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Average salinity as an index for environmental forcing on cod recruitment in the Baltic Sea

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Annual average deep-water salinity of the Baltic Sea was found to be usable as an index for environmental forcing that largely determines the level of recruitment of cod (*Gadus morhua*). Ricker's stock–recruitment equation with annually averaged salinity in the deepest basin of the central Baltic as an environmental factor explained 85% of the interannual variation in the recruitment of cod from 1974–2004 and closely predicted the drastic decrease in recruitment in the 1980s. The reproductive volume index, based on salinity and oxygen concentrations in the reproduction areas, does not provide such a high coefficient of determination. This finding is useful for multispecies modelling of the Baltic fish stocks, and also supports the hypothesis that hydrographic conditions play a dominant role in the recruitment success of cod. The most probable mechanisms are direct effects on the survival of eggs and indirect effects on the early phases of cod via the species composition of the planktonic food organisms.

Introduction

Large changes in the abundance of cod (*Gadus morhua*) have been typical in the Baltic Sea during the past three decades. Environmental factors, fishing and interactions between the fish species are currently assumed to be involved (Köster *et al*. 2005). In the Baltic Sea, the interacting fish community in the open sea areas is dominated by three species: cod, herring (*Clupea harengus*), and sprat (*Sprattus sprattus*). The cod stock has been at low level since 1990, whereas the sprat stock is currently abundant (ICES 2005; Fig. 1). Alheit *et al*. (2005) suggested that the dramatic changes in the abundance of fish stocks in the 1980s were linked to a general "regime shift" in the Baltic Sea.

The reproductive success of cod in the Baltic is coupled to hydrographic conditions in the spawning areas, mainly oxygen content and salinity (Köster *et al*. 2005 and references therein). In addition to direct hydrographic forcing, biological processes such as predation on eggs by clupeids (Köster and Möllmann 2000), cannibalism on juveniles (Neuenfeldt and Köster 2000, Uzars and Plikshs 2000) and food supply (Hinrichsen *et al*. 2002) have been suggested to affect the early life stage survival of cod. The concept of "reproductive volume" (RV) has been developed as an index for the environmental effect, combining two limiting factors, oxygen content and salinity (Plikshs *et al*. 1993, MacKenzie *et al*. 2000). This is the water volume that allows for successful cod egg development,

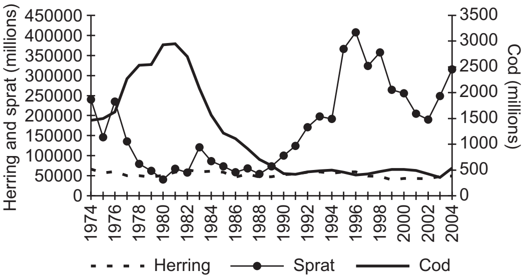

Fig. 1. Development of stock sizes of cod, herring and sprat (ages ≥ 1) in the Baltic Sea from 1974–2004. Note the different scale for the cod stock.

in some cases also taking into account temperature circumstances and oxygen consumption by biological processes (Köster *et al*. 2005). Despite being conceptually appealing, the reproductive volume explains only a limited amount of variance in cod recruitment (Sparholt 1996, Köster *et al*. 2005).

Multispecies virtual population analysis (MSVPA) has been used in the fish stock assessment of the Baltic with both a hind-cast VPA type mode and a forecast catch prediction mode (e.g. Magnusson 1995). Attempts with other types of multispecies models have also been made (Harvey *et al*. 2003). The factors affecting the recruitment of cod are still a problem in multispecies modelling. Recruitment models with environmental effects have been developed (Köster *et al*. 2001a, 2001b, Köster *et al*. 2005), and the best determination coefficients have been achieved for models with potential egg production and reproductive volume as independent variables. Until currently, in multispecies assessment the predictions for cod in the Baltic have been separately made for “good” and “bad” environmental conditions, with recruitment drawn from lognormal distributions derived from the observed recruitment according to hind-cast MSVPA assessment (ICES 2005). A simple index that would adequately represent the environmental forcing on cod recruitment, allowing for a single stock–recruitment equation in both “good” and “bad” periods, would be useful in cod stock assessment and multispecies modelling in the Baltic.

Large-scale climate patterns affect marine, terrestrial and limnic ecosystems via complex physical and biological processes (Stenseth *et al*. 2003, Alheit *et al*. 2005). Proxies for the overall climate condition such as the NAO (North Atlantic Oscillation) are useful in ecological studies because they provide a robust assessment of the ecological effects of climate fluctuations (Stenseth *et al*. 2003, Stige *et al*. 2006). Several studies have linked the variability in cod recruitment to the NAO (Stige *et al*. 2006 and references therein). Hänninen *et al*. (2000) and Zorita and Laine (2000) found that salinity changes in the Baltic Sea are connected to large-scale atmospheric circulation mirrored by climatic indices. In the 1980s, there was a shift of the NAO from a negative to a positive phase (Alheit *et al*. 2005), which led to increased western winds, increased rainfall and reduction in saline water pulses from the North Sea, and consequently, to decreased salinity in the Baltic Sea (Zorita and Laine 2000, Möllmann *et al*. 2003 and references therein). This induced a profound change, a “regime shift” in the ecosystem of the Baltic Sea, and simultaneously in the North Sea, involving all trophic levels in the pelagial (Alheit *et al*. 2005).

In this study, I hypothesized that the collapse of cod recruitment in the 1980s was at least partly a consequence of an ecological regime shift caused by the climatic forcing. As the NAO index is closely linked to salinity in the Baltic Sea, salinity could be a suitable proxy for the environmental effect. Accordingly, I used average deep-water salinity as an environmental index in Ricker’s stock–recruitment model for cod. This model was compared to the pure Ricker model and to a model with reproductive volume as an independent variable.

Material and methods

The time series of spawning stock biomass and recruitment of cod from 1974–2004 (Fig. 2) used in this study are from the MSVPA (Magnusson 1995), key run for the Baltic main basin (SGMAB: Study Group on Multispecies Assessment in the Baltic, ICES 2005). The recruitment of cod was at a high level during good environmental conditions in 1974–1985 (2000–5000 million age-0 recruits), but considerably lower during the period with poor environmental

Fig. 2. Spawning stock biomass (SSB) and recruitment (age 0) of cod in the Baltic from 1974–2004 according to MSVPA results.

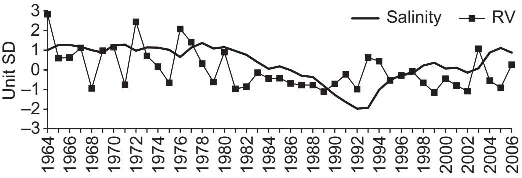

Fig. 3. Annually averaged salinity values below 100 m (Landsort Deep), and values of reproductive volume (RV) for cod according to M. Plikshs, Latvian Fisheries Research Institute (unpubl. data). The time series were normalized to unit SD with the average 0.

conditions from 1986–2004 (100–500 million) (ICES 2005; Fig. 2).

Three spawning stock–recruitment models were fitted to the data: (1) the pure Ricker model (Eq. 1; Hilborn and Walters 1992), (2) the Ricker model with the reproductive volume (RV) index as an environmental factor (Eq. 2), and (3) the Ricker model with the average annual salinity as an environmental factor (Eq. 2):

$$R = S\exp(a - bS) \quad (1)$$

where R = recruitment (1000 age-0 recruits), S = spawning stock biomass (1000 tonnes), a and b are constants.

The equation with the environmental effect is

$$R = S\exp[a - bS + c(E - \bar{E})] \quad (2)$$

where E is the environmental variable and $\bar{E}$ is the average value, and c is constant (Hilborn and Walters 1992).

The RV values (Fig. 3) are based on data from three spawning areas of cod: Bornholm Basin, Gdansk Deep and Gotland Basin. The estimation of reproductive volume is described by Plikshs *et al.* (1993) and MacKenzie *et al.* (2000), defined as the volume of water exceeding critical levels of salinity (> 11‰) and oxygen concentration (> 2 ml l^{-1}). RVs have also been calculated by the Institute of Marine Science, Kiel, using a different methodology and taking temperature into account (> 1.5 °C). There are differences between these time series but the peaks and troughs generally coincide (MacKenzie *et al.* 2000). Three to five basins of the central Baltic are usually included in the calculation of the reproductive volume, but the Bornholm Basin is the most important and has mainly determined the trend from 1980 onwards (MacKenzie *et al.* 2000, Jarre-Teichmann *et al.* 2000).

The salinity data were obtained from the Finnish Institute of Marine Research and from the database of the Swedish Meteorological and Hydrological Institute. Annual average salinity values from the deepest station BY 31 in Landsort Deep (58°35´N, 18°14´E, depth 450 m) were used, with the salinity averaged for depths ≥ 100 m similarly to Zorita and Laine (2000), to represent the large-scale environmental conditions in the Baltic Sea. The reproductive volume, on the contrary, is a direct measure of the conditions in the spawning areas. The general trends in the salinity and RV time series are similar, but there is larger interannual variation in the RV, and opposite patterns in the first half of the 1990s compared to the average salinity (Fig. 3).

Data from 1974–2004 were included in the stock–recruitment analysis. Nonlinear regression analysis was used to fit the three stock–recruitment models to the data. Linear regression with ln-transformed equations, which imply assumed lognormal distribution of residuals (Hilborn and Walters 1992), was also tried but the model fits were markedly worse as compared with those of the nonlinear method. Thus, normal distribution of the residuals of R was a more realistic assumption in this case. The three models were then compared on the basis of determination coefficients and information criteria (AIC and BIC). The significance of the parameters was considered on the basis of the confidence ranges, the residuals were examined for potential autocorrelation, and the predicted values were plotted with the observed recruitment data to check the goodness of fit of the models.

Results

According to nonlinear regression analysis, the Ricker model without the environmental effect gave the lowest coefficient of determination (Table 1), and the residuals were significantly autocorrelated, with first order autocorrelation of 0.82 and second order autocorrelation of 0.61 (Fig. 4). Fits of the models with the environmental effect, either reproductive volume or salinity, were better than that of the pure Ricker model (Tables 1 and 2). The Ricker equation with salinity as an environmental variable clearly best explained the variation in the recruitment of cod, with a mean corrected $R^2 = 0.85$ and the lowest values of Akaike's and Bayesian information criteria. There was first-order autocorrelation (0.52) in the residuals of the reproductive volume model, but not in the residuals of the salinity model (Fig. 4).

The salinity model also best predicted the recruitment of cod in 1974–2004, especially the latter part of the period when the recruitment level rapidly dropped at the beginning of the 1980s and then remained at a low level until the end of the time series (Fig. 5).

The confidence ranges of the compensatory coefficient *b* included 0 in all models, which means that the term was not significant. The environmental terms of the latter two models (reproductive volume and salinity) were significant.

Discussion

The results indicate that the recruitment of Baltic cod can be explained by the biomass of the spawning stock, and by environmental conditions. The fit of a stock–recruitment model was weak with the spawning stock biomass as the

Table 1. Results of the nonlinear regression analysis for three stock–recruitment models: coefficients of determination (R^2), Akaike's information criteria (AIC) and Bayesian information criteria (BIC) (smaller value indicates better model). Raw R^2 is the proportion of explained variation about zero; mean corrected R^2 is the proportion of explained variation about the mean; $R^2_{(\text{observed } vs. \text{ predicted})}$ is the squared correlation coefficient.

	Ricker	Ricker + repr. volume	Ricker + salinity
Raw R^2	0.714	0.796	0.915
Mean corrected R^2	0.505	0.647	0.854
$R^2_{(\text{observed } vs. \text{ predicted})}$	0.514	0.652	0.854
AIC	27.72	27.45	26.57
BIC	27.81	27.59	26.71

Table 2. Results of the nonlinear regression analysis for three stock–recruitment models: parameter values. A.S.E. is the asymptotic standard error. The term Param./A.S.E. is interpreted as a *t* statistic.

Parameter	Estimate	A.S.E.	Param./A.S.E	Wald 95% confidence interval
Ricker model				
a	8.200	0.452	18.124	7.275–9.125
b	–0.001	0.001	–0.662	–0.003–0.001
Ricker model + reproductive volume				
a	7.995	0.435	18.372	7.104–8.887
b	–0.001	0.001	–1.073	–0.003–0.001
c	0.002	0.001	3.840	0.001–0.004
Ricker model + average salinity				
a	7.576	0.376	20.152	6.806–8.346
b	0.000	0.001	–0.212	–0.001–0.001
c	1.549	0.265	5.849	1.007–2.092

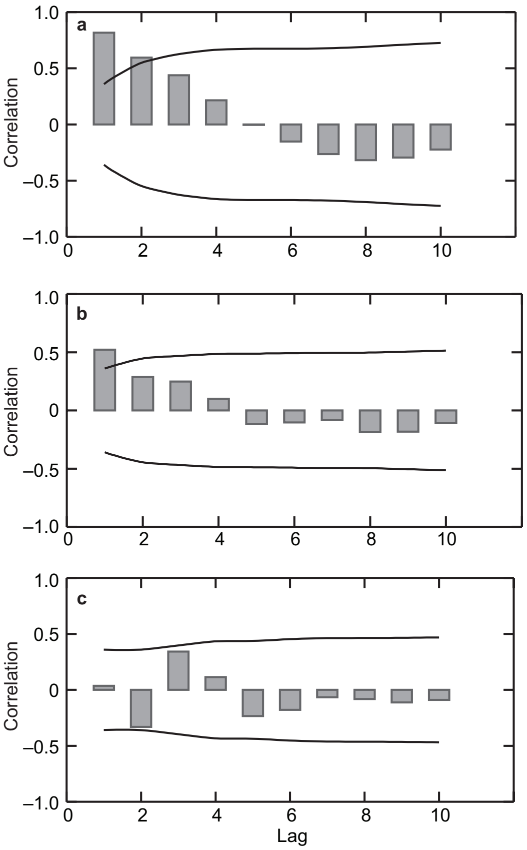

Fig. 4. Autocorrelation of the residuals of (**a**) the Ricker model, (**b**) the Ricker model with reproductive volume as an environmental variable, and (**c**) the Ricker model with average salinity as an environmental variable, with lines denoting the 95% confidence levels for the significance of each correlation.

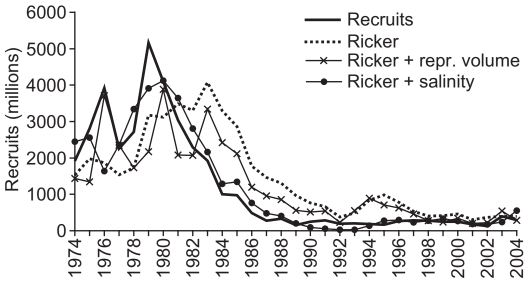

Fig. 5. Cod recruitment (0-year-old recruits) from 1974–2004 according to the MSVPA results, and predicted by three S/R models: a simple Ricker model, a Ricker model with reproductive volume as an environmental factor, and with average salinity as an environmental factor.

only independent variable. Annually averaged salinity in deep layers of the central Baltic as an environmental factor in the stock–recruitment model substantially increased the determination coefficient, and the fit was markedly better as compared with that of earlier models with reproduction volume or other independent variables, the highest determination coefficients of which were 0.5–0.7 (e.g. Köster *et al*. 2001b).

In all three models, the compensatory coefficient *b* was not significant, which would allow the recruitment to grow infinitely in predictive simulations. This non-realistic feature is most probably due to the narrow range of the spawning stock biomass data, lack of contrast (Hilborn and Walters 1992: p. 294). Thus, when using the model for prediction, a constraint has to be set, such as a hockey-stick type of equation (Barrowman and Myers 2000), in order to obtain realistic simulation results.

There is extensive literature on the factors that affect cod recruitment in the Baltic Sea (Sparholt 1996, Aro 2000, Cardinale and Arrhenius 2000, Köster and Möllmann 2000, Köster *et al*. 2001a, 2001b, Neuenfeldt and Köster 2000, Hinrichsen *et al*. 2002, Köster *et al*. 2005). Agreement exists on the fact that hydrographic circumstances, coupled with large-scale atmospheric circulation (Zorita and Laine 2000, Hänninen *et al*. 2000), are essential, and the effect is mediated via several physical and biological processes (Alheit *et al*. 2005). The directly constraining factors for the development of cod eggs are salinity, oxygen concentration and temperature (MacKenzie *et al*. 2000). Cardinale and Arrhenius (2000) suggested that the viability of cod eggs is also affected by parental stock structure. Among the biological processes, changes in the species composition of the zooplankton seem to play a significant role, especially the marine planktonic copepod *Pseudocalanus elongatus* that serves as a major food organism for larval cod (Hinrichsen *et al*. 2002, Möllmann *et al*. 2003). The abundance of this marine species is closely linked to salinity (Möllmann *et al*. 2003). In addition, egg predation by clupeid fish has been regarded as important (Köster and Möllmann 2000). Cannibalism of cod (Neuenfeldt and Köster 2000, Uzars and Plikshs 2000) has been incorporated in the MSVPA estimation, with the exception of intra-cohort cannibalism (ICES 2005). In the hind-cast calculation, this results in the estimated recruitment at age 0 being slightly higher than it would be without cannibalism.

The incorporation of these numerous processes or variables in models for fish stock assessment is problematic. Going into increasing detail in modelling attempts might not lead to the desired outcome, a larger proportion of explained variation. Reproductive volume represents a combination of different physical variables, calculated and summed for separate reproduction areas of cod, but only a limited amount of variance in cod recruitment can be explained with this variable (Köster *et al*. 2005). Biological variables such as sprat abundance (Sparholt 1996) or food availability (Hinrichsen *et al*. 2002) are also directly or indirectly coupled with the hydrographic conditions. For instance, the size of the sprat stock is negatively correlated with that of its predator cod (Fig. 1; ICES 2005). The same hydrographic parameters that regulate the mortality of eggs affect the vertical overlap of clupeids and cod eggs, and thus the predation on eggs (Köster *et al*. 2005). All this causes intercorrelations in the environmental and biological variables. Stige *et al*. (2006) stated that proxies for the overall condition may account for ecological processes better than local variables in cases where impacts on recruitment occur through a suite of different physical and biological processes. The use of average salinity as a proxy in the recruitment equation for Baltic cod is in line with this statement.

The reproductive volume incorporates both salinity and oxygen concentration, which are mostly assumed to be positively correlated, because inflows of salt water from the North Sea enhance the oxygen conditions in the deep basins of the Baltic (e.g. Köster *et al*. 2005). However, low-frequency averages of these variables show negative correlation (Zorita and Laine 2000). According to Zorita and Laine (2000), alternative mechanisms may lead to this negative relationship: The atmospheric circulation over the North Atlantic causes stronger westerly winds that increase rainfall and subsequent runoff in the catchment area, the conditions prevailing since the late 1980s (Matthäus and Nausch 2003), and this leads to decreased salinity. The oxygen concentration may be enhanced by weakened stratification due to decreased salinity (over long time scales), or more frequent inflows from the North Sea (over short time scales). However, there were no major inflows between the events in 1976 and 1993, and the latest inflow occurred in January 2003 (Matthäus 2006). The annually averaged oxygen concentrations in both the surface and deep layers have shown a rising trend since the mid-1980s, simultaneously with the decreasing salinity (Zorita and Laine 2000).

The model with average salinity accurately predicts the rapid decline in cod recruitment in the first half of the 1980s, which has been explained by the hydrographic conditions and high fishing effort (Köster *et al*. 2005). The recruitment started to decline even though the spawning stock biomass was still high until the mid-1980s (Fig. 2), and the number of eggs produced by old females was high (Cardinale and Arrhenius 2000). There was also no marked change in the fishing mortality (ICES 2005). This indicates at a decisive influence of other factors than fishing.

The model with reproductive volume seems to better simulate the fluctuations in recruitment in the late 1970s, with the exception of the peak in 1979. Köster *et al*. (2001b) also encountered underestimation of the recruitment in 1979 with all alternative models, and concluded that the "observed" recruitment derived by the MSVPA is biased, because the abundance of this year class at age 1 was above average but not extraordinary high. The predictions of the Ricker model and reproductive volume model deviate from the MSVPA results most obviously in the latter part of the 1980s and from 1994 to 1996, which is due to the high spawning stock biomass, and partly to the high reproductive volume in 1994, whereas the salinity was declining and remained below average until 1997 (Figs. 2 and 3).

It seems not probable in this case that the correlation between deep-water salinity and cod recruitment would be spurious. The significance of environmental conditions, largely coupled to salinity, in cod recruitment has been recognized (e.g. Köster *et al*. 2005), and the copepod *Pseudocalanus elongatus* is an obvious link between salinity and the survival of cod larvae (Möllmann *et al*. 2003, Alheit *et al*. 2005). The salinity in the deepest basin reflects the effects of atmospheric circulation, as well as hydrographic conditions in other deeps including the spawning areas of cod, and in surface waters (Zorita and Laine 2000). In brackish water, many species at different levels of the food web are dependent on salinity (Hänninen *et al*. 2000 and references therein). Most probably, hydrographic variables affect cod recruitment directly through survival of eggs, and indirectly as reviewed above, e.g. through species composition and availability of the food organisms important for survival of the early phases.

The high determination coefficient of the salinity model raises the question whether predation by sprat and herring on cod eggs (Köster and Möllmann 2000) played a significant role as a regulating factor of cod recruitment on a large scale. The environmental effect alone seems to be adequate to explain the drastic decline in the recruitment level in the 1980s, when sprat was not yet abundant, and the subsequent low-recruitment period. However, there is evidence from the northwestern Atlantic that predation on cod eggs may have a decisive effect on recruitment (Swain and Sinclair 2000), but the causal relationships in the Baltic Sea possibly differ because of its unique circumstances and the substantial influence of salinity on the ecosystem (Alheit *et al*. 2005, Möllmann *et al*. 2005).

The results of this approach support the hypothesis that hydrographic conditions play a dominant role in the recruitment success of Baltic cod, and that the dramatic decrease in cod recruitment in the 1980s was linked to an ecological regime shift in the Baltic Sea (Alheit *et al*. 2005). Moreover, it indicates that even if detailed knowledge of the processes affecting recruitment is essential for understanding the dynamics of fish stocks, it is not straightforward to incorporate this information in multispecies models. Problems arise from having many variables, some of which are strongly intercorrelated, and several interactions with large uncertainties. Climate indices are often found to be useful for assessment of the ecological effects of environmental fluctuations because they reduce complex space and time variability into simple measures (Stenseth *et al*. 2003, Stige *et al*. 2006). In the Baltic Sea, climatic circumstances are mirrored by the average deep-water salinity, which seems to function as an environmental index. In the case of cod, this index proved suitable for modelling the complicated effects that regulate recruitment and are either directly or indirectly coupled with the hydrographic conditions of the Baltic.

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