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Testing the implications of a permanent or seasonal marine reserve on
the population dynamics of Eastern Baltic cod under varying
environmental conditions

Christine Röckmann ^{1,2}, Michael St. John ³, Uwe A. Schneider ^{2,4}, Friedrich W.
Köster ⁵, Richard S.J. Tol ^{2,6,7}

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¹ *International Max-Planck Research School for Maritime Affairs, c/o MPI-priv,
Mittelweg 187, D-Hamburg, Germany*

² *Research Unit Sustainability and Global Change (FNU), Hamburg University and Centre for Marine
and Atmospheric Science (ZMAW), Hamburg University
Bundesstr.55, Pavillion, D-20146 Hamburg, Germany*

³ *Institute of Hydrobiology and Fisheries Science, Hamburg University and Centre for Marine and
Atmospheric Science, Hamburg University
Olbersweg 24, D-22767 Hamburg, Germany*

⁴ *International Institute of Applied Systems Analysis, Laxenburg, Austria*

⁵ *Danish Institute for Fisheries Research, Danmarks Fiskeriundersøgelser, Afd. for Havfiskeri (HFI),
Charlottenlund Slot, DK-2920 Charlottenlund, Denmark*

⁶ *Institute for Environmental Studies, Vrije Universiteit, Amsterdam, The Netherlands*

⁷ *Engineering and Public Policy, Carnegie Mellon University, Pittsburgh, PA, USA*

Corresponding author:

Christine Röckmann

Research Unit Sustainability and Global Change, ZMAW, Hamburg University

Bundesstr.55, Pavilion

D-20146 Hamburg, Germany

Tel: +49-40- 42838 2147

Fax: +49-40- 42838 7009

Email: roeckmann@dkrz.de

Abstract: In order to test the implications of the establishment of a marine reserve in the Baltic Sea, a spatially disaggregated, discrete time, age-structured model for the Eastern Baltic cod (*Gadus morhua callarias L.*) stock was constructed. Functional relationships for recruitment and predation mortality were developed by multiple regression analyses. The resultant model output compares well with observed data from the fishery. The model was then applied to simulate stock development over a 50 year time period using different management policies and a variety of environmental conditions. The investigated management policies reduce fishing mortality and range from a moratorium on the Eastern Baltic cod fishery via the establishment of a permanent or a seasonal marine reserve in ICES subdivision 25 to a fishing as usual scenario. The environmental conditions incorporated were based on the size of the reproductive volume (RV) and comprise a best case and a worst case of reproductive conditions, and two more realistic scenarios, where we assumed that a historic series of RV-sizes reoccurs over the simulation period. Our results show a strong dependence of stock dynamics on the environmental conditions. Under prevailing low RV, our model projects stock extinction by the year 2020, if fishing continues as usual. Under the restrictive scenarios, where fishing mortality is reduced either directly or by implementation of a marine reserve, the stock benefits from an increase in stock size and an improved age-structure. A seasonal closure of SD 25 as opposed to a closure of the entire Baltic Sea appears to be sufficient to prevent the Eastern Baltic cod stock from falling below safe biological limits.

Keywords: Baltic cod, management, age-structured model, population dynamics, MPA, environmental variability, reproductive volume

Introduction

Baltic Sea fish stock assessments show a large decline of the cod biomass since the mid-1980s (ICES, 2003). Recent estimates of spawning biomass fall below B_{lim} (the precautionary biomass level, below which recruitment is impaired), implying a reduced reproductive capacity of the stock (ICES, 2003, 2004b). Hence, the stock is classified “as being outside safe biological limits”, posing concerns for Baltic Sea fisheries management (IBSFC, 2004).

The principal policy instrument for managing the Baltic Sea Fisheries is annual ‘Total Allowable Catches’ (TACs), supplemented by technical regulatory measures, such as minimum landing sizes, mesh size regulations, and closed periods for fishing (IBSFC, 2002). Due to the persistently severe situation of the stock, the International Baltic Sea Fisheries Commission (IBSFC) adopted in 2002 a new recovery plan for the Eastern and Western Baltic cod stock, which focuses on meeting clearly defined stock reference points within several years (ICES, 2004b). Also, in addition to the catch quotas, a spawning closure has been established since 1995, prohibiting the cod fishery every year between 16 June and 15 August. Furthermore, the IBSFC implemented a seasonal area closure on all fishing in the Bornholm Deep. This ‘summer ban’ was extended by several weeks in 2005, lasting now from 15 May till 31 August 2005. Moreover, the IBSFC established additional spawning area closures in the Gdansk Deep and the Gotland Deep. Nonetheless, TACs are still in place and thus remain the main policy instrument. Their effectiveness, however, relies heavily on the quality of scientific fish stock assessments, which are highly susceptible to the variability and uncertainty of a number of input parameters (e.g. catch-at-age and weight-at-age data, mortality estimates for the terminal years, environmental parameters) and the difficulty in integrating complex processes, such as multispecies interactions and ecosystem functions (e.g. Botsford et al., 1997; ICES, 1998; Walters, 2001). Furthermore, black landings falsify the empirical data basis of the assessments.

Recently, interest has focused on the potential of marine reserves or marine protected areas (MPAs) as an alternative fishery management tool (e.g. Pauly et al., 2002; PROTECT, 2005; Roberts et al., 2001, 2005; Walters, 2001). Several field studies have illustrated that closed areas can lead to increases in fish biomass, density, and size, and ecosystem diversity (reviewed by Halpern, 2003). It is, however, important to recognise realistic limitations and expectations of the MPA approach and not to present reserves as a general panacea (Allison et al., 1998; Dayton et al., 2000; Kaiser, 2005): Whether MPAs can enhance the fisheries outside of their borders is still in question, as success depends on the setting, size and design of the reserve, on the life history and migratory behaviour of the species, on the specific characteristics of the ecosystem, and on the fishing activity surrounding the MPA. In contrast to the tropics, species variability is lower in temperate waters, but environmental conditions are much more variable, rendering the implementation of MPAs as fisheries management tool more complicated. Only very few empirical studies have investigated the effects of MPAs on mobile temperate fish and their related fisheries. MPAs in such studies either lack adequate size and proper enforcement (Martell et al., 2000) or were effectively used to enhance a fishery for sedentary species, e.g. sessile scallops instead of migratory Atlantic cod and haddock (Murawski et al., 2000). Since large reserves have as yet not been implemented, we can only rely on modelling studies to evaluate the implications of MPAs for migratory fish stocks and their respective fisheries in temperate regions.

Here, we present a spatially disaggregated, discrete time, age-structured model of the population dynamics of the Eastern Baltic cod (*Gadus morhua callarias* L.) to investigate the biological consequences of the establishment of a permanent or a seasonal marine reserve in a biologically highly productive area in the Baltic Sea. Our approach to the assessment of the implications of an MPA-based management policy and its potential importance on stock dynamics follows and extends the approach presented in Apostolaki et al. (2002), who simulated the potential of partial closures as rebuilding strategy for the Mediterranean hake

fishery. Our model is a single-species, but is fed with output from an area-disaggregated Multispecies Virtual Population Analysis (adMSVPA). Here, we decided not to implement the adMSVPA, but rather a simplified model, which compares favourably with the complex behaviour of the cod stock and the outputs of the adMSVPA. The advantage of this approach relative to the adMSVPA is its transparent structure and the ability to readily couple it to complex bio-economic models and thereby scenario test the implications of management options and environmental conditions on stock dynamics.

Since, at present, there are no quantitative data on Baltic cod migration available and qualitative descriptions vary widely, here we decided to investigate the situation as if there were three independent substocks of the Eastern Baltic cod in three particular subdivisions. Preliminary model runs with migration showed that the results are highly sensitive to the assumptions; the model runs do not add information. Although unrealistic, we believe, that such a simplified investigation serves as basis for future bio-economic modelling. Once quantitative data on cod migration becomes available, the present model can easily be extended.

We apply our model to simulate stock development of the Eastern Baltic cod over 50 years under various environmental conditions using different management policies. Our management scenarios investigate the biological effects of the establishment of an MPA in SD 25 (Fig.1), which encompasses the Bornholm Basin, as opposed to policies based on the overall reduction of fishing mortality in the Eastern Baltic Sea. Marine biologists and conservationists have already recommended the establishment of an MPA in SD 25 (MacKenzie et al., 1996), as the Bornholm Basin has been the most important spawning ground of Baltic cod during the last decades due to favourable hydrographic conditions (Nissling and Westlin, 1991; Nissling et al., 1994; Plikshs et al., 1993).

Baltic cod eggs, which are neutrally buoyant, need a minimum salinity ($S \geq 11$ psu) and a minimum concentration of dissolved oxygen ($c[O_2] \geq 2$ ml/l) to develop (e.g. Nissling et al.,

1994). The volume of water having these characteristics has been termed the “reproductive volume” (RV) for this species (e.g. MacKenzie et al., 2000; Plikshs et al., 1993) and been employed in the development of stock and recruitment models of Baltic cod (e.g. Köster et al., 2001b, 2003; STORE, 2002). In the Eastern part of the Baltic Sea, a reproductive volume usually only occurs below 50 m depth in the deep basins of the Baltic Sea, namely the Bornholm Basin, the Gdansk Deep, and the Gotland Deep, located in SD 25, 26 and 28, respectively (Fig.1) (Bagge et al., 1994). The bottom water in the deep basins regularly becomes anoxic due to the bacterial breakdown of organic material below the halocline combined with reduced replenishment due to bottom topography resulting in restricted horizontal and vertical circulation in the Baltic deep water (Matthäus and Lass, 1995).

The reproductive volume is replenished when inflows from the North Sea transport saline and oxygen rich water into the Baltic basins, termed “Major Baltic Inflows” (MBI) (e.g. Matthäus and Frank, 1992; Schinke and Matthäus, 1998). Its size mainly depends on the frequency and strength of such North Sea inflow events as opposed to the length of stagnation periods (e.g. MacKenzie et al., 2000; Oeberst and Bleil, 2000). A large reproductive volume, with hydrographic conditions favourable for successful cod egg development, occurs less frequently in the Gotland Deep and the Gdansk Basin than in the Bornholm Basin. Their location farther East/Northeast and hence more distant from the North Sea leads to stagnation periods which are much more pronounced and prevail much longer than farther West in the Baltic Sea (Köster et al., 2001a; Plikshs, 1993, 1996). Therefore, the Gotland Deep in SD 28 and the Gdansk Basin in SD 26 have become less important for cod spawning since 1986. These facts support our hypothesis that a closure of ICES subdivision 25 can result in a significant biological benefit to the Baltic cod stock recovery.

We focus on a comparison of a permanent versus a seasonal marine reserve, as temporary openings of an MPA to fishing might be the only opportunity for fishermen to accrue catches

of the protected part of the fish stock, in particular in cases where the fish do not frequently migrate out of the protected area.

Insert Fig. 1 here

Methods

Model construction

The Eastern Baltic cod stock is distributed over ICES subdivisions (SD) 25-32 (Aro, 1989), however, the majority of cod are found in the three ICES subdivisions 25, 26, and 28 (Fig.1), which our study is confined to (Sparholt et al., 1991). The cod in subdivisions 25, 26, and 28 are assumed to be a stock unit composed of age-groups 0-8 with the oldest age-group not handled as plus group. Based on maturity estimates from maturity ogives, we assume that cod of age 2 and older are mature and thus able to spawn (ICES, 2002; STORE, 2002). The age of entry into the exploitable fishery is also assumed to be age 2.

We use quarterly data on stock size, natural, predation and fishing mortality of cod for the ICES subdivisions (SD) 25, 26, and 28 from adMSVPA, covering the time period 1974 to 1999 (ICES, 1999, 2001b; Köster et al., 2001a, 2001b). Basin-specific data on reproductive volume for the time period 1976 to 1996 are specified based on estimates from MacKenzie et al. (2000) and Köster et al. (2001b), with estimates for the most recent years taken from ICES (2004a).

A discrete time, age-structured model is applied to calculate cod stock size (N) for each age-group (a) and for each subdivision (r), accounting for recruitment (R) and mortality due to fishing (F), predation (P) and natural mortality (M), using an extension of the standard equation of population dynamics (Beverton and Holt, 1954). There are three separate equations needed to incorporate recruitment, changes in age and year (y), and changes from one time-step (quarter q) to the next (Eq.1a-1c). For definition of symbols, refer to Table 1.

Insert Table 1 here

$$N_{a+1,r,q=q1,y+1} = N_{a,r,"q4",y} \cdot e^{-M_{a,r,"q4",y} - P_{a,r,"q4",y} - F_{a,r,"q4",y}} \quad (1a)$$

$$N_{a,r,q=q2 \vee q4,y} = N_{a,r,"q1 \vee q3",y} \cdot e^{-M_{a,r,"q1 \vee q3",y} - P_{a,r,"q1 \vee q3",y} - F_{a,r,"q1 \vee q3",y}} \quad (1b)$$

$$N_{a,r,q=q3,y} = N_{a,r,"q2",y} \cdot e^{-M_{a,r,"q2",y} - P_{a,r,"q2",y} - F_{a,r,"q2",y}} + R_{r,y} \Big|_{a="a0"} \quad (1c)$$

The endogenous variables in our model are stock size (N), recruitment (R), and cannibalism (P). For parameterisation of the two sub-models calculating recruitment and cannibalism, we performed multiple linear regression analyses.

Cannibalism (Predation mortality P)

Predation mortality refers to cannibalism by mature cod on the early and juvenile life stages of cod (ages 0, 1, and 2). In accordance with Köster et al. (2001b), predation mortality is linearly related to the cod spawning stock size (ssN), i.e., the sum of mature population numbers at ages 2-8, in the corresponding subdivision. Table A1 shows the parameters and statistical outputs of our regression analyses, performed to describe predation mortality of the early life-stages of cod (age-groups 0, 1, and 2) in the three subdivisions as a function of the size of the spawning stock. In this exercise, the independent variable (ssN) explains 70-88% of the variance of predation mortality, depending on the age-group and subdivision.

Recruitment (R)

In our approach, recruitment refers to 0-group cod. Here, young of the year enter the model in the third quarter every year, if a spawning stock exists, whereafter these early life stages are subject to cannibalism and to natural mortality. Köster et al. (2001b) have shown that cod recruitment in the Baltic Sea cannot suitably be described by a simple stock-recruit relationship such as the Ricker (1958) or Beverton & Holt (1954) curves, because environmental conditions in the deep basins play a crucial role for the recruitment success of Baltic cod (cf. introduction). Here, we calculate recruitment in each of the three subdivisions as a function of the basin-specific spawning stock size (ssN) and the size of the basin-specific

reproductive volume (RV). In Tables A2 and A3, we show functional forms and statistics of eight different possibilities (cf. equations #1 – #8) of combining the two explanatory variables ssN and RV. The tested functional forms explain 35-64% of the variance of recruitment in SD 25 and 0-85% in SD 26 and 28. In SD 25, the inclusion of RV as second explanatory variable increases the explained variance of functional forms # 2, #3, and #4 as opposed to #1, as well as for the Ricker-type functional forms #6 and #7 as opposed to #5.

Equation #2 has the highest predictive power in SD 28, explaining 85% of the variance of recruitment, whereas equation #6 explains 64% and 85% in SD 25 and 26, respectively. Equation #6, however, is not sensitive to the size of the spawning stock in SD 25 and SD 26 ($p(t\text{-stat.}) > 0.6$, cf. Tables A2&A3); hence, it is not used in this study. Since equation #2 explains 57%, 83%, and 85% of the variance of recruitment in SD 25, 26, and 28, respectively, here we chose this linear combination of ssN and RV for calculating recruitment in our scenario analysis. The regression parameters of the selected model #2, are significant at the 1% level of significance in SD 25 and 26 (cf. Tables A2&A3). In SD 28, the level of significance of the explanatory variable RV is 24%. As a matter of simplicity, we decided to apply the same functional form to calculate recruitment in all three subdivisions (instead of applying equation #1 in SD 28), and hence, we also chose equation #2 in SD 28.

$$R_{r,y} = a \cdot ssN_{r,q1,y} + b \cdot RV_{r,y} + c \quad (2)$$

The lack of density dependence in this linear model does not pose a problem in the case of the Eastern Baltic cod, as the stock is currently at a very low stock level. At such low level, the stock is limited neither by competition for food nor by cannibalism and predation. Historic stock records reveal that the Baltic cod spawning stock has not exceeded a quantity of 0.7 billion. We point out that the first part of the Ricker curve, with spawning stock number between 0 and 0.7 billion, can be approximated by a linear function.

Fishing mortality (F)

As our prime aim is an analysis of selected management policies, which constrain fishing mortality (F), here, F is an external forcing parameter, treated as exogenous variable. F differs between the investigated management scenarios, but is held constant during a management scenario. For the period 1976-1999 we apply the quarterly fishing mortalities derived by adMSVPA. During the simulation period, 2000-2050, the average fishing mortalities are modified according to the management policies, as described below.

Natural mortality (M)

Natural mortality was assumed to be 0.2/year, equally distributed over quarters, corresponding to standard MSVPA runs in the Baltic Sea (Sparholt, 1991).

Statistics and model validation

We tested the data for autocorrelation (Durbin-Watson test), checked the significance of variables (t-test) and the quality of the multiple regression between modelled and observed stock sizes. We omitted years 1976, 1979, and 1996 in our regression analyses for recruitment due to data inconsistencies and tuning problems of the adMSVPA during these years (Köster et al., 2001a, 2001b).

To assess the overall accuracy of our model, combined over subdivisions 25, 26, and 28, the projected stock sizes were summed over all ages and all three subdivisions, and the resulting total stock size was compared to corresponding estimates from the standard ICES stock assessment for the Central Baltic for the time series 1976-1999 (ICES, 2002).

Scenario analysis

(A) Management Scenarios

Our analyses focus on the establishment of a marine reserve in SD 25. Here, we compare the development of the stock size of Eastern Baltic cod under five selected management policies:

1. FasU Fishing mortality ‘as usual’, applying the average fishing mortality of 1990-1995 over the 50-year simulation period.
2. RoF70 overall reduction of fishing mortality by 70% in all three subdivisions (corresponds to ACFM advice for, 2003).
3. C25q1q2 seasonal closure of SD 25 in quarters 1 and 2; quarters 3 and 4 are open to reduced fishing (fishing mortality in quarters 3&4 is reduced by 50%).
4. C25 permanent closure of SD 25.
5. TC total closure, i.e., fishing mortality is zero in all three subdivisions (corresponds to ACFM advice for 2005).

Model runs are performed covering the years 1976-2050 with the different management scenarios initiated in year 2000. Quarterly estimates of fishing mortalities are available from adMSVPA until 1999 (Köster et al., 2001a). The management scenarios we have chosen can be implemented in our model by the following equation:

$$F_{a,r,q,y}^{MR} = \alpha_{r,q} \cdot F_{a,r,q,y} + \beta \cdot F_{a,r,SD25,y} \quad (3)$$

Fishing mortality in the individual subdivisions after marine reserve implementation ($F_{a,r,q,y}^{MR}$) is derived from the pre-reserve fishing mortality ($F_{a,r,q,y}$) and the degree of fishing effort redistribution from SD 25 into SD 26 or 28. As we neglect migration in this study, it makes no sense to study effects of effort redistribution, and hence, β is zero in the five presented management policies. Values for the coefficient α according to the corresponding scenarios are given in Table 2.

Insert Table 2 here

As pre-reserve fishing mortality, we take the average fishing mortality of the years 1990-1995 and apply it to the simulation period 2000-2050. We tested the effect of using other constant fishing mortalities for the simulation period, e.g. averages of the years 1986-1995

and 1974-1999. However, results of these simulations showed little variation from those using the average fishing mortality from 1990-1995.

(B) Environmental Scenarios

Data on reproductive volume are available until 1999. To perform simulations of the Baltic cod population dynamics, we also need to specify future environmental conditions. The size of the reproductive volume in the three spawning basins depends on the frequency and strength of major Baltic inflows from the North Sea, which are triggered by large scale and local atmospheric forcing conditions, such as the North Atlantic Oscillation (Hinrichsen et al., 2002; Schinke and Matthäus, 1998). There are, however, no climate models as yet available that project future atmospheric conditions. In the present study, we do not attempt to predict reproductive volume; instead, we look at trends of cod stock development based on the reoccurrence of historic environmental conditions. Thus, for the simulation period (2000-2050) we base our environmental scenarios on the observed reproductive volume as it was estimated for the years 1974-1999. Under environmental conditions 1, we apply the historic data set starting in 1974, when reproductive volume was high in all three subdivisions. Under environmental conditions 2, we assume that unfavourable conditions prevail in the first years of the simulation period; therefore, we start the simulation with the reproductive volume data of year 1981 and then repeat the historic data sequence from 1981 through 1999 followed by 1974 to 1980. We also investigate two extreme cases of having very large or very small reproductive volumes for a cycle of several years. The four environmental conditions can be characterised as follows:

- Environmental conditions 1 (“HighLow”): varying reproductive volume; the data sequence from 1974-1999 is applied repeatedly for the simulation period 2000-2050.
- Environmental conditions 2 (“LowHigh”): varying reproductive volume; the data sequence from 1981-1999 followed by 1974-1980 is applied repeatedly.

- Environmental conditions 3 (“HighHigh”): constantly high reproductive volume; data from year 1977.
- Environmental conditions 4 (“LowLow”): six year cycle of low reproductive volume; the data sequence from 1985-1990 is repeatedly applied.

Results

Model validation

A comparison of the development of the cod spawning stock size derived by our model #2 in contrast to the spawning stock size derived by extended survivor analysis (XSA), i.e., the ICES standard stock assessment technique, reveals that our model underestimates the spawning stock size in the first part of the validation period 1976-1999 whereas it overestimates values towards the end of the validation period. This problem can be attributed to flaws in the recruitment equation in SD 25, which does not accurately reproduce the observed recruitment, showing the same trends of under- and overestimation in the late 1970s/early 1980s, and in the early 1990s, respectively. Nevertheless, our combined model, applying recruitment equation #2, explains 72% of the variance of ICES standard stock assessment estimates (2002) (Fig. 2).

This correlation is based on the number of fish in millions. If we base the correlation on fish biomass instead of stock size in numbers by multiplying the number of fish in each age-group with the average weight-at-age of each age-group, the quality of the correlations diminishes ($r^2 = 66\%$): Errors with age-readings in Baltic cod, regional differences in the quality of the individual fish, as well as the standardised ICES procedure of determining mean weight-at-age data at the beginning of a year, derived from the 12 months average (thus neglecting fish growth) cause additional uncertainty, and hence a loss in precision (ICES, 2001; Reeves, 2001). For that reason, in the following we present results of the spawning stock in numbers instead of in biomass.

Insert Fig. 2 here*Scenario analysis*

The 50-year-simulations are initiated in the year 2000, when the size of the Eastern Baltic cod stock was very low and the fishery considered to be overexploited. The curves in figures 3-6 depict the trend of the development of the cod spawning stock in millions of fish, summed over SD 25, 26, and 28, for alternative environmental conditions that we will present separately.

Insert Figures 3-6 here*Environmental conditions 1 (“HighLow”)*

The simulation period under environmental conditions 1 starts with several years of large reproductive volume in the three subdivisions (large black, white, and grey bars in Fig.3). This leads to an erratic increase in the spawning stock size in 2004 under all five management scenarios (Fig.3). The reproductive volume decreases within four years after the major Baltic inflow event in 2002 and remains low for about 10 years from 2007 onwards. With a lag period of two years, the spawning stock size decreases gradually under all five management scenarios while reproductive volume remains low. The decrease in stock size is most evident for management scenario 1 (FasU) with fluctuations in stock size around a higher stock size dampened in scenario 5 (TC). Under management scenarios 2, 3, and 4, the spawning stock size increases by 80, 100, and 120%, respectively during the first seven years of the simulation period. Scenario 4 (C25) results in an initial increase in the cod spawning stock size to > 1 billion, a level similar to the spawning stock size at the end of the 1970s, beginning of the 1980s. Under management scenario 5 (TC), the spawning stock size increases by 160% to unprecedented high values. Under management scenario 1 (FasU), the spawning stock size initially increases by 50% to approx. 700 million cod within four years. While reproductive volume is low, spawning stock size then decreases to less than 200 million spawners. This situation resembles the extremely low level of the spawning stock in 1992 (ICES, 2003,

2004b). The stock does not go extinct under environmental conditions 1, because the reoccurrence of inflows after about 15 years leads to the replenishment of reproductive volumes and thus to stock recovery.

Figure 7 shows the age structure of the stock in 2050 under environmental conditions 1 for the five selected management scenarios. Under the FasU scenario, hardly any cod grows older than 4 years. In contrast, under the total closure and the permanent MPA scenario, the stock's age structure improves greatly, supporting around 30% of 5- to 8-year old cod. Under the seasonal MPA scenario, this fraction of older fish contributes around 20% to the stock size. If overall fishing mortality is reduced by 70%, the stock is composed of approx. 10% of fish of age 5 and older.

Insert Fig. 7 here

Figure 3 illustrates that, in general, the spawning stock size under the five management policies differs by a greater extent during periods of stagnation (low RVs) than during and shortly after major Baltic inflows (high RVs). The lines in figure 3, representing the five management policies, lie closer together in years directly after major inflow events. Moreover, the C25q1q2 line is lower than the RoF70 line during years of high RV, but after a stagnation period of approx. 10 years, the two lines intersect, and spawning stock size under C25q1q2 exceeds the spawning stock under RoF70. Considering the development of the spawning stock size towards the end of such a stagnation period, the ranking of management policies from highest to lowest spawning stock size is as follows:

1. TC,
2. C25,
3. C25q1q2,
4. RoF70,
5. FasU.

Environmental conditions 2 (“LowHigh”)

The simulation period under environmental conditions 2 starts with 12 years of low reproductive volume. This leads to a decrease in the spawning stock size under management scenario 1 (FasU) until 2011 (Fig.4). Spawning stock size under scenarios 2 (Rof70) and 3 (C25q1q2) fluctuates around 400 million. Again, the C25q1q2 line and the RoF70 line

intersect: after several years of low RV, spawning stock size under C25q1q2 exceeds the spawning stock under RoF70, whereas after the replenishment of RVs, spawning stock size under RoF70 exceeds ssN under C25q1q2.

Under scenarios 4 (C25) and 5 (TC), spawning stock size increases by 100% during the first 12 years of low RV. Afterwards, when RV is replenished by inflow events in 2013, 2016, 2021 and 2022, stock size increases even further.

In this “LowHigh” scenario, the spawning stock reaches levels similar to those reached under environmental conditions 1 (“HighLow”), however, it takes about two decades longer to achieve these levels. Likewise, the spawning stock shows similar dynamics to those under environmental conditions 1, i.e. the slope of the decrease in stock size is steepest for management scenario 1 (FasU) and weakest for scenario 5 (TC). Also, the ranking of management policies from highest to lowest spawning stock size is the same as stated above. Similar to environmental conditions 1, the stock does not go extinct under environmental conditions 2, because the reoccurrence of inflows after about 12-15 years leads to the replenishment of reproductive volumes and thus to stock recovery.

Environmental conditions 3 (“HighHigh”)

Albeit unrealistic, stock development under environmental conditions 3 (constant high reproductive volumes) is useful as a potential upper boundary of stock development. The spawning stock size increases under all five management scenarios (Fig.5). Equilibrium is reached after about ten years under all five management scenarios.

Under scenario 1 (FasU), the spawning stock size increases by more than 100% to approximately one billion cod, which is lower than historic stock sizes at the end of the 1970s. The stock benefits much more under management scenarios 2, 3, and 4, where spawning stock sizes increase by 140, 160, and 180% , respectively. Under management scenario 5 (TC), the spawning stock increases by 260% to an unprecedented high level of > 1.7 billion

spawners. The ranking of management policies from highest to lowest spawning stock size under these permanently favourable environmental conditions of high RV is as follows:

1. TC,
2. C25,
3. RoF70,
4. C25q1q2,
5. FasU.

In comparison to the ranking under environmental conditions 1 and 2, positions 3 and 4 are interchanged.

Environmental conditions 4 (“LowLow”)

Figure 6 depicts spawning stock development under the worst case of environmental conditions 4, i.e. no inflows for all five management scenarios. Except for a weak inflow event which reoccurs every six years to replenish a small reproductive volume in SD 25 and 26, only a small volume in SD 25 can permanently provide appropriate spawning conditions for successful cod egg development. Such unfavourable hydrological conditions combined with high fishing pressure (FasU) lead to the extinction of the cod stock after 18-20 years. If overall fishing pressure is reduced by 70% (RoF70), the spawning stock size falls below 300 million. The cod spawning stock can slightly recover and stabilise around a level of approximately 400 million spawners when temporarily closing SD 25 for fishing during the first and second quarter of the year (C25q1q2). Management scenarios 4 (C25) and 5 (TC) show that a slight stock recovery is possible despite unfavourable environmental conditions: The spawning stock increases by 50% within 20 years to 600 million. These two scenarios differ during the first 13 years, with stock size under a total closure exceeding stock size under the C25 scenario. Afterwards, both management scenarios result in the same spawning stock size.

Discussion

Model validation

As can be interpreted from figure 2, our model is able to reproduce the historic stock assessment estimates relatively well: The correlations of our model results with the ICES

standard stock assessment estimates (ICES, 2002) yield an explanatory power of 72%. Nevertheless, there is the problem of underestimating the size of the spawning stock in the first part of the historic time series and overestimating in the most recent part of the time series. One explanation for this is the comparatively poor coefficient of determination ($R^2 = 0.57$) for calculating recruitment in SD 25 as opposed to an $R^2 > 0.8$ in SD 26 and 28. The reproductive volume is probably not the only environmental factor, which influences spawning behaviour and recruitment, particularly in SD 25. Other processes have been implicated including predation of cod eggs by clupeids, transport to or retention in optimal habits, and larval feeding environment (Hinrichsen and Möllmann, 2002; Hinrichsen et al., 2003). These factors have the potential to be included in extensions of our model. Furthermore, the inherent uncertainty of standard fish stock assessment is equally present at the basis of our model exercises, since the underlying area-disaggregated data for recruitment, spawning stock size, and mortalities can be afflicted with an error of +/- 50% (Chen, 2003; Walters, 2001).

Scenario analysis

Our management scenarios 2-5 essentially represent policies that reduce fishing mortality, pursuing different approaches. The results of our simulations clearly show that the reduction of fishing mortality via the establishment of a marine reserve in SD 25 is beneficial for the cod stock under both favourable and unfavourable environmental conditions (Figures 3-6). Even in the case of prevailing unfavourable environmental conditions (“LowLow”), the stock stabilises around 400 million under the seasonal marine reserve scenario (C25q1q2) and recovers under the permanent marine reserve scenario (C25) and the total closure (TC) scenario (Fig.6). It also becomes obvious, that the cod stock can go virtually extinct, if unfavourable environmental conditions in the future prevail for a longer period of time while fishing continues as usual (Fig.6). Total stock size under management scenario 5 (TC) converges towards the total stock size under scenario 4 (C25) within 15 years (Fig.6). What is

happening? The subpopulations in SD 26 and 28 quickly go extinct under prevailing unfavourable environmental conditions. Since this has not occurred in the past, this result gives additional support to our conclusion that migration of cod in the Baltic Sea is of very high importance and needs to be incorporated into future models of the Baltic cod fishery. Without migration (as was assumed here), there would not be any cod left in the areas East Northeast of SD 25.

Management scenario 5 (TC) is probably the most unrealistic scenario from a management point of view; it corresponds, however, to the recent management advice given to the IBSCF by the ICES advisory committee for fisheries management (ICES, 2004b). Due to the high uncertainties in the Baltic fish stock assessments, the ICES Advisory Committee on Fishery Management was reluctant to present a catch forecast in any form, and its management advice was “no catch in 2005” (ICES, 2004b). Moreover, the total closure scenario (TC) can be interpreted as representing the environmental carrying capacity of cod in the Eastern Baltic Sea. According to our results, the carrying capacity ranges from approximately 600 million under unfavourable reproductive conditions (“LowLow”) to 1.7 billion under the best case of reproductive conditions (“HighHigh”). Supposing that historic environmental conditions reoccur in the future, the carrying capacity varies between 1 and 1.4 billion, depending on the actual future reproductive conditions.

When comparing stock dynamics under management scenarios 3 and 4, the intersecting lines under environmental conditions 1 and 2 lead to the conclusion that a seasonal marine reserve policy (C25q1q2) is more effective in protecting the spawning stock under unfavourable hydrographic conditions than an overall reduction of fishing mortality by 70% (RoF70). The different ranking of management policies 3 and 4 of the “HighHigh” and the “LowLow” environmental scenarios further supports this conclusion.. Again, this result supports our initial hypothesis that a protection of the spawning stock in SD 25 can be sufficient to rebuild the Eastern Baltic cod stock. This is due to the fact that a reproductive

volume will generally be present in the Bornholm Basin, despite unfavourable conditions, i.e., despite that lack of very strong inflow events from the North Sea, which could replenish the deep basins in SD 26 and 28.

Our simulations support the hypothesis that MPAs, both permanent and seasonal, can improve the age-structure of initially overexploited fish stocks (e.g. Apostolaki, 2001; Roberts et al., 2001), serving as positive feedback, in particular in the case of the Eastern Baltic cod (Fig.7). Here, the advantage of having more older fish in the stock results from the following: Older females lay many more eggs and they spawn over a longer time period than young females (Nissling et al., 1994, Vallin and Nissling, 2000). Moreover, the time period, when the eggs are at maximum quality, is longer for eggs of older females than for those of younger females.

In addition, our simulations support claims raised by several fisheries scientists that the size and location of the marine reserve is a crucial factor for evaluating its impacts (Beattie et al., 2002; Martell et al., 2000; Sumaila, 2002; Walters, 2000). In the Baltic Sea environmental conditions strongly drive the population dynamics of Baltic cod. Therefore, closing an area is useless, if unfavourable hydrographic conditions do not allow for successful cod egg development and, in turn, do not increase potential recruitment. Closures, not based on a sound biological basis, can even be counterproductive, as each negative example of marine reserve establishment can cause fishermen to become more reluctant to this type of management tool in the future. Furthermore, as Baltic cod is a highly migratory species with pronounced feeding and spawning migration, a small reserve size, such as the spawning ground closure, established by the IBSEFC since 1995, may very well dissipate any beneficial result for mobile species because of dispersal losses or effort concentration around the borders of MPAs (Walters, 2000).

As has already been stressed, our results have to be interpreted with caution due to our assumptions, which were described in the method section. For example, although commonly

applied, the concept of constant natural mortality is very unrealistic. This may be improved by incorporating more environmental variables, which impact on natural mortality rates, in particular of the early life stages (e.g. Köster et al., 2001b; MacKenzie et al., 1996). Furthermore, the management scenarios are derived from the assumption of a constant fishing mortality, the average of the years 1990-1995. For more realistic simulations, fishing mortality should be transformed into an endogenous variable that can reflect reactions to management measures. Including dynamic variation in fishing mortality requires an understanding of fishermen's behaviour and a complete analysis of the dynamics of the Baltic cod fishery (Kronbak, 2004). Hence, in the future, this biological model should be coupled to an economic model of the Baltic Sea cod fishery. The combined bio-economic model can then be used to evaluate the potential impacts of an area closure on the biology of the fish stocks on the one side and on the Baltic cod fishery on the other side.

Similar to the results drawn by Brander and Mohn (2004), our simulations reveal that stock development depends strongly on future environmental conditions, in particular hydrological conditions, which are triggered by inter-annual climate variability. There is a clear need to improve climate, meteorological, and hydrographic models which will allow to make better fish stock projections and provide scientifically sound advice to fishery managers and decision makers.

A major future goal in research has to be the integration of cod migration and movement rates. Tagging experiments are urgently needed to get quantitative information about cod migration.

Conclusion

In summary, our results suggest that the Eastern Baltic cod stock can significantly benefit from the implementation of an MPA that focuses on the protection of the spawning stock in SD 25. Under unfavourable environmental conditions, hydrographic conditions in the basins

East/Northeast of SD 25 do not allow for successful cod egg development anymore, and hence, it is particularly important, to protect the viable component of the spawning stock in SD 25. Then, the stock benefits more from a seasonal marine reserve policy, focussing on the protection of the spawning stock in SD 25, than from an overall reduction of fishing mortality in the Eastern Baltic Sea.

However, in contrast to the investigated seasonal marine reserve scenario, the seasonal closure that has been established in the Bornholm Basin is spatially too small and temporally too short to effectively reduce fishing mortality on the spawning stock. Furthermore, the additional closures in the Gdansk Deep and the Gotland Basin may only be effective sporadically, in the rare case of strong MBIs. During stagnation periods, these closures cannot lead to enhanced recruitment from SD 26 and 28.

According to our findings, a total moratorium on fishing in the entire Baltic Sea could be avoided by an MPA approach focussing on SD 25 to rebuild the Eastern Baltic cod stock. We conclude that MPAs as a policy instrument can and should be applied in areas, where the location of the stock's spawning concentration is known.

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Annex

Table A1. Results and statistics of regression analyses of age-specific predation mortality for cod age 0, 1, and 2 in SD 25, 26, and 28 ($P = a \cdot ssN + c$): parameter estimate, standard error, significance level of t-statistics, Durbin Watson statistics (indicating serial correlation in residuals if $DW < 2$), and r^2 values (indicating the proportion of the total variance accounted for by the linear influence of the explanatory variable ssN).

subdivision	prey age	Parameter	Std. Error	p(t-stat.)	DW	r^2
SD 25	age 0	a = 0.00082	0.00011	0.000	2.28	0.75
		c = 0.00293	0.04261	0.946		
SD 25	age 1	a = 0.00051	0.00006	0.000	1.79	0.80
		c = -0.00575	0.02308	0.806		
SD 25	age 2	a = 0.00005	0.00001	0.000	1.64	0.70
		c = -0.00026	0.00299	0.933		
SD 26	age 0	a = 0.00133	0.00015	0.000	2.66	0.83
		c = 0.02484	0.05253	0.642		
SD 26	age 1	a = 0.00089	0.00008	0.000	1.22	0.87
		c = -0.00048	0.03023	0.988		
SD 26	age 2	a = 0.00012	0.00002	0.000	1.08	0.70
		c = 0.00472	0.00698	0.508		
SD 28	age 0	a = 0.00285	0.00034	0.000	1.70	0.80
		c = -0.01466	0.05657	0.799		
SD 28	age 1	a = 0.00205	0.00018	0.000	1.12	0.88
		c = -0.01159	0.02975	0.702		
SD 28	age 2	a = 0.00023	0.00003	0.000	1.34	0.81
		c = -0.00003	0.00448	0.995		

Table A2: Results of regression analyses of stock-recruit relationships in SD 25: functional form of recruitment equation, parameter estimate, standard error, significance level of t-statistics, Durbin Watson statistics, and r^2 values.

Recruitment Equation [linearised from in brackets]	Parameter value	s.e.	p(t-stat.)	DW	r^2 (*)
SD 25					
#1 $R = a \cdot ssN + c$	a = 0.69481	0.23906	0.01	0.90	0.35
	c = 56.9188	86.7356	0.52		
#2 $R = a \cdot ssN + b \cdot RV + c$	a = 0.77217	0.20207	0.00	1.03	
	b = 1.44479	0.51662	0.01		
	c = -166.740	108.030	0.14		
#2, corrected for autoregression $R = a \cdot ssN + b \cdot RV + c + ar1 + ar2$	a = 0.769131	0.237	0.01	1.97	0.57
	b = 1.372792	0.325873	0.00		
	c = -163.2885	98.777	0.13		
	ar1 = 0.762269	0.241	0.01		
	ar2 = -0.629696	0.263	0.04		
#3 $R = a \cdot ssN \cdot RV + c$	a = 0.00493	0.00108	0.00	1.16	0.57
	c = 68.9399	55.5463	0.23		
#4 $R = RV \cdot (a \cdot ssN + c)$ [$R/RV = a \cdot ssN + c$]	a = 0.00736	0.00213	0.00	2.08	0.49
	c = -0.11076	0.77430	0.89		
#5 $R = ssN \cdot \exp(a \cdot ssN + c)$ [$\ln(R/ssN) = a \cdot ssN + c$]	a = -0.00052	0.00072	0.48	1.00	0.37
	c = -0.03224	0.26038	0.90		
#6 $R = ssN \cdot \exp(a \cdot ssN + b \cdot RV + c)$ [$\ln[R/ssN] = a \cdot ssN + b \cdot RV + c$]	a = -0.000278	0.000592	0.65	1.46	0.64
	b = 0.004525	0.001515	0.01		
	c = -0.73276	0.316729	0.04		
#7 $R = ssN \cdot RV \cdot \exp(a \cdot ssN + c)$ [$\ln(R/(ssN \cdot RV)) = a \cdot ssN + c$]	a = -0.00006	0.00065	0.93	1.73	0.57
	c = -5.02174	0.23634	0.00		
#8 $R = ssN^a \cdot RV^b \cdot \exp(c)$ [$\ln(R) = a \cdot \ln(ssN) + b \cdot \ln(RV) + c$]	a = 0.92336	0.20127	0.00	1.34	0.57
	b = 0.59092	0.21329	0.01		
	c = -2.62516	1.67092	0.14		

(*) When referring to the linear recruitment equations (#1-#3), the square of the Pearson correlation coefficient (r^2) is equal to the coefficient of multiple determination R^2 .

Table A3: Results of regression analyses of stock-recruit relationships in SD 26 and 28. For further explanations refer to Table A2.

Recruitment Equation [linearised from in brackets]	Parameter value	s.e.	p(t-stat.)	DW	r ² (*)
SD 26					
#1 $R = a \cdot ssN + c$	a = 1.295053	0.21899	0.00	1.32	0.69
	c = -73.88097	73.79343	0.33		
#2 $R = a \cdot ssN + b \cdot RV + c$	a = 0.974694	0.192394	0.00	1.67	0.83
	b = 2.119031	0.612369	0.00		
	c = -72.00417	56.83591	0.22		
#3 $R = a \cdot ssN \cdot RV + c$	a = 0.008195	0.001381	0.00	1.16	0.69
	c = 151.6722	46.7975	0.01		
#4 $R = RV \cdot (a \cdot ssN + c)$ [$R/RV = a \cdot ssN + c$]	a = 3.346399	2.00575	0.11	1.61	0.15
	c = -104.0102	675.8954	0.88		
#5 $R = ssN \cdot \exp(a \cdot ssN + c)$ [$\ln(R/ssN) = a \cdot ssN + c$]	a = 0.000746	0.000809	0.37	0.94	0.71
	c = -0.416527	0.272634	0.15		
#6 $R = ssN \cdot \exp(a \cdot ssN + b \cdot RV + c)$ [$\ln[R/ssN] = a \cdot ssN + b \cdot RV + c$]	a = -9.98E-05	0.000838	0.91	0.96	0.85
	b = 0.005591	0.002668	0.05		
	c = -0.411575	0.247667	0.12		
#7 $R = ssN \cdot RV \cdot \exp(a \cdot ssN + c)$ [$\ln(R/(ssN \cdot RV)) = a \cdot ssN + c$]	a = -5.93E-03	0.003775	0.14	1.25	0.15
	c = 0.57968	1.271986	0.65		
#8 $R = ssN^a \cdot RV^b \cdot \exp(c)$ [$\ln(R) = a \cdot \ln(ssN) + b \cdot \ln(RV) + c$]	a = 0.868428	0.211268	0.00	0.67	0.76
	b = 0.103038	0.047658	0.05		
	c = 0.411377	1.128871	0.72		
SD 28					
#1 $R = a \cdot ssN + c$	a = 1.388394	0.15375	0.00	1.74	0.84
	c = -34.87475	23.71123	0.16		
#2 $R = a \cdot ssN + b \cdot RV + c$	a = 1.396162	0.151571	0.00	1.73	0.85
	b = 0.718526	0.588287	0.24		
	c = -42.42439	24.15914	0.10		
#3 $R = a \cdot ssN \cdot RV + c$	a = 0.009536	0.009861	0.35	0.30	0.06
	c = 120.2287	37.7014	0.01		
#4 $R = RV \cdot (a \cdot ssN + c)$ [$R/RV = a \cdot ssN + c$]	a = 128.7795	20.40592	0.00	1.04	0.07
	c = -4526.896	3147.047	0.17		
#5 $R = ssN \cdot \exp(a \cdot ssN + c)$ [$\ln(R/ssN) = a \cdot ssN + c$]	a = 0.006479	0.001469	0.00	1.76	0.78
	c = -1.368814	0.226543	0.00		
#6 $R = ssN \cdot \exp(a \cdot ssN + b \cdot RV + c)$ [$\ln[R/ssN] = a \cdot ssN + b \cdot RV + c$]	a = 6.59E-03	0.001346	0.00	1.33	0.82
	b = 0.010576	0.005223	0.06		
	c = -1.479937	0.21448	0.00		
#7 $R = ssN \cdot RV \cdot \exp(a \cdot ssN + c)$ [$\ln(R/(ssN \cdot RV)) = a \cdot ssN + c$]	a = 8.10E-03	0.00717	0.28	1.69	0.06
	c = 1.693038	1.105708	0.15		
#8 $R = ssN^a \cdot RV^b \cdot \exp(c)$ [$\ln(R) = a \cdot \ln(ssN) + b \cdot \ln(RV) + c$]	a = 1.458096	0.121747	0.00	0.88	0.82
	b = 0.083543	0.050107	0.12		
	c = -2.243144	0.552074	0.00		

(*) When referring to the linear recruitment equations (#1-#3), the square of the Pearson correlation coefficient (r²) is equal to the coefficient of multiple determination R².

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Tables:**Table 1.** Variables, parameters, and indices used in our model.

variables and parameters		indices
$N_{a,r,q,y}$	Eastern Baltic cod stock size in number of fish [million]	r region (i.e., subdivision: SD 25, SD 26, SD 28)
$R_{a,r,y}$	Recruitment [million]	a age-group (ag0 – ag8)
$M_{a,r,q,y}$	Natural Mortality	q quarter (qu1 – qu4)
$P_{a,r,q,y}$	Predation Mortality	y year (y1976 – y2050)
$F_{a,r,q,y}$	Fishing Mortality	
ssN	Spawning stock size in number of fish	
RV	Reproductive Volume	

Table 2. Coefficient $\alpha_{r,q}$, defining management scenarios 1-5.

Management Scenario		SD 25	SD 26	SD 28
1. FasU		1	1	1
2. RoF70		0.3	0.3	0.3
3. C25q1q2	q1,q2:	0	1	1
	q3,q4:	0.5	1	1
4. C25		0	1	1
5. TC		0	0	0

Figure captions:

Fig. 1. Chart of the Baltic Sea, showing ICES subdivisions and important spawning grounds of Baltic cod. Source: after Bagge et al. (1994b).

Fig. 2. Linear regression of the spawning stock size, derived by our model (applying functional form #2 for calculating recruitment) with spawning stock estimates derived by ICES standard stock assessment; time series: 1976-1999.

Fig. 3. Simulations based on environmental conditions 1 (“HighLow”): data sequence from 1974-1999 is applied repeatedly for the simulation period 2000-2050. Management scenarios: (“NoC”) no closure = fishing “as usual”; (“70C25”) 70% closure of SD 25 & no fishing effort redistribution; (“100C25ER”) 100% closure of SD 25 & full effort redistribution; (“100C25”) 100% closure of SD 25 & no fishing effort redistribution; (“TC”) total closure = zero fishing. Bars: reproductive volume [km^3] in SD 25 (black), in SD 26 (white), in SD 28 (grey).

Fig. 4. Simulations based on environmental conditions 2 (“LowHigh”): data sequence from 1981-1999 followed by 1974-1980 is applied repeatedly. See Figure 4 legend for explanation of the graphs.

Fig. 5. Simulations based on environmental conditions 3 (“HighHigh”): constantly high reproductive volume; data from year 1977. See Figure 4 legend for explanation of the graphs.

Fig. 6. Simulations based on environmental conditions 4 (“LowLow”): six year cycle of low reproductive volume; the data sequence from 1985-1990 is repeatedly applied. See Figure 4 legend for explanation of the graphs.

Fig. 7. Age structure of the cod stock in year 2050 for the five different management scenarios under environmental conditions 1 (“HighLow”).

Figure 1

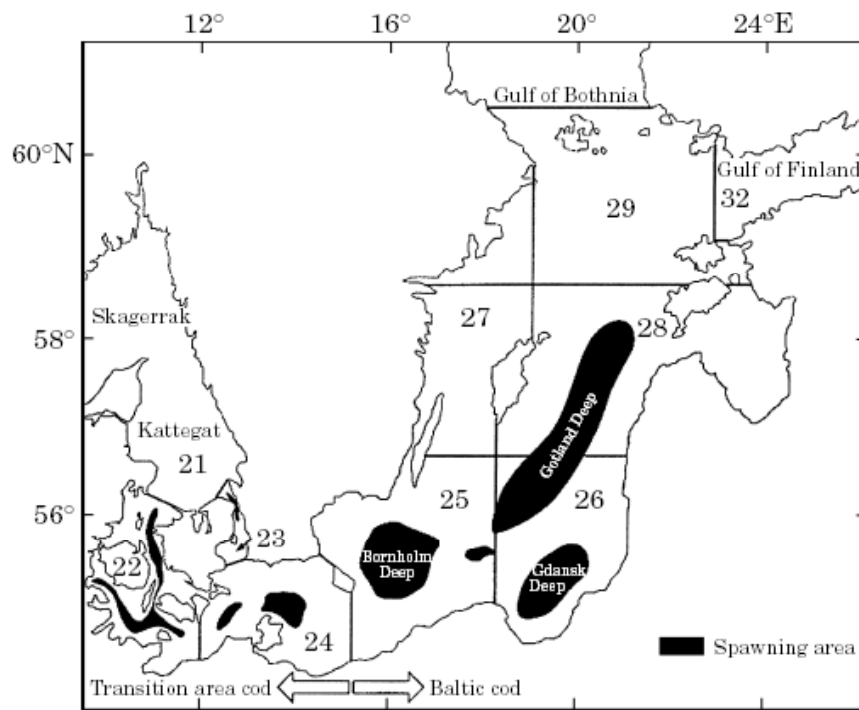


Fig. 1. Chart of the Baltic Sea, showing ICES subdivisions and important spawning grounds of Baltic cod. Source: after Bagge et al. (1994b).

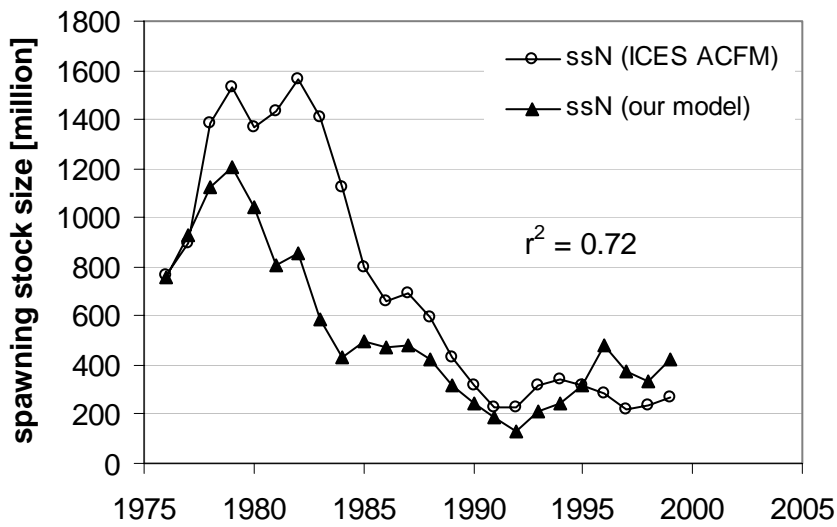
Figure 2

Fig. 2. Linear regression of the spawning stock size, derived by our model (applying functional form #2 for calculating recruitment) with spawning stock estimates derived by ICES standard stock assessment; time series: 1976-1999.

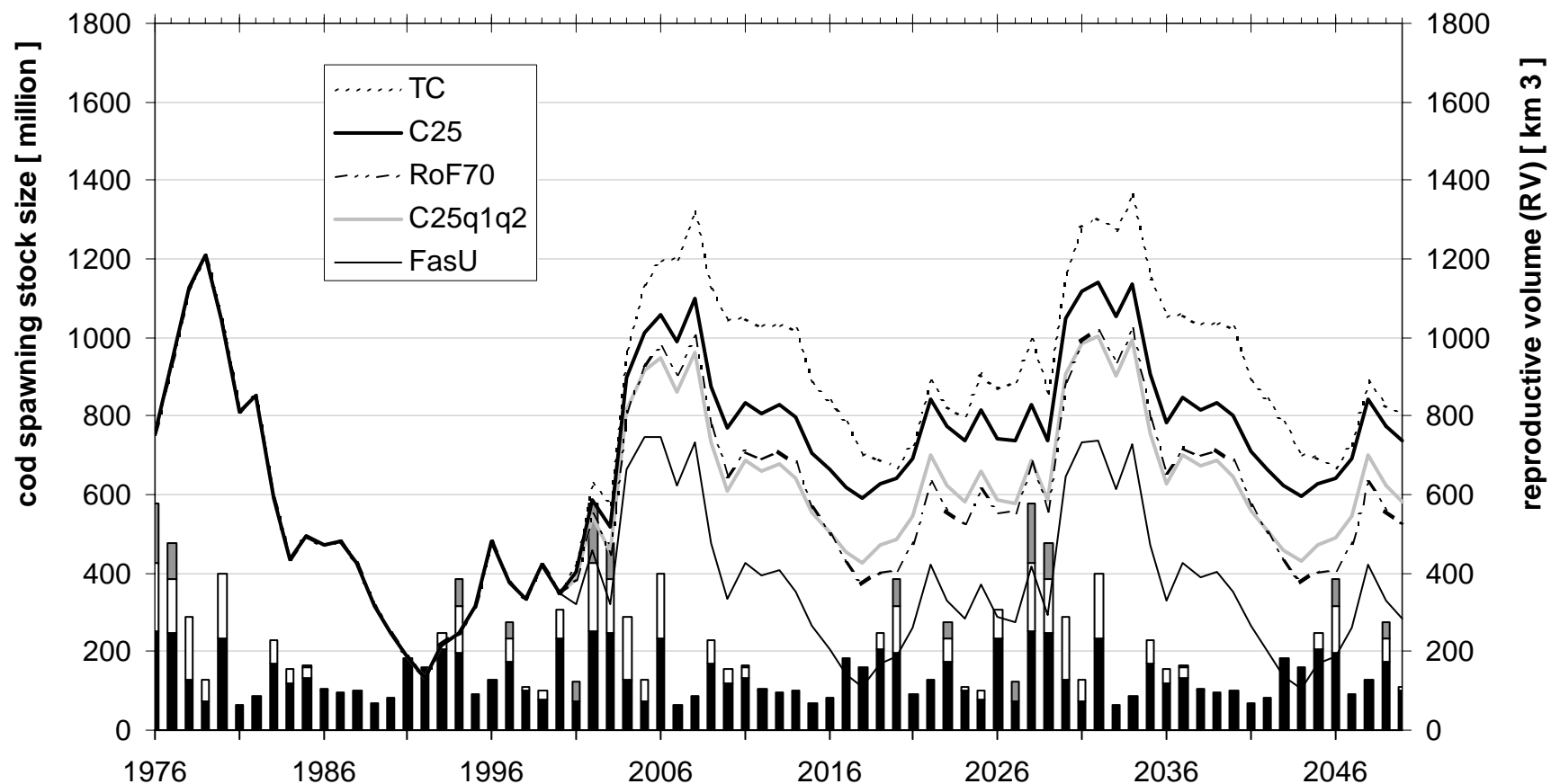


Fig. 3. Simulations based on environmental conditions 1 (“HighLow”): data sequence from 1974-1999 is applied repeatedly for the simulation period 2000-2050. Management scenarios: (“NoC”) no closure = fishing “as usual”; (“70C25”) 70% closure of SD 25 & no fishing effort redistribution; (“100C25ER”) 100% closure of SD 25 & full effort redistribution; (“100C25”) 100% closure of SD 25 & no fishing effort redistribution; (“TC”) total closure = zero fishing. Bars: reproductive volume [km^3] in SD 25 (black), in SD 26 (white), in SD 28 (grey).

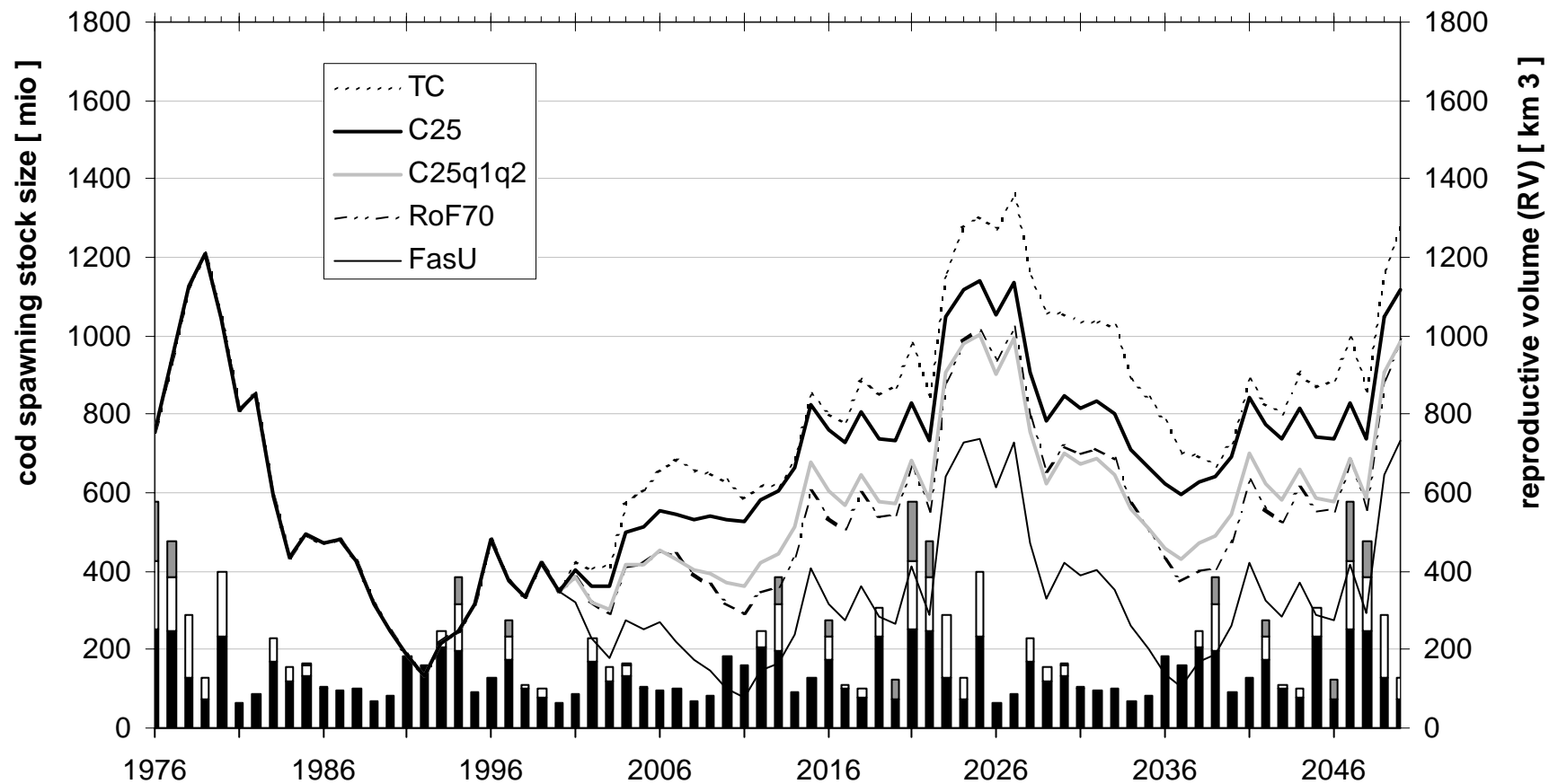


Fig. 4. Simulations based on environmental conditions 2 (“LowHigh”): data sequence from 1981-1999 followed by 1974-1980 is applied repeatedly. See Figure 4 legend for explanation of the graphs.

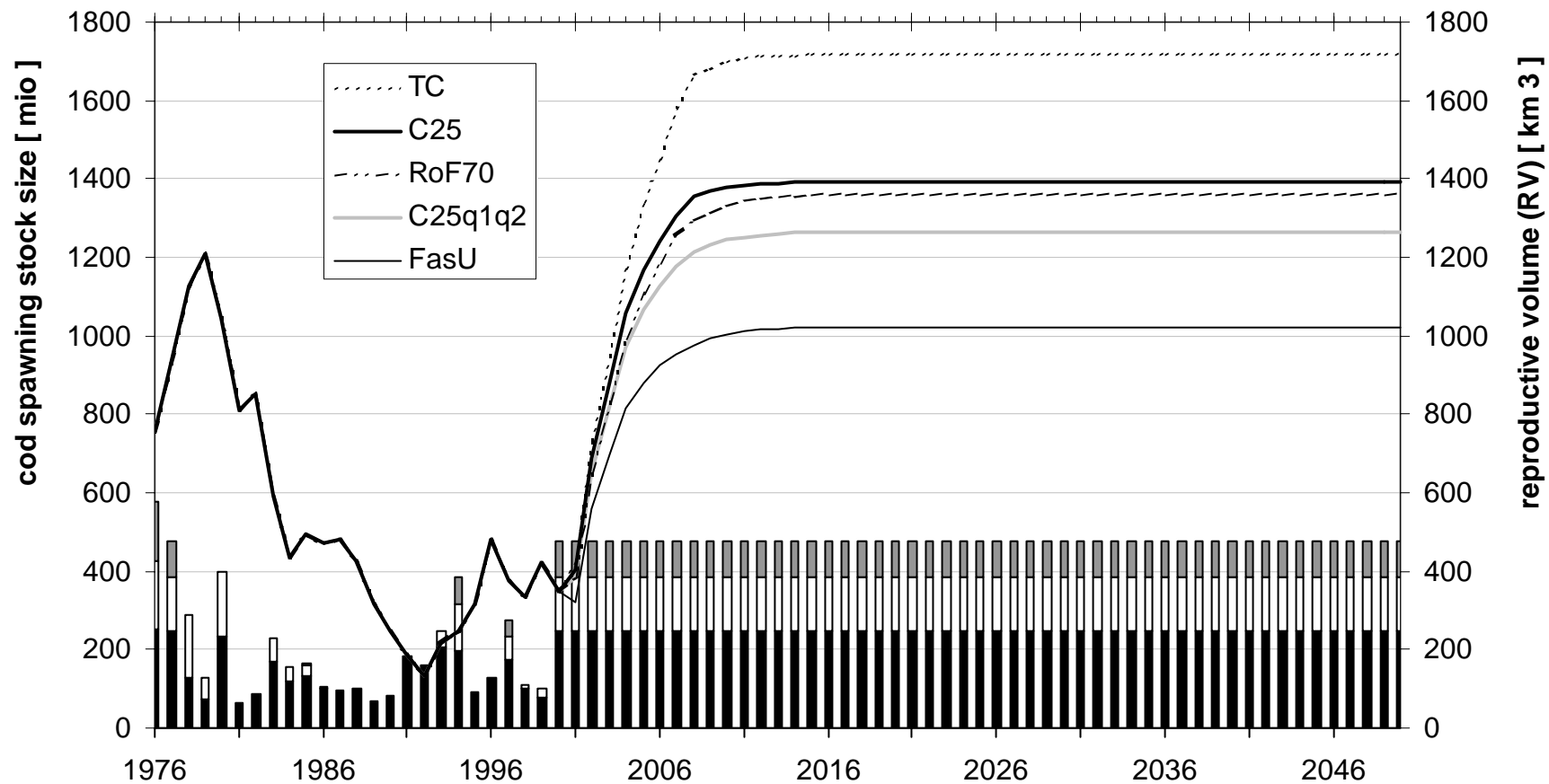


Fig. 5. Simulations based on environmental conditions 3 (“HighHigh”): constantly high reproductive volume; data from year 1977. See Figure 4 legend for explanation of the graphs.

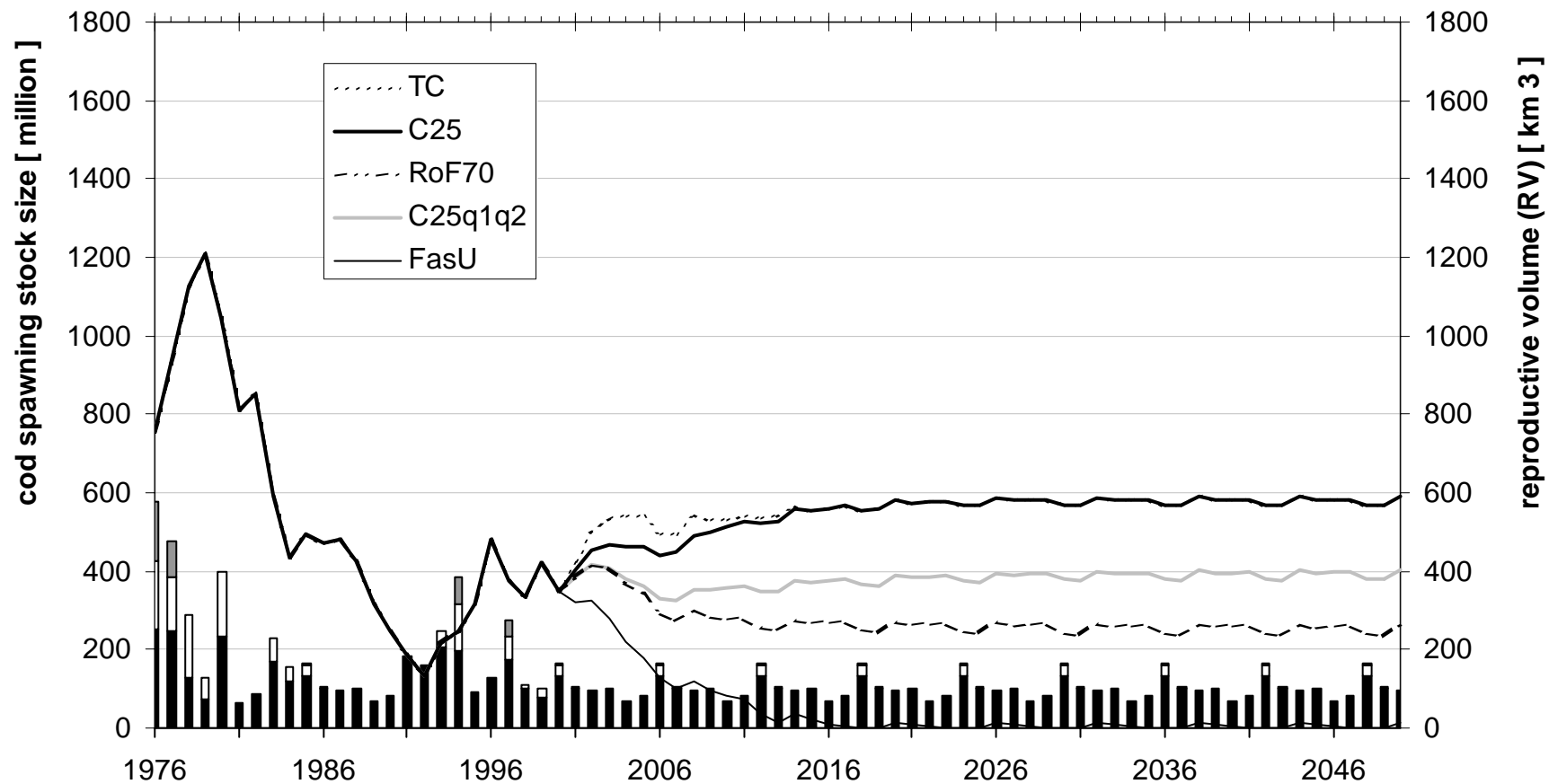
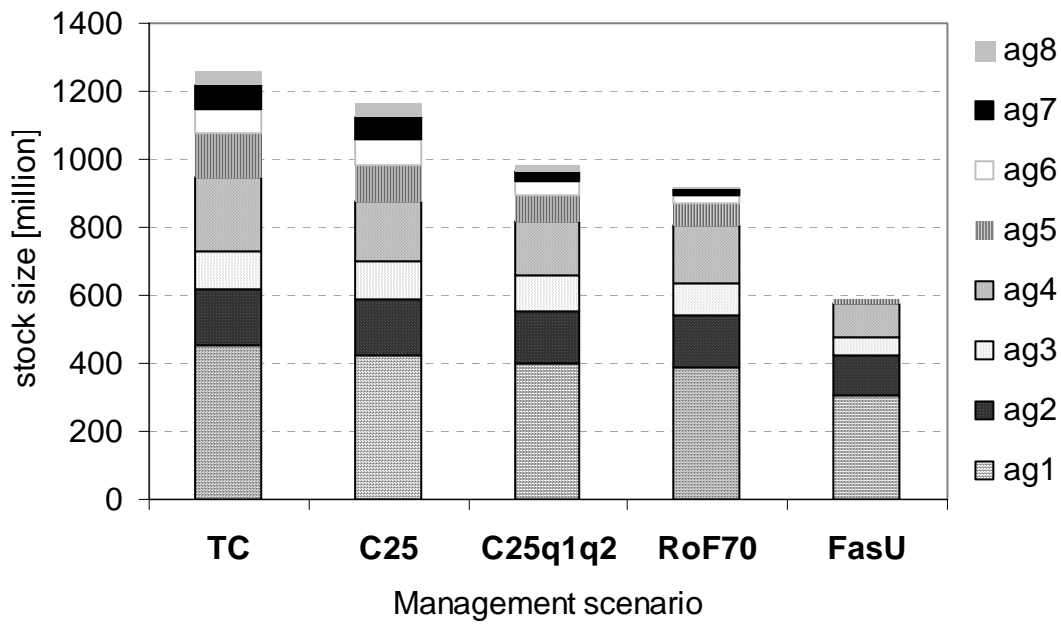


Fig. 6. Simulations based on environmental conditions 4 (“LowLow”): six year cycle of low reproductive volume; the data sequence from 1985-1990 is repeatedly applied. See Figure 4 legend for explanation of the graphs.

1 **Figure 7**

2



3

4 **Fig. 7.** Age structure of the cod stock in year 2050 for the five different management
 5 scenarios under environmental conditions 1 (“HighLow”).

6

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