

Gadget models of cod–shrimp interactions in Icelandic waters

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RH-03-2011

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May 2011

Abstract

In Icelandic waters there are known to be strong links between cod and shrimp, with shrimp abundance affected by predation by cod. Understanding the impact of cod predation might be expected to improve both the understanding of population dynamics and abundance estimates of shrimp. Modelling these scenarios requires multispecies, multiarea, multifleet models. The spatial overlap of the predator and prey needs to be taken into account. These species has different modelling requirements and differing levels of data availability. The development of models to address these issues is described, with levels of model complexity compared and evaluated.

Keywords: Gadget, multispecies, multiarea, statistical model, cod, shrimp, migration

1 Introduction

The marine ecosystem off Iceland contains several important players. Considered in isolation, the cod (*Gadus morhua*) stock is an important demersal species whose population dynamics have been studied extensively (e.g. Stefansson (1992) and Schopka (1994)). An interesting twist on the population dynamics is cannibalism, which appears to exist, though not of a dominating importance (Bogstad et al. 1994). The cannibalism has been taken into account when evaluating utilisation strategies for the cod stock (Baldursson et al. 1996).

Shrimp (*Pandalus borealis*) is also a commercially important species and there exists an important link between cod and shrimp, where predation by cod forms a considerable part of the mortality on the shrimp (Magnusson and Palsson 1991). This effect has been captured using models of interactions as a part of routine assessments of shrimp (Stefansson et al. 1994; MRI 2004).

The links between these species have been studied using simple regression analyses (Stefansson et al. 1998). The analyses support these conclusions but are difficult to convert into absolute numbers, though not impossible (Steinarsson and Stefansson 1996). These links have been used to develop harvest control rules for cod (Danielsson et al. 1997), as have sequences of more complex links (Stefansson et al. 1998a).

Models of marine ecosystems tend to be simplified in different ways depending on the purpose of the analysis conducted. As noted above, a very simple model can be in the form of a simple linear regression, possibly taking into account the statistical properties of the data. A very detailed model of the predation process could be a strictly mathematical model with no recourse to data fitting. Many model types fall somewhere in between these extremes, taking into account a varying level of detail in the mathematical model of the biological process and the statistical description of the data to which the model is fitted.

Although the simple models should be expected to illustrate the most important relationships, several problem issues arise. These include variable species overlap, seasonal and stage-dependent migratory behaviour as well as competing mortality factors which can only be sensibly considered in joint analyses.

The models to be developed in this paper are therefore implemented using the scheme set out in Stefansson and Palsson (1998) and implemented using a computer program, Gadget, described in detail by Begley and Howell (2004), Begley (2005) and Taylor et al. (2007). These models are statistical in nature, i.e. they are based on fitting to data using likelihood functions. They are also parametric in that a prediction is based on a parameter value alone, ideally using data only through the formal data fitting procedure. Finally, these models can take into account spatial and temporal variation in the species under consideration.

When developing these models it has proved important to first develop single-species models of fairly high quality for each species in question. Given the different data availability for e.g. cod and shrimp, these models become very different in nature. Thus, although the models may be internally age-disaggregated, there are no true age data for shrimp. Similarly, although most traditional assessments of cod in the North Atlantic use catches in numbers, disaggregated by age, such data are highly processed and the present paper uses data closer to the original samples, in accordance with common statistical procedure.

Earlier versions of such models have been used to analyse the cod-capelin interactions (Bjornsson 1998), based on Bormicon (Stefansson and Palsson 1997). Most of the earlier work has relied heavily on unproven and hardwired assumptions and weights given to different data sources. Given the problems in such approaches (Stefansson 1998), the emphasis in the present paper is on the cod-shrimp interaction, using appropriate statistical estimation methods at each stage of model development.

In multispecies models where spatial structure is considered necessary to account for predator-prey overlap, it is important to have a full understanding of the ability of the model to account for the observed dynamics and the ability of the data to define the spatial structure. If processes behind the spatial behaviour, such as migration and maturation (when life stages affect migratory behaviour), are poorly represented, or the data contain insufficient information on these processes, a spatially disaggregated model cannot be assumed to be an improvement on a simpler model. A simpler model ignoring predator-prey overlap, or assuming only a fixed proportion of the predator species consume the prey may be as able to represent the observed dynamics as a more complex model with poorly defined parameters. A single area model does not require modelling of migration, whereas even with two areas migration may be required which could make the model a worse representation of the population dynamics. Migration may vary between years and mark-recapture data do not typically represent random samples. While it may be possible to model the age structure of the population, the spatially disaggregated age structure might be considerably more difficult to determine.

The weights assigned to each negative log-likelihood component are of great importance and care needs to be taken (Methot 1989). In these models weights are calculated based on the method proposed by Stefansson (1998) & Stefansson (2003). A full description of the application of this method is given in Taylor et al. (2007).

2 Model definition: space

A variety of spatial definitions could be used to describe the relationship between cod and shrimp. In the initial stages of model development, however, it is prudent to consider the simplest spatial structures which can still account for the most important features of the species. For shrimp, only the overlap between cod and shrimp needs to be taken into account. For cod, modelling space is more complex as in a spatial model, seasonal and life stage migration can be taken into account.

2.1 Shrimp

The fishery for the offshore shrimp stock takes place mainly in the Gadget divisions 103, 104, 105 and 111 (figure 1). The definition of these areas is described in Taylor (2005b).

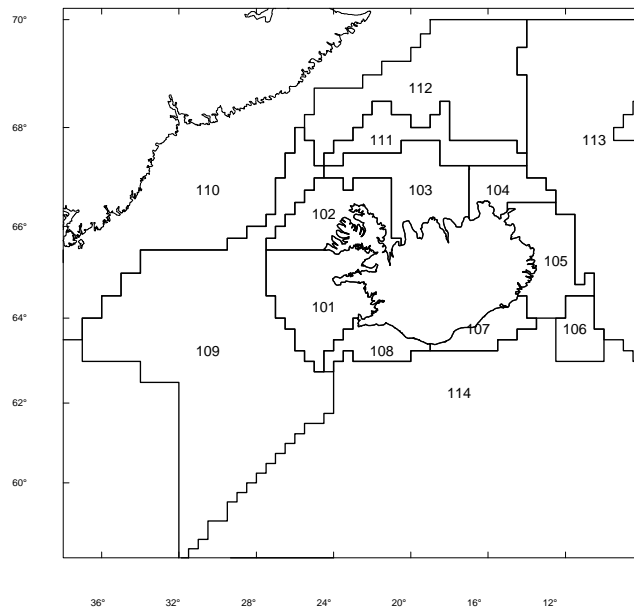


Figure 1: Map showing some of the datawarehouse divisions for the area around Iceland.

2.2 Cod

The cod stock, however, covers the entire area of the Icelandic shelf ($< 500\text{m}$). As the offshore shrimp stock occupies only part of the range of the cod population, use of the overlapping area by cod must be considered eg proportion of cod in this area, whether all ages of cod are present and whether presence of cod in the shrimp area is seasonal.

A further aspect of spatial distribution of cod is substock structure. Recent studies have indicated that the cod population in Icelandic waters can be classified into two main groups: northern and southern (Metacod 2007; Pampoulie et al. 2006; Jonsdottir et al. 2006). Mark-recapture data has shown that the northern cod display more resident behaviour with southern cod migrating further

to feed. To a large extent, these spawning populations can be considered spatially distinct. The main area where mixing of mature fish is to be expected is in the north west (area 102 in figure 1) as it is a feeding ground for some southern fish.

Immature cod are mostly in the north (areas 102, 103, 104 & 105 in figure 1 and NW, N & SE in figure 2) with juveniles from both substocks within this region. In some years, data from the Spring survey shows immature fish within the southern areas but these are mostly close to the boundaries with the more northern areas. The NW and SE in Figure 2 are areas of potential mixing of the immature with the southern mature stock with the northern stock in NW and N in figure 2.

The construction of population models is dependent on the availability of data and the removal of fish from the population is an important part of any fisheries model. Despite there being information from tagging, genetics and otoliths on substocks the disaggregation of the catch by substock is more problematic. The highest catches in numbers from the fishery are from the age groups 4 to 6. Most cod in these age groups are immature with < 10% mature at age 4, 20-30% at age 5 and 40-50% at age 6 (MRI 2005). While the mature components of each stock are predominantly separate throughout the year, with only a small amount of mixing, the juveniles, which constitute most of the fishery (in numbers) are mixed. Assumptions regarding the contribution of the juvenile components of each stock to the fishery are therefore very important.

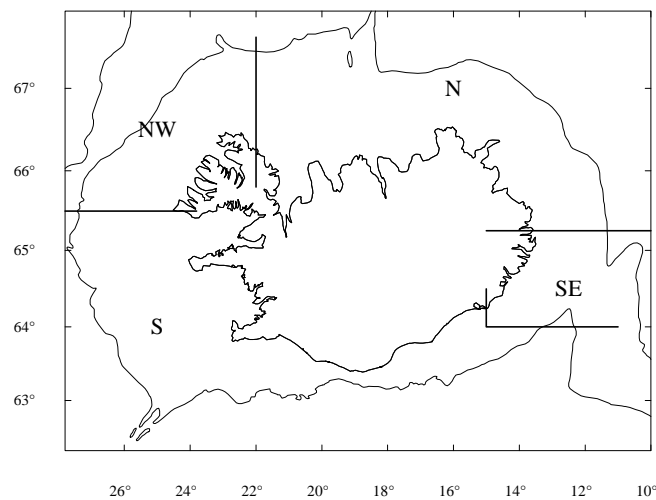


Figure 2: Spatial division of models of sub-stock structure of cod in Icelandic waters.

The available information suggests models with immature cod entirely (or predominantly) in the north, which mature into cod which can either remain in the north or migrate to the south and henceforth be resident there. While this conceptual model ignores the mixing of mature fish in the northwest and of southern mature and immature in the southeast, it should capture most of the observed dynamics. This system can either consider the mature cod to be in one population but spawning in separate areas and having different migration patterns or model the north and south spawning populations as separate substocks.

Modelling sub-stock structure in Gadget is, in many aspects, equivalent to modelling multiple species. The structural flexibility means that each sub-stock can have different characteristics and it is also possible for different data sets to be used for each sub-stock. A range of likelihood

data types can be used and these can be aggregated across sub-stocks and space. This means that observed data do not need to be assigned to a sub-stock and it is not necessary to partition the data artificially into sub-stocks. Neither is it necessary to assume the relative contribution of each sub-stock to the mixed fishery which is an important consideration for this population. Standard samples (eg length distributions and age-length frequencies) from the catch and surveys can therefore be used directly in optimisation. As the same data can be used for a range of structural models, the ability of the models to fit to the data can be compared.

2.3 Combining cod and shrimp

The simplest conceptual model consists of one area in which only juvenile cod are predators of shrimp. The majority of cod overlapping with shrimp are juveniles and any mature cod in this area will be expected to have low preference for shrimp. A single area model has several advantages including computational speed (there is only one area and there is no need for time consuming migration computations). In addition, migration is difficult to parameterise. Despite mark-recapture data being available, these do not represent random fish and cannot be considered to represent average behaviour whereas in a population model such as Gadget, average behaviour of the population is modelled.

The two area spatial structure which best combines the shrimp and cod populations has a northern area incorporating divisions 102, 103, 104 and 105 and a southern area of 107, 108 and 101 (figure 1). Within the model, shrimp only exist on the northern area (which covers a slightly greater area than required) whereas cod are on both. With this structure several conceptual models of cod population structure and migration can be tested.

Given the spatial structure of the final cod-shrimp model, preliminary single species models can be developed independently. This enables the impact of cod predation on shrimp to be assessed, and given the potentially computationally intensive models spatial models which can be developed it is more efficient to work with simpler models in the first instance. This is especially true for cod as shrimp is not considered to have a significant impact on the cod population and only top down effects are considered in the multispecies models.

The interest in linking cod and shrimp is in the impact of predation on shrimp rather than the effect of consumption on cod. As shrimp is not a major part of the diet of cod (Magnusson and Pálsson 1991), consumption of shrimp is not considered to have a significant impact on cod growth (Bjornsson 1998) and in this implementation cod growth is independent of consumption.

The approach to parameter estimation, through iterative weighting of each likelihood component is similar to that described in Taylor et al. (2007) and will not be described here.

Input data and likelihood component data were extracted from the datawarehouse described in Kupca and Sandbeck (2003) and Kupca (2005) with the original data sources and aggregation methods described in Taylor (2005a). In all cases the likelihood functions are those used for the cod models in Taylor et al. (2007).

3 Model definition: time

Require time scale which allows sufficient detail for processes. In particular migration and species overlap. Models with 12, 6 and 4 timesteps per year tested. 6 steps per year chosen as flexible enough to incorporate wide range of migration behaviour but still reasonable fast. On shorter timesteps, it is also necessary to model the fish on finer length divisions (to be able to model growth on the time scale of the model) which leads to further increases in the the time required

for model runs.

All the models operate on 6 timesteps per year with the population defined on 2cm length group intervals. Single area models have been used to test the performance of models on different temporal resolutions and the 6 step model was considered a sufficiently fine scale with which to model a range of migration strategies but all sufficiently fast to allow for the use of several models. The length of time required for an optimisation run is an important consideration when investigating model dynamics and testing different structures.

4 Shrimp model

4.1 Data and likelihood functions

Survey takes place over long time period which is not constant between years ie spans more than one time step in the model. In the model, the survey data have been combined into one time step for use as indices, but the length distributions have the data disaggregated by timestep as the shrimp will grow over the time covered by the survey.

Age data are only available for shrimp by using methods to disaggregate length frequency data (e.g MacDonald and Pitcher (1979)). Age disaggregation is problematic, especially for the older ages as the modes in the length distribution are difficult to identify. As can be seen in figure 3, only the modes of the first three cohorts are easily distinguished. For this reason it is preferable to estimate growth parameters within the population model using the available data rather than manipulating data independently of Gadget to derive ages. The growth parameters can also be used to calculate the mean length at age of the initial population.

Data used in the shrimp model are:

Input data:

- Landings data obtained from the Directorate of Fisheries data base.

Biological sampling likelihood data:

- Length distribution, aggregated on 1mm intervals, from sampling of commercial catches by month from 1988 to 2004.
- Length distribution, aggregated on 1mm intervals, from the main net of the offshore shrimp survey from 1988 to 2004 (Skuladottir et al. 2000).

Stock composition (female/male ratio) likelihood data:

- The proportion female at length in 2mm length classes from the main net of the offshore shrimp survey.

Survey index likelihood data:

- Five survey indices from the main net of the offshore shrimp survey (figures 3 & 4) with one datum for each group for the years 1988–2004.
- Two survey indices from the juvenile bag of the offshore shrimp survey (figures 3 & 4) with one datum for each group for the years 1988–2004.

Five indices are calculated for the main net (and two for the juvenile bag) by splitting the length distribution into groups, with the division based on the ‘typical’ structure of the length distribution for the survey over all years. The first three length groups are considered to be cohorts. The division of the length distributions into groups is illustrated for two years in figure 3. The length group divisions are identical for the two data sources and are derived from length distributions on 0.5mm intervals. The intervals in cm are: (0.60,1.10), [1.10,1.65), [1.65,2.15), [2.15,2.65) and [2.65,3.20) for groups 1–5. This provides two survey indices for the younger shrimp, with likelihood components that can be weighted simultaneously in the iterative weighting scheme. The

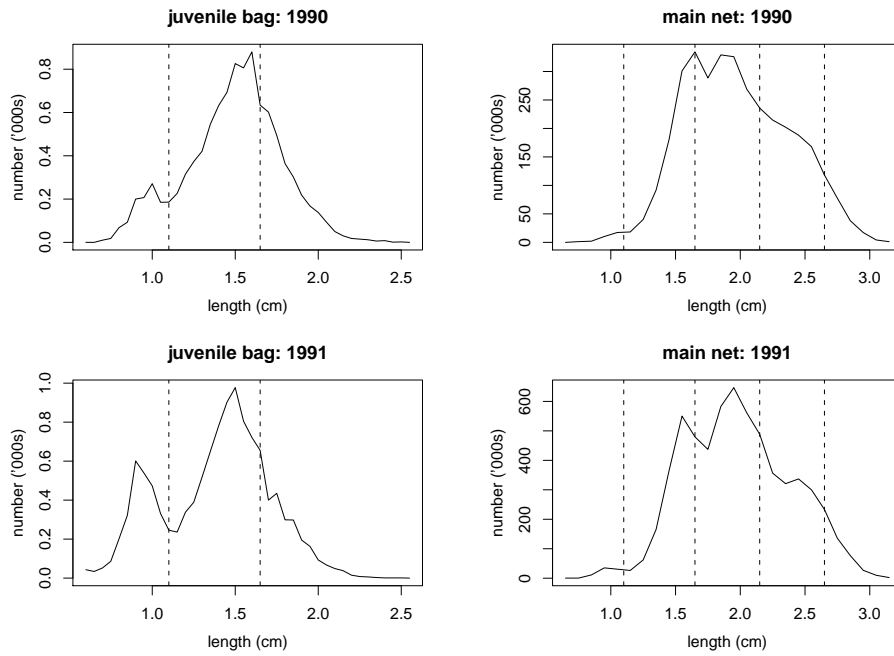


Figure 3: Length distributions from 1990 and 1991 for the juvenile bag and main net of the offshore shrimp survey. The vertical lines indicate the division into length groups for the survey index likelihood components.

appropriateness of these divisions as indicators of cohorts varies between years but as the indices are identified as length groups rather than age groups this is not a problem.

For the shrimp surveys, the power of the survey was fixed to 1 and only the intercept of the log-linear regression between the survey and modelled data estimated.

In figures 4 & 5 it can be seen that for length groups 1 and 2, the trends from the juvenile bag and main trawl net are similar for length group 1 (correlations between nets of 0.64 and 0.37 for length groups 1 and 2 respectively) although the time series do not entirely agree. For length group 2 the 1996 and 2002 cohorts are outliers. The selection of shrimp in the two nets is different, with the smaller meshed juvenile bag expected to be a more reliable indicator of length group 1 and the main net for length group 2.

Comparing length groups within nets by cohort (figure 6), the relationship between length groups 1 and 2 is considerably stronger in the main net than the juvenile bag (correlations of 0.63 and 0.37 respectively). There is also a strong correlation (0.57) between length groups 2 and 3 of the main net and between length group 1 of the juvenile bag and length group 2 of the main net (correlation of 0.56).

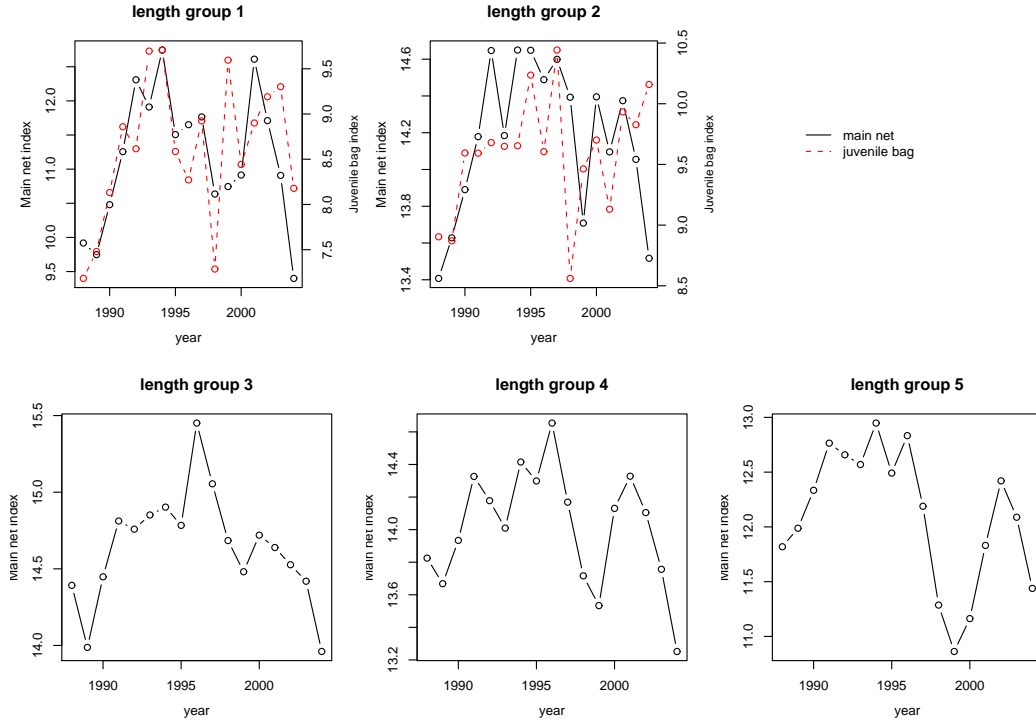


Figure 4: Survey indices for the offshore shrimp survey for both nets by length group. For length groups 1 and 2, the y axis for the main net is on the left and for the juvenile bag on the right with the index for the main net represented by the solid line and the juvenile bag by the dashed line.

4.2 Model Implementation

The model runs from 1988 to 2004, with six timesteps per year, on one area with two shrimp components – male and female. The males are aged 1 to 6 and the females 3 to 8, with the final age a plus group. Males become female through a maturation function and any not female by the end of their sixth year automatically move into the female stock component. A single commercial shrimp fleet operates along with a shrimp survey.

Variable natural mortality has been identified as an important control on the population dynamics of shrimp (Fu and Quinn 2000) and in Icelandic waters predation by cod has been estimated to be high in relation to the catch of the shrimp fishery (Magnusson and Palsson 1991). As the aim of developing the shrimp model is however to link it with a cod model to investigate the importance of cod predation on shrimp population dynamics, in this implementation natural mortality is constant for all years.

Length growth is according to the von Bertalanffy function as described in Taylor et al. (2007) with L_∞ fixed to 3.501 and k either fixed to 0.17 or estimated for both the male and female stock components. The von Bertalanffy parameters were calculated from data (Skuladottir pers. com.). The betabinomial parameter β is fixed at 20, with maximum length group growth $n = 20$ and length intervals of 0.05cm. The weight-length relationship is fixed, $W = aL^b$, with different values for the male and female components (Skuladottir pers. com.). Transition from male to female is implemented using the maturation function described in Taylor et al. (2007) as a function of length. The parameters defining sex change are estimated within the model. The fleet selection

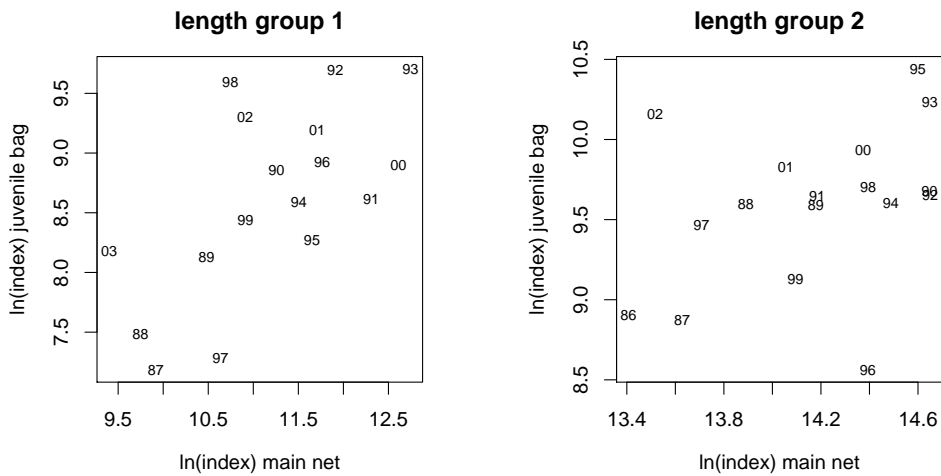


Figure 5: Scatter plots of the (ln transformed) offshore shrimp survey abundance indices. On the left, length group 1 from the main net is plotted with length group 1 from the juvenile bag and on the right, the equivalent plot for length group 2. Each point is labelled with the cohort, assuming group 1 is age 1.

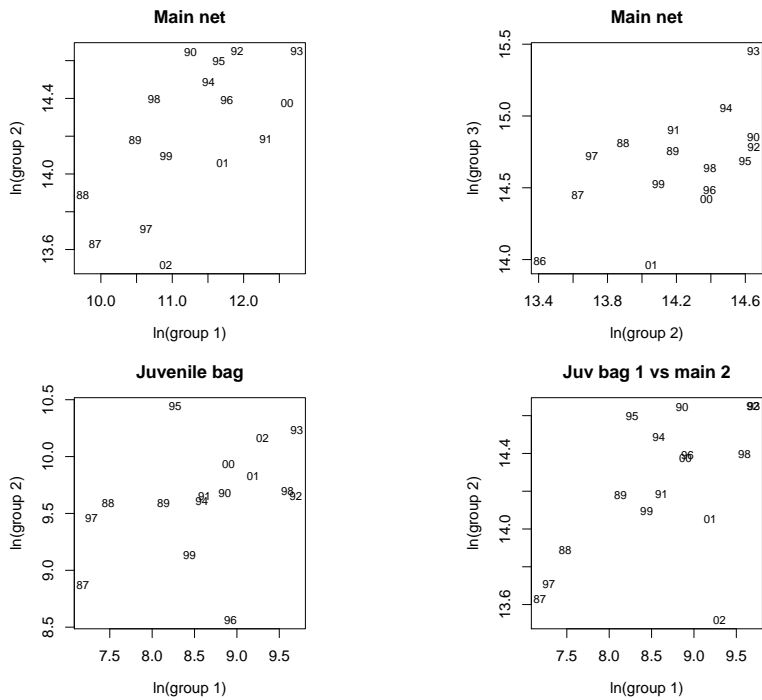


Figure 6: Scatter plots by cohort of the (ln transformed) offshore shrimp survey abundance indices. A) length group 1 vs length group 2 from the main net, B) length group 2 vs length group 3 from the main net C) length group 1 vs length group 2 from the juvenile bag and D) length group 1 from the juvenile bag vs length group 2 from the main net. Each point is labelled with the cohort, assuming group 1 is age 1.

pattern is the same as that used in Taylor et al. (2007) and the parameters estimated within the model.

Natural mortality at age is fixed for ages 1 and 2 to 0.3 and 0.2 respectively, 0.1 for males and females from age 3 to 6, and 0.2 and 0.6 for age 7 and 8 females. Appropriate values for natural mortality difficult to determine for this population. (Clark et al. 2000) report that mortality increases sharply after first hatching for mature females for Gulf of Maine shrimp. In some other areas however, natural mortality of males is believed to exceed that of females due to greater predation on smaller shrimp (Fu et al. 2001). As the purpose of these models is to evaluate cod predation on shrimp, the potential for predation induced mortality is ignored in the single species model.

The number at age of the initial population (ages 2 to 7) is estimated within the model. The standard deviation of length of the initial populations was fixed with the mean length at age calculated from the (estimated or fixed) von Bertalanffy parameters. The weight-length relationships used for weight growth were also used for the initial population. Similarly, the number of age 1 recruits for each year (1988–2004) is estimated within the model with the standard deviation of length fixed and the mean length calculated from the von Bertalanffy parameters.

The likelihood component weights are calculated using the method proposed in Stefansson (1998) & Stefansson (2003). To calculate the weights for the survey indices, the juvenile bag and main net are weighted simultaneously, similarly to the method in Taylor et al. (2007). For the shrimp survey however, there are no equivalent survey indices for the length groups containing larger shrimp. To estimate the weights for length groups 3 and 4, these indices were weighted simultaneously. While this is not ideal, it is more objective than the user defining the weights. For the final length group, it is assumed that the model fit to these data is poorer than the preceding two indices and it is given a weight lower than the fourth length group.

4.3 Results

Calculating the weights also provides information on the ability of the model to fit to the individual datasets and the relationship of the datasets with each other. The minimum sum of squares from the iterative reweighting procedure are shown in table 1.

The higher weight for length groups 1 and 2 is on the juvenile bag and main net respectively (table 2) which is the expected relationship given the survey design. Of length groups 3 and 4 which were weighted simultaneously, the calculated weight for length group 3 is considerably greater.

Parameters estimated for the single species shrimp model are compared in figure 7 for two different weighting schemes. The weights are identical apart from one component, the survey biomass index. The parameters estimated are similar, with the main differences for recruitment in later years and the initial population abundance for the older age groups. These are the parameters which are expected to be less well defined as in both cases there are fewer years of data for these cohorts.

Length group 1 is the survey group with the poorest fit of the model to the data for both the juvenile bag and the main net (figure 9 & 10). As the power term in the survey index is fixed for all indices, the slope of the regression represents the catchability. The catchability of shrimp in the main net of the survey is estimated to increase as length increases, apart from the final length group which has lower catchability than the previous two groups. The fit of the model to both survey indices from the juvenile bag is rather poor (figure 10).

| | mat | LDs | LDc | I1 | I2 | I3 | Nsse | Nsse2 |
|-----|---------------|--------------|--------------|--------------|--------------|--------------|--------|--------|
| mat | 13.690 | 429.700 | 391.400 | 77.360 | 21.790 | 292.600 | 21.040 | 21.140 |
| LDs | 0.636 | 0.084 | 0.147 | 0.361 | 0.872 | 1.118 | 0.099 | 0.098 |
| LDc | 3.517 | 1.233 | 0.864 | 5.261 | 4.701 | 6.648 | 0.053 | 0.870 |
| J1 | 78.430 | 11.290 | 13.070 | 2.193 | 6.347 | 33.790 | 14.010 | 16.310 |
| J2 | 19.840 | 3.466 | 5.548 | 6.703 | 1.782 | 10.020 | 4.867 | 6.254 |
| S1 | 66.830 | 11.780 | 15.040 | 2.966 | 12.140 | 27.940 | 14.600 | 15.170 |
| S2 | 15.770 | 4.585 | 3.938 | 5.590 | 0.517 | 4.340 | 2.583 | 3.019 |
| S3 | 10.260 | 5.437 | 2.364 | 5.975 | 1.818 | 0.143 | 1.572 | 1.657 |
| S4 | 13.290 | 5.535 | 1.684 | 8.372 | 3.934 | 1.644 | 1.352 | 1.482 |
| S5 | 35.590 | 10.790 | 5.262 | 15.330 | 14.350 | 13.460 | 2.004 | 1.891 |
| SB | 21.950 | 8.651 | 1.814 | 8.764 | 8.011 | 5.083 | 1.829 | 1.368 |
| tot | 43.430 | 23.273 | 20.296 | 15.921 | 9.598 | 26.757 | 64.809 | 69.257 |

Table 1: Minimum sums of squares from iterative optimisations with each column representing a run with that component heavily weighted. The values in bold are the sums of squares of the heavily weighted component in each optimisation. These components are from the biological sampling likelihood components (LD – length distribution, with s and c indicating whether survey or catch sampling), the ratio of immature to mature fish (mat) and the survey indices (I). For the indices, S_i , $i = 1, 2, 3, 4, 5$ are the length groups from the main net and the J_i , $i = 1, 2$ the juvenile bag. Length groups of the surveys are weighted simultaneously: column I1, weight on J1 and S1; column I2, weight on J2 and S2 and column I3, weight on S3 and S4. The columns Nsse and Nsse2 are the final scores for alternative optimisation runs.

| Component | Inverse weight | Weight | sse_{f1}/sse_m | sse_{f2}/sse_m |
|-----------|----------------|---------|------------------|------------------|
| mat | 0.0283 | 61.07 | 1.544 | 1.537 |
| LDs | 2.0412 | 7100.45 | 1.158 | 1.173 |
| LDc | 0.4155 | 2948.73 | 1.007 | 0.987 |
| J1 | 0.1191 | 7.75 | 7.437 | 6.389 |
| J2 | 0.3086 | 9.54 | 3.510 | 2.731 |
| S1 | 0.0962 | 5.73 | 5.115 | 4.922 |
| S2 | 0.5727 | 32.87 | 5.837 | 4.994 |
| S3 | 0.4464 | 118.55 | 11.555 | 10.962 |
| S4 | 0.1259 | 10.34 | 0.901 | 0.822 |

Table 2: Component weights: the inverse minimum sums of squares, the scaled weights calculated from the iterative reweighting procedure and the ratio of the sum of squares from the optimised model (sse_f) with the minimum from the weighting run (sse_m).

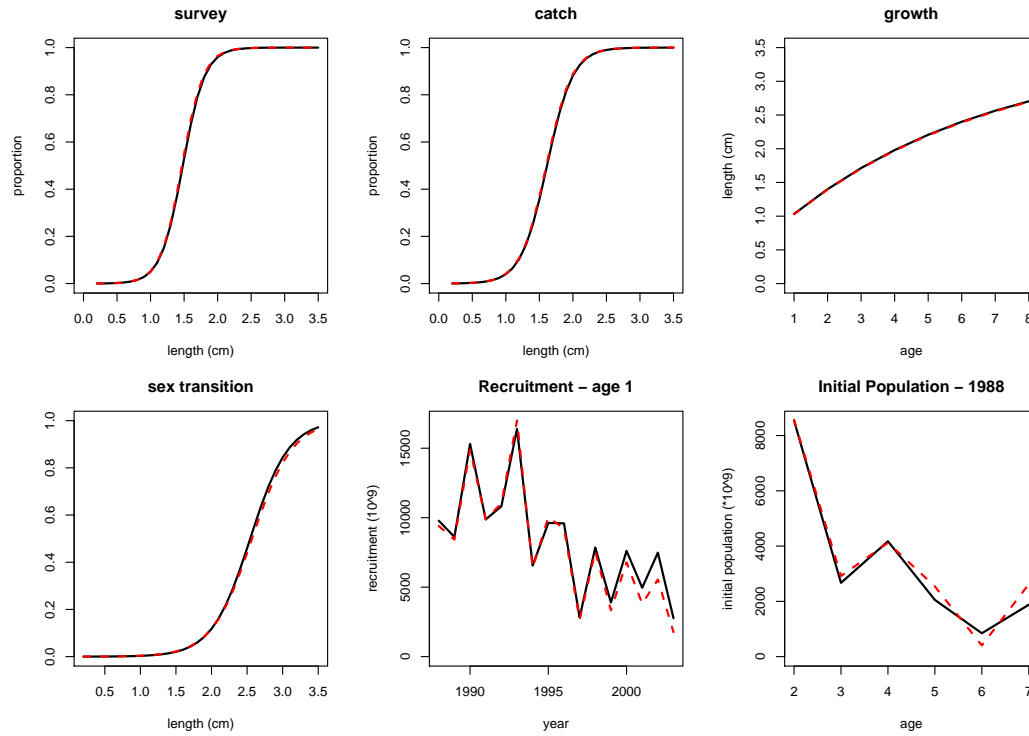


Figure 7: Parameter estimates from two optimisation runs with alternative weighting of the survey biomass component: selection patterns of the offshore shrimp survey and catch, growth, sex change (male to female), number of age 1 recruiting into the model and the initial population ages 2–7. The estimated stock biomass and the observed catch are also shown.

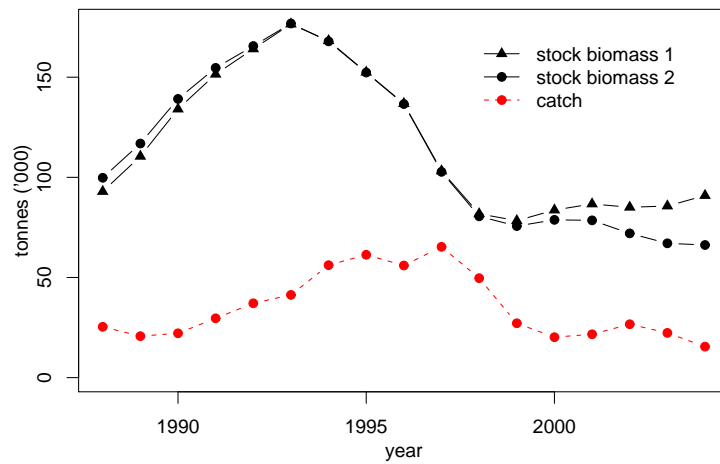


Figure 8: Parameter estimates from two optimisation runs with alternative weighting of the survey biomass component: selection patterns of the offshore shrimp survey and catch, growth, sex change (male to female), number of age 1 recruiting into the model and the initial population ages 2–7. The estimated stock biomass and the observed catch are also shown.

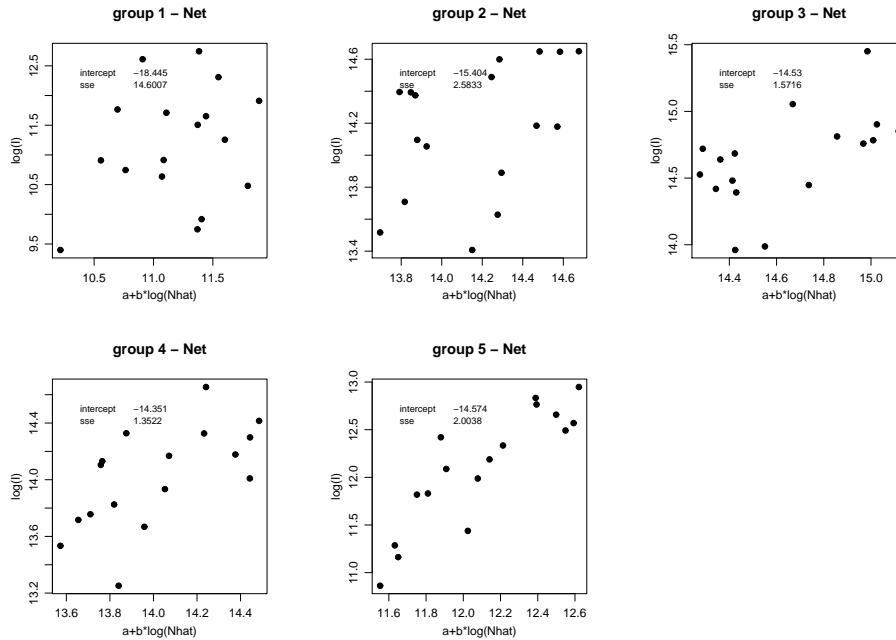


Figure 9: Plots of the log-linear regression as estimated in Gadget, with one plot for each likelihood component and the intercept and sse for each survey index are given. $\log(I)$ is the index and $a+b \cdot \log(\hat{N})$ the model estimate of the survey index.

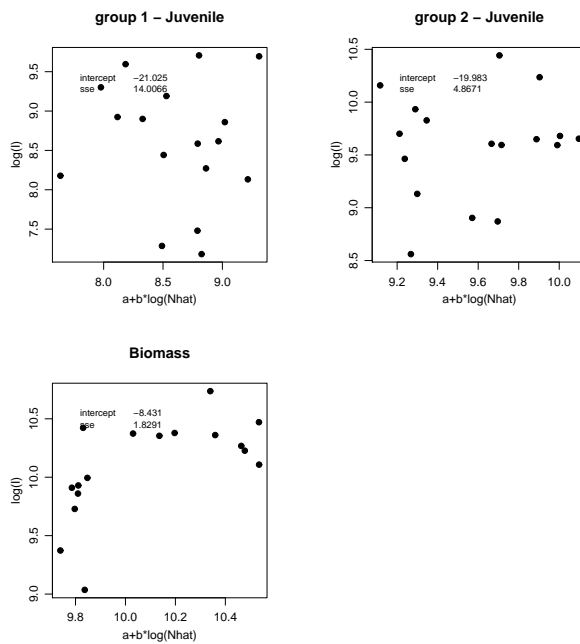


Figure 10: Plots of the log-linear regression as estimated in Gadget, with one plot for each likelihood component and the corresponding slope (estimated for length groups 1 and 2) and sse for each survey index. $\log(I)$ is the index and $a+b \cdot \log(\hat{N})$ the model estimate of the survey index.

The model is, in general, a better fit to the data from the indices comprised of older shrimp. These indices are smoother and less erratic than those for length groups 1 & 2 (figures 11 & 12). The model follows the main trends in the data fairly well, as would be expected, but cannot account for inconsistencies in the indices.

Abundance of all length groups is underpredicted for the final years (except the last year) (figure 11). The model can represent the rapid decrease in abundance around 1998 but not the subsequent increase. The plot of biomass (figure 12) shows that the model is accounting for the main trends in the survey biomass.

This is reflected in the biomass plot in figure 8 where the total stock biomass can be seen to increase from 1998 onwards, whereas the catch decreased in these years. As the first two length groups fit the index data for this time, the problem is entirely due to an over prediction of the abundance of older shrimp. It is possible that this is a result of not taking into account annually varying mortality. With mortality constant for all years and fixed growth and fleet selectivity, recruitment and catch determine the modelled stock structure and abundance. For a stock, such as shrimp, with high predation mortality, natural mortality can be a more important determinant of stock dynamics than recruitment (Fu and Quinn 2000). Another possible cause for the over prediction of older shrimp could be the increased mortality of females after hatching which has been observed for Gulf of Maine shrimp (Clark et al. 2000).

The landings from the shrimp fishery remained high after the data indicate a stock collapse as the TAC (total allowable catch) remained high. Contemporary assessments did not show a collapse in the stock which was apparent in later assessments.

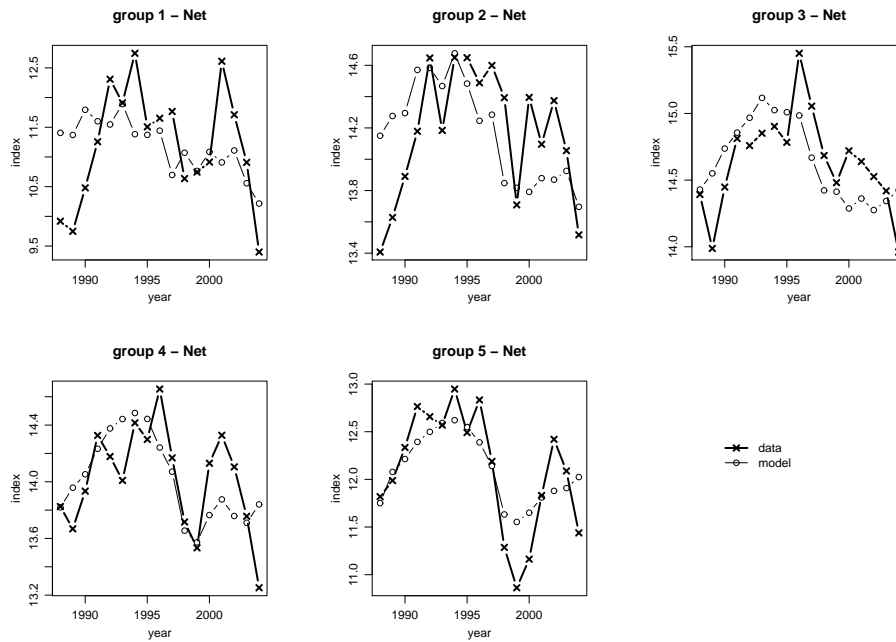


Figure 11: Plots of the log-linear regression as estimated in Gadget, with one plot for each likelihood component and the corresponding slope (estimated for length groups 1 and 2) and sse for each survey index. $\log(I)$ is the index and $a+b*\log(\hat{N})$ the model estimate of the survey index.

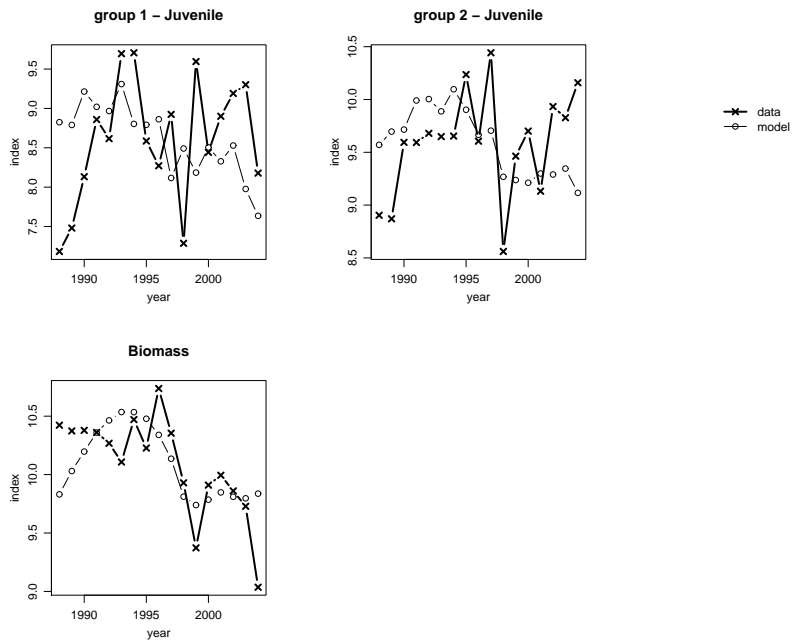


Figure 12: Plots of the log-linear regression as estimated in Gadget, with one plot for each likelihood component and the corresponding slope (estimated for length groups 1 and 2) and sse for each survey index. $\log(I)$ is the index and $a+b*\log(N)$ the model estimate of the survey index.

5 Single area cod model

A single area model similar to that described in Taylor et al. (2007) but with six time steps per year.

6 2–area cod model

To construct the most appropriate 2 area model of cod a hierarchy of models was developed and tested. The aim being to identify the model which can explain the key aspects of the population dynamics. A relatively simple model is desirable, both to reduce computational time and to limit the model to those processes for which there is evidence in the data. An overly complicated model, with more processes and parameters may contain many parameters which are poorly defined, introducing more error and uncertainty into the model.

All models are based around the same core structure. The main differences in structure between models is in the spatial distribution of the immature and mature components and whether the population is modelled as a single spawning unit or with two spawning substocks.

Within these structures, the combination of likelihood data in the objective function required for parameter estimation is also evaluated. Both, in the type of data used and the spatial disaggregation of the data. The use of statistical models in this manner allows the evaluation of whether increasing model complexity is desirable. Questions which can be considered include: ‘Do more detailed models provide a better fit to the observed data?’ and ‘Is there sufficient information to test whether increasing the complexity of the model is justified?’ It is possible that quite different conceptual models of the population dynamics fit equally well (or badly) to observed data.

The maximum time range of the model is from 1984 until 2004 with the population defined for ages 1 to 12 (with the final age a plus group) on two areas. All individuals are classified as being immature or mature. Immature fish mature according to a length based maturation function and any not mature by the end of their tenth year move into the mature component. Fishing is by a single commercial fleet with catches spatially disaggregated. 2 surveys take place, one each in the 2nd and 6th timesteps.

The power term for the survey indices is fixed equal to 1 in all cases with only the catchability parameters estimated. Results from single area models have shown that while the increased model flexibility from estimating the power term improves the fit to the survey indices, there is no significant difference in population abundance or biomass (Taylor et al. 2007) for the time period modelled. Given the increased time demands of multi–area, multi–species models and the need to test many model structures, fixing the power term to 1 reduces the computational time required.

6.1 Model parameters

The parameters estimated in these models represent: the growth rate, catch and survey selection patterns, the number of recruits (age 1) entering the population in each year, the number at age (for ages 2 – 11) in the initial year and where necessary migration parameters. Migration parameters are always considered to be constant for all years. While annually varying migration would increase model flexibility, it would not be informative when forecasting. An alternative to estimating migration is to estimate the proportion of fish which mature into the northern sub-stock, with all fish maturing into the southern stock then migrating south. A single maturation ogive is used for both stocks (using optimised parameters from a single stock model) as it is not possible to identify the immature by stock. This assumption also allows for a combined immature

stock component in the model which reduces the required computing time. A full optimisation procedure is performed for every model.

6.2 Single stock models on two areas

The two area models aggregate NW, N and SE in Figure 2 into a single northern area.

The model structures start from the most simple abstraction of the cod population dynamics. These structures are:

1. **Immature in north, mature in south (S1):** All immature cod are in north and move south when mature where they remain. All mature cod in the initial population start in the south.
2. **Immature in north and south, mature in south (S2):** All immature cod start in the north and all move south when mature. Immature cod can also migrate south before maturation with the migration rate estimated. All mature cod in the initial population start in the south.
3. **Immature in north, mature in north and south (S3):** All immature cod are in the north and the migration of mature cod to the south is estimated (ie some stay in the north) but all mature cod in the initial population start in the south.
4. **Immature in north, mature in north and south (S4):** All immature cod are in the north and the migration of mature cod to the south is estimated (ie some stay in the north). The abundance of mature fish in the initial population is estimated for north and south.

The simplest model (S1) assumes that all immature cod are in the north and when mature they migrate into the southern area. Given a small northern sub-stock this model would be expected to explain most of the population dynamics. Model 2 allows for some immature to move into the southern area as the data indicate that this does happen and the importance of it needs to be evaluated. Model 3 allows for some immature fish upon maturing to remain in the north as the proportion migrating south is estimated. Model 4 is an extension of model 3, if a large proportion of mature fish are estimated to remain in the north then the model needs to be initialised with mature fish in the north.

6.3 Two stock models on two areas

Only one population structure is used for this scenario. There are two mature stocks (north and south). All immature cod are in a single mixed stock, when they mature they enter either the northern or southern mature stock with the distribution into the north and south mature stocks estimated (and constant for all years). All juveniles start in the north and stay there until mature. When they mature, those entering the southern mature stock all move south, with those moving into the northern mature stock remaining in the north. The initial populations of mature fish in the north and south are estimated separately with no relationship assumed between them.

The immature cod are grouped into one mixed stock as there is no information with which to separate them and the only information (available for a substantial number of fish) which can be used to split the mature stocks is the spatial distribution.

Models constructed on this basis are also used to consider different growth rates for the areas.

6.4 Likelihood data

The likelihood data are of two main types: biological samples from the commercial catch and surveys and survey indices from both surveys. All categories of fish (ie maturity stages and stocks) are aggregated but can be spatially disaggregated. Constructing likelihood components by maturity stage would greatly reduce the data available and there is almost no data (and it is not random) on substock structure. The biological samples are: length distributions (LD), age-length frequencies (ALF) and age compositions (AC) with the age compositions only used for model comparison and not included in the optimisation process. The survey indices are length disaggregated into three groups which represent age 1, age 2 and age 3+. The use of the likelihood data in this form is described in detail in Taylor et al. (2007)

The survey indices are always spatially disaggregated with all three length groups in the north in all models but typically only one group (the largest) in the southern area. The exception is for model structure 2 for which all indices are used in both areas. The biological samples are used in three forms: all data aggregated into one area, area disaggregated but combined in the same component and area disaggregated into separate components.

Models are optimised using survey indices with age-length frequencies, in which case the fleet selection patterns are fixed or with survey indices, age-length frequencies and length distributions. These are referred to as:

| | Likelihood data |
|----|---|
| D1 | ALF aggregated into one area & survey indices |
| D2 | LD & ALF aggregated into one area & survey indices |
| D3 | LD & ALF disaggregated by area but in same component & survey indices |
| D4 | LD & ALF disaggregated and in separate components & survey indices |

By using spatially aggregated data in the objective function there is a link between the single area model to the two area model as both models can be parameterised from the same observations. This clear progression in model hierarchy and use of data helps to evaluate the appropriateness of the more detailed models before introducing the use of spatially disaggregated data.

Despite migration being estimated in some of these models, tagging data have not been used (although it is possible to include tagging data as a likelihood component in Gadget (Hannesson et al. 2004; Begley 2005)). In Icelandic waters, mark-recapture of cod in recent years have targeted spawning fish on spawning grounds, whereas in all the scenarios the focus has been on modelling the migration of immature fish when they first mature, with mature fish remaining in the same area thereafter. Data on fish which are already spawning is too late to use in these model structures. Migration is therefore driven by the fit of the model to the survey indices and sampling data (the length distributions and age-length frequencies) rather than to direct observations of fish movement.

Within both surveys there is a strong log-linear relationship between the number of fish in length group 1 (correlation = 0.90) and length group 2 (correlation = 0.88) in the following year for the northern area (Figure 13). This indicates both the suitability of these length categories as indicators of cohort strength and that the majority of fish within these length ranges remain in the north. In the northern area, there is also a strong relationship within the equivalent length groups between the surveys (Figure 14), with the exception of group 3. In the southern area, the agreement between the surveys is good except for 2001 (correlation of 0.81 if 2001 excluded) which indicates that the assumption that mature fish remain in the southern area throughout the year is reasonable (or at least that a fairly constant proportion are migrating out of the area to feed). The outlying point could be the result of immigration of fish into the southern area from Greenland between the Spring and Autumn surveys of 2001. The northern area also shows an increase in 2001 in the north without a corresponding increase in the south which could also be

due to immigration. The group 3 indices in the north can be split into two groups within which the surveys show agreement ie 1996 to 1998 and 2001 to 2004. In the later time period the autumn index is relatively high compared with the spring index. This could indicate a change in survey catchability on the north. The indices are also shown as time series in Figure 15).

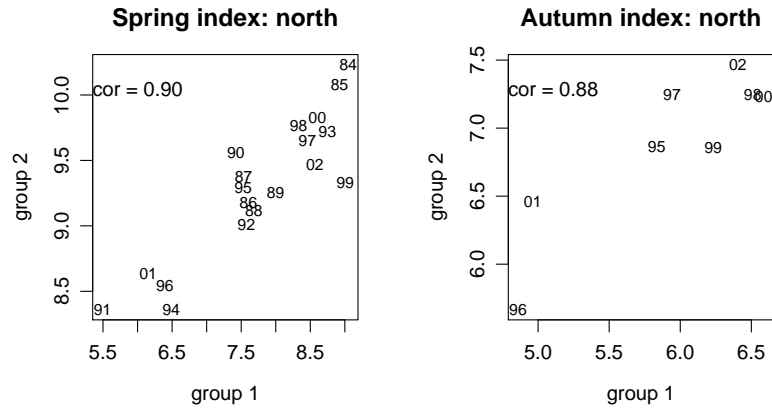


Figure 13: Log transformed scatter plots of the survey indices by survey with the length group 2 index plotted against the length group 1 index of the previous year by survey. Each point is indicated by the year in which length group 1 was sampled. The correlation is also given.

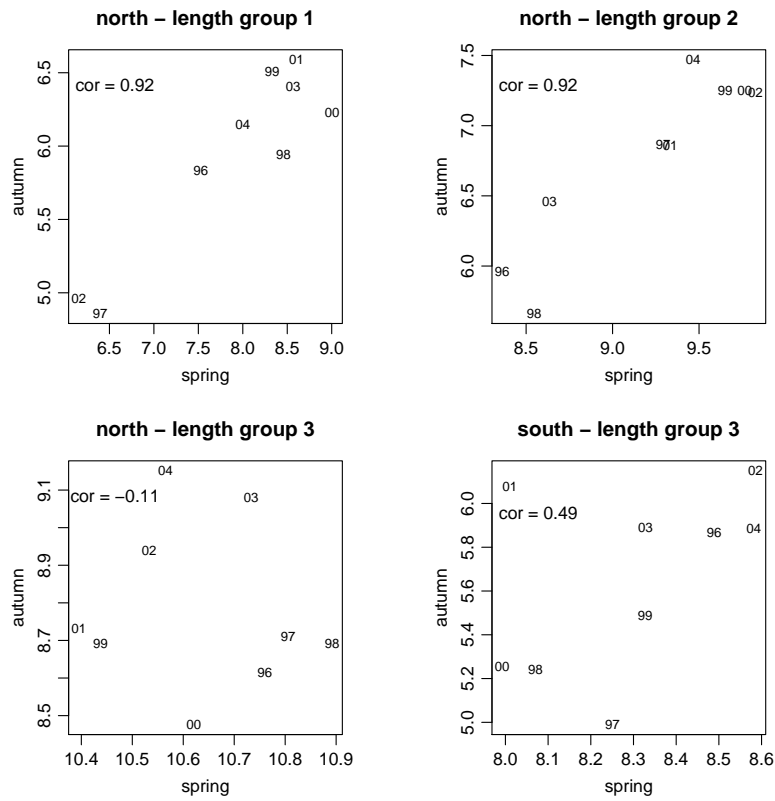


Figure 14: Log transformed scatter plots of the survey indices by length group with the autumn survey index plotted against the equivalent spring survey index. Each point is indicated by the year of sampling. The correlation is also given.

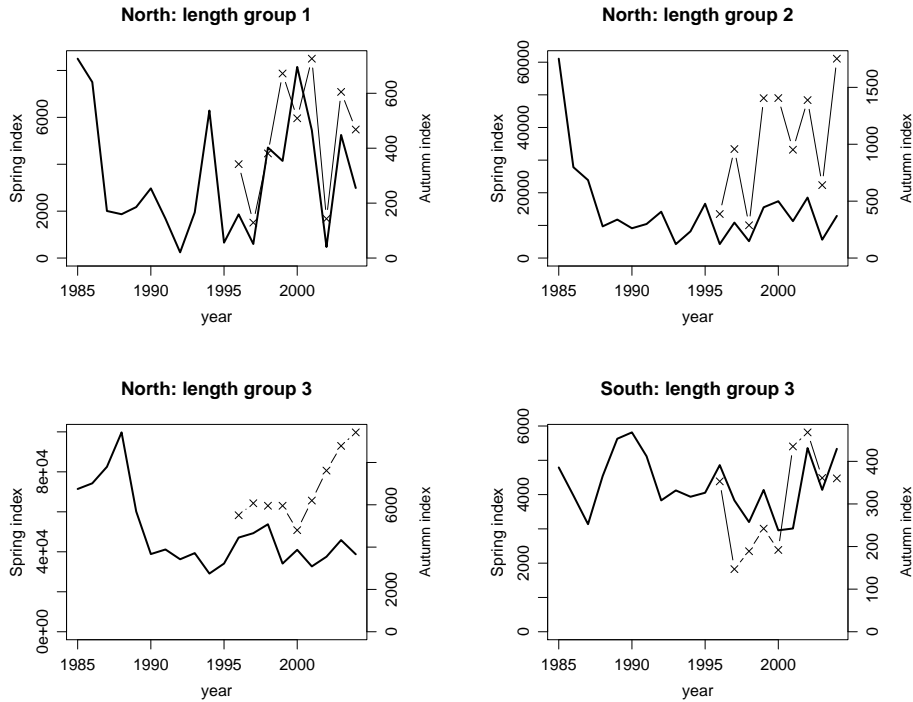


Figure 15: Time series of the survey indices by area, with the Spring survey indicated by the solid line and the Autumn survey by the crosses.

6.5 Model comparison

There are two main aspects consider here, the structure and the data. For the same data, how does the structure affect the optimisation? And within a model structure, how does the data affect the optimisation? It is, of course, possible that the model could fit equally well to different structures which generate different results if there is insufficient information in the data to distinguish between them.

When the model structure is a better representation of the population structure, the spatial aggregation of the likelihood component data is of less importance. Where the model structure does not adequately describe the population structure the format of the likelihood data affects the ability of the model to optimise. Consideration of these factors is part of the model evaluation process. For example, a model might be able to fit to length distributions aggregated over the entire space but not to the spatially disaggregated length distributions. The distribution of abundance could be correct but not the size structure.

6.5.1 Single stock models: negative log-likelihoods

The fit of the model to the likelihood data can be used to compare models, as described in Taylor et al. (2007). In the hierarchy of model structures, many models use the same likelihood data and the same parameters are estimated. Even likelihood datasets not used in the optimisation can be used to compare models.

With the biological sampling likelihood data spatially aggregated (D1), ie the datasets easiest for

the model to fit to, the likelihood scores show that S2 is not an improvement on S1, whereas S3 fits the data better than S1 in most cases (figure 16). The differences between the likelihood scores for the models, are not however, large. This shows that it is important to have mature fish in the north but immature fish in the south is not an important part of the population dynamics. It is important to realise that it is not just the spatially disaggregated survey indices that are affected by changing the distribution of the population. Catches are spatially disaggregated so even the aggregated LD and ALF generated by the model can be affected by migration. As S4 initialises with mature fish in the north rather than just allowing some mature fish to remain there it is expected to be a more appropriate model than S3. For most components S4 does fit the data better than S3 but just as the Spring survey length–group 3 index is a poorer fit for S3 than S1, S4 is worse again than S3 (figure 17). Mature fish being present in the north improves the fit to the northern indices, along with the Autumn survey in the south, but not the the Spring survey in the south.

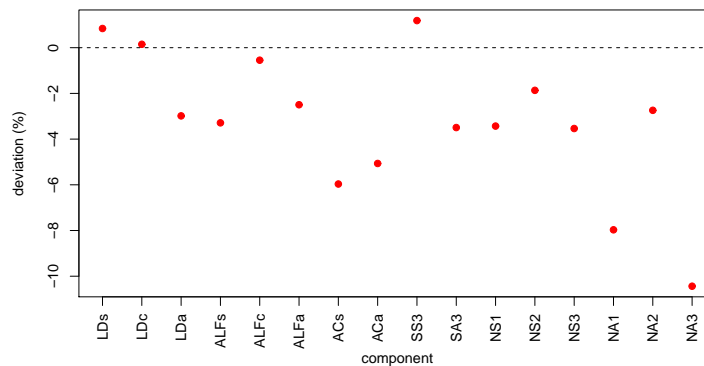


Figure 16: The difference in negative log-likelihood scores by component for the Structure 3 and Structure 1 models as a percentage of the Structure 1 model $((S3-S1)/S1)*100$

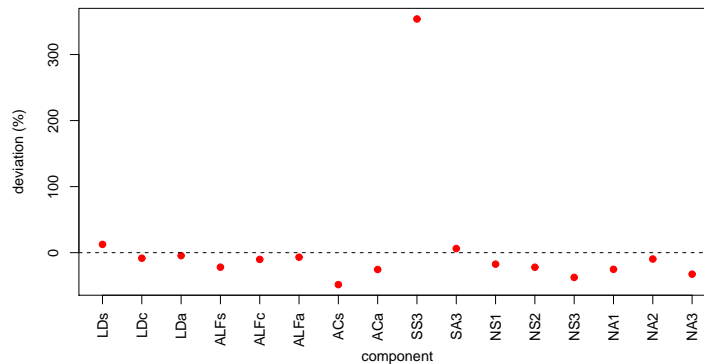


Figure 17: The difference in negative log-likelihood scores by component for the Structure 4 and Structure 3 models as a percentage of the Structure 3 model $((S4-S3)/S3)*100$

When models of the same structure but with datatypes D1 and D2 are compared, no clear conclusions can be drawn but there are some indications that the greater flexibility (additional parame-

ters estimated) is an improvement. In the case of structure 4 it is not surprising that the length distributions fit better and the age-length frequencies and age compositions tending to fit worse (figure 18). The fit to most indices is improved, the exceptions being length-groups 2 and 3 of the Spring survey in the north and the Spring survey in the south.

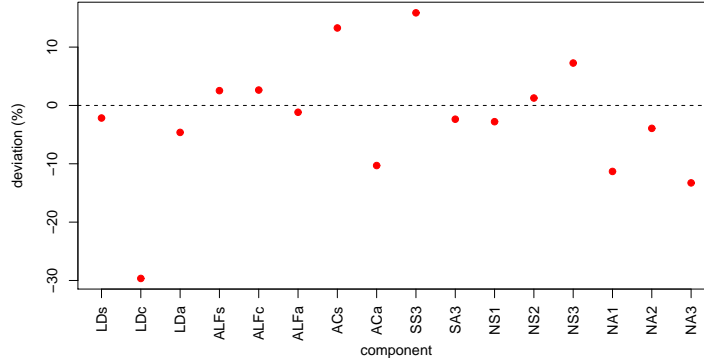


Figure 18: The difference in negative log-likelihood scores by component for S4 with datatypes D1 and D2 as a percentage of D1.

By disaggregating the data but not separating the areas into different components, the implicit assumption is that the model is able to fit to both areas equally well. It is not expected that this will be the case. Disaggregating the biological sampling data within the same likelihood component – surveys fit better for S4 but other indices worse (even when take into account they are twice the size).

Fully spatially disaggregated data is the ideal format and a model must be able to fit to data of this type if it is to be considered an adequate representation of the population. The likelihood scores for the indices for S4 with D4, are only better than those for D2 for two components. There are, however, more components to fit to with D4 which would be expected to affect the ability of the model to fit to any one dataset.

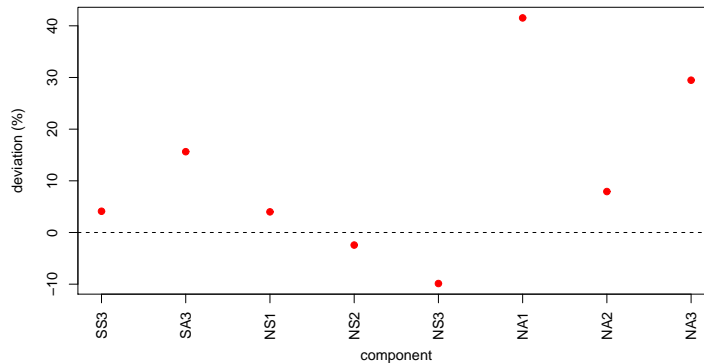


Figure 19: The difference in negative log-likelihood scores by component for S4 with datatypes D2 and D4 as a percentage of D2.

6.5.2 Single stock models: stock biomass

While there is not much difference in the negative log-likelihoods between the model structures, the corresponding projected end of year biomasses show large differences (figures 21 & 22). When the objective function is comprised of spatially disaggregated sampling data, it is clear that the simpler structures (S1 and S3) fail to fit to these data resulting in ever increasing biomass trends (figure 22). In models where the northern population is restricted to immature fish (or in the case of S3 the initial population is restricted to immature fish) in order for the north to have sufficient biomass, recruitment is required to be very high leading to extremely high values of biomass in the south. Increasing the detail of the model increases the biomass in the north with a reduction in southern biomass. With aggregated data in the objective function (figure 21) the biomass trends are similar for all model structure but not with the disaggregated data (figure 22). Model performance is dependent on the form of the data in the objective function. The most complicated model structure (S4) is the most stable in terms of projected biomass with the different data types and best able to represent the disaggregated data. This indicates that it is a more suitable model of the population.

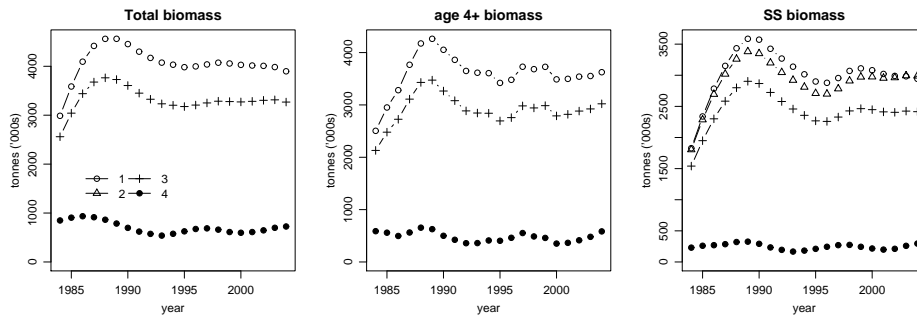


Figure 20: End of year biomass for four model structures with area aggregated sampling data in the objective function. Total biomass, age 4+ biomass (assumed fishable biomass) and spawning stock biomass.

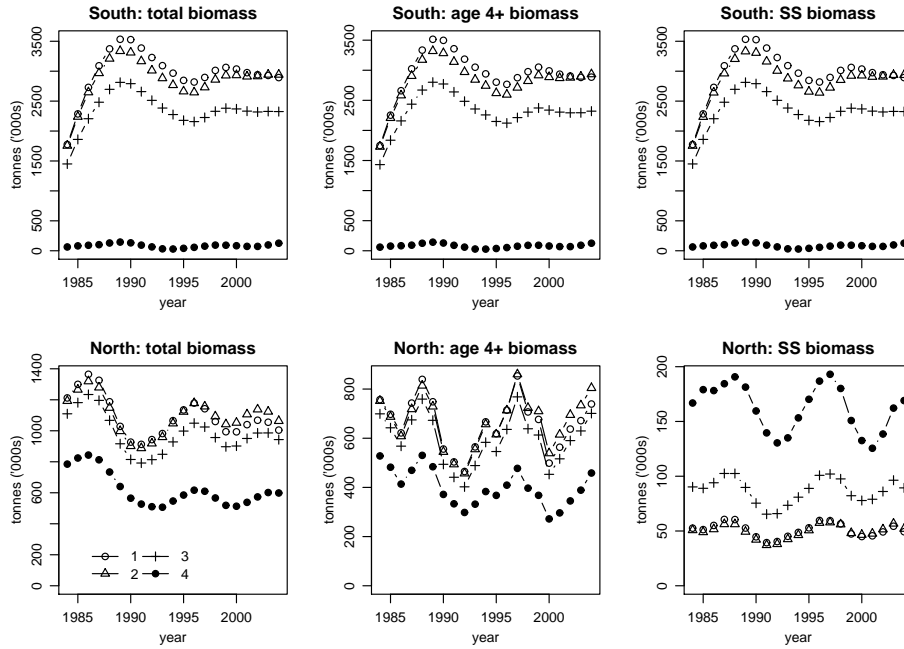


Figure 21: End of year biomass for four model structures with area aggregated sampling data in the objective function. Total biomass, age 4+ biomass (assumed fishable biomass) and spawning stock biomass.

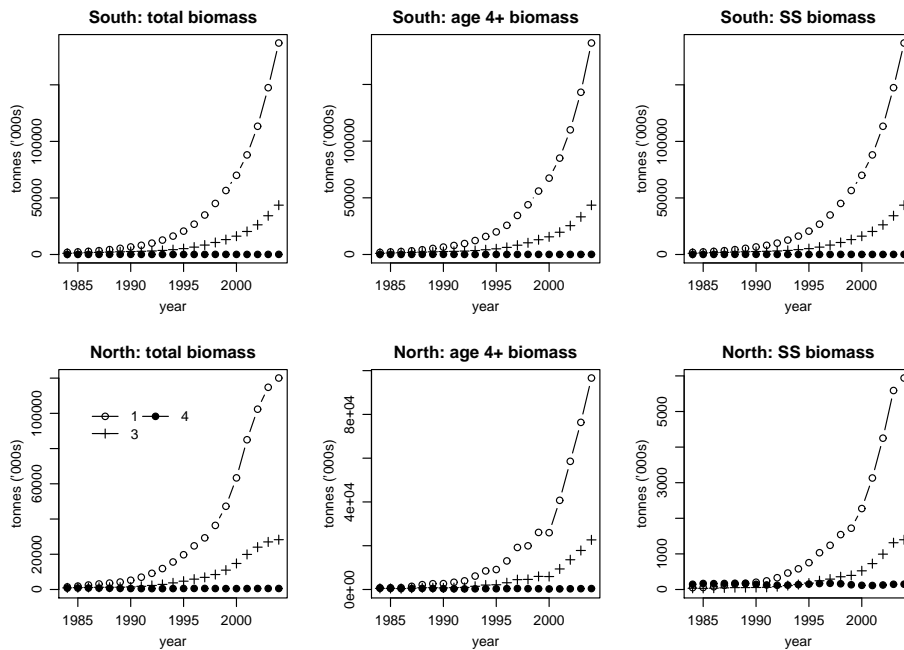


Figure 22: End of year biomass for three model structures with area disaggregated sampling data in the objective function. Total biomass, age 4+ biomass (assumed fishable biomass) and spawning stock biomass.

6.5.3 Two stock model

The model with two mature sub-stocks (S5) is similar to structure 4 but with the mature fish in the different areas modelled as separate sub-stocks. In Gadget, this increases the potential for the sub-stocks to have different characteristics. The increased flexibility unfortunately, also results in slower running times. There is also a difference in migration behaviour, although a two mature sub-stock model could be structured more like S4. For S5, any fish maturing into the southern stock and migrating south does so upon maturation, whereas with S4 individuals can migrate south and behave as southern spawners at any time after maturation. There can, therefore, be a substantial difference in the length and age of the fish migrating south in these models as there are several age groups after maturation.

The response to the level of aggregation of the sampling data in the objective function is similar for S5 as S4 and only the results of models optimised with the fully disaggregated data are considered further. S5 with same parameters as S4 fits better to more components than than the corresponding S4 model (figure 23). In particular, the fit to the sampling data and indices from the south is improved, although the fit is mostly worse for data from the north.

The projected end of year total biomass and fishable biomass (age 4+) for the entire area is similar for S4 and S5 (figure 24) with S4 predicting slightly lower biomass, particularly towards the end of the time period. When compared with results from a single area model, S4 is the most similar at the beginning of the time period but S5 towards the end. The pattern of spawning stock biomass predicted from the two structures is however quite different at the start of the time period. The pattern, and abundance level, of S5 is closer to that predicted from the single area model than that from S4.

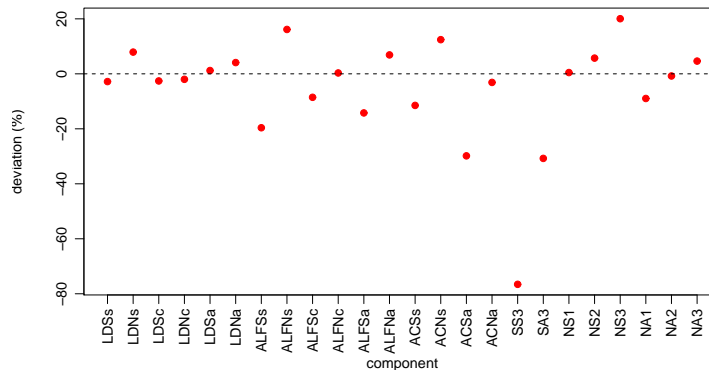


Figure 23: The difference in negative log-likelihood scores by component for S5 and S4 with datatypes D4 as a percentage of S4.

Despite the spatially aggregated biomasses being similar, the distribution of biomass between the two areas is quite different for S4 and S5 (figure 25). The two sub-stock model (S5) predicts higher biomass in the south than with one mature stock. There is less difference in the north, apart from spawning stock biomass (SSB), with the two sub-stock model predicting considerably higher SSB at the start of the time period.

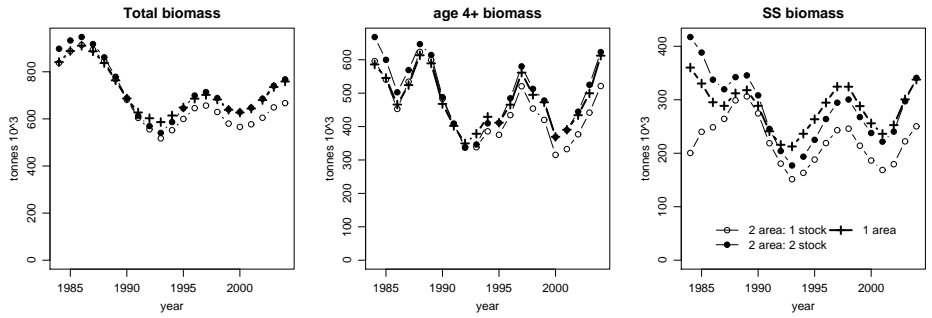


Figure 24: End of year biomass for three model structures with area disaggregated sampling data in the objective function. Total biomass, age 4+ biomass (assumed fishable biomass) and spawning stock biomass.

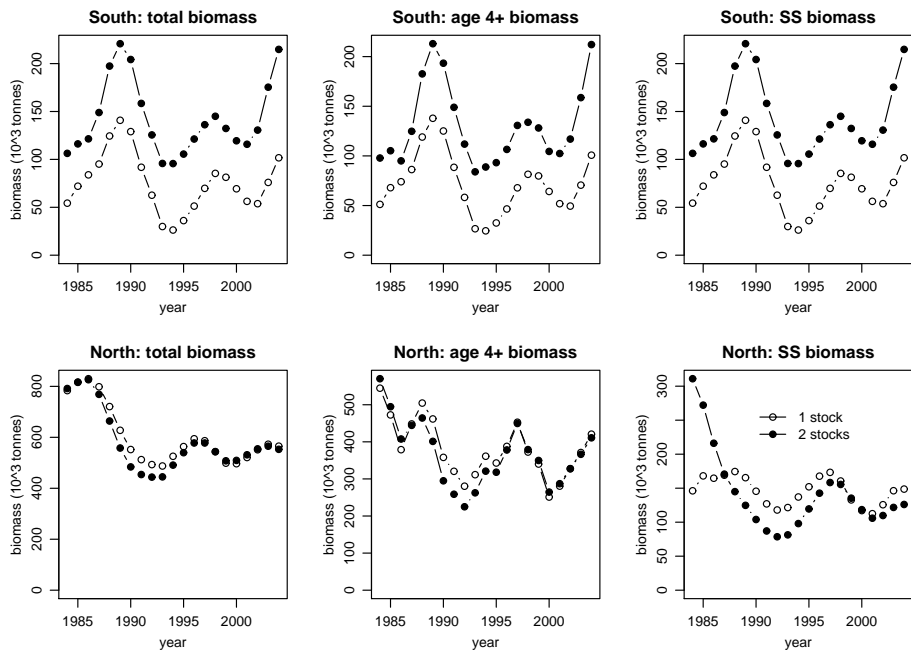


Figure 25: End of year biomass for three model structures with area disaggregated sampling data in the objective function. Total biomass, age 4+ biomass (assumed fishable biomass) and spawning stock biomass.

6.5.4 Summary

The simplest multi-area models are clearly incapable of adequately representing the population dynamics. When constructing a two area model, oversimplifying the system results in optimisation problems. While it has traditionally been considered that most of the spawning takes place in the south, the fit of the model to the data indicates that ignoring the presence of mature cod in the north is not appropriate. It should be noted that an overly simplistic 2 area model is not an advantage over a single area model. When constructing a multi-area model, the need to model the spatially disaggregated size structure clearly has the potential to cause problems as migration must be taken into account.

A model with mature fish in the north and south, whether modelled as two distinct spawning stocks or as separate parts of the same stock is a better representation of the observed spatially disaggregated data. Which of these models most accurately represents the behaviour of the population is more difficult to determine.

Given the large differences in the projected end of year biomasses from the different structures and data types, it is unfortunate that there is little corresponding difference in the negative log-likelihoods. This suggests that there is either insufficient information in the data being used in the objective function or that work is required to find a model which can more adequately represent the population.

Structure 5 represents a clearer distinction between the mature sub-stocks, as in structure 4 a fish can be mature in the north for several years before migrating to the south. Mark-recapture data have shown that cod in Icelandic waters display strong loyalty to spawning grounds (Pampoulie et al. 2006) which would suggest that S5 is a more suitable model of the stock structure. The spatially aggregated end of year spawning stock biomass predicted from S5 is also closer to that of the single area model, although that alone cannot be taken as proof that S5 is the better model. With its potential for greater flexibility in modelling biological characteristics and the indications that it may be the better structure the following analysis focuses on results from models with two mature sub-stocks.

6.6 Two stock models: model behaviour

Use of a statistical modelling framework enables the modelled population to be compared with direct observations of the population as well as being able to plot population summaries such as total biomass or abundance. These direct comparisons can be used to identify deviations in the modelled population from the observations, indicating where improvements can be made to the model structure. By modelling the mature fish in the north and south as separate sub-stocks they can have different characteristics such as growth rates or weight-length relationships.

Various small changes to the two-stock model were found to make little difference to the predicted biomass. These included estimating separate growth rates for the mature fish in the north and south, some changes to the likelihood data files and reducing the time period of the model.

End of year biomass trajectories are shown in figure 26 for three two-stock models along with a single area model. The two-stock models are: alternative 1 has a single value of the growth rate, alternative 2 has separate growth rates for the two mature stocks and 89+ starts in 1989 rather than 1984. Differences between these models are mainly due to the start of the time series and in a forward projection model the first year is expected to have the greatest parameter uncertainty. The model starting in 1989 also has a similar trajectory for most of the time series — the exception being again for the first two years. It is encouraging that the more complex models optimise to solutions which generate essentially the same population trends regarding not just the total biomass but also the age 4+ biomass and spawning stock biomass.

The area disaggregated biomass is shown in Figure 27 for alternatives 1 and 2. As all the immature population is in the north (and the north is geographically a larger area), it is not surprising that the total biomass is greater in the north with more than 60% of the biomass (Figure 28). The proportion of the initial spawning stock biomass in the north is, however, higher than might have been expected. The survey indices for length group 3 show high abundance for the north at the start of the time series (Figure 15) but this group includes many immature fish. The Spring survey age-length frequency data used in the objective function starts in 1989, despite the survey starting in 1985, as sampling prior to 1989 was not random. Starting the model in 1989 generates trajectories from 1989 onwards very similar to those for the same time period from the models started in 1984. Additional indices could be used which would provide more information on the

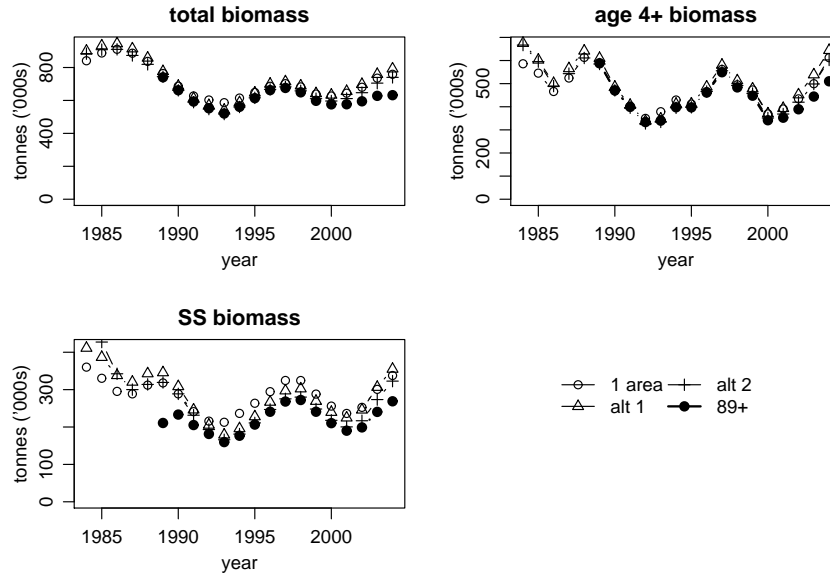


Figure 26: End of year biomass trajectories for both areas combined for two alternative two stock models and a single area, single stock model. Alternative 1 has the same growth rate for both mature stocks whereas alternative 2 has a separate growth rate for mature fish in the south. Total biomass, age 4+ biomass (assumed fishable biomass) and spawning stock biomass.

distribution of the larger fish for the first few years. Alternatively, likelihood components could be created using data from fish for which the maturity stage is known.

The model fit to the length group 1 survey indices is good for both surveys and for all length groups in the north (Figures 29 & 30). Model fit to the Autumn survey groups 2 & 3 is poorer than for the Spring survey but the time series for these is much shorter and the fit to the single area model was also found to be relatively poor (Taylor et al. 2007). For both models the fit to the southern survey indices is worse than for the north. This is not surprising as the model does not take into account the presence of immature fish in the south. While these are a small proportion of the total abundance of immature fish, they do account for some of the fish in the likelihood data (including the survey indices) for the southern area and as such affect the ability of the model to fit to these data. The two sub-stock model might be improved by the addition of some immature fish to the southern area and the reintroduction of this type of behaviour to the model should be evaluated in future model developments.

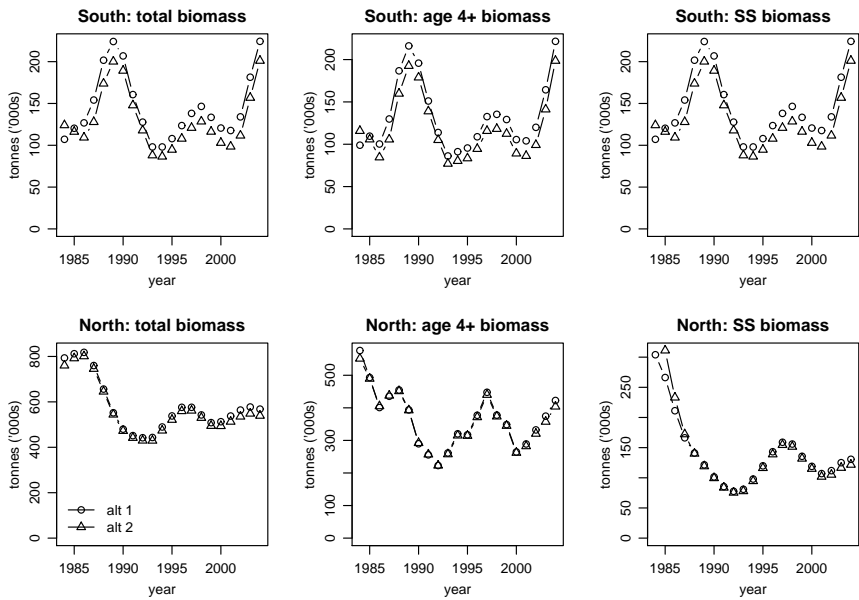


Figure 27: End of year biomass trajectories by area for two alternative two stock models models. Total biomass, age 4+ biomass (assumed fishable biomass) and spawning stock biomass.

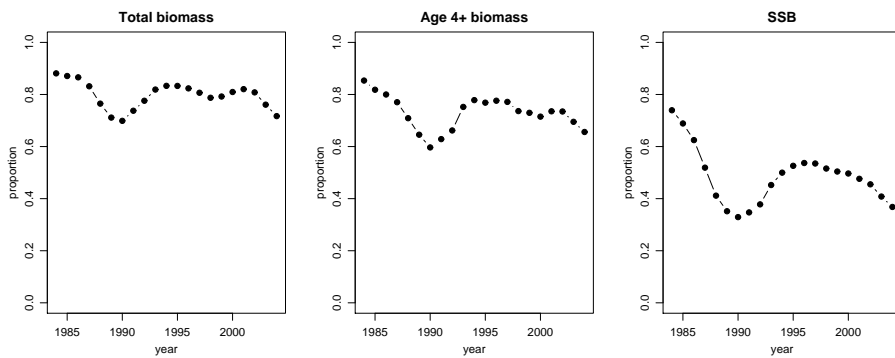


Figure 28: Proportion of the biomass in the north for the alternative 2 model for the total biomass, fishable biomass (age 4+) and spawning stock biomass.

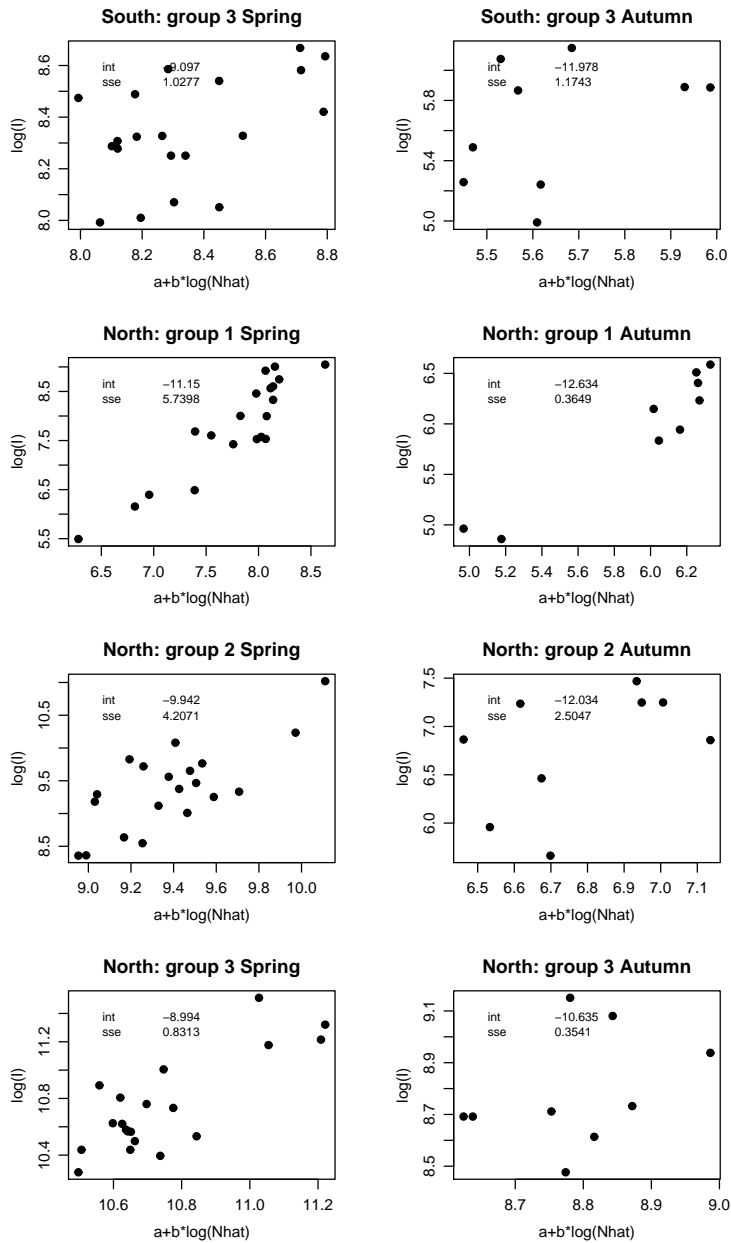


Figure 29: Plots of the log linear regression as estimated in Gadget for alternative 1, with one plot for each likelihood component and the $\ln(\text{catchability})$ is the intercept and sse given for each survey index. $\log(I)$ is the index and $a+b*\log(N)$ the fitted regression to the modelled population.

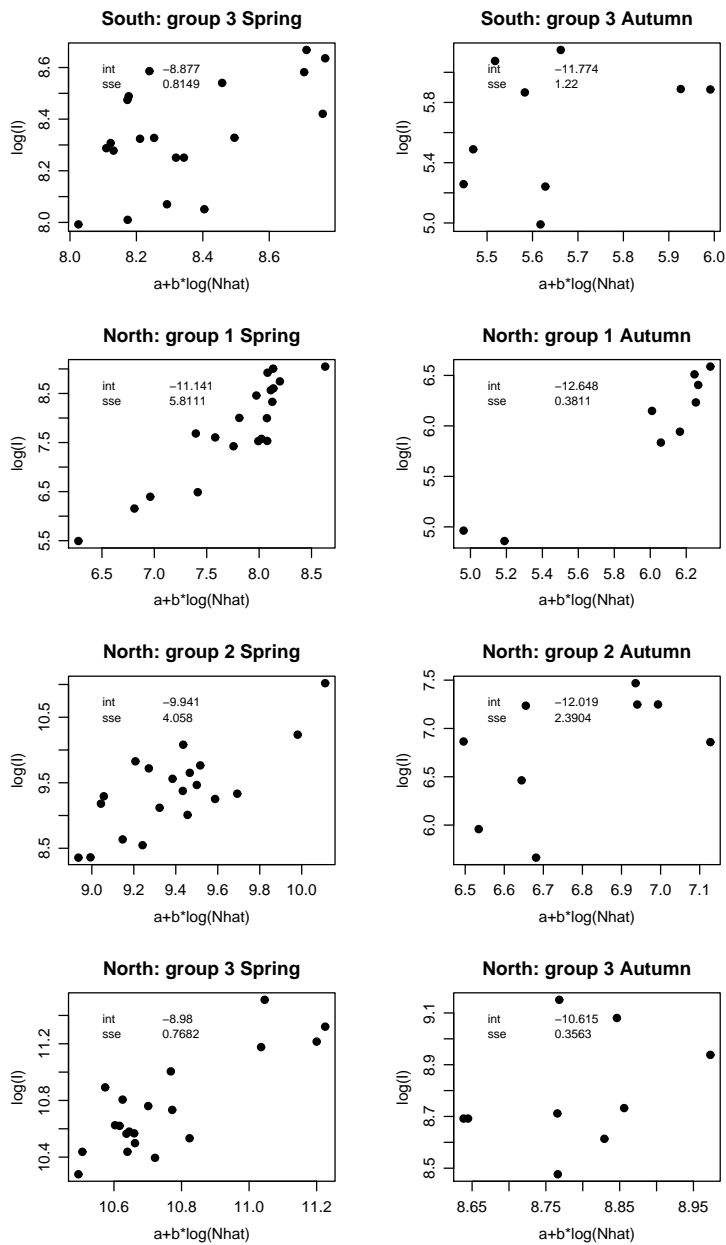


Figure 30: Plots of the log linear regression as estimated in Gadget for alternative 2, with one plot for each likelihood component and the $\ln(\text{catchability})$ is the intercept and sse given for each survey index. $\log(I)$ is the index and $a+b*\log(N)$ the fitted regression to the modelled population.

There is little difference between the catchabilities estimated for the alternative models (Tables 3 & 4) with the main differences for the south as the fit of the indices to the data will be affected by the estimation of a separate growth rate for the sub-stock in this area. For both surveys, the estimation of a faster growth rate has slightly increased the catchability of the fish.

| Survey | Index | Area | ln(catchability) |
|--------|---------|-------|------------------|
| Spring | group 1 | North | -11.15 |
| Spring | group 2 | North | -9.94 |
| Spring | group 3 | North | -8.99 |
| Autumn | group 1 | North | -12.63 |
| Autumn | group 2 | North | -12.03 |
| Autumn | group 3 | North | -10.63 |
| Spring | group 3 | South | -9.10 |
| Autumn | group 3 | South | -11.98 |

Table 3: Estimated catchability of the surveys by length group and area for the alternative 1 model.

| Survey | Index | Area | ln(catchability) |
|--------|---------|-------|------------------|
| Spring | group 1 | North | -11.14 |
| Spring | group 2 | North | -9.94 |
| Spring | group 3 | North | -8.98 |
| Autumn | group 1 | North | -12.65 |
| Autumn | group 2 | North | -12.02 |
| Autumn | group 3 | North | -10.62 |
| Spring | group 3 | South | -8.88 |
| Autumn | group 3 | South | -11.77 |

Table 4: Estimated catchability of the surveys by length group and area for the alternative 2 model.

If the likelihood scores of the models are compared directly (Figure 31) there is little to discriminate between these two models in their fit to the observed data, with the greatest difference in scores less than 20%. The added flexibility of the separate growth rate for the mature sub-stocks does however improve the fit of the model to most of the length distributions, age-length frequencies and age compositions.

The models can also be compared directly with a single area, single stock model, even though these data were not used in the optimisation process (Figure 32). Of the eight comparable components, even though the single area model is a better fit to six of the datasets, for most datasets there is little difference in the fit of the models to the data.

The fit of the model to the data for each timestep can be plotted (Figures 33 & 34) to highlight areas in which the model deviates from the observed data or indicate areas where the model flexibility could be increased.

For the Spring survey (Figure 33), the age composition has two outlying points for the south for 1990 and 1991 (and the age-length frequencies for 1991). These are considered to be years with immigration into Icelandic waters from Greenland (Shepherd and Pope 1993). These data would indicate that most of this immigration was into the south as there are no comparable outliers for the northern area, although the values are among the highest for the area. The length distributions and age-length frequencies display similar trends, with the fit to the data improving in the south over time but declining in the north.

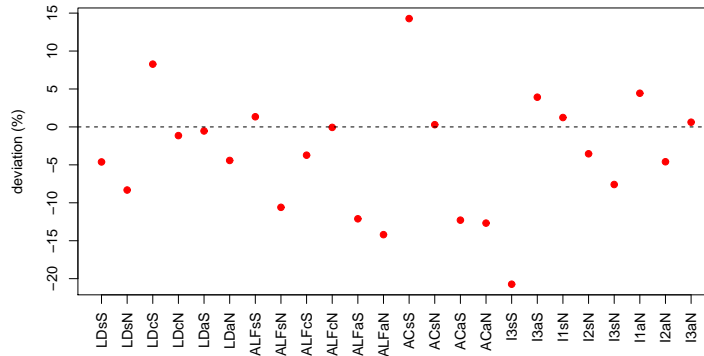


Figure 31: Deviation of model scores with two growth rates (alternative 2) from the equivalent model with a single growth rate (alternative 1). Scores below the zero line indicate that alternative 2 is a better fit to the observed dataset than alternative 1. LD: length distribution, ALF: age-length frequency and AC: age composition

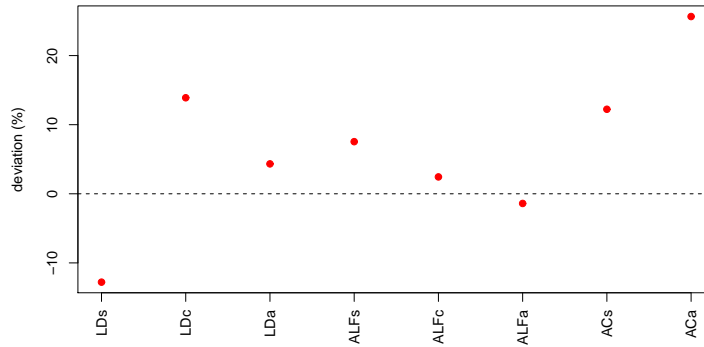


Figure 32: Deviation of alternative 2 (a two sub-stock, two area model) model scores from the single area model.

Conversely, the fit of the model to the Autumn survey age-length frequency data decreases in the north over time. Ideally, improvements to the model which increase the model flexibility and more accurately use the data would reduce the extent to which the different data sources are inconsistent.

The fit of the model to the age composition data (which were not used in the optimisation of the model) provides more detail to evaluate the modelled population. The observed age compositions from the surveys are plotted with the modelled age compositions in Figures 35 to 38. The model is capable of representing the different age structures (within the same age groups) in these two areas. These are years where the fit of the model to the data is poor, but the main instances of this is for the south in 1990 and subsequent years which can be associated with the immigration of age 6 fish into the south from outside Icelandic waters. For most years, and both surveys, the model is predicting a higher proportion of age 1 fish than there are age readings for. This could be due to the level of natural mortality assumed for these fish in the model, or an under

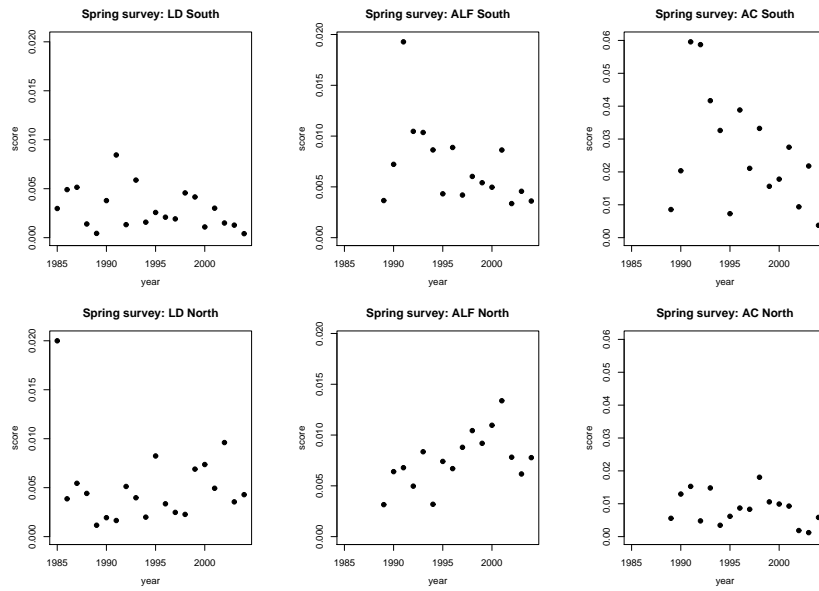


Figure 33: Likelihood scores (residuals) for the Spring survey for the alternative 2 model.

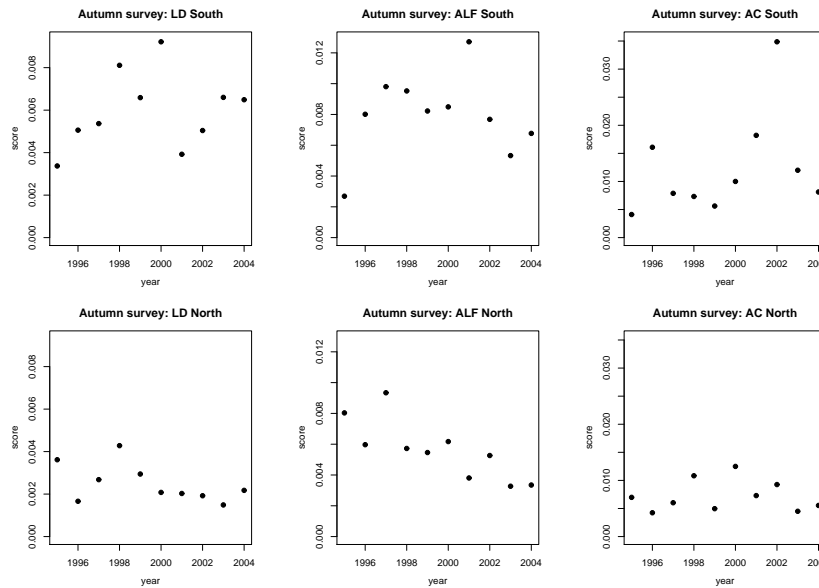


Figure 34: Likelihood scores (residuals) for the Autumn survey for the alternative 2 model.

representation of age 1 fish in samples for age reading. These data (along with the survey indices) indicate a more recent, but considerably smaller, immigration event than that in 1990 and 1991. In 2001, there were relatively few age 5 fish in the Spring survey (as this was a poor year class) but relative number increased by the Autumn survey and subsequently remained at a higher level. This agrees with the outlying point in the north group 3 survey indices (Figure 14). The model can be adapted to include these immigrations of fish into Icelandic waters and to estimate the abundance of immigrating fish.

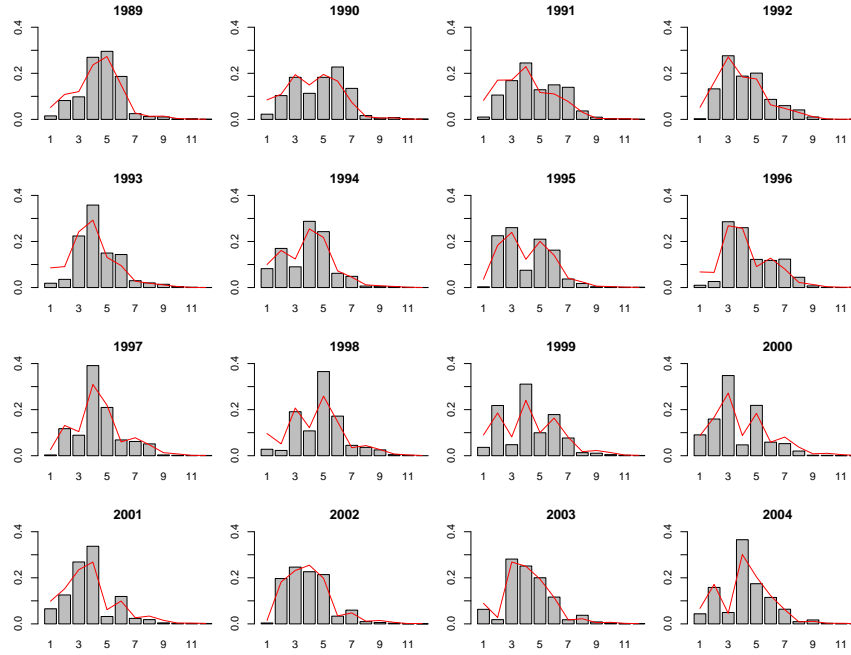


Figure 35: Age composition from the Spring survey in the north. Observed data as bars and modelled age structure as lines.

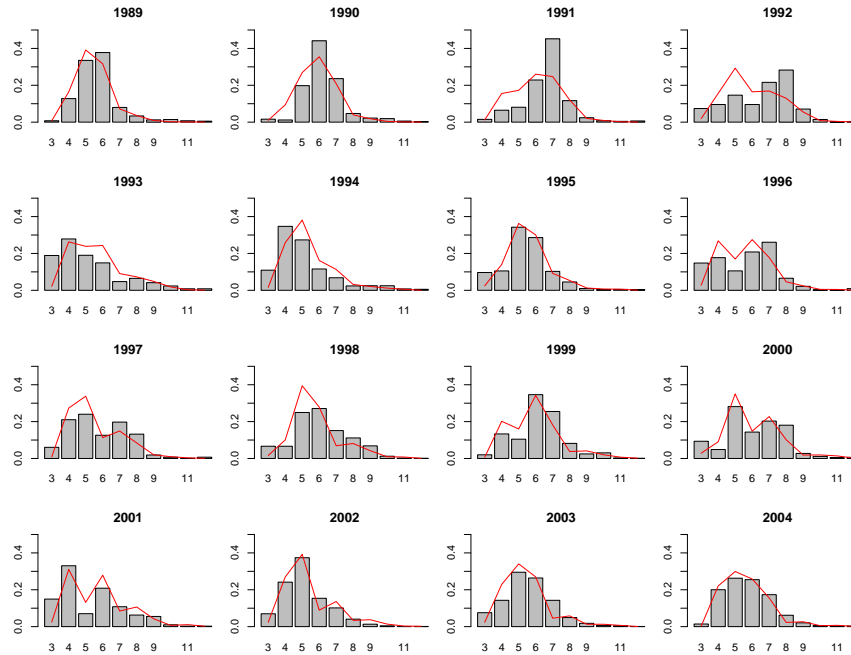


Figure 36: Age composition from the Spring survey in the south. Observed data as bars and modelled age structure as lines.

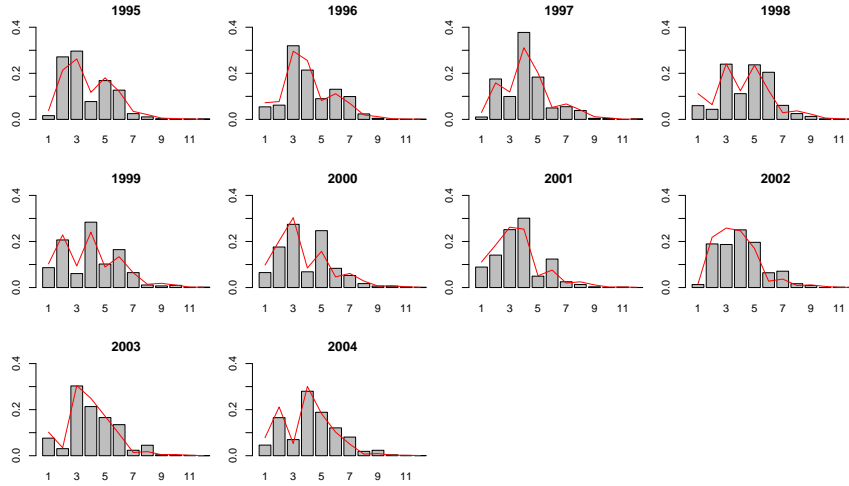


Figure 37: Age composition from the Autumn survey in the north. Observed data as bars and modelled age structure as lines.

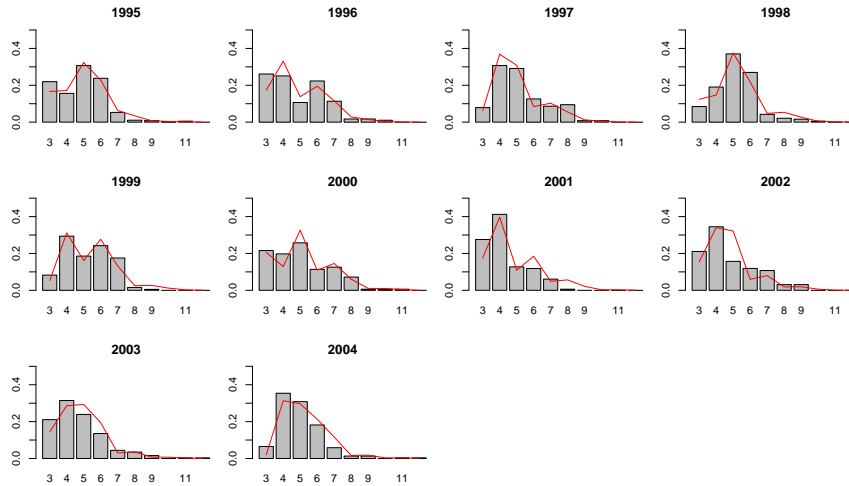


Figure 38: Age composition from the Autumn survey in the south. Observed data as bars and modelled age structure as lines.

6.7 Conclusions

Can model the cod population on two areas and predict similar total biomass as a single area model. The best models contained two mature spawning components. Simpler conceptual models for two areas performed considerably worse and led to optimisation problems, especially when spatially disaggregated sampling data included in the objective function. A clear finding is that the mature cod in the north are an essential component of a two area model.

These models have shown that it is not trivial to construct multi-area models and it should not be assumed that more complex multi-area models will necessarily be an improvement on single area models. The requirement to model migration, in particular migration dependent on size or stage requires that assumptions are tested rigorously. Statistical models such as can be developed in Gadget allow for the formal testing of model assumptions and evaluate what the data can prove and the behaviour which it cannot distinguish between. The flexibility of Gadget also makes it easy to construct a hierarchy of models with which the models can be compared and tested.

The basic two area two sub-stock models described here have the potential to be developed further but there are some aspects of the population which are harder to include in the model. While there is some evidence of different lengths of maturation for the two spawning sub-stocks, as there is a single immature component it is not possible to separate the maturation process in the model. In addition, in terms of the observed data, calculating maturity ogives for each area cannot be considered to represent the length at maturation as the south predominantly contains mature fish, whereas there are many immature fish in the north. Any ogive calculated for the northern spawning stock is affected by the presence of considerable numbers of immature individuals which when mature would spawn in the south. Spatially disaggregated maturity ogives can only be calculated for sub-stocks which do not mix and ideally for populations with the immature and mature occupying the same space.

The structure of the two area model includes an area (the northwest) where immature fish mix with the southern mature and possibly northern mature with the southern mature. In the context of cod-shrimp models, this area is outside the area of the offshore shrimp fishery and would ideally be excluded from a shrimp model. The structure of the two area model includes an area (the northwest) where immature fish mix with the southern mature and possibly northern mature with the southern mature. In the context of cod-shrimp models, this area is outside the area of the offshore shrimp fishery and would ideally be excluded from a shrimp model. Initial work on a simple three area model predicts similar biomass trajectories as the single area model for the whole area. The three area structure can be extended to allow for the migration of southern fish into the north-west for feeding. With this extension to the model, most of the key issues in the spatial structure of the population will be accounted for.

Initial work on a simple three area model predicts similar biomass trajectories as the single area model for the whole area. The three area structure can be extended to allow for the migration of southern fish into the north-west for feeding. With this extension to the model, most of the key issues in the spatial structure of the population will be accounted for.

7 Cod shrimp model

7.1 Introduction

The simplest manner in which to combine the cod and shrimp models is to have cod as predators of shrimp and other food, ignoring cod cannibalism. Cannibalism does not appear to have a large impact on the stock dynamics and with no cannibalism the cod parameters can be fixed to those from a single species model, substantially reducing the number of parameters estimated.

The preference for shrimp by cod, in Icelandic waters, decreases as predator length increases (Magnusson and Pálsson 1991) and as shown in figure 39. Magnusson and Pálsson (1991) also found that for small cod there is an increase in prey length as predator length increases. For some areas, predation on male shrimp is considered to exceed that on females as predation is largely by young cod Fu et al. (2001) and data from the north of Iceland indicate that most consumption of shrimp by small cod is on shrimp which are probably male.

Recent data indicate that shrimp constitute approximately 10% of the biomass in cod stomachs (figure 39) which is the same value found by Magnusson and Pálsson (1991). For both Icelandic waters (Magnusson and Pálsson 1991) and the Flemish Cap (Parsons et al. 1998) no significant relationship has been found between the stock biomass/CPUE of the shrimp fishery and the level of predation by cod.

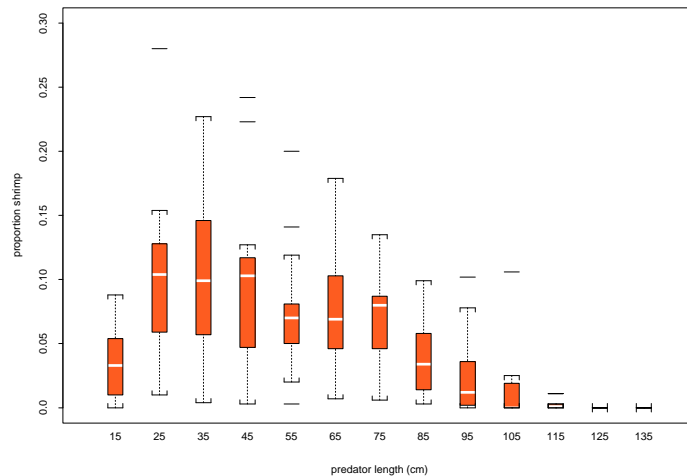


Figure 39: Boxplots of the proportion of shrimp in cod stomachs by predator length from the Spring groundfish survey.

In the stock production model of Stefansson et al. (1994) the consumption index was based on the abundance of the immature part of the cod stock. In this study, predation by cod on shrimp is considered in models of two spatial structures: a single area model with only immature cod as predators of shrimp and a two area model with all cod in the north as potential predators of shrimp.

7.2 Data and likelihood functions

The only data required in addition to those described previously are stomach content likelihood data:

- Species composition of stomach content data as ratios of prey biomass by species (ie shrimp or other) aggregated over all predator lengths from the Spring groundfish survey for 1988–2004.
- Species composition of stomach content data as ratios of prey biomass by species (ie shrimp or other) aggregated in predator length groups of 10cm from the Spring groundfish survey for 1988–2004. These data are only used for comparison and are not included in the objective function.
- Length distribution of prey by predator length groups as biomass ratios from the Spring groundfish survey for 1988–2004. Predators are aggregated into 20cm length groups and prey into 4mm length groups.

7.3 Cod–shrimp indices

In recent years, the number of cod being caught in the shrimp survey has increased markedly for all length groups (figure 40). As there is no corresponding increase in cod abundance over the whole of the north (figure 41) it appears that there must have been a change in the spatial distribution of cod in the north, for at least the summer (when the offshore shrimp survey takes place).

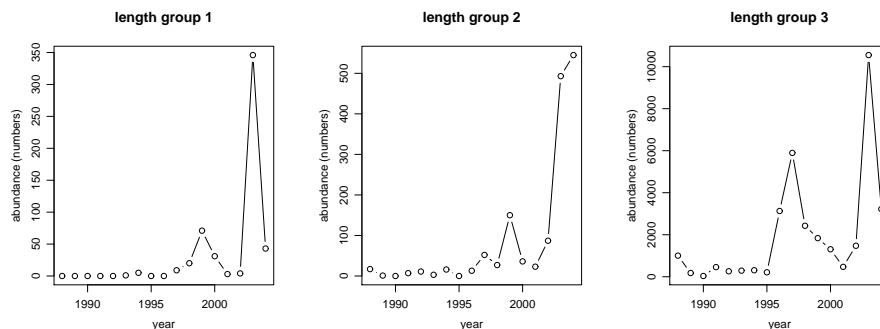


Figure 40: Offshore shrimp survey abundance indices of cod by three length groups (representing age 1, age 2 and age 3+ as described for the cod model).

Data indicate that preference of cod for shrimp is related to availability of shrimp (figure 42). Even comparing data from the Spring survey (for stomach data) and shrimp survey the correlation is 0.48. Despite restricting the data from the Spring survey to areas of the offshore shrimp fishery the spatial coverage of these surveys is not the same and they take place at different times of the year. As the the long tows of the shrimp survey lead to problems with using the cod stomach content data, the Spring survey data are considered more appropriate.

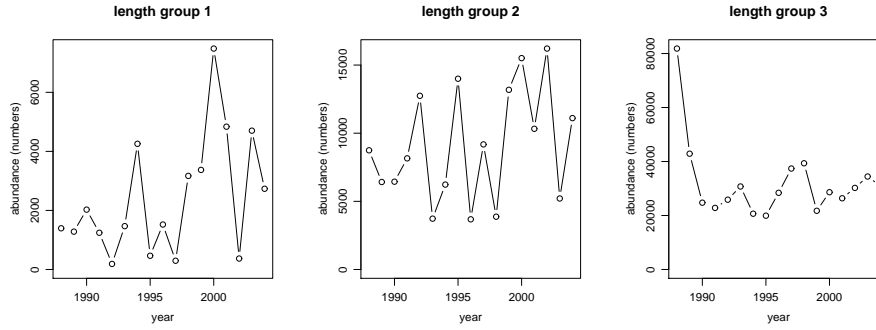


Figure 41: Spring survey abundance indices of cod in the north (areas 103, 104 & 105 in figure 1) by three length groups (representing age 1, age 2 and age 3+ as described for the cod model).

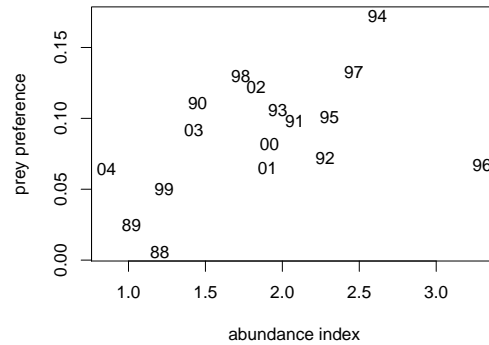


Figure 42: The proportion of cod stomach contents (biomass) which are shrimp (from the Spring survey) versus the abundance of shrimp in the offshore shrimp survey.

7.4 Model Implementation

As the assumption is that shrimp do not affect the cod population, cod parameters were fixed to those estimated from an equivalent single species cod model.

The implementation of consumption is described in Taylor et al. (2004) for cod cannibalism and the approach is similar for the two species model with maximum consumption fixed to half the maximum measured by (Jobling 1988) in feeding experiments on cod. The predator-prey length suitability parameters were fixed with a single otherfood parameter estimated and otherfood is constant for all steps and years.

The stocks are structured as for the single species models described earlier. There are five fleets: a commercial fleet targeting each species, two cod surveys and one shrimp survey. The time frame of the model is from 1988 to 2004 as this is the period for which shrimp data are available.

The cod-shrimp model is implemented either on one area or two areas. In the single area model, all juvenile cod are potential predators of shrimp but mature cod do not consume shrimp. With two areas, all cod in the northern area are predators of shrimp and shrimp are only present in the northern area.

7.5 Results: single area model

In a single area model with only juvenile cod as predators of shrimp, the consumption by cod of shrimp is closely related to the total biomass of shrimp (figure 43) ie changes in the modelled cod population have less impact than changes in the modelled shrimp population. Throughout the modelled time period, consumption of shrimp is considerably greater than the landings from the shrimp fishery (figure 43). As for the single species model, the modelled shrimp biomass does not display the marked drop in shrimp abundance observed by the shrimp survey.

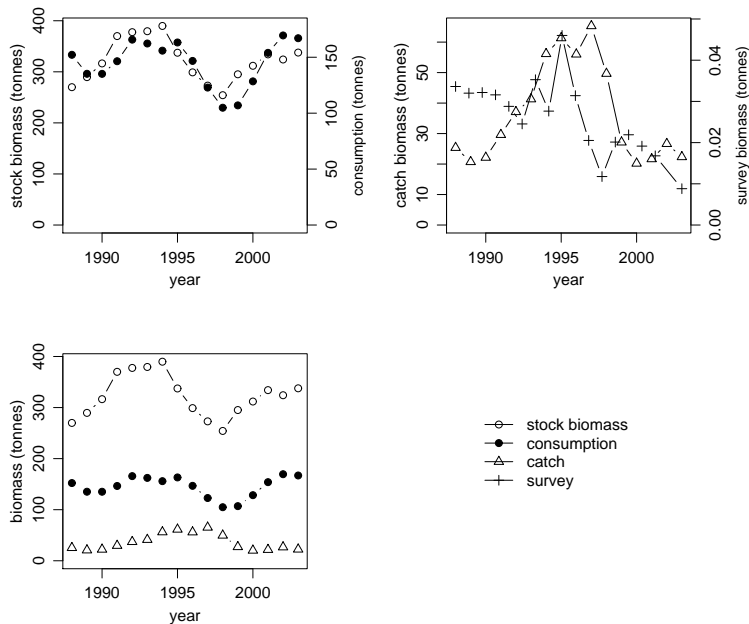


Figure 43: Modelled shrimp biomass, modelled cod consumption of shrimp and shrimp landings from the fishery.

The modelled cod preference for shrimp by predator length is shown in figure 44 and compared with observed data (not included in the objective function) in figure 45. The modelled results are unsurprisingly much smoother than the stomach content data which are a notoriously noisy data type. The overall trend indicates that the model is able to replicate not only the trends in the data but also the length structure preference for shrimp. The main deviations from the data are for the smallest and largest cod, which are also the length groups for which the least data are available.

If the time series of cod preference for shrimp in the Spring survey is considered (which was included in the objective function) then, while the data are much noisier than the modelled results, the model represents the overall trend in the data (figure 46). The main difference between the model and the data is that the model overpredicts preference for shrimp at the start of the time period. As the preference for shrimp is strongly related to shrimp abundance, this might indicate that the model is overpredicting shrimp abundance at the start of the time period.

The fit of the model to the survey indices from both the juvenile bag and main net shows that the model is over predicting the number of small shrimp in the survey (length groups 1 and 2 and to a lesser extent group 3) at the start of the time period (figures 47 & 48). It can be seen from the indices however, that these shrimp are required by the model to account for the number of shrimp in the larger length groups later in the model. The overprediction at the start in the indices agrees

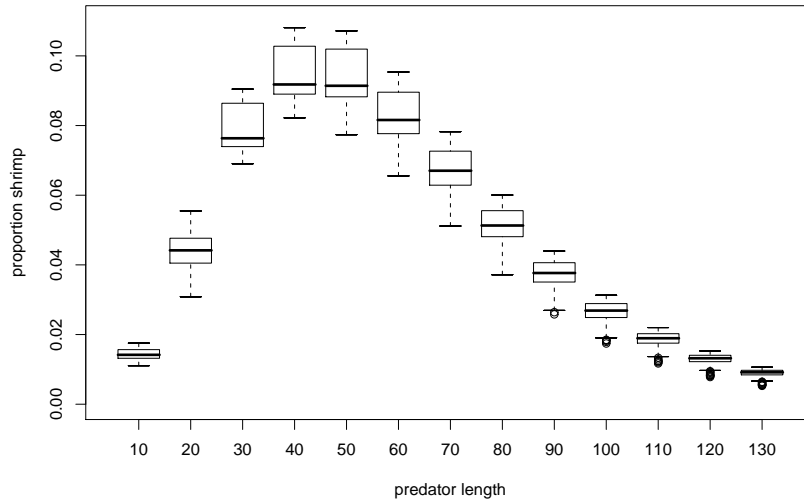


Figure 44: Modelled preference of cod for shrimp by predator length.

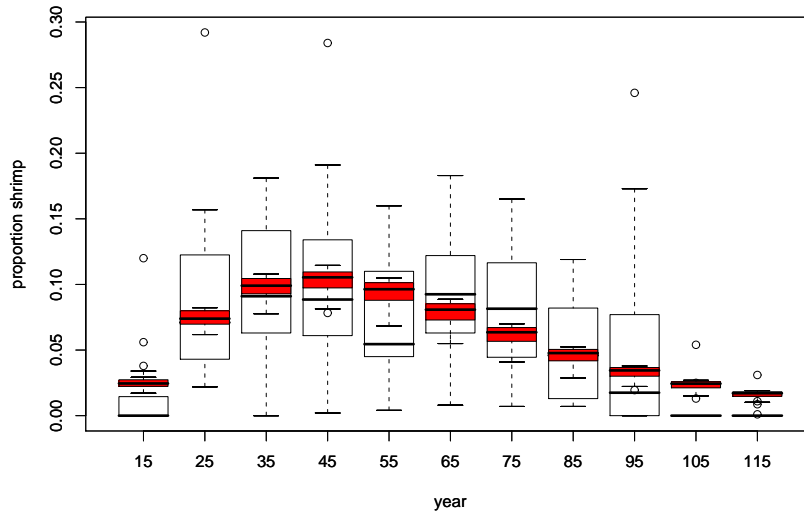


Figure 45: Modelled preference of cod for shrimp by predator length compared with observations from cod stomachs.

with the overestimate of cod preference for cod at the start of the time series (figure 46).

Ideally, the inclusion of cod predation in a model of shrimp should improve the fit of the model to the observed data. If not then the validity of the model is in doubt or there is no indication of the importance of that form of predation in controlling the population dynamics of the prey species. In this case including cod predation in a model of shrimp population dynamics improves the fit of the model to many of the likelihood components (figure 49). The use of shrimp likelihood components is identical between these models (with neither including a biomass index or a total shrimp abundance index in the objective function) except for the inclusion of stomach data in the

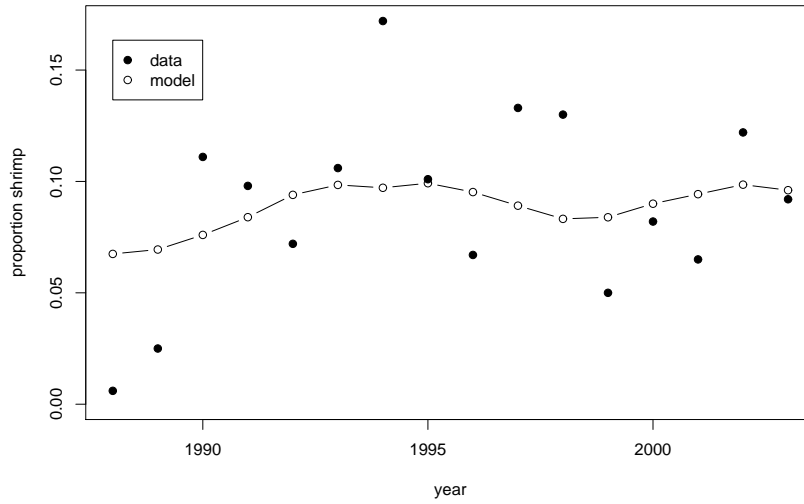


Figure 46: The biomass proportion of shrimp in cod stomachs from the Spring survey. The data are shown by points and the model by the line.

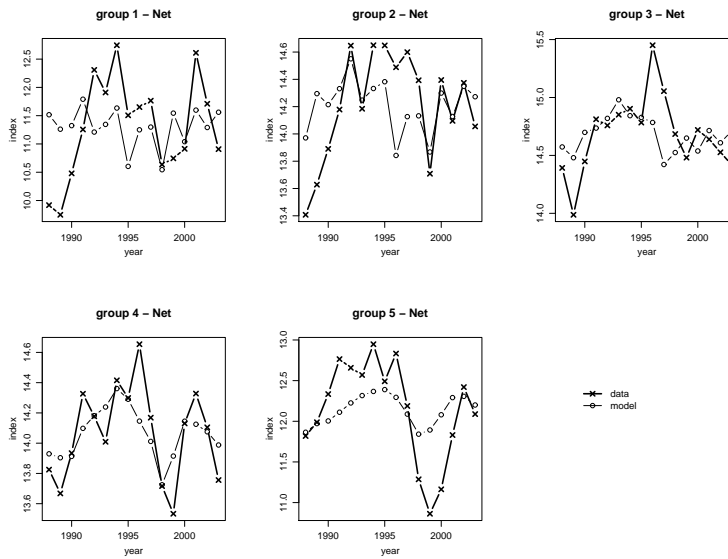


Figure 47: Time series plots of the fit of the model to the survey index data for the main net of the offshore shrimp survey.

predation model. The only component included in the objective functions for which the single species model is a better fit to the data is the largest survey length group. This might be in part to the relatively low preference of juvenile cod for shrimp of this size. It should be noted that adding a likelihood component to the objective function reduces the impact of the original likelihood components. As most of the original likelihood components are a better fit with consumption, this is a strong indication that the inclusion of cod predation is a better representation of the shrimp population dynamics.

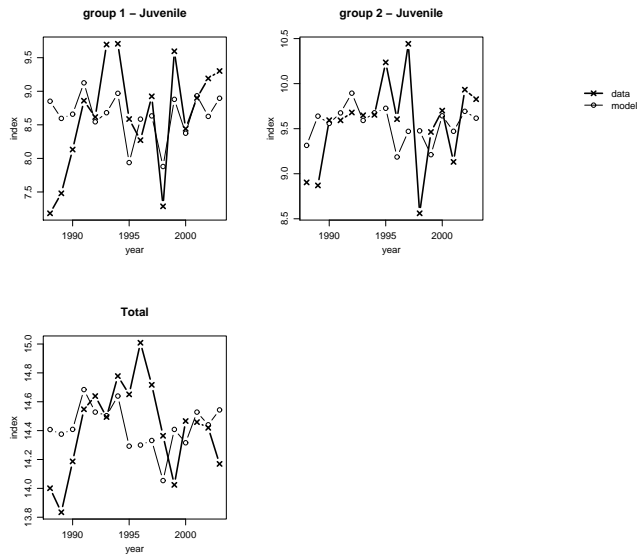


Figure 48: Time series plots of the fit of the model to the survey index data for the juvenile bag and the total abundance of shrimp in the offshore shrimp survey.

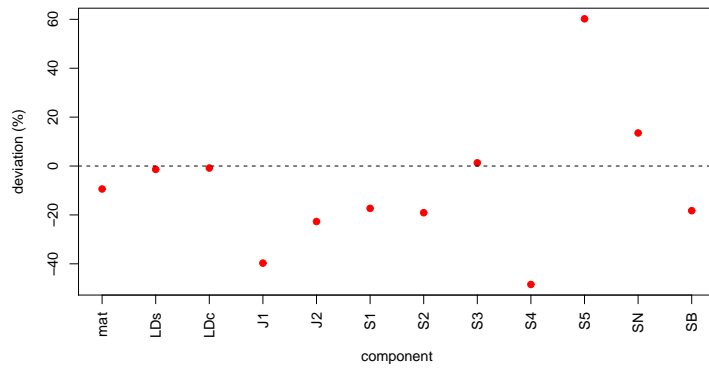


Figure 49: Difference in likelihood component scores between two equivalent shrimp models. The difference is expressed as the percentage difference between the single species and two species models as a percentage of the single species model.

7.6 Results: two area model

The 2 area model is a poorer fit than the single area model to all the shrimp survey indices (figures 50 & 51). Comparison of the end of year biomass trajectories for the single and 2-area models shows that despite similarities in the biomass of immature cod in the north and the total amount of consumption, the modelled shrimp biomass is considerably greater in the 2-area model (figure 52). Some of this difference could be due to optimisation problems with the 2-area model requiring further parameter optimisation. In addition, starting the the 2-area model in 1989 rather than 1988 could have caused some problems. It should be noted that the single area model displays an increase in consumption in the final years (as the number of juveniles increases), whereas this does not occur in the 2-area model. This increase could help with the fit to the shrimp indices as overpredicting biomass in the final years is a fault of the models without predation.

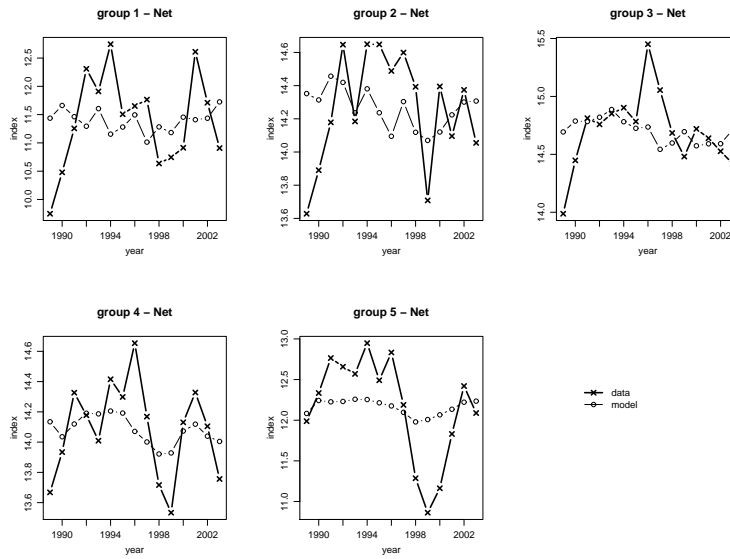


Figure 50: Time series plots of the fit of the model to the survey index data for the main net of the offshore shrimp survey.

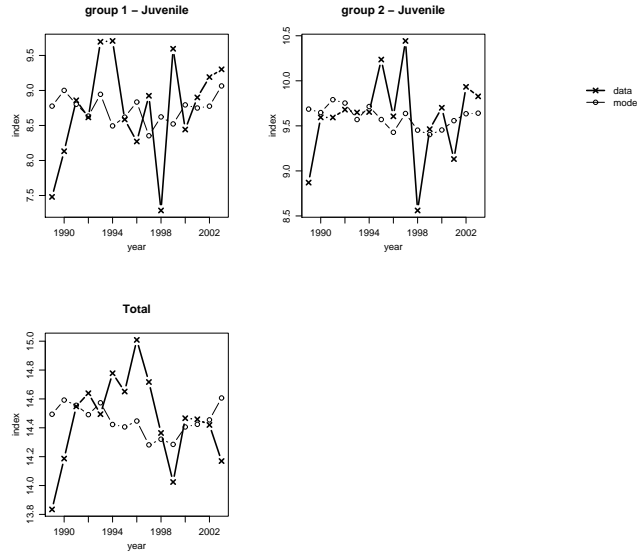


Figure 51: Time series plots of the fit of the model to the survey index data for the juvenile bag and the total abundance of shrimp in the offshore shrimp survey.

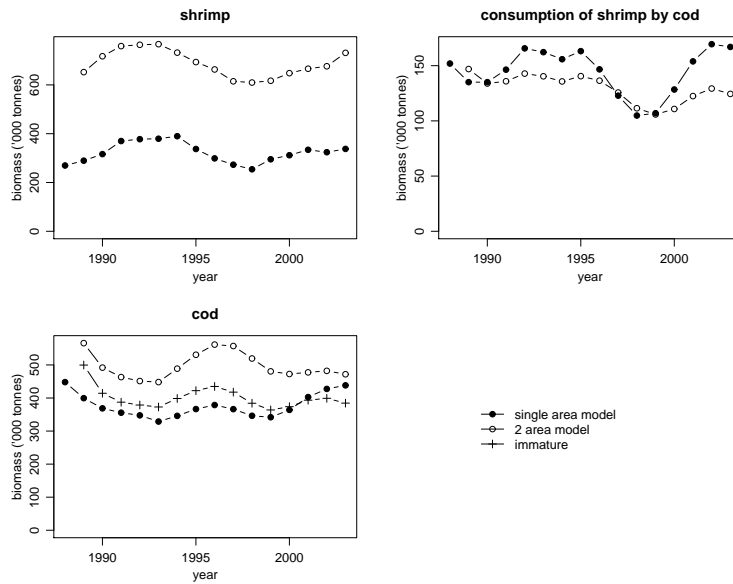


Figure 52: Time series plots of the fit of the model to the survey index data for the main net of the offshore shrimp survey.

8 Discussion

8.1 Shrimp

The single species shrimp model consistently estimates sex change and growth parameters from data in the objective function. This capability is very important as it removes the requirement to assign ages to the shrimp outside of Gadget. By assigning ages externally, bias can be introduced as the external age calculations would not take into account the length based selection of the survey gear or the impact of length based selection by the shrimp fishery on the population.

The fit of the model to the survey indices, however, is more problematic. While the model can fit to the larger shrimp survey indices, fitting to the smaller shrimp causes more problems with the model overpredicting the abundance of shrimp in length groups 1 and 2 at the start of the modelled time period. At the same time, however, the model under predicts the stock biomass at this time. Some of these problems may, in part, be due to the rather inconsistent and noisy data from the offshore shrimp survey as shown in figure 4 to 6. The survey consists of long tows (which can be variable in length) over a several weeks and the time period taken to complete the survey has varied over time. These factors could have contributed to some of the irregularities in the data. Naturally, taking the variable mortality inflicted by cod on shrimp into account may diminish some of these inconsistencies.

8.2 Two area cod

Simpler modelling scenarios of two area cod population dynamics are inadequate. They cause optimisation problems and perform more poorly than more detailed models. Two mature spawning components are necessary and even a simple model of sub-stock structure improves the fit of the model to spatially disaggregated data. The presence of mature cod in the north was found to be an essential if the model is to fit spatially disaggregated data.

The methodology used here highlights the importance of testing models with data. In particular, some commonly made assumptions regarding the length/age structure of the Icelandic cod population are too simple if a model is required to fit to spatially disaggregated data. These models also indicate the additional problems when assumptions need to be made regarding less understood phenomena such as migration. It is considerably more straightforward to model the length structure and abundance of a global population rather than to construct a model which accounts for seasonal migration and the resulting spatially disaggregated length structure.

Spatially explicit models provide additional information on the interaction between the fishery and population which is not available from single area, single stock models. In particular, spatial and temporal information is available on fishing mortality. An important aspect of constructing models such as these in Gadget, is that the statistical modelling framework allows for the formal testing of whether additional model flexibility is required. It is also a useful tool in highlighting discrepancies between the modelled and observed population.

Many extensions and elaborations of these models are possible. For example, the importance of separating the fleet into different gear classes may be of greater importance with two area models than single area models.

Initial work on a simple three area model predicts similar biomass trajectories as the single area model for the whole area. The three area structure can be extended to allow for the migration of southern fish into the north-west for feeding. With this extension to the model, most of the key issues in the spatial structure of the population will be accounted for.

These models indicate that this approach to sub-stock modelling has the potential to be an extremely useful tool in modelling the spatial structure of populations.

8.3 Cod and shrimp

Any simple model of the relationship between cod and shrimp requires some degree of compromise. A model is, after all, an abstraction. There are two main strategies by which models of cod and shrimp can be combined: a simpler option with cod predation of shrimp limited to immature cod or to construct spatially explicit models of cod population dynamics with all cod in the relevant area predators. The latter requires models which can represent the size/age dependent migration patterns of cod in Icelandic waters. As predation is a length based process, it is particularly important that the modelled length structure of the predator is reasonable.

As for the single species shrimp model, the cod–shrimp model overpredicts the abundance of small shrimp at the start of the time period (and the total abundance). Given that the relationship between the proportion of shrimp in cod stomachs and the shrimp survey indices is so strong and that these years are not outliers it does seem that the model is overpredicting the population at this time and it is not a problem with the indices (figures 42 & 46).

The single area predation model, with only juveniles as predators of shrimp improves the fit of the model to most of the shrimp likelihood data compared with the single species shrimp model. This shows that cod predation is an important facet in modelling shrimp population dynamics and that to a certain extent the predation model is correct. The consumption data also shows that the model is able to reflect the main dynamics of these populations and the relationship between them.

The two area model is also capable of representing the main aspects of the cod–shrimp relationship but the model fit to the shrimp data is poorer than that of the single area model. In all cases, however, shrimp consumption by cod is significantly greater than landings by the shrimp fishery.

It is possible that the preference of cod for shrimp is not entirely length dependent and that older cod display a lower preference for shrimp than juvenile cod, in which case the single area model is a more appropriate model of cod–shrimp predation. Alternatively, the single area model is a better model of cod than the more complex two–area model. An additional problem with the two–area model could be the additional time required to optimise the model and a longer optimisation might be required. It is known that statistical models can have a problem reducing abundance if started with the abundance at too high a level. Given that the level of consumption for the two–area model is similar to that of the single area model further optimisation of the model is required.

As the models indicate the importance of cod predation on the shrimp population, the rapid change in the abundance of cod in the offshore shrimp survey should be expected to be of importance in modelling shrimp. As the overall pattern of the cod population in the north does not display the massive increase in cod, a more spatially detailed model would be required to include this behaviour. Given the complications and assumptions required in modelling migration this is not a trivial task.

Acknowledgements

Much of the work described here was undertaken while the author was employed at the MRI (Marine Research Institute, Reykjavik) and uses data from the MRI databases. The Gadget code has been in development for more than a decade by many programmers at the MRI and IMR (Institute of Marine Research, Bergen). The work was supported in part by EU grants dst² (QLK5-CT1999-01609), METACOD (QLRT-2000-00953) and BECAUSE (FP6 TP8.1 502482), as well as a grant from The Icelandic Centre for Research (Rannis).

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