Causal correlation between recruitment and spawning stock size of central Baltic cod?

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A biologically sensible model for cod recruitment in the central Baltic is proposed. The model takes into account, in a simple way, (1) the spawning stock size of cod, (2) the annual spawning conditions in terms of salinity and oxygen content, and (3) the predation on cod eggs by sprat. The parameters are estimated using regression analysis methods. All three factors are shown to be statistically significant, although sprat predation is the least clear effect. The model residuals are not correlated (no auto-correlation). The model is successfully evaluated against independent data. According to the model, cod recruitment at age 0 is proportional to the spawning stock biomass (SSB) for realistic ranges of SSB, for a given set of spawning condition and sprat predation. It is further shown that it is important to use recruitment data from an MSVPA, where cod cannibalism is included, in stock recruitment analysis of central Baltic cod.

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Introduction

For fisheries management it is important to know whether and to what extent recruitment depends on spawning stock biomass, because the stock–recruitment relationship determines the sustainability of a particular harvest at varying levels of fishing mortality.

However, the analysis of stock–recruitment data is never easy. Due to environmental factors like temperature, salinity, feeding conditions for larvae and predation of eggs and larvae, recruitment varies considerably from year to year. These variations are superimposed on a possible relationship between recruitment and spawning stock size, often blurring the results of standard regression analyses.

Even if regression analysis shows a significant correlation between spawning stock and recruitment, there is a problem in interpretation. If favourable conditions for recruitment persist over a number of years, this will lead to an increase in spawning stock size and, as a consequence, a positive correlation may emerge. This problem is illustrated in Figure 1. Sometimes, this is clearly indicated in the data series when trends in recruitment appear before trends in spawning stock size. In statistical terms, the simulations reflect autocorrelation in the "dependent" variable (here recruitment, R)

and dependence, with some time lag, of the "independent" variable (here the spawning stock biomass, SSB) on the dependent variable (R). A basic assumption for regression analysis is thus not fulfilled. The possible effects created by autocorrelation in stock–recruitment relationships have also been simulated by Walters (1990), Armstrong and Shelton (1988) and Myers and Barrowman (1995), who clearly show that it may cause serious problems. Walters (1985) and Hilborn and Walters (1992) have also described a bias problem in estimation of SSB–R relationships which is caused by the dependence of SSB of R with time lag. The problem arises because it is not possible to freely select the level of SSB in the "experiment" and because the level of SSB changes when R changes level (with some time lag). Fortunately, problems of the above kinds are often revealed by autocorrelation in the residuals (Wonnacott and Wonnacott, 1970; Armstrong and Shelton, 1988) and may be overcome if, as in this case of Baltic cod, the contrast in the data is large. If autocorrelation is found little faith can be put into the estimated relationship from a standard regression analysis.

Another problem often ignored in SSB–R analysis is whether R is defined in a sensible way. As shown by Sparholt (1995) for the central Baltic cod stock, because of cannibalism, the relationship depends on whether R is
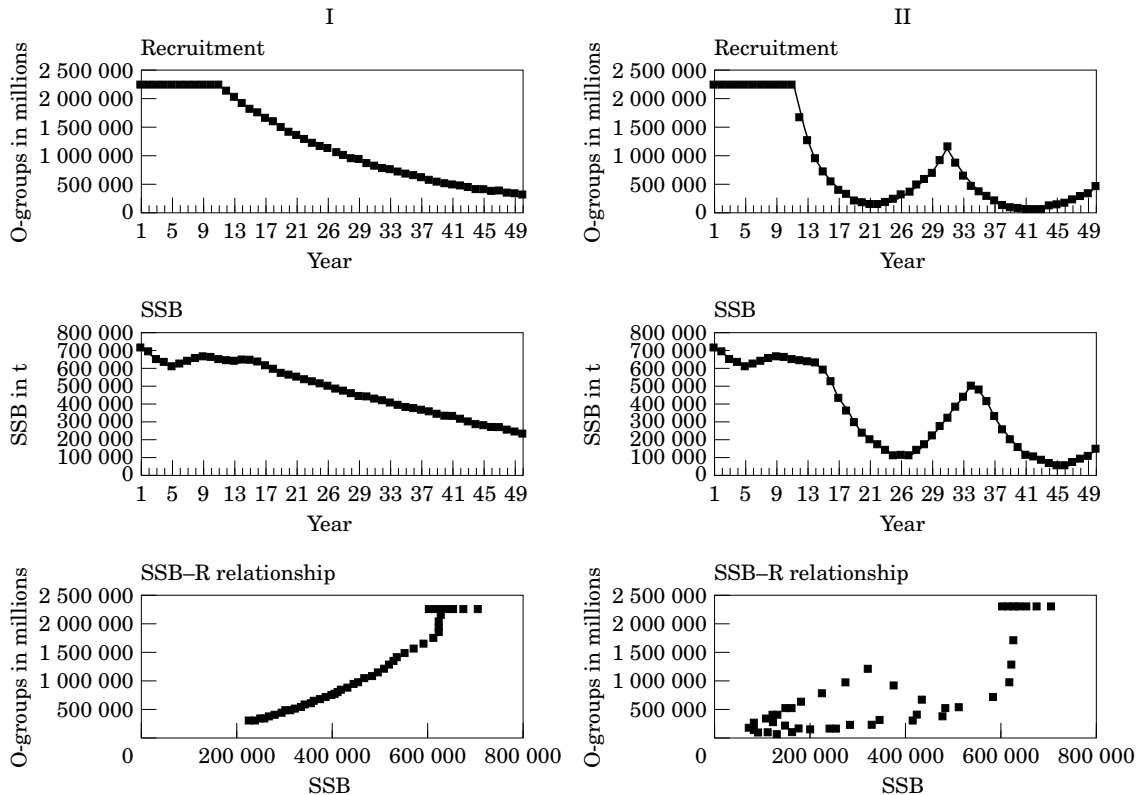
Figure 1. Two simulations (I and II) of R–SSB relationships when R varies independent of SSB. (a) Forced variation in R; (b) how SSB develops due to the variation in R according to the MSVPA/MSFOR model (Sparholt, 1994); and (c) the resultant plot of R against SSB. Even though R is forced to vary independent of SSB (for instance due to environmental conditions), the plots of R against SSB indicate that R is positively correlated to SSB.

measured as the number of 0-, 1-, or 2-years old cod. Paulik (1973) noted the same problem for salmon in Canada. Myers and Cadigan (1993a) have shown density-dependent juvenile mortality in several marine demersal fish stocks, indicating a more general problem. The central Baltic cod stock is especially interesting to consider in stock–recruitment studies because there are large contrasts in the data and because our knowledge has increased significantly in recent years regarding cannibalism, multi-species interactions and environmental factors affecting recruitment.

Of course, environmental effects might be (almost) the sole factor responsible for recruitment variability. Since it is not possible to carry out repetitive experiments in a given year with constant environmental conditions and to vary SSB, the appropriate way to elucidate the effects of environmental factors is to find and analyse them, as also suggested by Beverton and Iles (1992). The factors can then be included in a regression analysis in order to estimate the actual SSB effect, "cleaned" for the other factors. The number of parameters that might be included in a model of recruitment is virtually unlimited. However, since the number of observations of SSB and R is rather low, it is necessary to be parsimonious and

practical by considering only those factors which have been demonstrated to be of potential importance, and only to consider one or a few measures of these factors. The aim of this paper is to analyse whether a sensible model of the stock–recruitment relationship of central Baltic cod can be established if relevant environmental parameters are taken into account.

Oxygen content and salinity have been shown experimentally to be important for Baltic cod egg fertilization, development and survival (e.g. Nissling and Westin, 1991; Westin and Nissling, 1991; Waller *et al.*, 1993). These results are supported by *in situ* observations. For instance, Plikshs *et al.* (1993) observed that the fraction of viable cod eggs in samples from April–June 1954–1990 was related to both of these factors. Both the oxygen content and the salinity must exceed certain values. As the oxygen concentration generally increases and salinity decreases from bottom to surface in the Baltic Sea, it is reasonable to consider the available "spawning volume" (spvol) (Plikshs *et al.*, 1993) at a given time. The spvol is defined as the volume of the water masses with oxygen concentration above 2 ml/l and salinity above 11. Therefore, it seems appropriate to include spvol in a model of recruitment.

Furthermore, sprat predation on cod eggs has been shown to be substantial in some years (Köster, 1992; Anon., 1994a). So the inclusion of the stock size of sprat in a model of recruitment needs to be evaluated. However, other factors such as temperature and feeding conditions for cod larvae have never, convincingly, been demonstrated to be of importance in explaining the variation in Baltic cod recruitment.

Model and method

If cod eggs can only survive in water masses constituting the spvol, the most simple relationship between R and spvol is a proportional one. However, the distribution of cod in the central Baltic seems to be contracted towards the water masses with suitable spawning conditions when the spvol is reduced. In recent years, only the Bornholm Deep has offered suitable spawning conditions and the cod stock distribution has largely been restricted to this area (Sparholt and Munck-Petersen, in prep.). Thus, a more reasonable model would be that R is proportional to spvol^b, where 0<b<1.

Predation on cod eggs by sprat might be modelled by R being proportional to exp[− c^1*SB(spr)], where SB(spr) is the sprat stock biomass. It has been shown that fish predators in both the North Sea and the Baltic do not switch prey type as a function of prey abundance; predation mortality is approximately proportional to the amount of predators (Rice *et al.*, 1991; Anon., 1992; Larsen and Gislason, 1992). As SB(spr) has only varied by a factor of about 5 in the past, the above relationship can be approximated by R being proportional to SB(spr)^c, which is mathematically more convenient.

The relationship between cod SSB and R is also modelled as a proportional one. Density dependent mortality in the larval stage is not very likely because of the low density of cod larvae compared to other fish larvae (e.g. Anon., 1994a). Grauman (1973) found that cod larvae were not food limited because differences in food composition between years with high and low larvae abundance were not evident. Furthermore, Grauman found that the abundance of cod larvae was significantly correlated to the number of eggs in stage IV, indicating that recruitment is not determined in the larval stage. No major predator on cod larvae has been reported so far from the central Baltic.

The three factors influencing recruitment (SSB of cod, the spawning volume and the sprat stock) have been included in a linear model of logarithmic transformed data:

$$Log(R)=a+log[SSB(cod)]+b*log(spvol)+c*log[SB(spr)].$$

The effects of the different factors are thus regarded as multiplicative in the untransformed mode, and the variance structure is assumed to be lognormal with constant and equal coefficient of variation. Standard regression procedures were applied to estimate the model parameters and associated statistics by means of SAS Statistical Computer Software (Anon., 1988).

Material

Cod spawning stock biomass estimates were derived from Virtual Population Analysis (VPA) (Anon., 1994b), extrapolated backwards to 1966 using the proportion of F (fishing mortality) and M (natural mortality) before spawning and weight-at-age in the stock for 1966–1973, as used by Anon. (1994b) for 1974. The reliability of the VPA SSB estimates has been evaluated by Sparholt and Munck-Petersen (in prep.) who found that they correlated well with an SSB index from the international research vessel bottom trawl survey (r^2=0.96 for 1982–1992).

Recruitment (R$_0$) is defined as numbers of 0-group cod at 1 July from Multi-species VPA (MSVPA) for the years 1977–1992 (Anon., 1994a). For the years 1966–1976, recruitment figures were obtained by running a VPA with adjusted values of natural mortality (M) for 0-, 1-, and 2-groups. These M values were obtained from regression analysis of M on cod spawning stock biomass for the period 1977–1992 as estimated from MSVPA. The procedure was evaluated by comparing the numbers of 0-, 1-, and 2-groups from the MSVPA (1977–1992) with the numbers estimated by the VPA with adjusted M values. The deviations were in no cases more than 2%. Spawning volume is given by Plikshs *et al.* (1993) for February–May and August. Here the means of these values were used.

Biomass of 1-group and older sprat in 1977–1992 was taken from the MSVPA for sub-divisions 25–26 and 28 (Anon., 1994a). 0-group sprat are unimportant as predators on cod eggs because most of the young of the year hatch later than the spring–summer when cod eggs are present. In order to extend the time series backwards, the commercial catch of sprat in the Baltic (Anon., 1975 and 1994b) was assumed to represent a measure of the sprat biomass in 1966–1976. A conversion factor was obtained as the ratio between biomass and catch in 1977–1981.

All input data to the regression analysis are shown in Table 1. Data from 1992 onwards were not used because of convergence problems with VPA and MSVPA in the most recent data years (e.g. Pope, 1972). The data for 1977–1991 were regarded as the most reliable and used to estimate the parameters in the regression analysis. Data for 1966–1976 were used to test the model obtained.

Results

Figure 2a,b shows the time series of spawning stock biomass and recruitment at age 0 and age 2, respectively.

Table 1. The data used in the analysis. Data from 1977–1991 are used to estimate the parameters in the recruitment model and data from 1966–1976 to test the model.

Year/ year class	Cod SSB	Cod stock numbers			Sprat SB	Spawning volume	Sprat landings
		Age 0	Age 1	Age 2			
1966	228	704	501	339	341	220	92
1967	296	635	421	284	266	270	72
1968	300	506	334	227	337	80	91
1969	287	545	365	252	463	390	125
1970	262	625	430	302	561	345	151
1971	237	846	597	414	682	85	184
1972	259	1039	717	491	778	425	209
1973	276	670	454	298	782	240	210
1974	342	751	476	297	898	320	242
1975	426	1325	771	483	749	75	201
1976	424	2360	1381	846	724	605	195
1977	399	2339	1190	637	586	575	211
1978	488	2774	1104	472	491	255	132
1979	727	6583	1893	733	337	135	78
1980	828	5238	1512	723	231	380	58
1981	780	2801	1048	477	312	70	47
1982	806	1868	658	313	441	100	49
1983	783	1469	529	256	667	245	37
1984	759	1363	543	263	874	235	53
1985	616	1393	589	341	713	160	69
1986	451	569	325	209	523	120	75
1987	372	303	185	120	530	100	88
1988	354	246	156	109	501	75	80
1989	284	96	70	52	583	110	86
1990	216	134	102	83	1001	45	86
1991	146	286	218	—	1324	155	103
1992	72	165	—	—	1688	150	142

Weights in $t \times 10^{-3}$; numbers in millions; spawning volume in km^3.

The corresponding stock recruitment plots are given in Figure 2c,d. The relationship shows less variation for age 0 than for age 2. However, there is a very strong autocorrelation in the residuals as suggested by the lines joining observations from subsequent years.

The results of the regression analysis are shown in Table 2. Possible simplifications of the ultimate model are included as a means for evaluating the model fit.

In model 1, R_0 is simply regressed against cod SSB. The correlation is highly significant ($r^2 = 0.63$). However, the high value of the slope indicates that R_0 is almost proportional to SSB squared in the untransformed mode. Moreover, the residuals are significantly autocorrelated at the 5% level according to the Durbin–Watson D statistic (Wonnacott and Wonnacott, 1970). Thus, we cannot rely on this relationship.

The slope was fixed to 1 in model 2. The "restrict" parameter measures the sensitivity of the sum of squares to the restriction constant, which in this case is equal to 1 (Anon., 1988). When the value equals 0, the restricted estimates are the same as the unrestricted estimates. The significance of the restriction parameter here is 0.065, i.e. the restriction constant is close to being significantly different from 0 at the 5% level.

In models 3 and 4, R_0 is regressed against Log spvol and Log SB(spr), respectively. Both factors are significantly correlated to R_0. The probabilities given are one-sided values since negative parameters for spvol and positive values for SB(spr) have no biological meaning. As in models 1 and 2, the residuals are still significantly autocorrelated.

Models 5, 6, and 7 combine the three factors by pairs. They all have rather high r^2 values (0.59–0.67) but only in model 7 with factors spvol and SB(spr) are the residuals not autocorrelated.

Model 8 includes all three factors. This model can be regarded as an extension of model 7 by inclusion of SSB(cod). This leads to a significant improvement of the model and the residuals are not autocorrelated. The value of the slopes are sensible from a biological point of view. However, the parameter value for SB(spr) is no longer significantly different from 0 and the parameter value for SSB(cod) is rather high, 1.36, not significantly different from 1.

In the final model (model 9) the parameter value for SSB(cod) has been fixed to 1. This model is the model described in the model section above, and it is estimated to be:
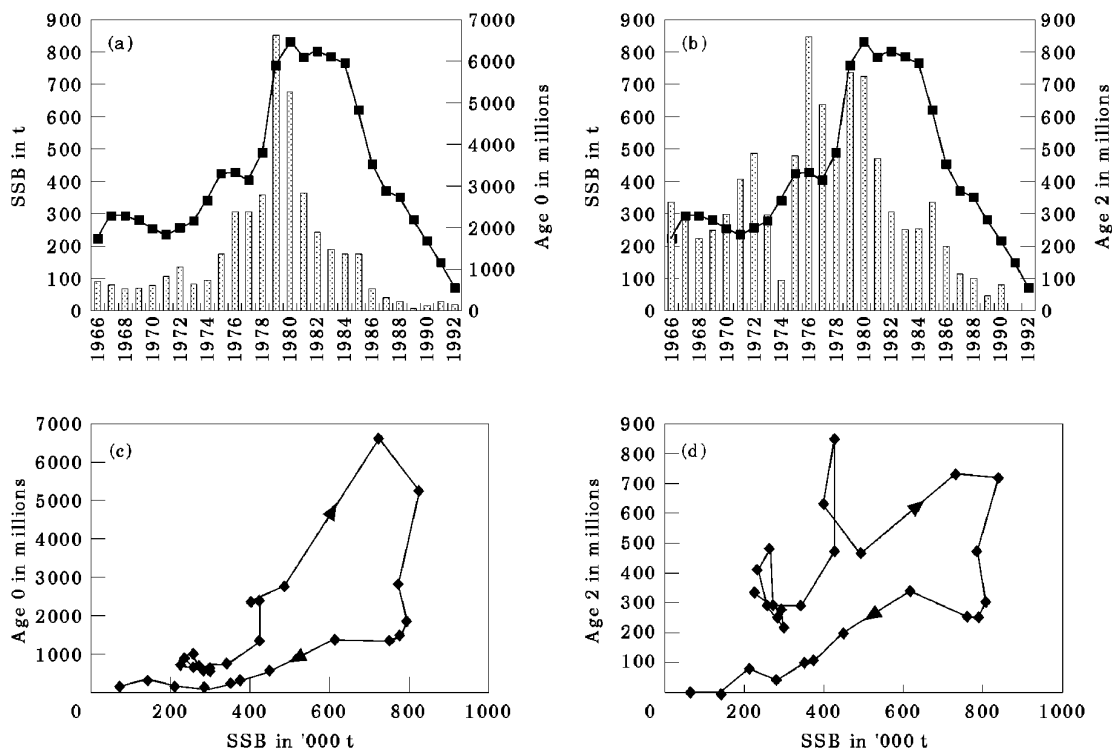
Figure 2. SSB and recruitment at age 0 and at age 2 for central Baltic cod 1966–1992: (a) and (b) show SSB and R plotted against year and (c) and (d) show R plotted against SSB with points from neighbouring years joined by lines. Bars=age 0; ■ =SSB.

$$\text{Log } R_0 = 2.19 + \log[SSB(cod)] + 0.79 * \log(spvol) - 0.86 * \log[SB(spr)].$$

Compared to model 8, the correlation coefficient is slightly smaller, 0.75 compared to 0.76, but one degree of freedom has been gained (by fixing the slope of Log(SSB(cod))) and the autocorrelation of the residuals is lower. More importantly, model 9 makes more sense from a biological point of view. The parameter value for SB(spr) is again significantly different from 0 but the restrict parameter is far from being significantly different from 0 (p=48%). The 10% upper and lower confidence limits are between ± 0.99 and 1.11 from the predicted values in 1977–1991, depending on the values of the independent parameters. This means that in one of ten cases the actual R_0 value will be smaller than about 35% of the predicted value and in one of ten cases it will be larger than about 280% of the predicted value.

In all models where spvol is included, the variation in the estimates for this factor is rather low (0.73–1.10). The parameter value for SSB(cod) varies between 1.36 and 1.96, except of course when it is fixed to 1. The parameter value for SB(spr) is more variable, from − 1.78 to − 0.59, and is not even significantly different from 0 in model 8.

The residuals from model 9 are plotted against year and R_0 in Figure 3a,b, indicating no clear trends, while the residual of the 1989 point is large.

The model can be further evaluated by examining its performance on the data set for 1966–1976. Figure 4 shows the predicted values of R_0 from model 9 and the observed values, as well as the 10% upper and lower limits. The predicted and observed values of R_0 agree quite well and the latter generally lie within the confidence limits. Values of R_0 can be normalised against the mean spvol and SB(spr) values by:

$$\text{Adj. Log } R_0 = \text{Log } R_0 - 0.79 * [\text{Log}(spvol) - \overline{\text{Log}(spvol)}] + 0.86 * \{\text{Log}[SB(spr)] - \overline{\text{Log}[SB(spr)]}\}.$$

The adjusted R_0 values are plotted against SSB(cod) for 1966–1991 (Fig. 5) as suggested by Beverton and Iles (1992). Median values and the 10% upper and lower limits are also shown. The wide confidence limits of the relationship between R_0 and SSB(cod) under average conditions of spvol and SB(spr) are evident, but the important point in the present context is that there is a clear relationship.

Table 2. Results of multiple regression analysis of cod recruitment against cod spawning stock biomass [SSB(cod)], spawning volume (spvol), and sprat stock biomass [SB(spr)] for 1977–1991.

Model	Parameter estimates		Prob.>t	r^2	Durbin–Watson D	1st order autocorrelation	Autocorrelated at 5%?
1	Intercept	− 5.23	0.065	0.63	0.488	0.606	Yes
	Log SBB(cod)	1.96	0.000				
2	Intercept	0.70	0.014	0.48	0.288	0.811	Yes
	Log SBB(cod)	1.00	—				
	(Restrict	3.86	0.065)				
3	Intercept	1.39	0.550	0.31	0.811	0.537	Yes
	Log (spvol)	1.10	0.015				
4	Intercept	18.12	0.000	0.37	0.496	0.716	Yes
	Log SB(spr)	− 1.78	0.080				
5	Intercept	− 3.59	0.041	0.67	1.081	0.459	Indecisive
	Log SBB(cod)	1.00	—				
	Log (spvol)	0.86	0.008				
	(Restrict	2.55	0.116)				
6	Intercept	7.03	0.053	0.59	0.545	0.628	Yes
	Log SBB(cod)	1.00	—				
	Log SB(spr)	− 1.00	0.038				
	(Restrict	1.63	0.241)				
7	Intercept	12.19	0.010	0.61	1.458	0.264	No
	Log (spvol)	0.97	0.009				
	Log SB(spr)	− 1.61	0.006				
8	Intercept	− 1.39	0.821	0.76	1.377	0.243	No
	Log SBB(cod)	1.36	0.011				
	Log (spvol)	0.73	0.018				
	Log SB(spr)	− 0.59	0.163				
9	Intercept	2.19	0.506	0.75	1.510	0.206	No
	Log SBB(cod)	1.00	—				
	Log (spvol)	0.79	0.008				
	Log SB(spr)	− 0.86	0.033				
	(Restrict	0.74	0.48)				

Discussion

There have been several attempts in the past to relate the recruitment of central Baltic cod to spawning stock size and environmental parameters. They have not been very successful, however, possibly because cannibalism and auto-correlation were not considered.

Lablaika *et al.* (1989) analysed 34 parameters of cod spawning stock biomass, salinity, oxygen content and temperature for relationships to recruitment at age 2 (R_2) from VPA. They considered data from the Gotland Deep area in 1966–1985. Generally, SSB(cod), salinity and oxygen concentration were positively correlated to R_2 but with low correlation coefficients (− 0.04–0.45). However, their results were not tested for autocorrelation and, as there was a general increase in recruitment during this period, it is likely that this represented a serious problem. Cod cannibalism was not quantified at that time and was not taken into account. Berner *et al.* (1989) found that R_1 (from VPA) in 1969–1983 was correlated to spawning stock biomass of cod and a weighted mean of the oxygen concentration in March and August in the Gotland Basin in a multiple regression analysis. These factors were selected out of 37 alternative factors listed. The selection was based on "best fit" considerations, so it is not unlikely that they made a "type I error", i.e. rejecting a hypothesis (the null hypothesis saying that no relationship exists) that is true. Bagge (1993) found a positive correlation between both R_1 from MSVPA and R_2 from VPA and the vertical extension of water with a salinity higher than 11, an oxygen content of more than 2 ml/l and a mean (April–June) temperature higher than 1.5°C for the period 1979–1991. However, r^2 values were rather low and he concluded that other factors must be involved. Plikshs *et al.* (1993) developed a rather complex model in a stepwise regression analysis of data for the period 1960–1990. R_2 was positively related to egg abundance, cod spawning stock biomass and spawning volume, and negatively to cod spawning stock biomass multiplied by egg abundance. They applied an additive model which is more difficult to justify biologically than a multiplicative model as used here. Whether the overall effect of cod spawning stock biomass on R_2 is positive is difficult to judge, because it is confounded with the effects of egg abundance and the combined factors of spawning stock size and egg abundance.
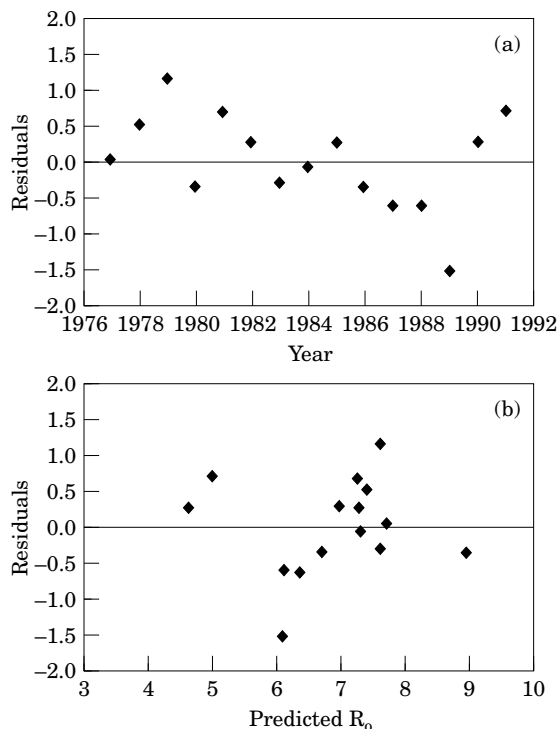
Figure 3. Residuals from the recruitment (age 0) model plotted against (a) year and (b) predicted value of R_0.
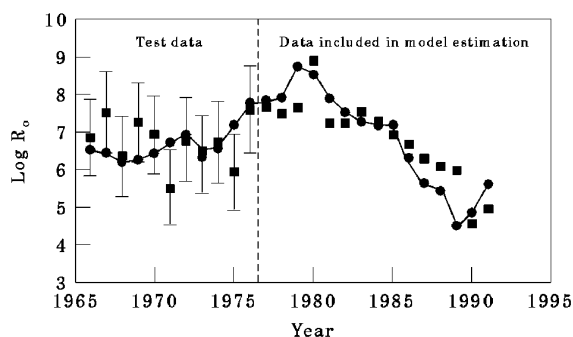

Figure 4. Observed and predicted value of R_0 plotted against year. Data from 1966–1976 are test data not included in the estimation of the model parameters. For these points the 10% upper and lower limits are shown. ● =Observed; ■ =predicted.

Figure 5. R_0, adjusted for the effects of spawning volume and sprat predation, plotted against SSB.
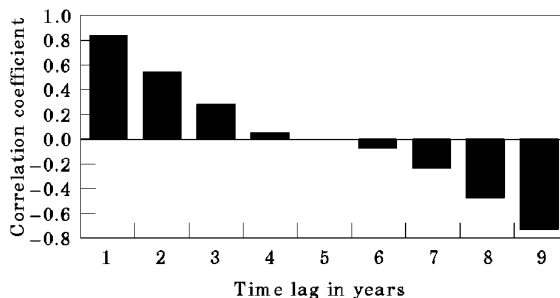
Figure 6. Auto-correlation in R_0 plotted against time lag in years.

By including spawning volume and sprat biomass in the regression of recruitment against spawning stock size of cod in a biological sensible way, the explanatory power of the variations in recruitment has been increased but, more importantly, the autocorrelation in the residuals has been virtually eliminated. Therefore, more faith can be placed in the relationship obtained. Ricker (1954, 1975) or Beverton and Holt (1957) type stock–recruitment curves do not seem to apply for central Baltic cod when recruitment is measured at

age 0, as the curve tends to bend upwards rather than downwards with increasing spawning stock biomass, according to model 8 (Table 2). Whether the curve will bend downwards at very high levels of spawning stock biomass remains a hypothetical question. Whether the observed relationship between recruitment and spawning stock biomass is causal cannot be proven. By applying statistical methods there is always a risk of making a "type I error". However, in this case the results have been verified on the basis of independent data, indicating that a causal relation is involved. Although the model explains 75% of the variability in recruitment of 0-group cod observed in the past, predictions in individual years are not very precise. In two out of ten cases, observed recruitment may be either smaller than 35% or larger than 280% of the predicted values. For short-term predictions, recruitment in the most recent year may be a better predictor than the model because the 1st order autocorrelation of recruitment is very high (Fig. 6). The usefulness of the model is, thus, mainly restricted to long-term predictions where 1st order autocorrelations are not of much use.

MSVPA has radically changed our perception of the actual recruitment to the central Baltic cod stock (Sparholt, 1994). Cannibalism on 0- and 1-group cod

Figure 7. Observed and predicted (by a "model 8"-type regression of R_2) value of R_2 plotted against year. Data from 1966–1976 are test data not included in the estimation of the model parameters. ● = Observed; ■ = predicted.

has been much higher than previously perceived. Using MSVPA estimates of recruitment that take account of cannibalism instead of VPA estimates is therefore ess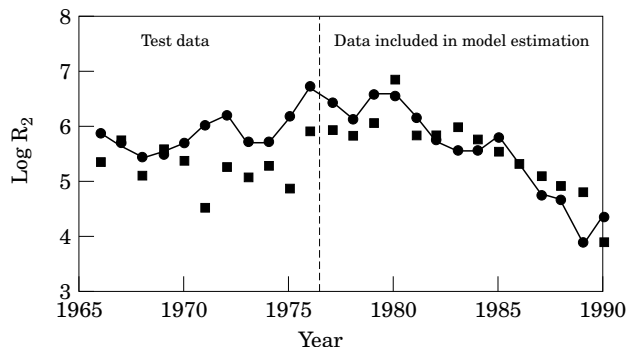ential in studies of stock and recruitment in relation to environmental factors. The problem is illustrated in Figure 7 where model 8 has been applied to recruitment at age 2 and used to predict recruitment at age 2 for 1966–1976. The correspondence between the observed and the estimated recruitment is not as good as for age 0 (Fig. 4), as recruitment at age 2 is under-estimated in the majority of the years. Model 8 is used here instead of model 9 because, in the latter case, cannibalism can be implicitly allowed for. In line with the expectation that the parameters for SSB(cod) is less than 1, the regression analysis results in a parameter estimate of 0.86.

Inclusion of MSVPA estimates for the years prior to 1977 would allow a more precise analysis and would only need catch data by quarter for each stock and year in the MSVPA. The values of sprat biomass used for 1966–1976 in the present paper would be especially interesting to verify by MSVPA estimates. An ordinary VPA would probably be too uncertain for sprat because F is very low compared to M for this stock. Pope (1972) has shown that low F values compared to M make an ordinary VPA imprecise, i.e. very dependent on the terminal F values used. These F values are "guestimated" for sprat. Contrary to this, the MSVPA for the central Baltic is very robust to the "guestimates" of terminal F for sprat (Sparholt, 1994). Another problem with the use of sprat stock biomass as a measure of sprat predation on cod eggs is the timing of cod spawning. Köster (1992) has shown that sprat predation on cod eggs decreases in summer when alternative food items become more abundant. Thus, adjusting sprat biomass for annual variations in cod spawning might improve the model fit.

The spawning volume data used are only a crude measure of the suitability of the environmental conditions during spawning. It is based on measurements at only five hydrographical stations. The value for 1989

appears to be high compared to values given by Bagge (1993) for the suitable part of the water column during this year. The predicted value of the 1989 year class represents an outlier in the data series, which might be due to an over-estimate of the spawning volume. Furthermore, the index does not distinguish between water masses with oxygen concentration just above and far above the limit of 2 ml/l. Waller *et al.* (1993) showed that hatching rate of cod eggs from the Bornholm Basin increased by a factor of about three when oxygen content increased from 2 ml/l to 8 ml/l. Thus, refinements of spawning volume seem possible.

Egg quality has been shown to vary with the size of female Baltic cod. According to Grauman (1973), eggs from large females are larger, more buoyant and have a higher survival rate than eggs from small cod. Thus, the spawning stock parameter used in the present analysis as a measure of the number of eggs produced might be improved by correcting for the size distribution of female cod.

According to Figure 4, the 1979 year class of cod is about 3 times and the 1989 year class only about 1/4 of the predicted size. A careful analysis of these two outliers might give valuable information to be used in future improvements of the present model.

Myers and Cadigan (1993b) have shown that inter-annual variability of the density-independent component of juvenile natural mortality is not a major source of variability in the abundance of marine demersal fish. Except for cannibalism, it is not likely either that any density-dependent mortality on the juvenile stage of central Baltic cod can account for the variability in abundance. Food competition seems not to take place to any major extent as there are only weak indications of density-dependent growth in central Baltic cod (Sparholt, 1991; Bagge *et al.*, 1992). Thus, environmental factors related to juvenile survival need not be considered as a first priority in this context. A causal relationship between stock and recruitment has important implications for management of the fishery. Based

on the results presented, the central Baltic cod stock has to be managed in a way that secures a certain level of the spawning stock. Sparholt (1995) has estimated that, if the spawning stock becomes much higher than 0.5 million t, cannibalism will reduce the survivors to age 3 more than can be compensated by higher recruitment of 0-groups. This spawning stock will therefore provide the maximum yield from the stock and can be reached within a ten year period by an F of 0.4, even when environmental conditions for cod recruitment remain poor.

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