# EVALUATION OF LONG-TERM OPTIMAL EXPLOITATION OF COD AND CAPELIN IN THE BARENTS SEA USING THE BIFROST MODEL

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## Introduction

The multispecies model for the Barents Sea Bifrost (Boreal integrated fish resource optimisation and simulation tool) has evolved over a long time. The main problem for management of the Barents Sea capelin stock is that since the capelin dies after spawning the logical management variable is the spawning stock, for which there are no measurements. One has to rely on modelling the spawning stock's evolvement from the yearly measurement in September to spawning in April. The starting point was a single species model for capelin that was used in what probably was the first evaluation of a target reference point in the ICES area (Hamre and Tjelmeland, 1982). In this model – CAPELIN – the dynamic entity was number of capelin by age. Later, in recognition of the different dynamics of male and female capelin, the number by age was distributed on sex (Tjelmeland and Bogstad, 1993). This model (CAPSEX) was then the foundation of Multspec in which the capelin model framework was parameterised for different species which were connected through a predation module (Tjelmeland and Bogstad, 1998). The emphasis was on the dynamics of the predation of pre-spawning capelin by cod. Even if Multspec as a multispecies model was more complex than CAPSEX, limiting the management-related study to this subsystem was tractable because during the modelled period there also was conducted a cod-directed survey. Thus, the cod dynamics could to a large extent be disregarded. Multspec had area structure and a migration module and was used for estimating the predation mortality prior to spawning during the yearly assessment of the capelin stock. Bifrost is in many respects a step back from Multspec, in that the area structure is removed in order to make the model a more robust and versatile instrument for management-close multispecies analyses in the Barents Sea.

The management of Barents Sea capelin is in practice conducted using the spreadsheet based model CapTool (Gjøsæter et al., 2002), which gets its dynamics from Bifrost. There is thus an unbroken line of model development since 1982 that always has been close to the assessment and management of Barents Sea capelin.

The present-day management of Barents Sea capelin has a multispecies basis in that the consumption by cod in the pre-spawning period of capelin is accounted for. In the present paper, the cod-capelin dynamics is extended throughout the year. Also, a recruitment module for cod is added. When there is a large year class of Norwegian spring spawning herring in the Barents Sea, the recruitment of capelin is severely hampered (Gjøsæter, 1998). The herring stock is assessed with the model SeaStar (Tjelmeland and Lindstrøm, 2005) and during prognostic simulations Bifrost and SeaStar are connected, so that the herring model used in Bifrost is essentially the same as the SeaStar prognostic simulation. Bifrost is thus now a multispecies simulator with which harvesting control rules in the cod-capelin-herring system can be studied.

Figure 1 shows the development of cod 1+ biomass from 1946, from the Arctic Fisheries WG assessment. Good recruitment conditions in 1962-1964 and 1969-1970 led to a temporary increase 1966-1977. However, the general trend is a decline since 1946 that lasted until 1982, after which the stock has stablized. The present yield form the stock is much smaller than it was in the period 1946-1982. This may naively be interpreted as the catch regulations in the recent period preventing good catches. There may be two alternative interpretations of recent history. One interpretation is that the present regime is different in that decreased harvesting of harp seals and minke whales – both preying on cod – and increased harvesting of capelin – which is the most important food item for cod – gives smaller prospects of yield from the cod stock than in the pre-1982 period. The other interpretation is that the yield before 1982 was not sustainable. The spawning stock was kept so small by fishing that the recruitment on the average failed to replenish the stock.

The value of the spawning stock for future recruitment is crucial to the management of the stock, as the size and structure of the spawning stock is the way humans affect future stock development. In order to properly understand the spawning stock – recruitment dynamics one must understand the cannibalism on the pre-recruiting part of the stock. This is a multispecies problem, in that large abundance of alternative food (e.g. capelin) partly may shield cod recruits from cannibalism. It is an important part of the present paper to clarify the spawning stock – recruitment relation in cod by estimating recruitment parameters taking cannibalism on pre-recruiting cod into account.

**Input data**

The capelin stock is surveyed in a joint Russian-Norwegian survey with 4 vessels each September (Gjøsæter, 1998). The vessels follow a pre-agreed sailing plan. Using a model for the uncertainty connected to this survey (Tjelmeland, 2002) survey replicates by year, age, length and sex are constructed prior to any Bifrost estimation of parameters.

The joint IMR-PINRO stomach content data base (Bogstad and Mehl, 1997) comprises nearly 200 000 stomachs, most of them from cod. For each predator the stomach content has been grouped on capelin, cod and other food. Since the evacuation rate depends on the temperature, the temperature from the closest station is added to each stomach content data point. If there is no temperature station near by, the closest temperature station in an adjacent year is used, scaled with the difference of temperature between the two years as observed in the Kola section data.

The stomach evacuation rate of cod has been measured in laboratory experiments at the university of Tromsø (Santos and Jobling, 1992). These data are used in yearly calculations of consumption of various prey species by cod (Bogstad and Mehl 1997) using the expression:

$$consumptionModelCod = \ln 2 \frac{S_i^{\xi} W^{\delta} e^{\gamma T}}{S_0^{\beta} \alpha_i}$$

where $S_i$ is the stomach content of species *i*, W the weight of the predator, $S_0$ the total stomach content immediately after the last meal and $\alpha_i$ a species-specific constant. $\xi$, $\delta$, $\gamma$, $\beta$ and $\alpha$ are parameters that are estimated from laboratory data.

This expression, however, involves the initial meal size, which is not known in the field. Following the argument of Temming and Andersen (1994) a consumption model without the initial meal size is fitted to the data by forcing $\beta$ to zero during the estimations. Repeated estimations are performed and the replicates stored for later use by Bifrost. It should noted that when $\xi$ is zero, the stomach size dependency is represented by the parameter $\xi$, which is estimated. When $\xi$ is different from 1 (exponential model), the stomach content data cannot be summed before the estimation of consumption is carried out, but must be treated individually.

**Calculation of consumption**

The parameters in the predation function are estimated by comparing modelled consumption to consumption calculated from stomach content data. In addition, comparison between modelled and estimated stock abundance at October 1 has some bearing on the predation parameters. Exogeneously to the model, replicates of consumption per cod by age and degree of maturation is calculated quarterly using the following information:

> Stomach content data
> Replicates of evacuation rate parameters
> Temperature from stations, with uncertainty
> Swept area estimates of cod

The area dimension is necessary because it cannot be assumed that the stomach sampling is in proportion to cod abundance. The calculations are done several times, each time drawing temperature data from the assumed distribution and each time using a different replicate of evacuation rate parameters. The replicates of consumption per cod are stored on file for later use by Bifrost.

When the empirical consumption is calculated for the likelihood terms, the consumption per cod is multiplied to the number of cod of the appropriate maturation degree using number at age from the Arctic Fisheries WG assessment.

**Estimation of parameters**

There are two different classes of parameters, those that are determined iteratively on historic data and those that are estimated using a likelihood function. This distinction is purely practical. In each simulation run during likelihood estimation the historic period is run 10 times, during which the number of cod recruits as 0 year old, the number of 1-group capelin and the residual mortality of capelin are found iteratively. The number of modelled 0-group is scaled so that the modelled number of 3 year old cod matches the number of 3 year old cod from the assessment. The number of 1-group capelin is scaled so that the simulated number of 2-group capelin matches the measured number of 2-group capelin the following year. The residual mortality of 1-4 year old capelin is determined to that value which yields the number

of 2-5 year old capelin the next year. Thus, the number of recruits of both cod and capelin are consistent with consumption of cod and capelin by cod.

Parameters other than residual mortality of capelin, capelin 1-group and cod recruits are simultaneously estimated using maximum likelihood estimation. The probability of observing the data, given the model is correct, can be partitioned by data sources:

$$L(obs|par) = L_{cap}(obs_{cap}|par) \; L_{cons}(obs_{cons}|par)$$

L is the likelihood of the observations, i.e. the probability of having observed the actual data, given that the model formulation is correct and that the parameters *par* have correct values. $obs_{cap}$ is the number of 4 year old capelin, females and males taken separately. Only the period 1973-1980 has been used for the capelin observation data in the likelihood. In this period the population dynamics of capelin was relatively stable, and problems caused by a possible sex-dependent mortality are probably less severe. $obs_{obs}$ is the exogeneously estimated consumption of capelin, cod and other food in the period 1984 and later. $L_{cap}$ is the probability of observing the capelin data and $L_{cons}$ is the probability of observing the exogeneously estimated consumption. The parameters *par* are described in the sections below.

The assumption of a normal distribution of data on log-basis is used throughout. The standard deviations of the capelin data and the consumption are parameters that are estimated along with the biological parameters. In the present version of the Bifrost model the information about uncertainty in the exogeneously estimated consumption that is inherent in the number of stomachs used in each quarter and in each year is not used, so that outliers stemming from too few stomach content data can have unduly large weight in the estimation.

**Maturation**

For cod and herring, the proportion mature at age is taken from the VPA data during simulations over the historic period. For capelin, for which the mature and immature part of the stock are considered different dynamic entities, the following length-based model is used:

$$m(l) = \frac{1}{1 + e^{capelinP_1(capelinP_2 - 1)}}$$

where *capelinP1* and *capelinP2,* which are both sex-dependent, are parameters that can be estimated from data. *capelinP1* is fixed to 0.6 for both males and females, a value that is commonly obtained when the above function is estimated on empirical maturation data. *capelinP2* is estimated. Here, as elsewhere in the paper, the name of parameters and variables is the same as used in the model software, although sometimes abbreviated.

For the prognostic period, the proportion mature by age for capelin is taken from the pool of estimated proportion mature by age during the historic period. For herring the proportion mature by age is kept constant. For cod, a model for maturation as function of biomass, temperature and individual weight is used. Figure 2 shows the proportion mature at age during the historic period, from which the tendency to earlier maturation in later years (Nakken, 1994) is evident. Figure 3 shows the proportion mature as function of stock biomass

and weight for each age group. The proportion mature is modelled as a linear function of total biomass, temperature and weight at age:

*codOgiveAtAge = codOgiveConstant + codOgiveTemperaturePar codOgiveTemperature + codOgiveBiomassPar codOgiveBiomass + codOgiveWeight weightAtAge*

*codOgiveConstant*, *codOgiveTemperaturePar*, and *codOgiveBiomassPar* are parameters that are estimated from historic data for each cod age group in each prognostic iteration. *codOgiveTemperature* is the mean yearly temperature at the Kola section.

## Growth models

The weight at age for capelin during prognostic simulations is taken from historic data, selected at random for each year prognostic year. Alternative runs where the historic period is used cyclically have been performed, and show no significant deviation in mean long-term yield from the runs where the weight at age has been drawn at random. Thus, neglecting possible autocorrelations does not seem to be a serious deficit.

Strong year classes of cod tend to be distributed further east, thereby experiencing slower growth (Michaelsen et al 1998). This form of abundance dependence should not be confused with abundance effects related to consumption. Figure 4 shows the weight as function of SSB the year before for different age groups. Each point has been coloured from blue to red according to the mean temperature along the Kola section the year before.

It is difficult to see a definite temperature effect, so the model for weight at age for cod is given by:

codWeightAtAge = codWeightAgeConstant + codWeightAgeBiomass (0.6 – codSSB) + codWeightAgeCapelin capelinConsumption, codSSB > 0.6
codWeightAtAge = codWeightAgeConstant + codWeightAgeCapelin capelinConsumption, codSSB < 0.6

*capelinConsumption* is the total consumption of capelin in the preceding year, *codSSB* is the spawning biomass of cod, *codWeightAgeConstant* and *codWeightAgeCapelin* are constants that are estimated from historic data for each cod age group in stochastic iteration run.

The weight at age for herring during prognostic runs is assumed constant.

## Recruitment models

The capelin recruitment model has a Beverton-Holt formulation with effects from herring, cannibalism, and 0-group cod in the denominator. Thus, predation on the capelin recruits determines good or bad recruitment conditions, but does not affect the asymptotic value. The temperature effect is made a proportional effect, affecting the asymptotic value as well as recruitment for medium and low values of the spawning stock. The mathematical formulation of the number of capelin recruits is:

$$capMax * e^{capTemp*tempdiff} \frac{SSB}{capHalf + cap\Pr ed + SSB}$$

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where:

$$capPred = capHerProp(herring + capHerOffset)^{capHerExp} + capCodProp * zeroCod + capcapProp * capelin$$

SSB is the capelin spawning stock biomass, *capelin* is the biomass of capelin that may be considered predators on 0-group capelin, *tempdiff* is the difference between the mean temperature during August-December and the mean temperature during January-April in the Kola section. Herring is the biomass of young herring in the Barents Sea, taken as herring of age 1 and age 2 in the VPA, *zeroCod* is the 0-group cod from the model, *capHerProp*, *capHerOffset*, *capHerExp*, *capCodProp* and *capCapProp* are parameters that are estimated prior to a prognostic run.

Figure 5 shows modelled and measured recruitment as 2 year old capelin. The mean value of $R^2$ for the prognostic runs is 0.83. Figure 6 shows modelled and measured recuitment when cannibalism on cod is not modelled. The mean value of $R^2$ is 0.78. It is clear from comparing the two figures that the cod's predation on juvenile cod affects the predation on capelin and hence the capelin recruitment model.

There is no built-in predation term in the recruitment model for cod, because the historic simulated 0-group is consistent with subsequent consumption by cod until the recruits are 3 years. As for capelin, the recruitment model for cod is built on the Beverton-Holt formulation. However, the spawning stock effect is made a power function of the spawning stock, thus accommodating a somewhat more flexible formulation. As for capelin, a temperature effect is built into the proportional term. Also, effects of mean age and mean weight are built into the proportional term. The rationale for building in mean age is the possibility that older females have a higher value as parents because of their large eggs and longer spawning time (Solemdal, 1997). The rationale for building in mean weight is the possibility of a higher degree of skipped spawning when the condition is poor (Filina, 2002). In Icelandic cod the spawning stock-recruitment relationship is improved by including age information of the spawners (Marsteinsdottir and Thorarinsson, 1998) and a simulation study shows that the recruitment deteriorates when the percentage of repeat spawners falls (Scott et al., 1999). Using mean weight as a (inverse) proxy for skipped spawning has also an age effect. However, skipped spawning occur at a larger frequency for younger fish. These amendments of the recruitment function are key activities in the joint IMR-PINRO programme "Evaluation of long-term yield of cod" (Filin and Tjelmeland, this symposium). The recruitment model is:

$$codMaxRec * e^{codTemp*temp + meanWeightPar*meanWeight + meanAgePar*meanAge} \frac{SSB^{codExpRec}}{codHalf^{codExpRec} + SSB^{codExpRec}}$$

*codTemp*, *meanWeightPar*, *meanAgePar*, *codHalf* and *codExpRec* are parameters that are estimated from data during each prognostic run. *temp* is the mean temperature in the Kola section during August-October, *meanAge* is the mean age and *meanWeight* is the mean weight.

Figure 7 shows the modelled recruitment and the VPA age 3 as function of SSB. Figure 8 shows the modelled recruitment and the VPA age 3 as function of SSB without modelling effects from temperature, mean age or mean weight. Figure 9 shows the modelled recruitment vs. VPA age at 3 years without modelling cannibalism. Figure 10 shows the modelled

recruitment vs. VPA age at 3 years without modelling effects from temperature, mean age, mean weight or cannibalism.

The mean value of $R^2$ without modelling cannibalism or including temperature, mean weight or mean age is 0.17, see Figure 10. When temperature, mean weight and mean age is included it is 0.59, see Figure 9, when cannibalism is included it is 0.50, see Figure 8, and when all of the factors temperature, mean age, mean weight and cannibalism are included, $R^2$ is 0.78, see Figure 7. Attempts of estimating the spawning stock -recruitment relation for cod have earlier resulted in values of $R^2$ well below 0.30 (Godø, 2003). An $R^2$ of 0.43 was obtained using total lipid content, wind stress and temperature as explanatory variables (Matrshall et al., 2000). Those regressions were performed for a considerably longer time series of data, however. Sparholt (1996) demonstrated that the number of recruits of Baltic cod must be evaluated by a multispecies model (MSVPA) in order to achieve good recruitmet models, as the present result demonstrates this also seems to be the case for North-east arctic cod.

**Predation**

In the model, cod is a predator on cod and capelin. Other predation interactions are capelin and herring preying on capelin larvae, but those interactions are built into the recruitment function for capelin.

Predation is determined on the one hand by the spatial overlap between predator and prey and on the other hand by the density of the predator and prey stocks in the overlap area. Bifrost has no explicit spatial structure. However, the geographical extent of both capelin and cod are dependent on stock size, and it may be necessary to take into account the dynamics of the size of the overlap area. Both the part of capelin that overlaps with cod and the part of cod that overlaps capelin, as well as the feeding level, are modelled with functions of the form $\dfrac{abundance^k}{cons\tan t^k + abundance^k}$, where *constant* and *k* are to be determined from the data.
Figure 11 shows an example of how the overlap model may be interpreted. As the capelin abundance increases, the capelin area (yellow) expands and the overlap (magenta) between cod and capelin increases. As the cod abundance increases, the cod area (blue) expands northwards, aslo increasing the overlap. The total area (red), which determines the area density of other food is assumed constant with size 1.

The predation by cod on capelin is modelled by:

$$consumptionCapelinByCod = P\,F\,\frac{capelinFood}{totalFoodCapelinArea}$$

where P is the predation pressure exerted by cod on capelin and F is the feeding level of cod in the overlap area. Here:

$$P = maxConsCod * predationAbilityCodOnCapelin * overlapping$$

$$\mathrm{F} = F = \frac{totalFoodCapelinArea^{consExponent}}{halfCodExtension^{consExponent} + totalFoodCapelinArea^{consExponent}}$$

$$predAbilityCodCapelin = \sum_{age} suitCap * codN * (1 - codOgive) * (1 - svalbComp) * codW^{0.801 + codWExp}$$

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$$overlapping = partOfCapelinOverlappedByCod * partOfCodOverlappingCapelin$$

$$partOfcapelinOverlappedByCod = \frac{capelinFood^{capExtensionExp}}{halfCapelinExtension^{capExtensionExp} + capelinFood^{capExtensionExp}}$$

$$partOfCodOverlappingCapelin = \frac{codBiomass^{codExtensionExp}}{halfCodExtension^{codExtensionExp} + codBiomass^{codExtensionExp}}$$

*suitCap* represents the size-specific suitability for cod consuming capelin and is a vector where the first two element (ages 0 and 1) are zero, the third element (age 2) is 0.5 and the elements for older ages are 1.0. The cod starts eating capelin at age 2 (Dalpadado and Bogstad, 2004). However, further studies are needed in order to establish the suitability for age 2 on data, and the value of 0.5 remains at the moment somewhat speculative. *codN* is the number by age of cod, *codW* is the weight at age of cod, *svalbComp* is the proportion by age of cod that during the first quarter reside in the Svalbard area (B. Bogstad, pers comm). *consExponent*, *halfCodExtension*, *codWExp*, *capExtensionExp*, *halfCapelinExtension*, *codExtensionExp*, *halfCodExtension* are parameters that can be estimated from data.

Cannibalism is one of the potential most important processes for cod dynamics. For relatively long-living species having highly dynamic recruitment cannibalism can be an important source of food (Longhurst, 1999). Usually, cannibalism is incorporated into the recruitment function using a Ricker model. In Bifrost, cannibalism is modelled directly as cod is one of the food items of cod, and the recruitment as 3 year old cod is thus dependent not only of the consumption of juvenils by adult cod, but also of the relative abundance of juvenile cod with respect to capelin and other food.

**Simulation**

The investigation of harvesting control rules is based on 150 years of prognostic simulation, where the first 50 years are discarded to avoid initial effects. Maturation and weight at age of cod are explicitly modelled, as is recruitment for all stocks. For processes that are not modelled (e.g. temperature, maturation and residual mortality of capelin), the values used during prognostic runs are drawn at random from the historic values. If, alternatively, these entities are used cyclically, the results do not differ much. Hence, neglecting a possible autocorrelation in these variables does not seem to be a serious problem.

**Harvesting control rules**

The simulations have been performed with a target spawning stock of capelin of 0 (removing capelin from the system), 0.25, 0.50, and 1.5 million tonnes and F-value for cod of 0.125, 0.4, 0.75, 0.875, 1.0, 1.125 and 1.25 relative to current exploitation. Figure 12 shows the mean longterm catch of cod and capelin for F-values for herring of 0.125, 0.20 and 0.30. The maximum long-term yield of cod corresponds to a fishing mortality of about half the current fishing mortality, and the optimal fishing mortality is about constant, irrespective of the fishing mortality applied for herring. However, as the fishing mortality for herring increases, the long-term yield of cod increases substantially for all levels of fishing mortality of cod, due to increased availability of capelin.

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Naturally, the long-term yield of capelin increases substantially with increased fishing pressure on herring. In order to maintain an average capelin yield above 0.5 million tonnes, the fishing pressure on cod should not be reduced from the present level.

The long-term yield of herring is 0.81, 0.73 and 0.46 million tonnes for F-values of 0.125, 0.20 and 0.30, respectively. The present-day F-value on herring of 0.125 is nearly optimal, and increasing the fishing pressure above this reduces yield of herring considerably.

It should be noted that the strong dependence of long-term yield of cod on the fishing pressure on herring (and thereby on the availability of capelin) mainly is an effect of the capelin partly shielding cod recruites from cannibalism. Only to a little extent does the effect of capelin abundance on cod growth contribute to the long-term yield, in the present model. The amount of other food is kept constant during all model runs, and it may be dubious whether this assumption holds true when the cod stock gets very large.

It should be noted that the present work is preliminary. Sub-models and estimation procedures can be significantly improved. Therefore the presentation in this paper has deliberately been made somewhat sketchy. I believe the main result that the fishing pressure on cod must be lowered in order to obtain maximum long-term yield will stand the test of time, however. Whether the low maximum long-term yield calculated here of about 0.4 million tonnes will change when the model is improved, for instance by including cannibalism for cod of age 3 and older, remains to be seen.

**Bifrost and Russian-Norwegian efforts to estimate long-term yield of cod**

Bifrost is a simulator for cod, capelin and herring in the Barents Sea, where the interaction between these species has been taken into account, and in the present paper it has been demonstrated that it can be used to evaluate 3-species harvesting control rules. The Russian-Norwegian Fishery Commission has mandated IMR and PINRO to evaluate the long-term yield of cod taking into account the interaction between species and the influence from the environment. Formally, Bifrost could be used for that purpose as it stands. However, other multispecies models may be as useful. Bifrost relies solely on estimating historic consumption by cod from stomach samples, while the Russian model STOCOBAR (A Filin, this symposium) uses stomach content data only for partitioning consumption on species, while the total consumption is estimated from the observed weight increase. Both approaches should be tried and compared before the final choice of multispecies model is made.

A part of the future work with Bifrost should be to include the effect of consumption on growth in the likelihood function, thereby bringing it closer to STOCOBAR. Also, effects from harp seals and minke whales on capelin and cod should be included, using results from the corresponding sub-projects (see below).

The formally comprehensive results regarding longtime yield from a multispecies model should not distract the attention from the fact that a chain is not stronger than its weakest link. A multispecies model is comprised of a number of sub-models, some of which deal with interactions between species, some of which deal with processes pertaining to a single species. The IMR-PINRO response to the request from the Commission is to define subprojects in which sub-models can be built from studies of historic data. The results from

these sub-projects (e.g. skipped spawning in starving cod, eggs from older cod more viable than eggs from younger cod) will be used in several multispecies models. As the work goes on, the results from the sub-projects are also combined into a model that evolves with the project – EcoCod. This model can also serve as a candidate for the final multispecies model.

## Implementation in management

Once the general guideline for management is found by long-time simulation the question arises of implementation in the year to year management. As pointed out by Walters and Punt (1994) the best way of conveying the uncertainty to managers is by using a graph that shows the risk of not meeting the objective next year as function of catch. In the present context of a 3-species harvesting control rule, in order to arrive at a single-valued objective value must be attributed to the catch of each of the species. This is complicated by the fact that the stocks are shared between countries which may want to value the species differently, depending on the use of catches in each country. This complication might partly be avoided by the two countries delivering fish and fish products on the world market, but still large regional differences may prevail (e.g. the use of capelin). Thus, aiming at a comprehensive management where the species interactions are taken into account may lead to complications in the economic domain, where the countries must co-operate. Also, the biological science must connect to the economic science in order to provide adequate background for managers.

In recent years, the question whether large fishing pressure leads to evolutionary changes has arisen. Heino (1998) discusses management implications of evolutionary evolving fish stocks using a simple simulation model as example. The technical problems of extending this type of simulations to a more complicated management-oriented model like Bifrost should be modest.

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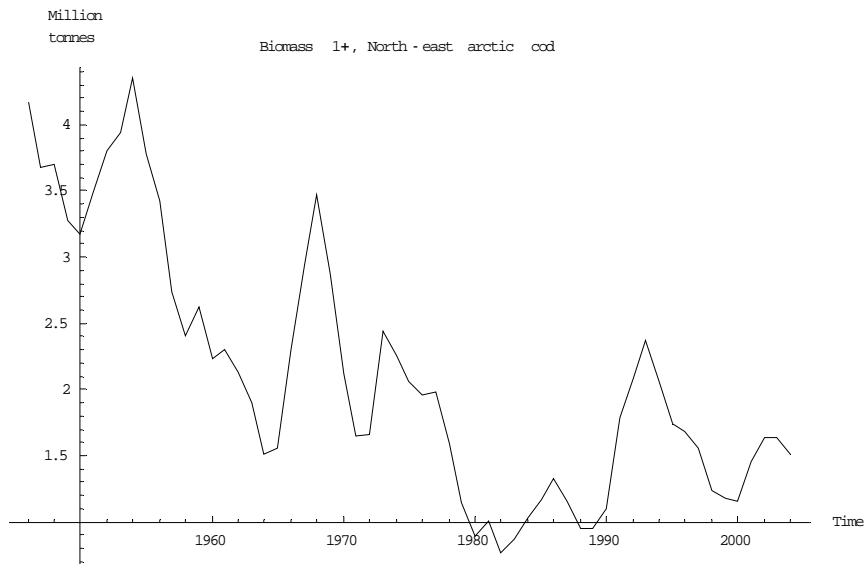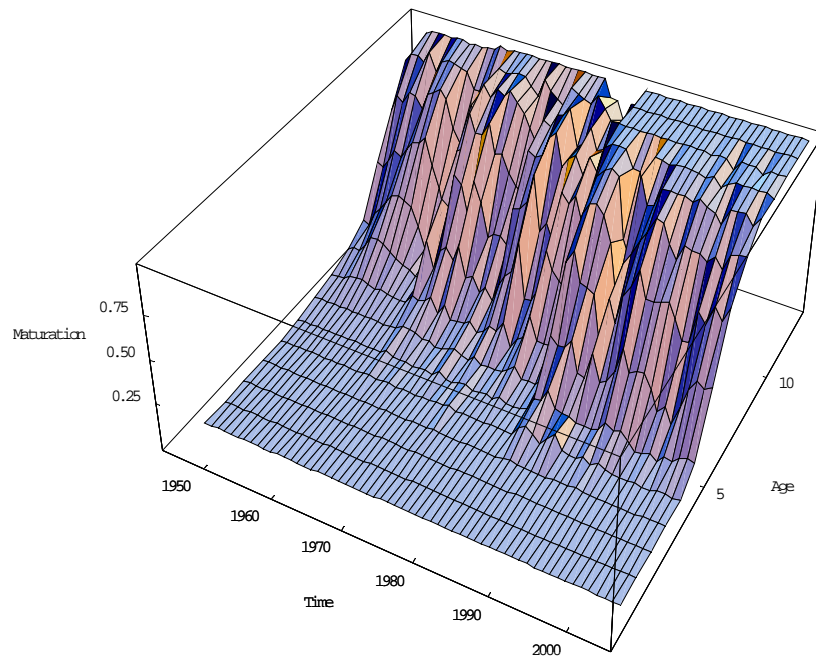
Figure 1. Biomass of 1+ cod, VPA data



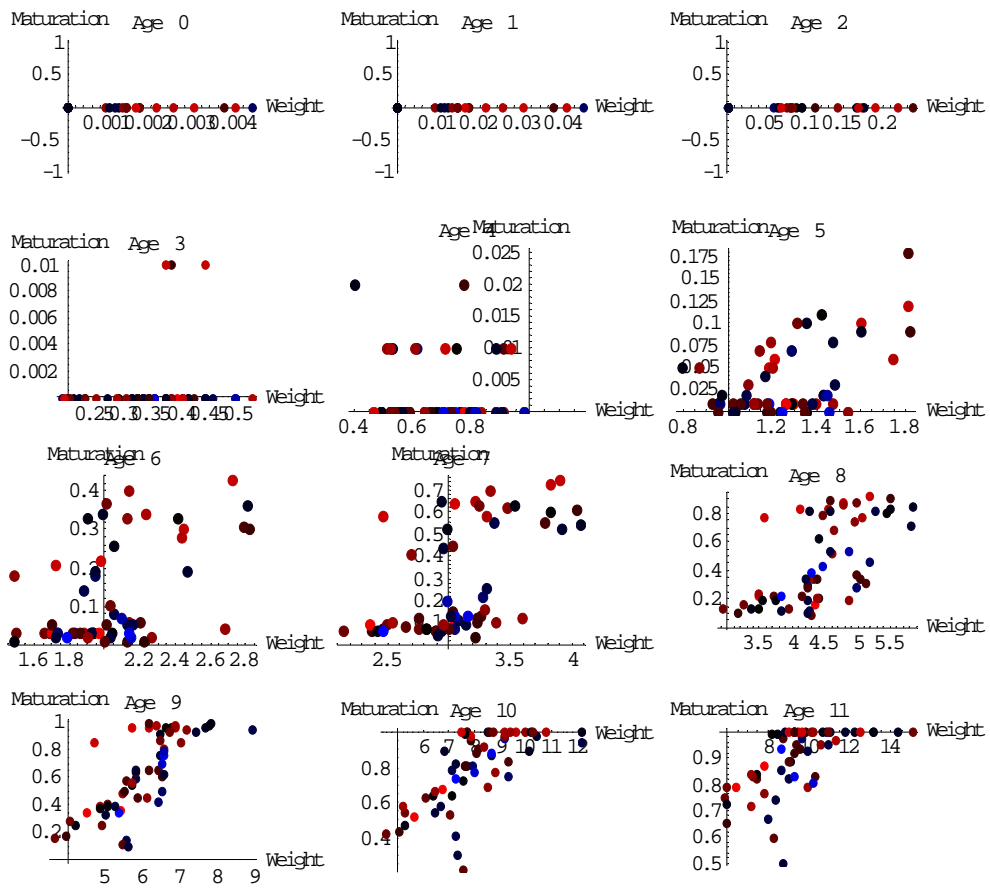Figure 2. Proportion mature for cod, VPA data.

Figure 3. Proportion mature for cod as function of individual weight for different age groups, VPA data. Points are coloured according to temperature, red is warm, blue is cold.
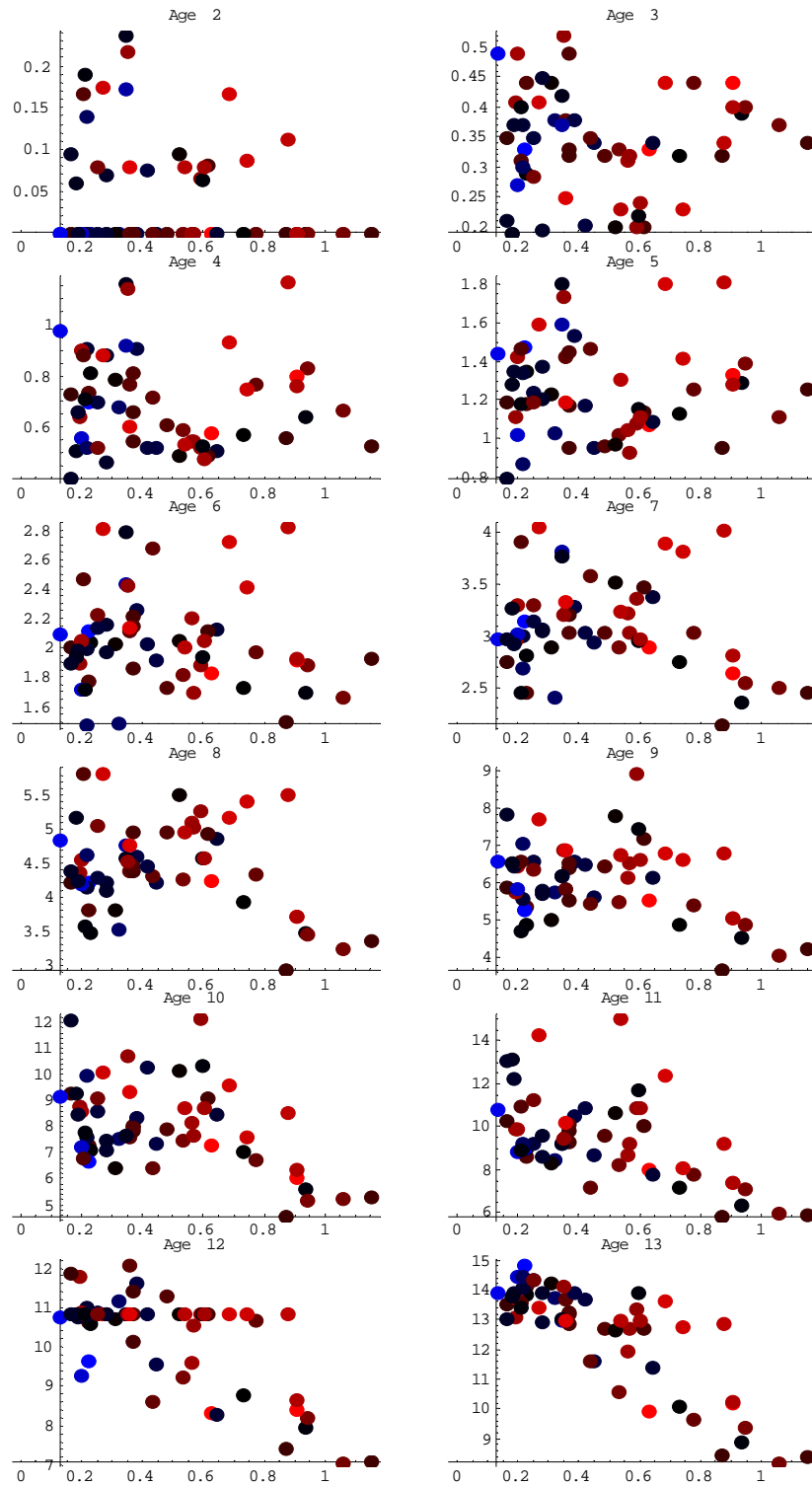
Figure 4. Individual weight of cod vs SSB for different age groups. Points are coloured according to temperature, red is warm, blue is cold
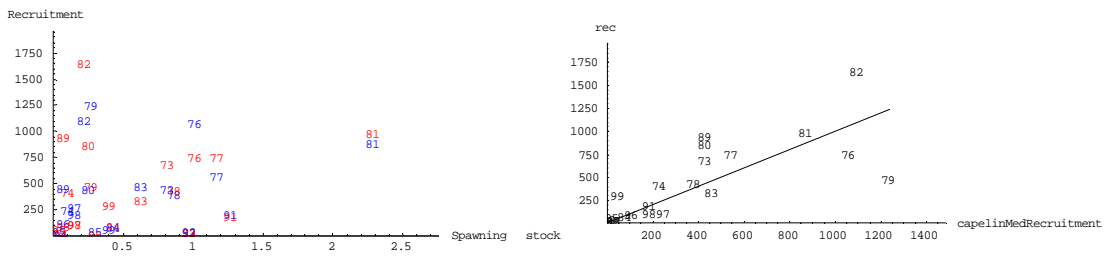
Figure 5. Capelin recruitment. Left panel: Measured (red) and modelled (blue) recruitment as 2 year old capelin vs spawning biomass. Right panel: Measured (vertical axes) vs modelled (horizontal axis) recruitment as 2 year old capelin
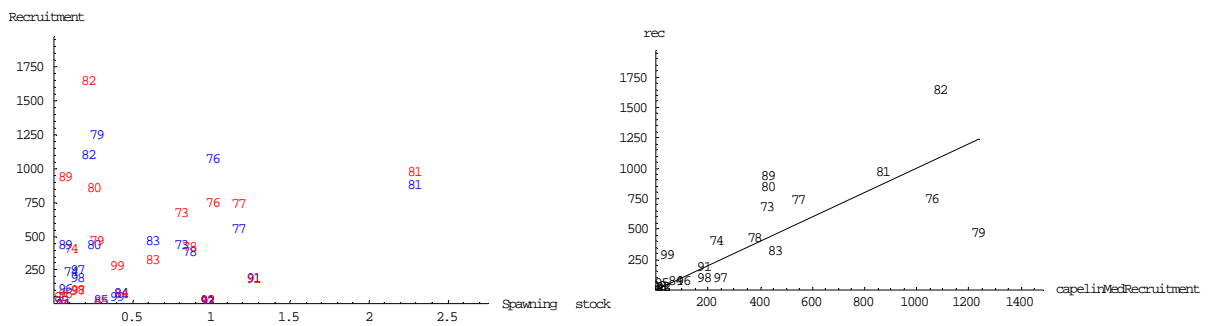


Figure 6. Recruitment of capelin. Same data and explanations as for figure 5, but without cannibalism of cod in the model
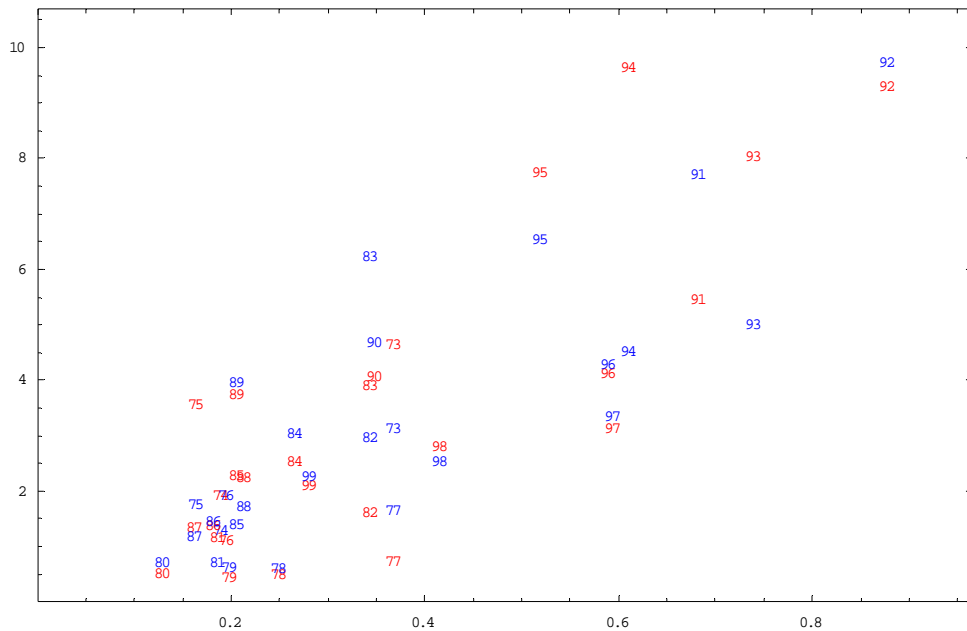


Figure 7. Recruitment of cod with cannibalism, temperature, mean age and mean weight vs spawning stock biomass. Red is number of 0 year old cod as fitted to 3 year old cod in the VPA, blue is modelled recruitment

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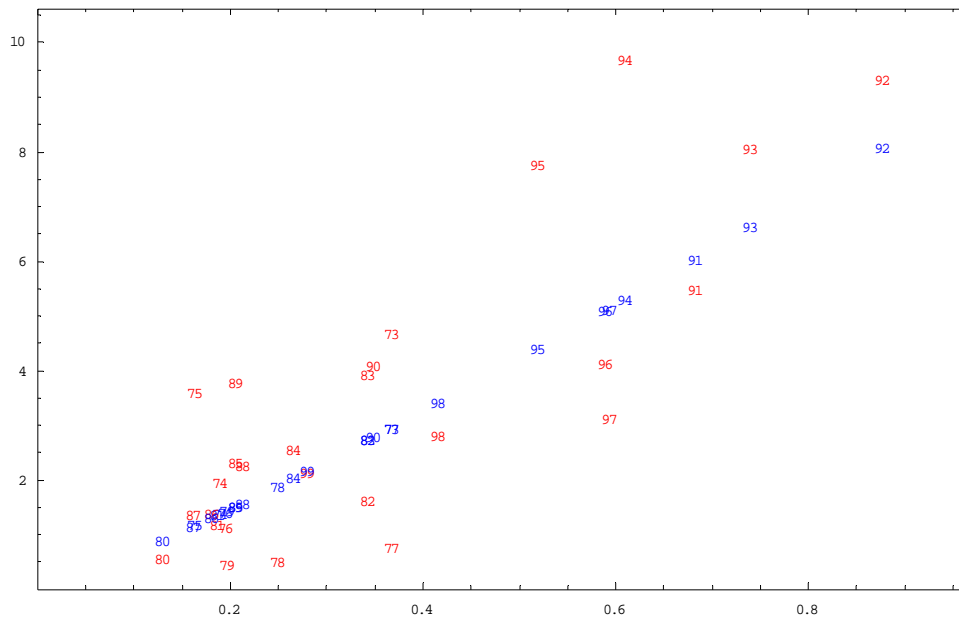
Figure 8. Cod recruitment (billion) with cannibalism, but without temperature, mean age and mean weight in the model. Red is number of 0 year old cod as fitted to 3 year old cod in the VPA, blue is modelled recruitment. Horizontal axis is spawning stock biomass
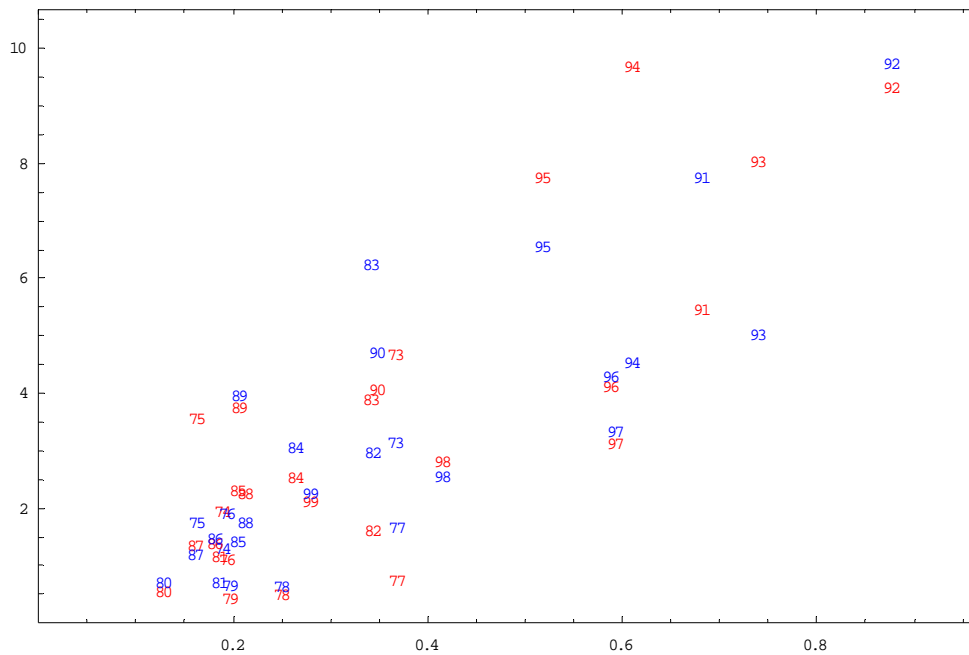


Figure 9. Cod recruitment (billion) with temperature, mean age and mean weight in the model, but cannibalism is excluded. Red is number of 0 year old cod as fitted to 3 year old cod in the VPA, blue is modelled recruitment. Horizontal axis is spawning stock biomass
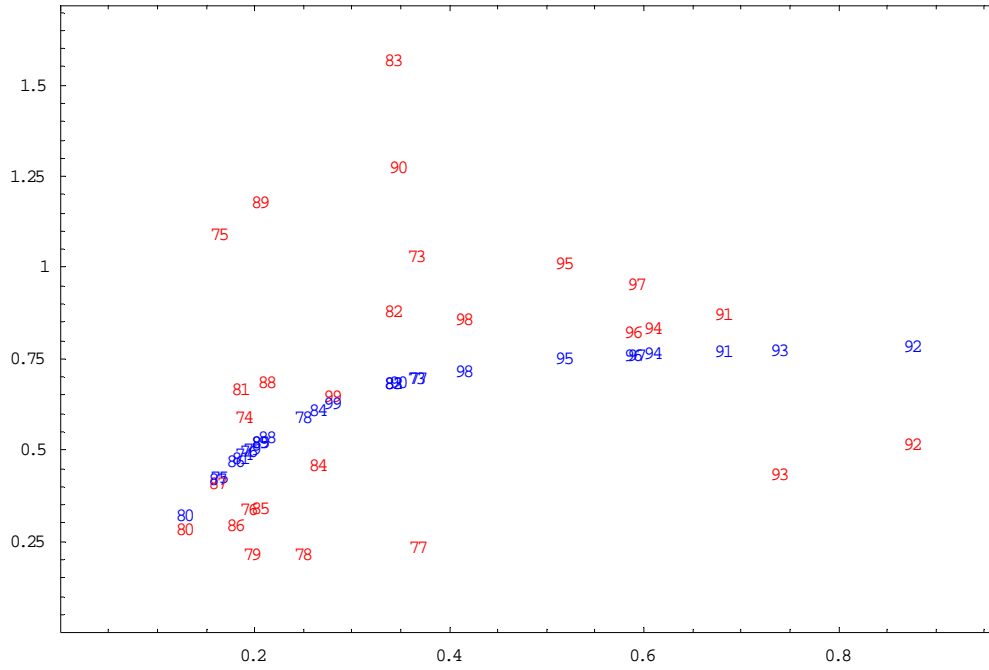
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Figure 10. Cod recruitment (billion) when neither cannibalism, temperature, mean age or mean weight affect recruitment in the model. Red is number of 0 year old cod as fitted to 3 year old cod in the VPA, blue is modelled recruitment. Horizontal axis is spawning stock biomass
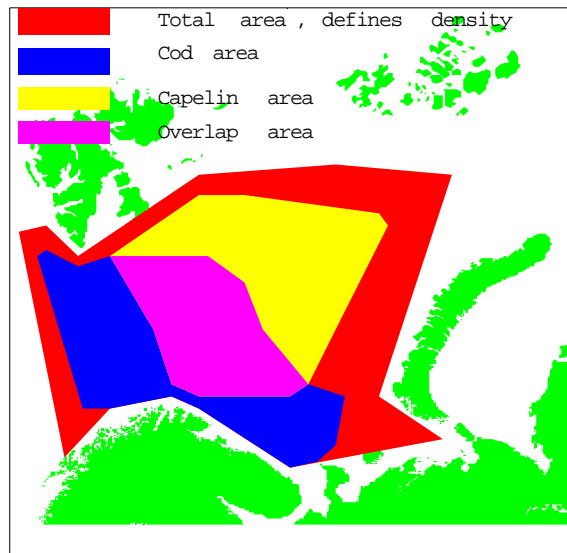


Figure 11. Example of overlap. Yeallow: capelin area, blue: cod area, magenta: overlap area, red: total area.
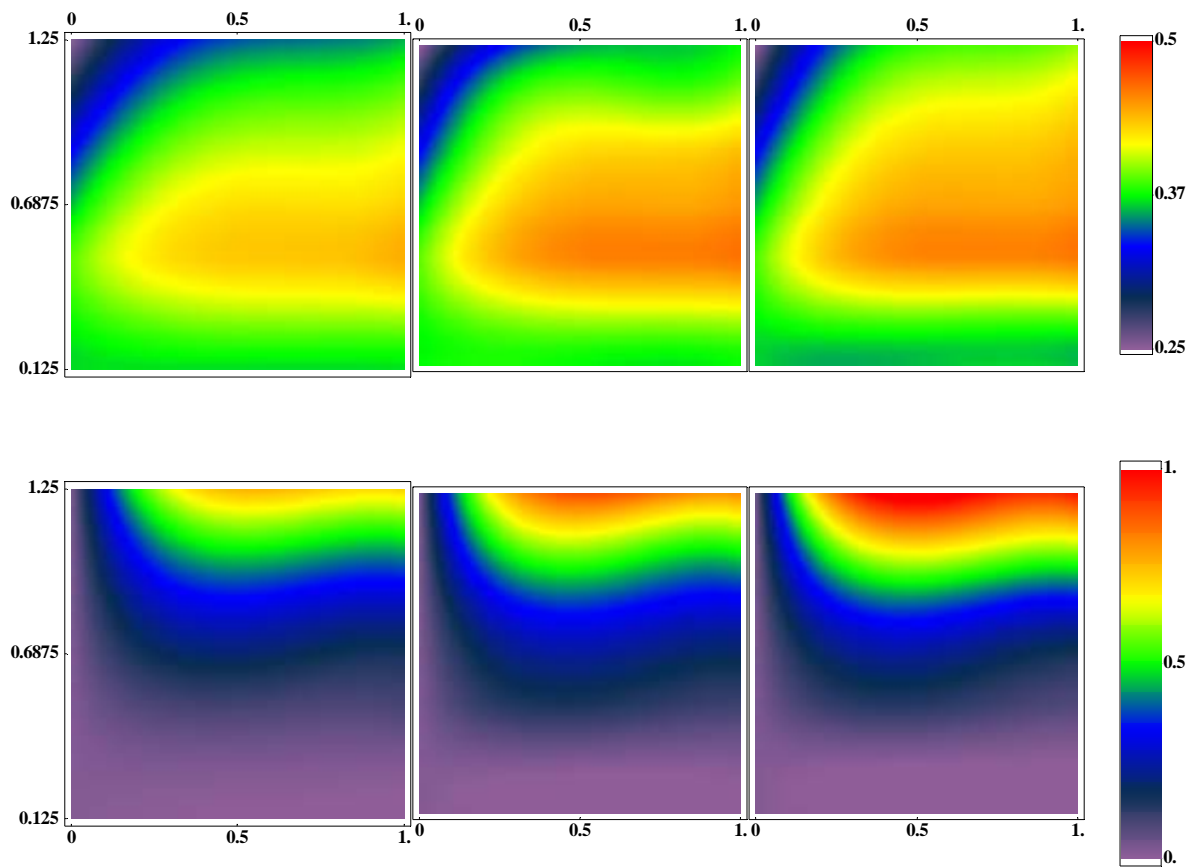
Figure 12. Long-term yield of cod (upper panel) and capelin (lower panel) for a two-dimensional cod-capelin harvesting control rule, given fixed harvesting control rule for herring. Horizontal axis: target spawning biomass of capelin. Vertical axis: F-value of cod, relative to present. Left figures: $F_{herring} = 0.125$, middle figures: $F_{herring} = 0.20$, right figures: $F_{herring} = 0.30$. Colouring according to mean long-term yield, values correspond to panel on the far right

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