad \text{stomachs.}
\end{aligned}
$$

Re-writing this as

$$W_S = \frac{\left(\frac{W_{TOT}}{N_F}\right)(N_F + N_{SR} + N_R)}{N}$$

makes it clear that equation 3 yields that average stomach contents weight for all fish, including the non-feeding ones, since it is the product of the mean weight of valid stomachs (W_{TOT}/N_F), times the number of feeding fish ($N_F + N_{SR} + N_R$) (giving the total stomach contents weight across all fish) divided by the total number of fish N. This suggests that the "Total weight all prey" in the tables is indeed that average weight of the total prey over all fish.

We now have nearly all the information we need,

$$
\begin{aligned}
f_{a,q} \times W_{a,q} \quad &\equiv \quad W_S \\
\pi_{a,q,i} \quad &\equiv \quad \text{Weight \% by major taxa.}
\end{aligned}
$$

Numbers at age

For the numbers at age $(n_{a,q})$ we have annual estimates for our five predator species in the ICES reports, corresponding to the numbers in the first quarter $(n_{a,1})$. If $N_{a,y}$ is the ICES assessed number of age a fish in year y, and we assume that mortality is constant over the year we can estimate the mean quarterly abundances from

$$n_{a,q} = N_{a,y}e^{-\mu(q-1)/4}(1 - e^{-\mu/4})/(\mu/4)$$

where

$$\mu = \ln(N_{a,y}/N_{a+1,y+1}).$$

Length at age

We calculate mean length at age in a given quarter $(l_{a,q})$ by integrating the von Bertalanffy growth curve for each species to give

$$l_{a,q} = l_\infty - \frac{l_\infty - l_0}{(\gamma/4)}e^{-\gamma(a+q/4)}(1 - e^{\gamma/4}),$$

where l_∞ is the asymptotic length, l_0 is the hatchling length and γ is the von Bertalanffy growth rate.

Temperature dependence

Typical values for the Q_{10} for gastric evacuation in fish seems to be in the range 2–3 (Bromley, 1994, and references therein), so a value of 2.5 would seem reasonable in the absence of more specific information. Daan *et al* (1989) give North Sea temperatures as 6°C in quarter 1, 7°C in quarter 2, 10°C in quarter 3, and 8°C in quarter 4.

The 1981 stomach contents data

The report by Daan *et al* (1989) contains the same information about the diets of cod, haddock and whiting in 1981 as we have considered for 1991. For saithe the 1981 diet data differs in two ways. Firstly the data are grouped by winter (Q1 and Q4) and summer (Q2 and Q3) half years because of low sampling at some times of the year. This means that the relevant W_s and $\pi_{a,q,i}$ values are each assigned to two quarters, with separate numbers at age, and temperature (as described above) used for each quarter. Secondly the saithe are grouped by length, rather than age, with the length classes being 250, 300, 400, 500, 700 and 1000. No definition is given for these but it seems reasonable to assume they are lengths in millimetres. We assume that these are the lower end of the length class and use the following average lengths (cm) for each

575 class in (2): 27.5, 35, 45, 60, 85, 110. To attribute the mean stomach contents for each length class to the

576 appropriate numbers of fish we assign each class to an age as shown in Table 7.

Calculating confidence intervals for the stomach contents data

578 To calculate the annual mean diet percentages (Π_i) we make use of the average total weight of prey in the

579 stomach by age and quarter ($f_{a,q} \times W_{a,q}$) and the weight percentages of stomach contents ($\pi_{a,q,i}$) from the

580 stomach sampling data. In addition we calculate the numbers at age and quarter ($n_{a,q}$) and length at age

581 and quarter ($l_{a,q}$). To calculate the standard deviation in these percentages we also need to make use of the

582 average number of prey items ($p_{a,q}$) and the average weight per prey item ($v_{a,q}$).

583 To calculate the variability in the diet percentages we assume that predators encounter and consume

584 prey as a Poisson process, with the mean rate $\pi_{a,q,i}$ and that all items of prey leave the stomach after a

585 fixed period of time, $\tau_{a,q}$ (the stomach residence time considered when calculating the mean of the stomach

586 contents). The variance in the rate of a Poisson process is equal to the mean and we use the delta method

587 (Powell, 2007) to estimate the variability of our diet percentages.

The delta method allows us to approximate the variance of a function of a random variable from the
variance of that random variable. The variance can be calculated as

$$var(G) \approx \sum_{i=1}^{n} var(X_i) \left[\frac{\partial f}{\partial X_i} \right]^2 .$$

For our purposes the f we are interested in is Π_i and our X_i are the $p_{a,q}$ that come from the data. To make the
differentiation of Π_i easier to follow we will consider that $\Pi_i = A/B$, with $A = \sum_{a=0}^{N} \sum_{q=1}^{4} p_{a,q} v_{a,q} n_{a,q} \pi_{a,q,i} / l_{a,q} Q_{10}^{(-T_q/10)}$
and $B = \sum_{a=0}^{N} \sum_{q=1}^{4} p_{a,q} v_{a,q} n_{a,q} / l_{a,q} Q_{10}^{(-T_q/10)}$. We will differentiate by the quotient rule so we note that
$\Pi_i' = (A'B - AB')/B^2$. Differentiating (2) with respect to $p_{a,q}$ we have

$$\frac{\partial \Pi_i}{\partial p_{a,q}} = \frac{(n_{a,q} v_{a,q} / l_{a,q} Q_{10}^{(-T_q/10)})(\pi_{a,q,i} B - A)}{B^2} .$$

Applying the delta method we find

$$var(\Pi_i) \approx \sum_{a=0}^{N} \sum_{q=1}^{4} p_{a,q} \left(\frac{(n_{a,q} v_{a,q} / l_{a,q} Q_{10}^{-Tq/10})^2 (\pi_{a,q,i} B - A)^2}{B^4} \right) .$$

588 We find the standard deviation of Π_i, which is what is used as the confidence interval in our plots, as

589 $s(\Pi_i) = \sqrt{var(\Pi_i)}$.

1991 grey gurnard diets

The report by Hislop (1996) also features information on the diet of grey gurnard in 1991. Like the saithe data in 1981 this data is in terms of length classes of predator, rather than age. The length classes used are 100, 120, 150, 200, 250, 300, 350 and 400, which we take to be lengths in millimetres. Since grey gurnard is not an assessed species we do not have assessed values for numbers at age. Instead we use the values of catch-per-unit-effort (CPUE) from the North Sea International Bottom Trawl Survey as a substitute for numbers at length.

As before we calculate the stomach contents percentages from (2), though here a denotes length classes, rather than age classes. We are missing the $n_{a,q}$, the numbers of fish in each class. Instead we consider $n_{a,q} = \nu_q \eta_{a,q}$, where ν_q is the total average number of grey gurnard during the quarter and $\eta_{a,q}$ is the proportion that are in a given length class. We now assume that in all quarters the CPUE, $\kappa_{a,q}$, is a fixed fraction p of ν_q, so that $\kappa_{a,q} = p\nu_q$. Substituting for $n_{a,q} = \eta_q \kappa_{a,q}/p$ in (2) our p's cancel and we have

$$\Pi_i = \frac{\sum_{a=0}^{N} \sum_{q=1}^{4} f_{a,q} \kappa_{a,q} \eta_{a,q} \pi_{a,q,i} W_{a,q}/l_{a,q} Q_{10}^{(-T_q/10)}}{\sum_{a=0}^{N} \sum_{q=1}^{4} f_{a,q} \kappa_{a,q} \eta_{a,q} W_{a,q}/l_{a,q} Q_{10}^{(-T_q/10)}}.$$

Confidence intervals for grey gurnard stomach contents

The data for grey gurnard stomach contents in 1991 is in a different form to that for the other predators. The information we have here is the total average weight of stomach contents, the average proportions that are different prey, and the number of stomachs sampled, for several length classes of predator. Since we do not know the average numbers of prey items we are forced to make different assumptions about the variability. We assume that the proportions of stomach contents ($\pi_{a,q,i}$) are binomially distributed, such that they represent the probability that an item of stomach contents is the given prey.

The standard error can be calculated by $SE = \sqrt{p(1-p)/n}$, where p is the proportion of the diet that is the chosen prey and n is the number of predator stomachs sampled. An alternative formulation of standard error is $SE = s/\sqrt{n}$, where s is the sample standard deviation. Setting these two forms to be equal we can rearrange to estimate the standard deviation, $s = \sqrt{p(1-p)}$, and therefore the sample variance is $var(\pi_{a,q,i}) = p(1-p)$. We once again use the delta method to approximate $var(\Pi_i)$. In this case we differentiate Π_i with respect to $\pi_{a,q,i}$,

$$\frac{\partial \Pi_i}{\partial \pi_{a,q,i}} = \frac{f_{a,q} \kappa_{a,q} \eta_{a,q}/l_{a,q} Q_{10}^{-T_q/10}}{\sum_{a=0}^{N} \sum_{q=1}^{4} f_{a,q} \kappa_{a,q} \eta_{a,q}/l_{a,q} Q_{10}^{-T_q/10}},$$

and applying the delta method we find

$$var(\Pi_i) \approx \sum_{a=0}^{N} \sum_{q=1}^{4} \pi_{a,q,i}(1 - \pi_{a,q,i}) \left(\frac{f_{a,q}\kappa_{a,q}\eta_{a,q}W_{a,q}/l_{a,q}Q_{10}^{-T_q/10}}{\sum_{a=0}^{N} \sum_{q=1}^{4} f_{a,q}\kappa_{a,q}\eta_{a,q}W_{a,q}/l_{a,q}Q_{10}^{-T_q/10}} \right)^2.$$

In most cases, as before, our error bars are the standard deviation of Π_i, which we find from $s(\Pi_i) = \sqrt{var(\Pi_i)}$. However, for the proportions of the diet that are whiting and dab the standard deviation calculated is greater than the mean, so we truncate the lower error bar at 0.

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Table 1: Species-specic model parameter values for the piscivorous length-structured species.

Description	Symbol	Units	Cod	Haddock	Whiting	Saithe	Grey gurnard
No. length class	jmax	-	140	70	70	70	90
Egg dev. time	τ_e	d	11	15	15	9	7
Hatchling length	L_0	cm	0.3	0.5	0.5	0.35	0.35
Settlement length	L_s	cm	7	5	5	6.5	5
Mean maturation length	L_m	cm	60	27	22	55	29
S.d. maturation length	s_m	cm	11	8	8	8	1
Max. modelled length	L_{max}	cm	110.7	58.5	40.85	72	42.75
Asymptotic length	L_∞	cm	123	65	43	80	45
Growth rate	γ	y^{-1}	4.25×10^{-4}	8×10^{-4}	0.0013	8.22×10^{-4}	8×10^{-4}
Fecundity	ρ	eggs g^{-1}	500	500	880	750	3000
Spawning start	S_0	day of yr.	90	75	0	1	150
Spawning end	S_1	day of yr.	120	105	120	120	240
Effective land size	L_l	cm	45	34 (28 pre-1989)	35	35	35
Density-independent mortality rates							
Egg	m_e	d^{-1}	0.74 (0.8 pre-1970)	0.67	0.014	0.16	0.073
Pre-settlement	m_p	d^{-1}	0.74 (0.8 pre-1970)	0.67	0.014	0.16	0.073
Post-settlement	m_s	d^{-1}	7.0×10^{-6}	0.0024	5×10^{-7}	2×10^{-4}	0.001
Biomass-dependent mortality							
Pre-settlement	δ_p	g^{-1} m^2 d^{-1}	0.001 (0.068 pre-1970)	5×10^{-4}	1.6	0.006	5×10^{-8}
Post-settlement	δ_s	g^{-1} m^2 d^{-1}	5×10^{-4}	0.0015	1×10^{-5}	4.5×10^{-4}	0.0015
Assimilation efficiency	ϵ	-	0.6	0.6	0.6	0.6	0.6
Metabolic cost	η	d^{-1}	0.001	0.001	0.001	0.001	0.001
Weight at length const.	a	g cm^{-b}	0.0104	0.0052	0.0098	0.0104	0.0054
Weight at length power	b	-	3.0	3.155	2.926	2.972	3.13
Preferred prey/pred ratio	Φ_{opt}	-	0.3	0.1	0.2	0.3	0.35
Min. prey/pred ratio	Φ_{min}	-	0.04	0.005	0.01	0.04	0.01
Max. prey/pred ratio	Φ_{max}	-	0.4	0.4	0.5	0.4	0.4
Pref. function tightness	β	-	1.1	1.1	1.06	1.1	5

Table 2: Species-specic model parameter values for the benthivorous and planktivorous length-structured species.

Description	Symbol	Units	Dab	Plaice	Norway lobster	Sandeel	Herring	Norway pout
No. length class	jmax	-	45	60	50	40	80	65
Egg dev. time	τ_e	d	7	24	1	90	7	7
Hatchling length	L_0	cm	0.25	0.625	0.7	0.5	0.8	0.8
Settlement length	L_s	cm	1	45	1	4	6	1
Mean maturation length	L_m	cm	24.5	30	9	14	22	14.5
S.d. maturation length	s_m	cm	2	6	1	1.5	1.5	2
Max. modelled length	L_{max}	cm	38	42.75	18	19	28.71	18.315
Asymptotic length	L_∞	cm	40	45	20	20	29	18.5
Growth rate	γ	y^{-1}	0.0016	9.59×10^{-4}	4.38×10^{-4}	0.00238	0.00145	0.0027
Fecundity	ρ	eggs g^{-1}	1000	800	100	783	400	980
Spawning start	S_0	day of yr.	60	30	90	0	330	60
Spawning end	S_1	day of yr.	150	120	180	30	360	120
Effective land size	L_l	cm	30	27	8.5	10	20	8
Density-independent mortality rates								
Egg	m_e	d^{-1}	0.15	0.28	0	0.009	0.05 (0.06 post 2002)	0.1
Pre-settlement	m_p	d^{-1}	0.15	0.28	0.16	0.06	0.05 (0.06 post 2002)	0.1
Post-settlement	m_s	d^{-1}	0.008	3.5×10^{-6}	1×10^{-5}	1×10^{-5}	8×10^{-4}	4×10^{-6}
Biomass-dependent mortality								
Pre-settlement	δ_p	g^{-1} m^2 d^{-1}	5×10^{-5}	8.5	0.5	5×10^{-6}	7×10^{-4}	3
Post-settlement	δ_s	g^{-1} m^2 d^{-1}	5×10^{-4}	1×10^{-4}	0.008	0.001	2.3×10^{-4}	0.002
Assimilation efficiency	ϵ	-	0.6	0.6	0.6	0.6	0.6	0.6
Metabolic cost	η	d^{-1}	0.001	0.001	0.001	0.001	0.001	0.001
Weight at length const.	a	g cm^{-b}	0.005	0.009	0.090450	0.0015	0.006	0.0068
Weight at length power	b	-	3.14	3.031	2.91	3.169	3.09	3
Preferred prey/pred ratio	Φ_{opt}	-	0.1	0.1	0.03	0.03	0.03	0.03
Min. prey/pred ratio	Φ_{min}	-	0.01	0.01	0.01	0.01	0.01	0.01
Max. prey/pred ratio	Φ_{max}	-	0.2	0.2	0.3	0.1	0.1	0.1
Pref. function tightness	β	-	10	10	10	10	10	10

Table 3: Diet preferences. Herring predation is on eggs and larvae of the prey species.

Predator	Cod	Haddock	Whiting	Saithe	Grey gurnard	
Prey						
Cod	5	-	2	-	0.002	
Haddock	2		7	1	0.00005	
Whiting	5	-	3.5	1	0.015	
Saithe	-	-	-	-	-	
Grey gurnard	-	-	-	-	-	
Dab	0.5	-	-	-	0.00015	
Plaice	-	-	-	-	-	
Norway lobster	0.8	-	-	-	-	
Sandeel	0.2	8	0.5	0.125	0.002	
Herring	0.4	0.15	1	0.8	-	
Norway pout	0.7	12	1	3	0.0005	
Zooplankton	-	-	-	-	-	
Benthos	0.15	0.4	0.01	0.25	20	
Other fish	0.1	1	0.03	0.12	0.0008	

Predator	Dab	Plaice	Norway lobster	Sandeel	Herring	Norway pout
Prey						
Cod	-	-	-	-	6	-
Haddock	-	-	-	-	2	-
Whiting	-	-	-	-	1	-
Saithe	-	-	-	-	-	-
Grey gurnard	-	-	-	-	0.8	-
Dab	-	-	-	-	1	-
Plaice	-	-	-	-	-	-
Norway lobster	-	-	-	-	-	-
Sandeel	-	-	-	-	-	-
Herring	-	-	-	-	1	-
Norway pout	-	-	-	-	15	-
Zooplankton	-	-	-	1	1	1
Benthos	1	1	1	-	-	-
Other fish	-	-	-	-	-	-

Table 4: Catchability parameters used in (2).

species	l_h	ω	γ
cod	18	5	1
haddock	42.5	15.5	1
whiting	20	5	1
saithe	40	10	1
grey gurnard	15	1	1
dab	10	2	1
plaice	24	6	1
Norway lobster	34	7	1
sandeel	17	2.5	1
herring	10	5	1
Norway pout	12	5	1

Table 5: Proportion of fishing mortality that comes from beam trawl (BT); otter trawl targeting fish (OTF); otter trawl targeting Norway lobster (OTN); and seine gear (SG).

species	BT	OTF	OTN	SG
cod	0.1041	0.6736	0.1066	0.1157
haddock	0.0047	0.7125	0.0320	0.2508
whiting	0.0683	0.6490	0.1094	0.1734
saithe	0.0002	0.9857	0.0021	0.0120
plaice	0.7926	0.1373	0.0542	0.0159
Norway lobster	0.0060	0.2728	0.7191	0.0020
grey gurnard	0.0683	0.6490	0.1094	0.1734
dab	0.1041	0.6736	0.1066	0.1157

Table 6: Percentage changes of equilibrium TSB of all species of reducing by 10% the fishing by beam trawl (BT); otter trawl targeting fish (OTF); otter trawl targeting Norway lobster (OTN); and seine gear (SG).

species	BT -10%	OTF -10%	OTN -10%	SG -10%
cod	+4.45	+30.8	+3.60	+4.08
haddock	-0.331	-1.71	-0.180	-6.34×10^{-3}
whiting	-0.372	-2.09	-0.174	-0.129
saithe	$+6.08 \times 10^{-4}$	+3.00	$+6.38 \times 10^{-3}$	+0.0365
grey gurnard	+0.0477	+0.405	0.0287	+0.0403
dab	+0.599	+3.92	+0.636	+0.688
plaice	+3.64	+0.630	+0.249	+0.0729
Norway lobster	-0.986	-6.30	-0.506	-0.771
sandeel	-0.459	-3.49	-0.152	-0.264
herring	-0.307	-2.66	-0.111	-0.152
Norway pout	-19.6	-71.4	-7.66	-23.1

Table 7: Assignment of length to age for 1981 saithe stomach contents data.

length class	250	300	400	500	700	1000
ages	1	2	3	4,5	6,7,8,9	10+

Fig. 1 - Time series of modelled (lines) and observed (bars) total stock biomass (TSB) of each of the length structured species in the model

Fig. 2 - Time series of modelled (lines) and observed (bars) spawning stock biomass (SSB) for the ICES assessed fish species

Fig. 3 - Time series of modelled (lines) and observed (bars) recruitment for the ICES assessed fish species

Fig. 4 - Time series of modelled (lines) and observed (bars) landings of each of the length structured species in the model

Fig. 5 - Modelled (lines) and observed (bars) length distributions for selected length structured species in the model. Distributions are from the first quarter of 1991.

Fig. 6 - Modelled and observed diet of cod (% by wet weight). Observed values (points with error bars of $\pm s$) are from 1981 and 1991 year of the stomach projects.

Fig. 7 - Modelled and observed diet of haddock (% by wet weight). Observed values (points with error bars of $\pm s$) are from 1981 and 1991 year of the stomach projects

Fig. 8 - Modelled and observed diet of whiting (% by wet weight). Observed values (points with error bars of $\pm s$) are from 1981 and 1991 year of the stomach projects

Fig. 9 - Modelled and observed diet of saithe (% by wet weight). Observed values (points with error bars of $\pm s$) are from 1981 and 1991 year of the stomach projects

Fig. 10 - Modelled and observed diet of grey gurnard (% by wet weight). Observed values (points with error bars of $\pm s$) are from 1991 year of the stomach project

Fig. 11 - Modelled mean mortality rates (proportion per timestep τ) of settled, immature fish in quarter 1

Fig. 12 - Modelled mean mortality rates (proportion per timestep τ) of mature fish in quarter 1

Fig. 13 - Changes between 1977 and 1985 modelled flux of biomass of unstructured species to predation by structured species: thickness of lines are proportional to log($50\times$ change of flux). Black lines indicate positive change and grey lines indicate negative change

Fig. 14 - Changes between 1977 and 1985 of modelled flux of biomass of structured species to predation, density dependent (DD) mortality and fishing: thickness of lines are proportional to log($500\times$ change of flux). Black lines indicate positive change and grey lines indicate negative change

Fig. 15 - Changes between 1985 and 2005 modelled flux of biomass of unstructured species to predation by structured species: thickness of lines are proportional to log($50\times$ change of flux). Black lines indicate positive change and grey lines indicate negative change

Fig. 16 - Changes between 1985 and 2005 of modelled flux of biomass of structured species to predation, density dependent (DD) mortality and fishing: thickness of lines are proportional to log($500\times$ change of

flux). Black lines indicate positive change and grey lines indicate negative change
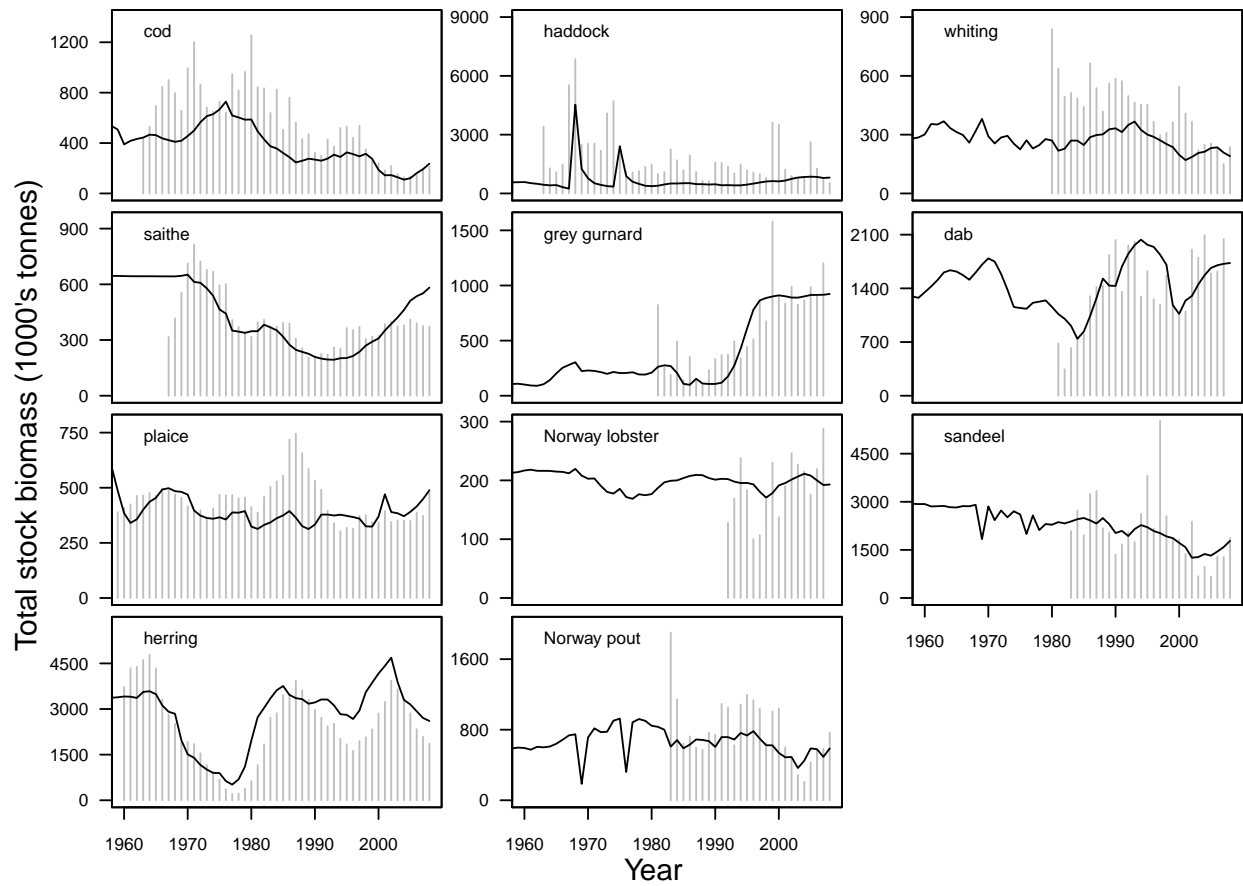
Figure 1: Time series of modelled (lines) and observed (bars) total stock biomass (TSB) of each of the length structured species in the model
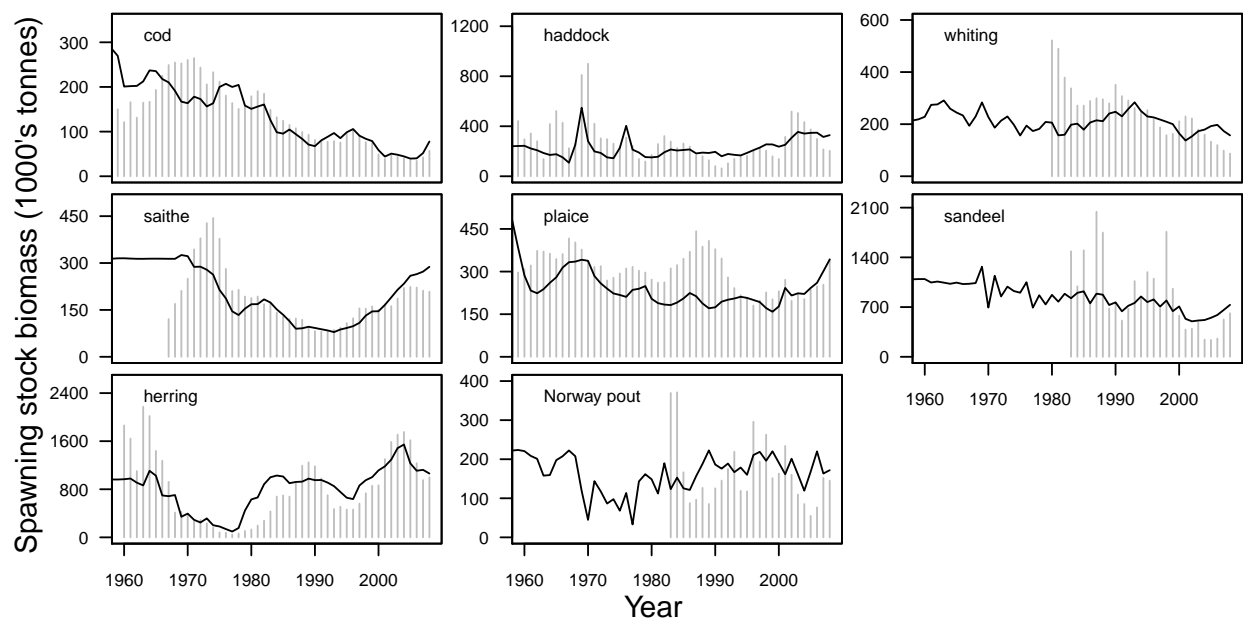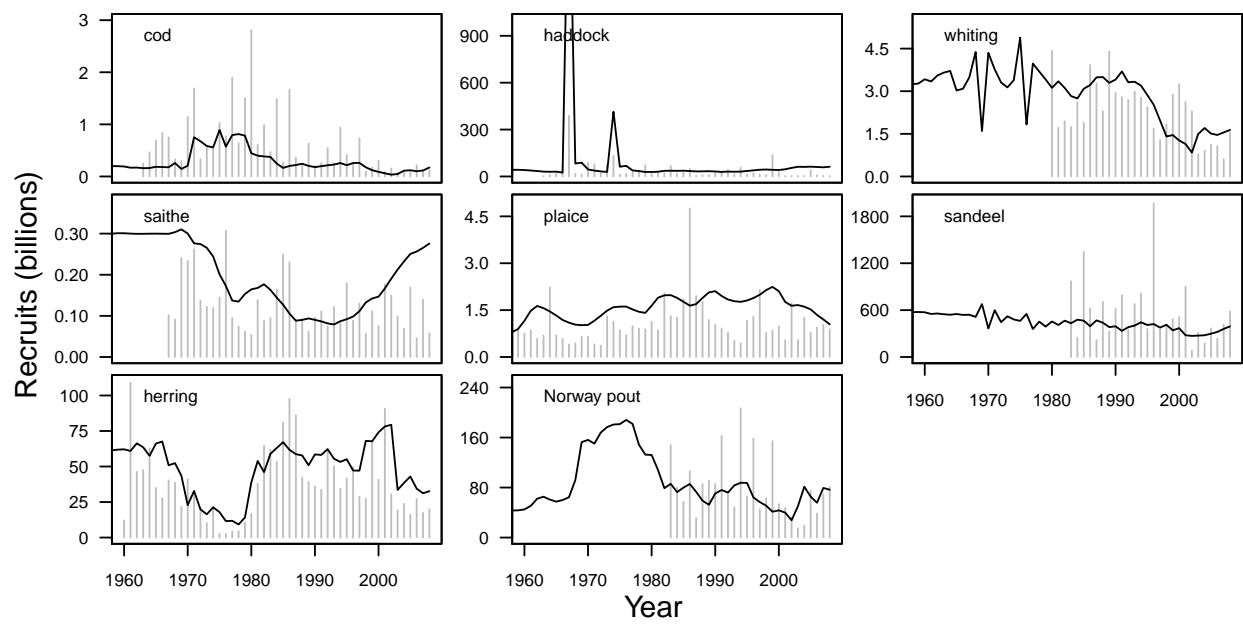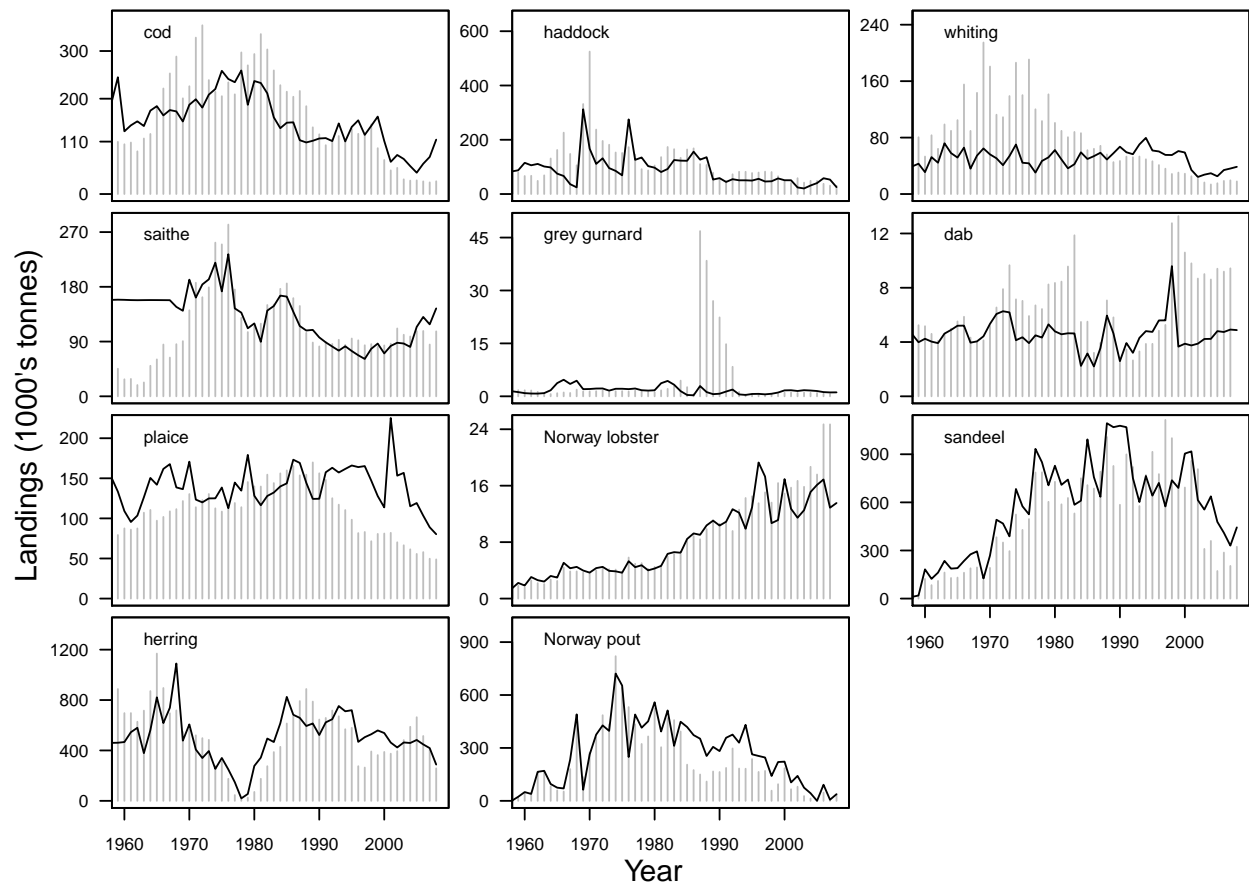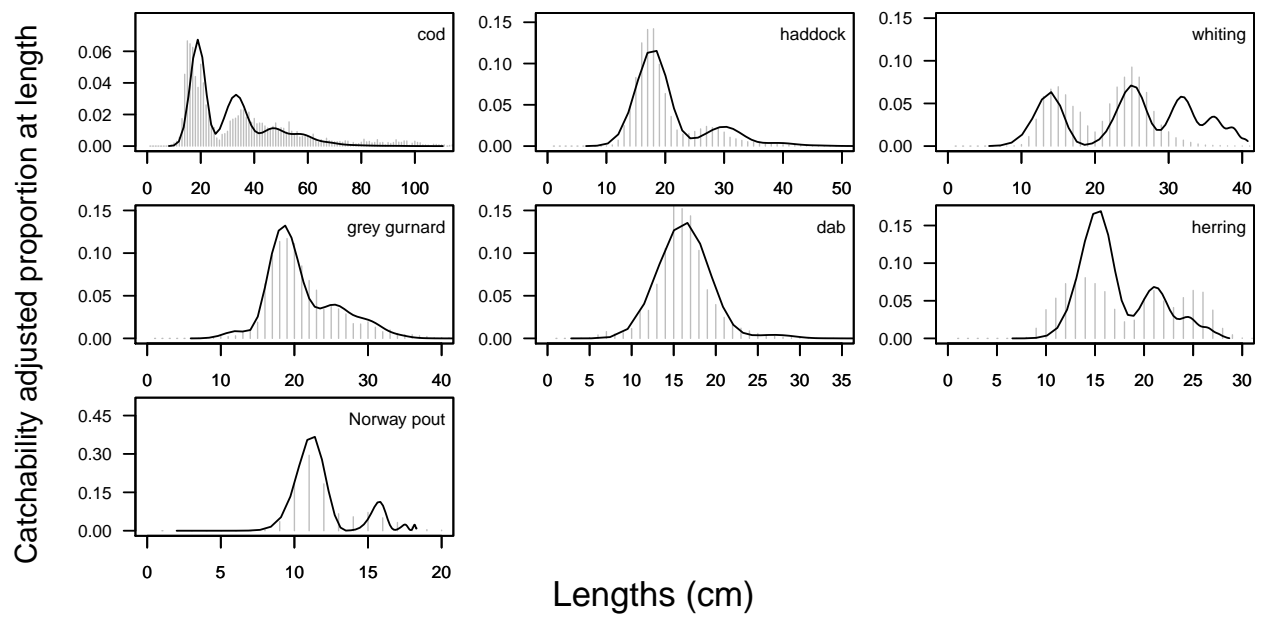
Figure 2: Time series of modelled (lines) and observed (bars) spawning stock biomass (SSB) for the ICES assessed fish species

Figure 3: Time series of modelled (lines) and observed (bars) recruitment for the ICES assessed fish species

Figure 4: Time series of modelled (lines) and observed (bars) landings of each of the length structured species in the model

Figure 5: Modelled (lines) and observed (bars) length distributions for selected length structured species in the model. Distributions are from the first quarter of 1991.
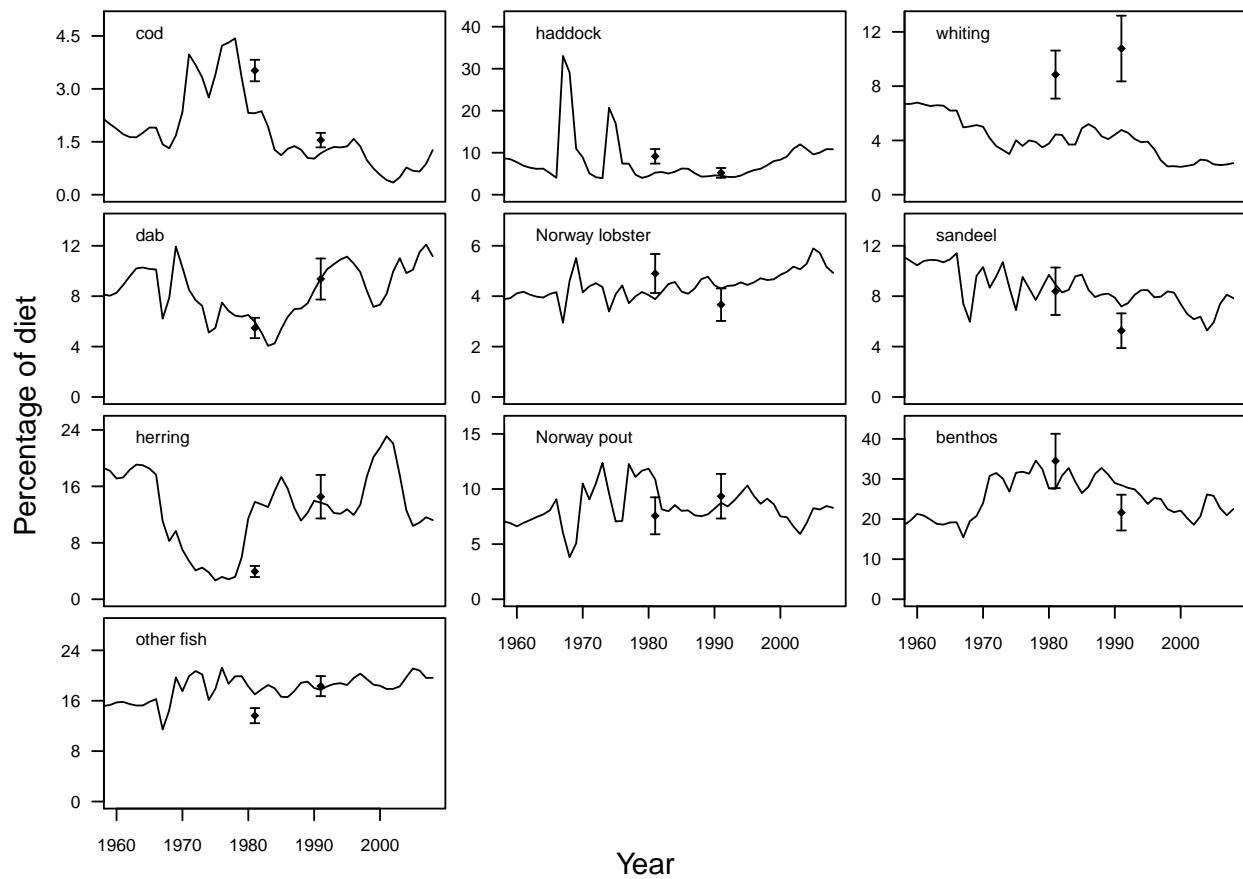
Figure 6: Modelled and observed diet of cod (% by wet weight). Observed values (points with error bars of $\pm s$) are from 1981 and 1991 year of the stomach projects.
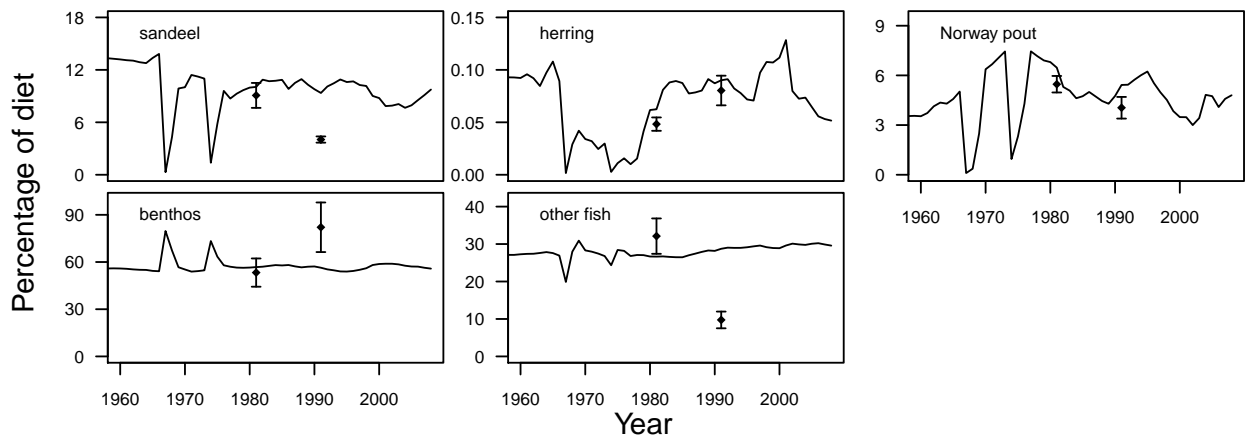
Figure 7: Modelled and observed diet of haddock (% by wet weight). Observed values (points with error bars of $\pm s$) are from 1981 and 1991 year of the stomach projects.
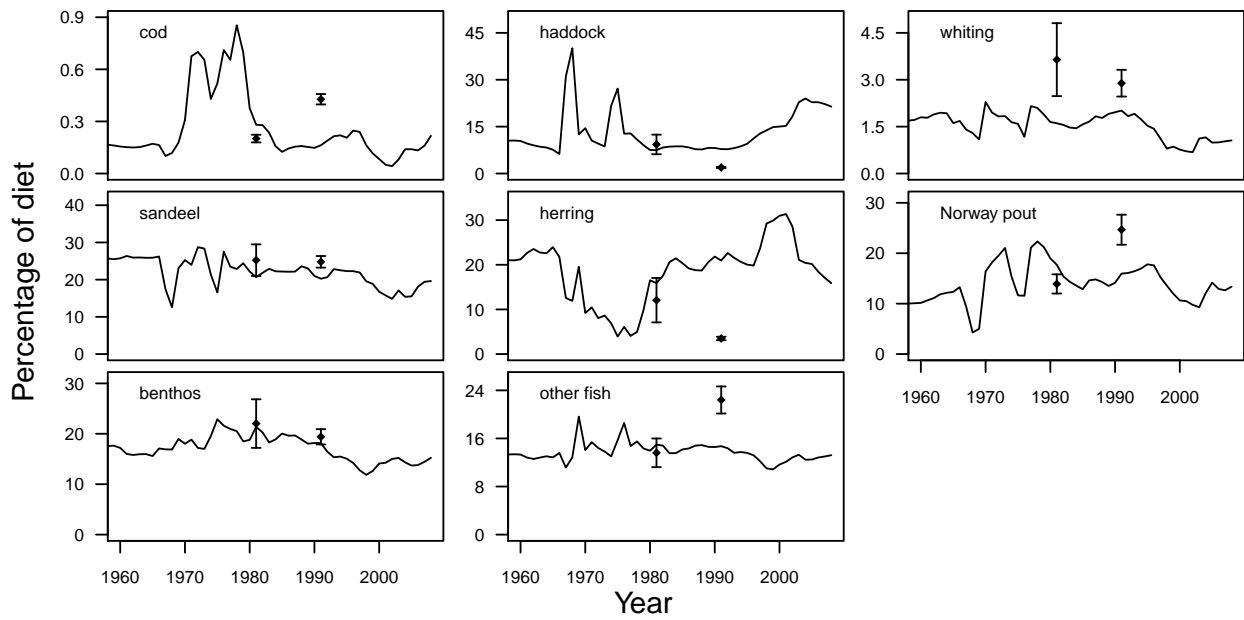
Figure 8: Modelled and observed diet of whiting (% by wet weight). Observed values (points with error bars of $\pm s$) are from 1981 and 1991 year of the stomach projects.
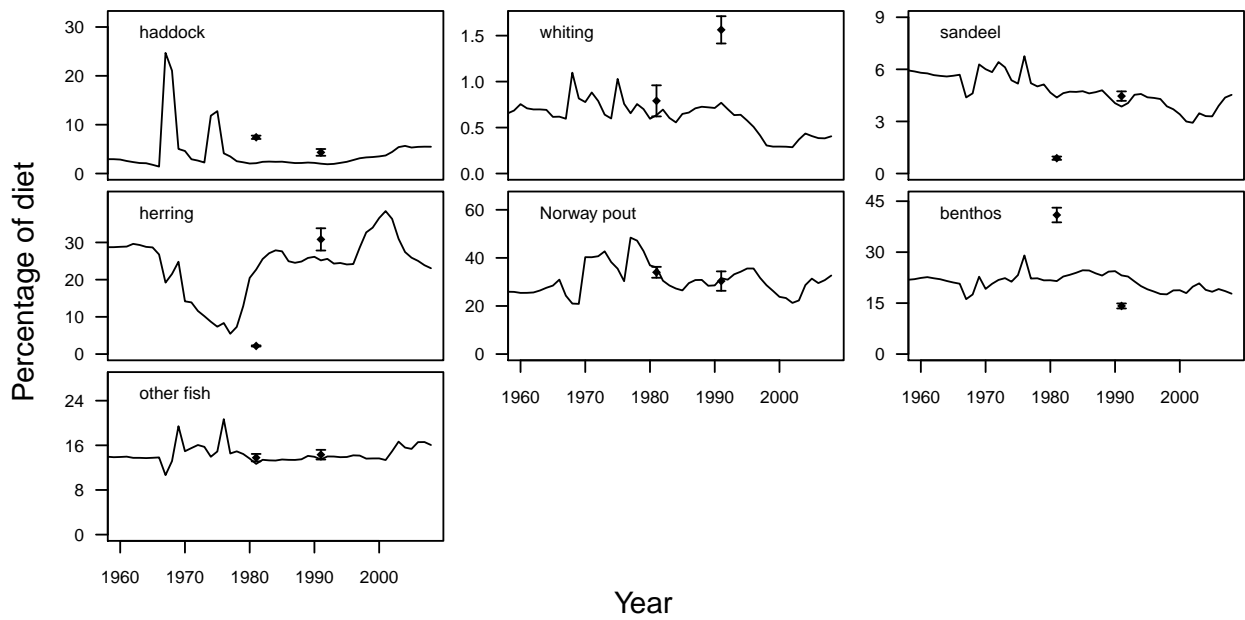
Figure 9: Modelled and observed diet of saithe (% by wet weight). Observed values (points with error bars of $\pm s$) are from 1981 and 1991 year of the stomach projects.
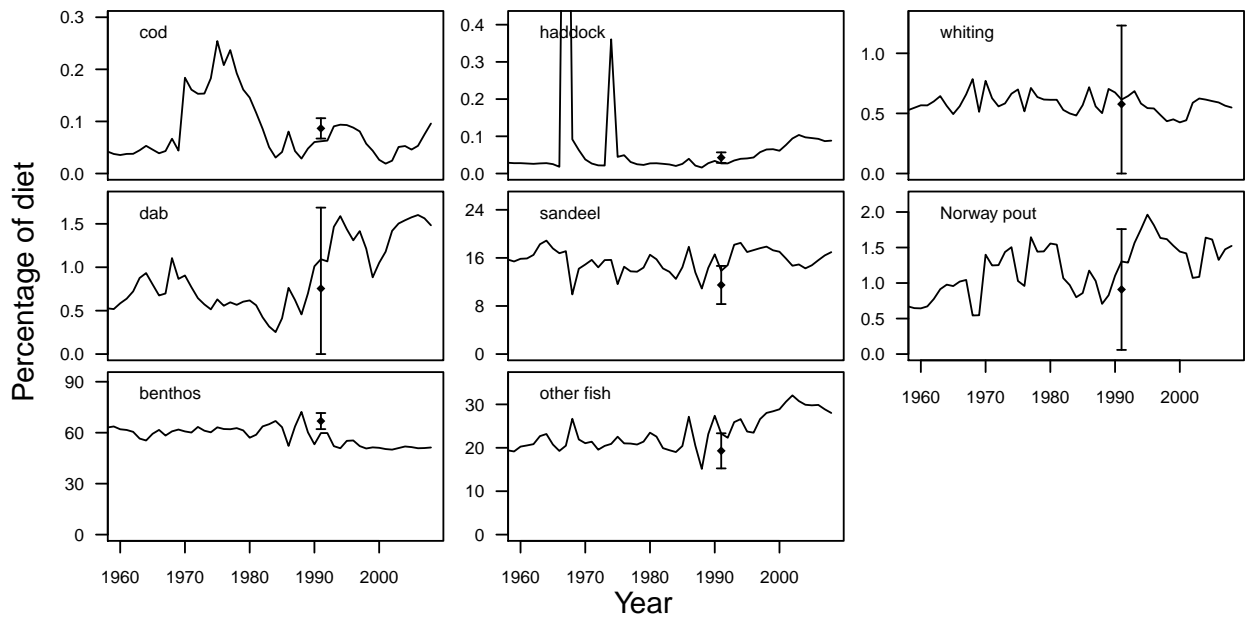
Figure 10: Modelled and observed diet of grey gurnard (% by wet weight). Observed values (points with error bars of $\pm s$) are from 1991 year of the stomach project.
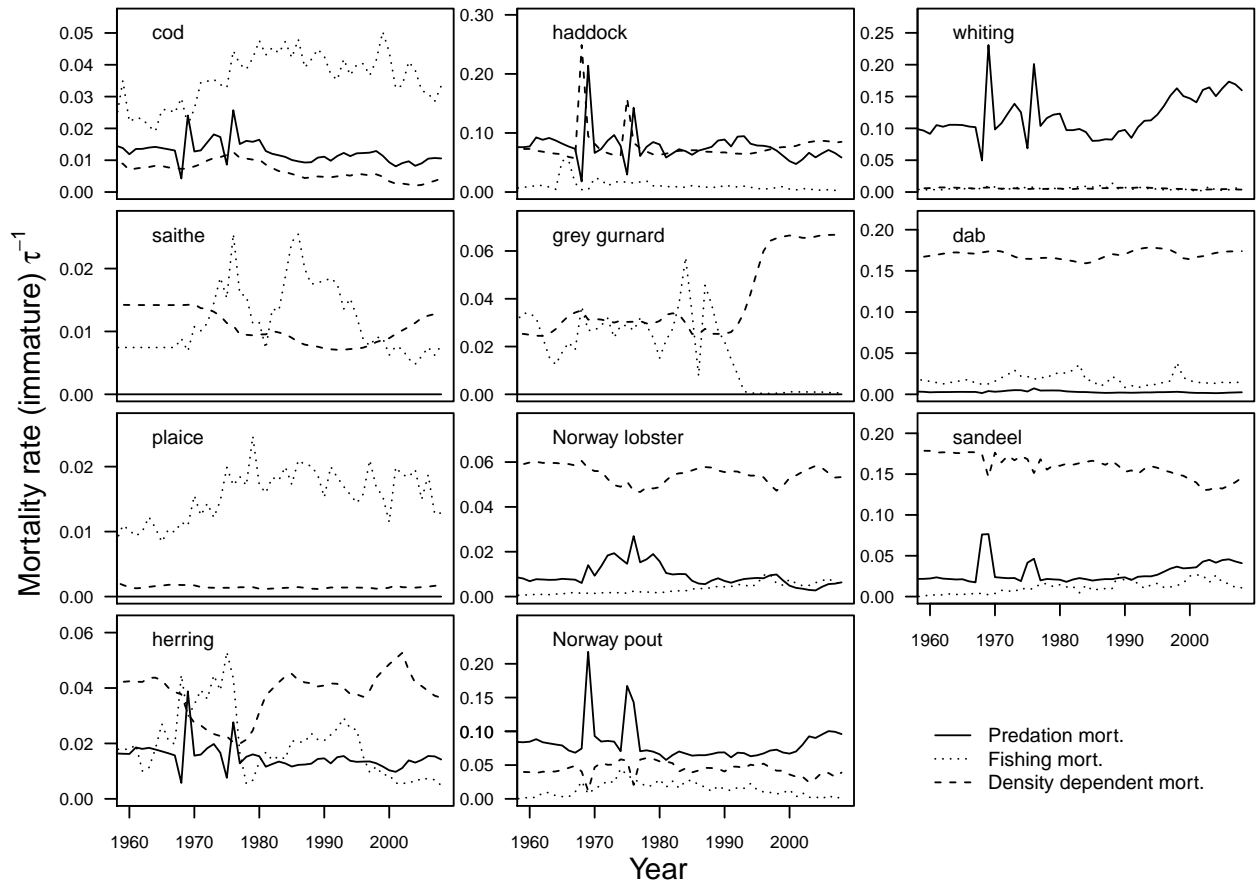
Figure 11: Modelled mean mortality rates (proportion per timestep τ) of settled, immature fish in quarter 1.
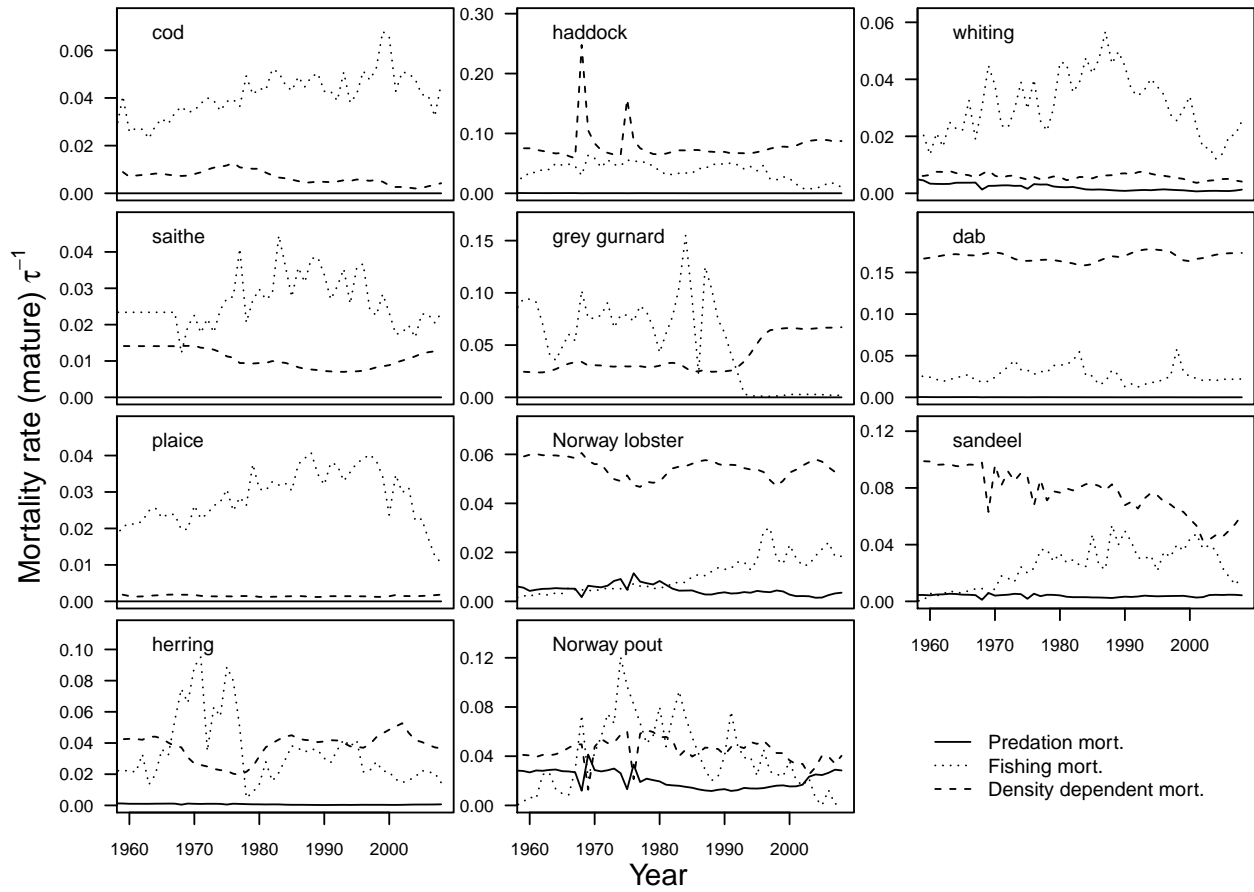
Figure 12: Modelled mean mortality rates (proportion per timestep τ) of mature fish in quarter 1.
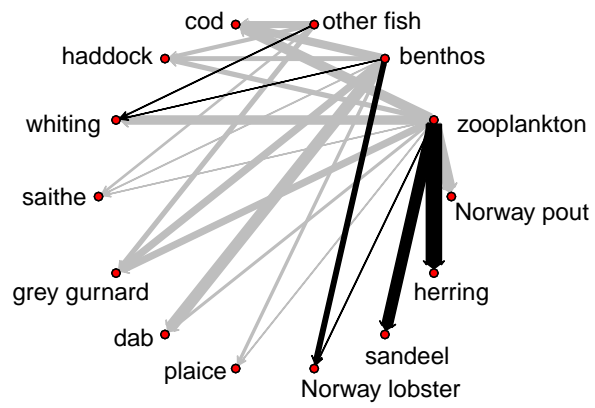
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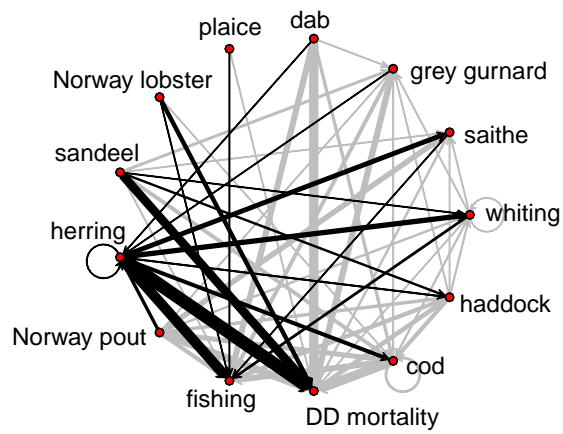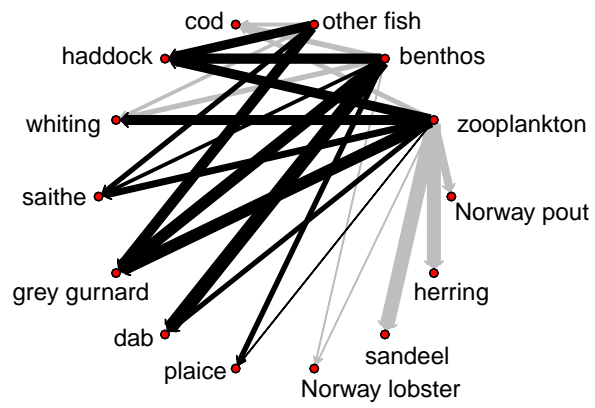
Figure 14: Changes between 1977 and 1985 of modelled flux of biomass of structured species to predation, density dependent (DD) mortality and fishing: thickness of lines are proportional to log(500× change of flux). Black lines indicate positive change and grey lines indicate negative change.

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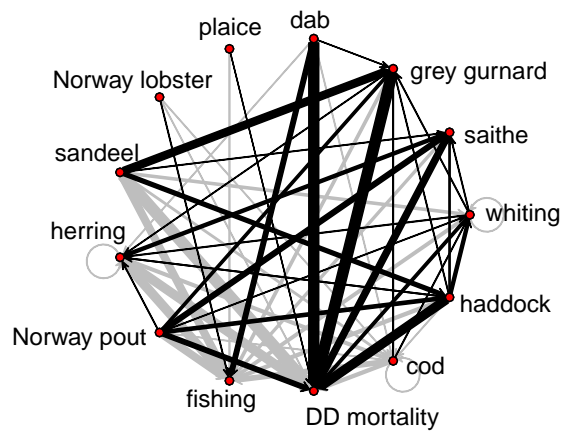
Figure 16: Changes between 1985 and 2005 of modelled flux of biomass of structured species to predation, density dependent (DD) mortality and fishing: thickness of lines are proportional to $\log(500\times$ change of flux). Black lines indicate positive change and grey lines indicate negative change.