

## Stock-recruitment relationships for cod (*Gadus morhua* L.) in the central Baltic Sea incorporating environmental variability

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### Abstract

Recruitment of central/eastern Baltic cod critically depends on favourable oceanographic conditions in the deeper basins of the Baltic Sea creating a suitable habitat for the development of early life stages. The decline in the size of the spawning stock since the mid-1980s initiated a series of investigations on recruitment, which were continued through a partial recovery of the stock in the mid-1990s. The principal factors influencing recruitment and recognized at present are: (i) the volume of water with temperature, oxygen and salinity conditions which meet the minimum requirements for successful egg development ('reproductive volume'); (ii) the age-structure of the spawning stock; (iii) the timing of spawning; and (iv) predation mortality on eggs due to sprat (*Sprattus sprattus*) and herring (*Clupea harengus*), as well as cod cannibalism. We relate recruitment at age 2 to parent stock size using updated time series of these variables, comprising the period 1966 to 1994. Spawning stock biomass and egg production are compared as measures of parent stock size. The influence of wind energy and zooplankton abundance on cod recruitment are discussed. A modified Ricker model is outlined explicitly accounting for environmentally-induced oscillations around the two observed levels of cod stock size.

### Kurzfassung

Bestand-Nachwuchsbeziehungen beim Dorsch (*Gadus morhua*) in der zentralen Ostsee unter Einbeziehung der Umweltvariabilität

Die Rekrutierung des Dorschbestandes in der zentralen Ostsee hängt zwingend davon ab, dass günstige ozeanographische Bedingungen in den tieferen Becken der Ostsee einen passenden Lebensraum für die Entwicklung der frühen Lebensstadien bieten. Der Niedergang in der Größe des Laichbestandes seit der Mitte der achtziger Jahre veranlasste eine Reihe von Untersuchungen über Rekrutierung, die durch die teilweise Erholung des Bestandes in der Mitte der neunziger Jahre fortgesetzt wurde. Die zur Zeit anerkannten Hauptfaktoren, die die Rekrutierung beeinflussen, sind (i) Wasserkörper mit Temperatur-, Sauerstoff- und Salzgehaltsbedingungen, die den Mindestanforderungen für erfolgreiche Eientwicklung genügen („Reproduktionsvolumen“), (ii) die Altersstruktur des Laichbestandes, (iii) der Zeitpunkt der Hauplaichaktivität,

und (iv) die Wegfraßsterblichkeit (Eifraß) durch Sprotte (*Sprattus sprattus*) und Hering (*Clupea harengus*), sowie durch Kannibalismus beim Dorsch. Wir erstellen Beziehungen zwischen der Rekrutierung von zweijährigen Dorschen und der Elternbestandsgröße auf der Grundlage von aktualisierten Zeitserien dieser Hauptfaktoren im Zeitraum 1966 bis 1994. Laichbestandsgröße und Eiproduktion werden als Maße für die Elternbestandsgröße verglichen. Der Einfluss von Windenergie und Zooplankton-Abundanz auf die Dorschrekrutierung werden diskutiert. Eine modifizierte Rickerkurve wird skizziert, die die umweltinduzierten Schwankungen der Dorschbestandsgröße um zwei beobachtete Niveaus ausdrücklich berücksichtigt.

## Introduction

Central Baltic cod is one of the commercially most important fish stocks in the Baltic Sea. As knowledge on the relationship between parent stock and recruitment is essential for producing sound scientific advice on fisheries management, this relationship has been subject to many analyses, but it is still not fully understood to date.

Several factors have been identified to influence the recruitment of Baltic cod. Cod spawn in the deeper basins of the Baltic Sea, i.e., the Bornholm Basin, the Gotland Deep, and the Gdansk Deep (Figure 1). The importance of hydrographic factors in the spawning areas, particularly the inflow of saline and oxygenated water, has been pointed out by Lablaika *et al.* (1989), Kosior and Netzel (1989) and Berner *et al.* (1989). The annual extent of favourable hydrographic conditions was recently estimated as the available reproductive volume, defined as the water mass characterized by temperature, oxygen and salinity conditions which meet the minimum requirements for successful egg development (Plikshs *et al.* 1993).

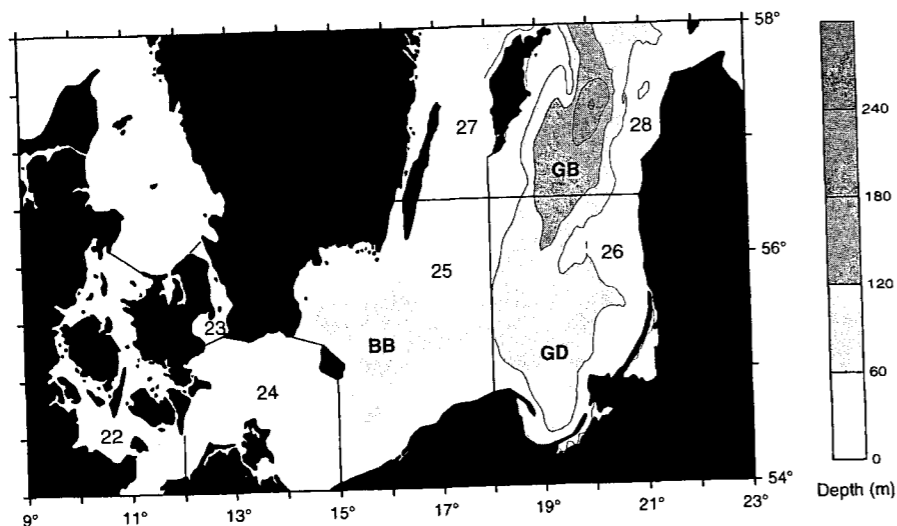


Figure 1: Western and central Baltic Sea, ICES Subdivisions and spawning areas of central/eastern Baltic cod. BB: Bornholm Basin, GD: Gdansk Deep, GB: Gotland Basin.

Also, the stock size of females aged 5 to 7, as a proxy for egg production, contributes significantly to year-class strength (Lablaika *et al.* 1989). Viable egg production should in principle be a more adequate estimator of the relationship between parent stock and recruitment. Fecundity-size relationships and sex ratios were recently updated for the central Baltic (ICES 1997a), allowing for improved estimates of total egg production. However, as characteristics of the parent stock influence the probability of survival of the eggs, the fraction of viable eggs may vary between years (MacKenzie *et al.* 1996a; Nissling and Vallin 1996).

Cod eggs are heavily preyed upon by sprat and herring when prey and predator distributions overlap (Köster and Schnack 1994). While sprat is the dominant predator on cod eggs in the Bornholm Basin in spring, herring prey on cod eggs during summer. Following the observed delay in cod spawning time (Wieland *et al.* 2000), the importance of herring as a predator may have become more important during recent years (Köster and Möllmann 1997, 2000). In turn, both sprat and herring are preyed upon by cod (*e.g.* Uzars 1989), and there is evidence for top-down control (Rudstam *et al.* 1994, Jarre-Teichmann 1995).

Bagge *et al.* (1994) indicated that processes acting on cod larvae and young juveniles may not justify the assumption of constant mortality for these groups. While cod eggs are usually retained in the spawning areas (Wieland 1988), larvae are drifted out of the basins into areas of shallow water where they settle. Simulation models are being developed to analyse possible drift routes (Aro *et al.* 1991; Hinrichsen *et al.* 1997). Mortalities during the larval period can be quite different between years (Wieland 1995; Grønkjær *et al.* 1995; Voss 1996). Food availability, *i.e.* the occurrence of zooplankton of the right type and size together with cod larvae, is likely to be an important factor for the survival of the larvae (MacKenzie *et al.* 1996a, Grønkjær *et al.* 1997).

Juvenile cod are subject to cannibalism, which is higher in periods of high cod abundance (Uzars 1995). Variations in rates of cannibalism on 0- and 1-group is taken into account in multispecies stock assessment (Jensen and Sparholt 1992; ICES 1997b).

Sparholt (1996a) related 0-group abundance to cod spawning stock biomass (SSB), reproductive volume, and sprat SSB for the period 1977-1991. Solari *et al.* (1997) proposed a new type of model that was considered more appropriate to describe the spawning stock-recruitment relationship of Baltic cod than the classical models of Ricker (1954) or Beverton and Holt (1957). This new model was based on the assumption of multiple steady-states, each limited by a particular carrying capacity, as well as density-independent transitions between them, and applied to data from the assessment of Baltic cod in 1993.

We update the time series of variables, which have been identified to affect cod reproduction. These key variables are subsequently analysed in view of the relationship between cod spawning stock and recruitment, incorporating environmental variability.

## Materials and methods

### Cod

Data series on spawning stock biomass and recruitment at age 2 (Figure 2) were taken from ICES (1997a). The spawning stock biomass increased sharply towards the end of

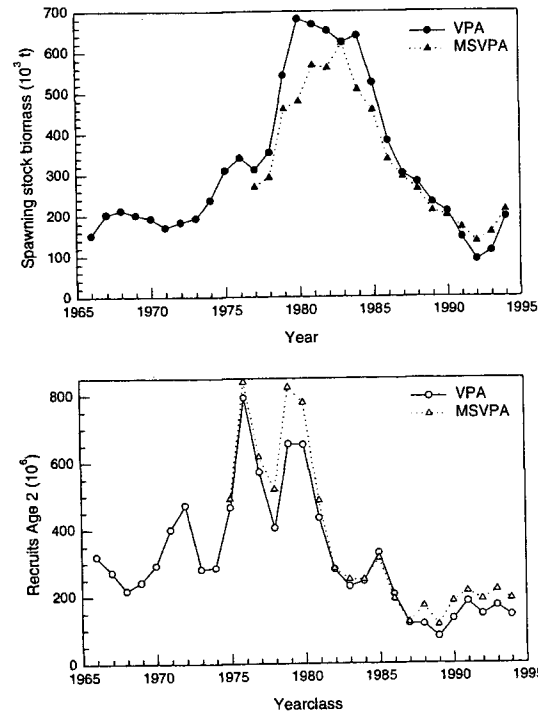


Figure 2: Spawning stock biomass and numbers of recruits at age 2 of central Baltic cod (ICES Subdivisions 25-32) as estimated by VPA and MSVPA, 1965-1994. Note that recruit numbers are shifted two years back in time corresponding to SSB in the year they were born.

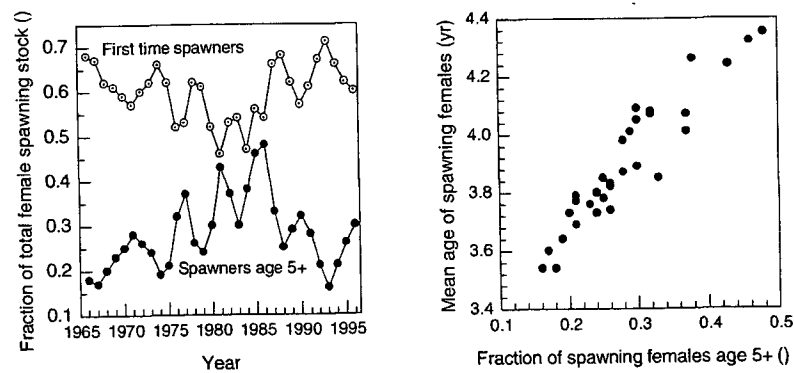


Figure 3: Characteristics of the mature female population of central Baltic cod: Fractions of first time spawners and of spawners age 5+, and correlation between mean age of the spawning population and the fraction of age 5+ spawners.

the 1970s, and maintained a high level during 1980-1986. Subsequently, SSB declined sharply, and the minimum SSB in 1992 corresponded to only about half the value estimated for the late 1960s. Since the mid-1990s, cod biomass has recovered to about the level of the late 1960s. Recruitment was on a moderate level during the late 1960s and early 1970s, followed by a series of strong year classes in 1976 to 1979, and then declined consistently, reaching a minimum for the 1989 year class. The current level is still below the long-term average.

The dynamics of both SSB and recruitment at age 2 from multispecies virtual population analysis (MSVPA) are very similar to those of the (single-species) VPA (Figure 2), even though SSB was estimated lower and recruitment at age 2 higher by MSVPA than by VPA during the late 1970s.

The fraction of first time spawners in the total female cod population, and the fraction of mature females of age 5+, as well as the mean age of the spawning stock in the central Baltic were also based on ICES (1997a; Figure 3). The changes in the age structure of the stock were less pronounced than those in biomass. Although 4 to 6 years cycles are visible in the stock structure, the fraction of spawners of age 5+ increased from the mid-1960s to the first half of the 1980s, and subsequently decreased to a level corresponding to that of the early 1970s. The fraction of first time spawners constitutes around 60 % of the population on a 30 years average, with a contrasting pattern to that of the fraction of older spawners. The mean age of the spawning stock, and the fraction of spawning females of age 5+ are closely correlated (Figure 3).

Potential egg production for cod was estimated from stock numbers, weight-at-age, maturity ogives and sex ratios (ICES 1997a). Egg production was first estimated for each ICES Sub-division, and then summed across Sub-divisions to obtain the total production. Within a Sub-division, the total number of fish was determined by applying the spatial distribution of adult cod to the total population numbers in the Baltic. Numbers of eggs produced by age group were calculated by combining the results of five studies of cod fecundity in the Baltic, which express egg production relative to body weight (Table 1). Most studies also provide a relationship between fecundity and body length. However, as assessment data are limited to weight-at-age, the weight-fecundity relationships were preferred since conversion of weights to lengths would have involved another source of error.

It is unknown whether the parameter values are significantly different and whether their use should be restricted to particular years or areas. We therefore decided to implement a method, which aggregates all the available information by estimating the range in

Table 1: Relationships between individual fecundity (F; numbers of eggs) and body weight (W in g) for Baltic cod.

Relationship	Sampling years	Subdiv.	Reference
$F = 859 \times W^{0.9936}$	1968	24, 25	Schopka 1971
$F = 526 \times W + 173.8$	1959-1962	26	Kosior and Strzyzewska 1979
$F = 558.07 \times W + 186279$	1994	25	Bleil and Oberst 1996
$F = 410.99 \times W^{1.0682}$	1992	25	Kraus 1997
$F = 740.59 \times W^{1.0164}$	1996	25	Kraus 1997

through the 1980s, a steady decrease was estimated in the VPA assessment. MSVPA estimates fluctuate around 2 million t from the late 1970s through the early 1980s, followed by a marked decrease and a continuation around 1 million t since 1988. We used the multispecies assessment for analyses from 1977 onwards, but omitted herring from the analysis of the entire time series.

### Reproductive Volume

Estimates of reproductive volume, defined to be all water exceeding critically low levels of salinity, temperature and oxygen content ( $S > 11$  psu,  $T \geq 1.5$  °C, and  $O_2 \geq 2$  ml/l) were obtained from MacKenzie *et al.* (2000). Since a delay in cod peak spawning time has been observed in the Bornholm Basin during recent years (Wieland *et al.* 2000), the reproductive volume was adjusted to account for these changes on the assumption that a similar shift had taken place in the entire central Baltic cod population. The peak spawning season lasts for about three months. We thus used mean values for the period April to June for 1966 to 1989, May to July for 1990 to 1992, and June-August from 1993 onwards. When no monthly estimate was available for a basin, the missing value was obtained by linear interpolation. The adjusted reproductive volumes are shown in Figure 6A for the period of interest here, 1966 to 1994. They are relatively close to the mean summer conditions used by Sparholt (1996), stronger deviations occur for the period of early spawning until the late 1970s than for the mid- and late 1980s and 1990s (Figure 6B).

The Bornholm Basin has traditionally been the most important area for cod reproduction, while the Gdansk Deep and the southern Gotland Basin each regularly contributed about half the size of the reproductive volume in the Bornholm Basin. The central Gotland Basin was often oxygen depleted, but it contributed a volume equivalent to that of the Bornholm Basin in some years.

The reproductive volume has always fluctuated strongly. However, it was on average much higher before 1980 than thereafter, and it was never for more than one year in a row that the Bornholm Basin constituted the only relevant reproductive volume for cod. However, during 1981 and 1982, the Bornholm Basin represented the only suitable area for cod reproduction for two consecutive years. This happened at a time, when about 80 % of the cod population was distributed the Gdansk Deep and Gotland Basin (ICES 1997a). In the following years, the percent contribution of the other Basins to the total reproductive volume remained very small until 1993 and 1994, after major inflows of highly saline and oxygenated water into the Baltic Sea (Matthäus and Lass 1996). Consequently, the average reproductive volume has been much lower in the 1980s and early 1990s than during the late 1960s and 1970s.

Estimates on the breakdown of the cod stock by subdivision are available since 1980 (ICES 1997a) and indicate that the distribution has changed. Therefore, we constructed an alternative time series, which was weighted by the abundance in each Sub-division (Figure 6C). The importance of the Bornholm Basin has apparently increased since the mid-1980s, due to a general southward shift in distribution of the stock. Because it is unlikely that the distribution would have been constant during the period 1966 to 1980, when large biomass changes were observed, we did not try to extend the series backwards in time.

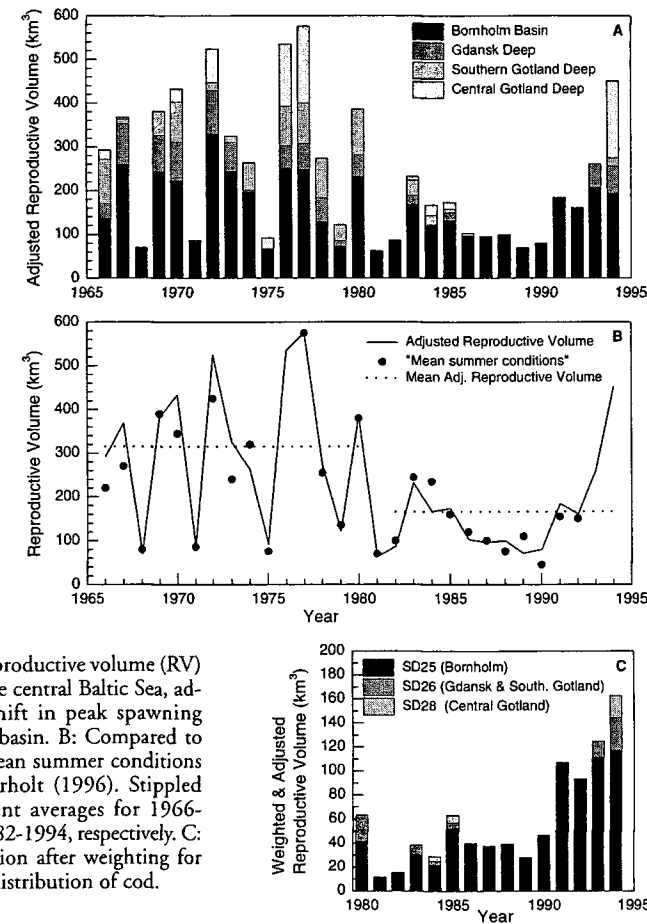


Figure 6: Reproductive volume (RV) for cod in the central Baltic Sea, adjusted for shift in peak spawning time. A: By basin. B: Compared to values for mean summer conditions used by Sparholt (1996). Stippled lines represent averages for 1966-1980 and 1982-1994, respectively. C: By Sub-division after weighting for the relative distribution of cod.

### Wind energy

Hinrichsen *et al.* (in press) developed a wind index of larval drift based on a three dimensional eddy resolving baroclinic model of the Baltic Sea (Lehmann 1995), driven by a time series of wind measurements at Christian's Island (located approximately 10 nautical miles north-east off Bornholm) and using a Lagrangian particle tracking technique (Hinrichsen *et al.* 1997). We used the basic calculations underlying this wind index to derive estimates of cumulative wind energy during peak spawning time as determined by Wieland *et al.* (2000). On Christian's Island, the wind sensor was replaced and modified in 1979, resulting, on average, in significantly higher wind speed measurements. Assuming that the mean wind speed had not changed during the mid-1960s through mid-1990s, a regression was established to intercalibrate the two time series. Cumulative wind energy was calculated from three hourly wind speed measurements. Earlier studies

(Hinrichsen *et al.* 1995) suggest that drift towards the west and north is correlated to winds from westerly and southerly directions. To distinguish between different directions of larval transport, wind energies were provided with a positive sign if southerly or westerly winds predominated, and with a negative sign, if northerly or easterly winds predominated. The three-hourly values were summed over a period of 60 days, corresponding to the average duration of the larval drift. Dates of peak spawning are not available for all years. Therefore, the value for 1970 was used in calculating the wind energy for 1966 to 1968, the 1980 value for 1981 to 1984, and the 1989 value for 1990. For each year, the calculation from the peak spawning date onwards was repeated for the period starting 10 days before, 5 days before, 5 days after and 10 days after the peak, and the 5 values obtained were averaged. The resulting time series is given in Figure 8 (middle panel).

Cumulative wind energy fluctuated around a level of 80 kW·m<sup>-2</sup> during the mid-1970s to the early 1990s. Strong northerly to easterly winds were noted in 1971, resulting in a negative anomaly. There is an indication that wind energy around cod peak spawning time has increased in the early 1990s.

### Zooplankton

Long time series of zooplankton abundance exist for some areas of the Baltic Sea. Time series of zooplankton abundance for the Bornholm Sea, the Southern Gotland Sea, the Gotland Deep, and the Gdansk Deep are available for 1979 to 1994 from HELCOM (1996). We weighted these series by the relative abundance of cod by Sub-divisions to obtain a combined zooplankton abundance series.

### Analyses

As density-dependent processes are known to be important for cod because of cannibalism (Uzars 1995), we expect a stock recruitment curve of the Ricker-type (Ricker 1954). We used the linearized form of recruitment per unit parent stock in our computations:

$$\ln(R/P) = \ln \alpha - \beta \cdot P \quad (1)$$

where R is a measure of stock recruitment, P a measure of the parent stock (biomass, egg production, etc.), and a and b are coefficients of the density-independent and density-dependent terms, respectively.

Note that recruit numbers at age 2 were shifted two years back in time to match cod SSB and other data series for the year they were born.

As it is likely that the relationship between the environment and cod recruitment (or recruitment per unit parent stock) is nonlinear, we used the Alternating Conditional Expectation algorithm (ACE) developed by Breiman and Friedman (1985) for optimal variable transformation. This algorithm has successfully been applied in recruitment studies before (e.g., Mendelsohn 1989, Cury and Roy 1989). The dependent variable y and the independent variables x<sub>i</sub> (i = 1...n) are replaced by transformation functions T<sub>0</sub>(y), T<sub>i</sub>(x<sub>i</sub>). The algorithm estimates these functions by minimizing

$$e^2 = E\{(T_0(y) - \sum_i T_i(x_i))^2\} / \text{Var}(T_0(y)) \quad (2)$$

The transformation functions do not belong to a particular parameterized family, and are not necessarily monotone. However, we restricted the transformation of the de-

pendent variable to monotone functions in order to allow for straightforward retransformation. If the values of all but one variable are fixed, and the problem of which new transformation will minimize the normalized residual sum of squares is solved, then the solution is a conditional expectation that can be estimated empirically based on a smoothing algorithm. The algorithm converges to an optimal solution and produces an empirically smoothed function for each variable. The shape of the function is found by plotting the transformed values of a variable versus the original values. As the transformation is free of *a priori* assumptions on relationships between response and predictor variables, it may be used to confirm existing ideas on the relationship, or provide new insights.

### Results

Stock-recruitment curves for central Baltic cod (Figure 7; Table 2) were estimated for the entire time series and for two periods separately (1966 to 1980 and 1982 to 1994), corresponding to the observed shift in reproductive volume level (Figure 6). The variance explained by the regressions ranged from 27 to 45 % for the entire time series, and 21 to 44 % and 45 to 54 %, respectively for the two periods, depending on whether spawning stock biomass, total egg production, or egg production by females of age 5+ was used as a

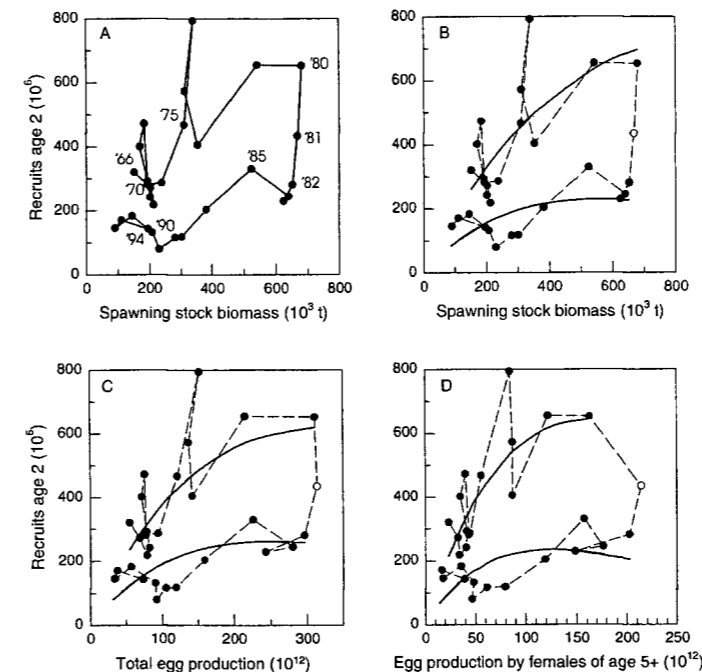


Figure 7: Recruitment (R) of central Baltic cod at age 2 for different measures of parent stock size, and fitted Ricker curves (Table 2). A: Trajectory, B: SSB, C: Total egg production D: Egg production by females of age 5+.

Table 2: Parameter values of Ricker stock-recruitment curves for Baltic cod. Dependent variable was number of recruits at age 2 (millions) per unit of parent stock in all cases. Parent stock was taken as spawning stock biomass (SSB), total egg production (TEP) or egg production by age 5+ females (5+EP).

Parent stock	Period	ln( $\alpha$ )	$\beta$	$r^2$	d.f.	P
SSB ( $10^3$ t)	66-94	0.538	0.002	0.27	27	0.004
	66-80	0.691	0.001	0.21	13	0.084
	82-94	0.103	0.002	0.45	11	0.013
TEP ( $10^9$ )	66-94	1.452	0.004	0.32	27	0.002
	66-80	1.622	0.003	0.31	13	0.031
	82-94	1.047	0.004	0.48	11	0.009
5+EP ( $10^9$ )	66-94	2.151	0.009	0.45	27	<0.001
	66-80	2.350	0.006	0.44	13	0.007
	82-94	1.630	0.008	0.54	11	0.005

measure of parent stock size (Table 2). All regressions were significant at  $P < 0.05$ , except for the fit of the upper branch (1966 to 1980) for spawning stock biomass. The best fit was obtained in all cases using egg production of 5+ females, while the worst fit was obtained using spawning stock biomass. All curves suggest that recruitment can be adequately described by Ricker curves, and that the optimal recruitment had just about been reached for the high recruitment regime 1966 to 1980, whereas the "right hand side" of the Ricker curve was reached during the present regime of low recruitment at spawning stock biomasses of around 400 000 to 550 000 t, or a total egg production of about  $250 \times 10^{12}$  eggs.

Time series of reproductive volume, wind energy, and sprat biomass, and scatterplots of log-transformed recruitment and the residuals of the fitted Ricker curve with total egg production as the measure of parent stock size are given in Figure 8. While recruitment and residuals increase with reproductive volume, suggesting a slightly curvilinear relationship, correlations are less obvious for wind energy, or sprat biomass. While there is some indication that recruitment increases with increasing (westerly) wind energy when considering the two periods separately, there is only a trend in the residual plots for the later period. While recruitment appears to be negatively influenced by sprat biomass for each period, there is no trend in the residuals for the early period and the trend for the later period is positive, contradicting the negative trend indicated by plotting log recruitment *versus* sprat biomass.

Multiple linear regressions of log-transformed recruitment per number of eggs produced on total egg production, and reproductive volume were highly significant ( $P < 0.005$ ). The regressions explained 51 % of the variance of the entire time series when reproductive volume was used linearly or and 50 % when log-transformed. Neither wind energy nor sprat biomass were significant.

ACE-transformation revealed a slightly nonlinear relationship between recruitment per unit of egg production as dependent variable, and total egg production and reproductive volume as independent variables (Figure 9). A markedly nonlinear relationship was suggested for cumulative wind energy, with a minimum at  $60 \text{ kW}\cdot\text{m}^{-2}$ , and two maxima corresponding to strong easterly winds (approximately  $-190 \text{ kW}\cdot\text{m}^{-2}$ ), and moderate

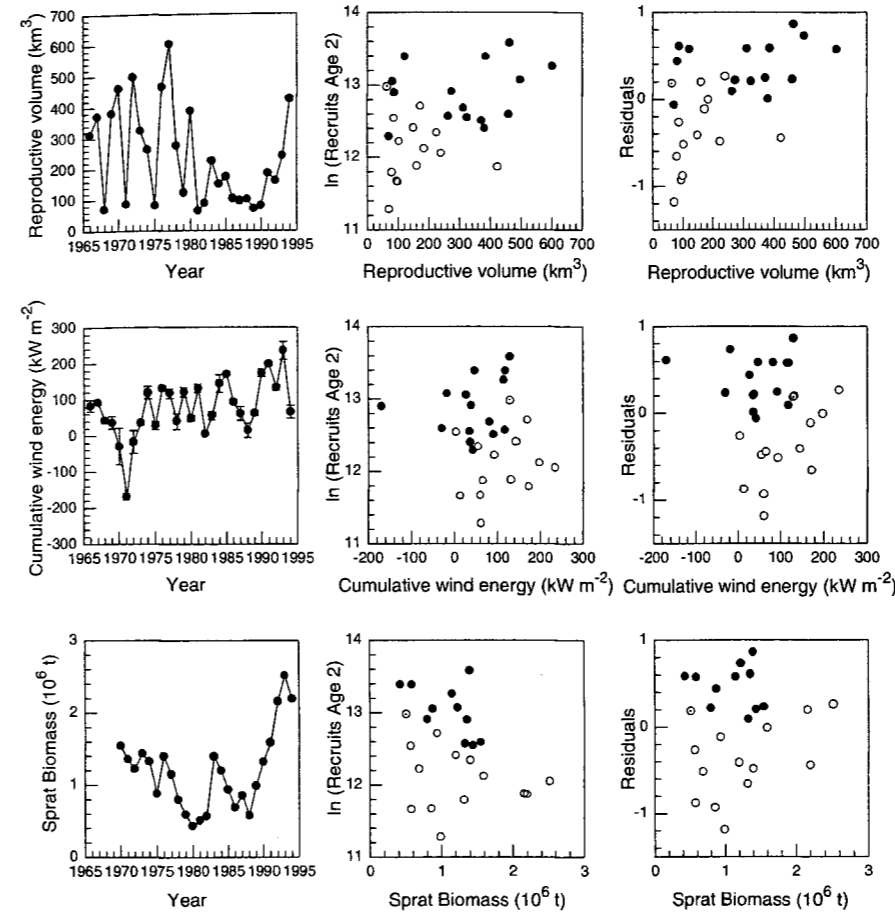


Figure 8: Time series of variables used in multiple linear regression 1966 to 1994, scatterplots of these variables versus number of recruits at age 2, and versus the residuals from the fitted Ricker curve: Upper panel: Adjusted reproductive volume; Middle panel: cumulative wind energy ( $\pm$  standard error); lower panel: sprat biomass. Filled circles: 1966 to 1980; dotted circle: 1981; open circles: 1982 to 1994

south-westerly winds ( $110 \text{ kW}\cdot\text{m}^{-2}$ ), respectively. The three independent variables were highly significant ( $P < 0.001$ ), whereas sprat biomass was not. A multiple linear regression using only total egg production and reproductive volume explained 61 % of the variance, while 81 % was explained when wind energy was added.

Similar calculations for egg production of females of age 5+ explained even 84 % of the variance for the full model and 66 %, when wind energy was deleted. The transformation of the egg production was also smoother than before (Figure 10). As before, sprat biomass was not significant.

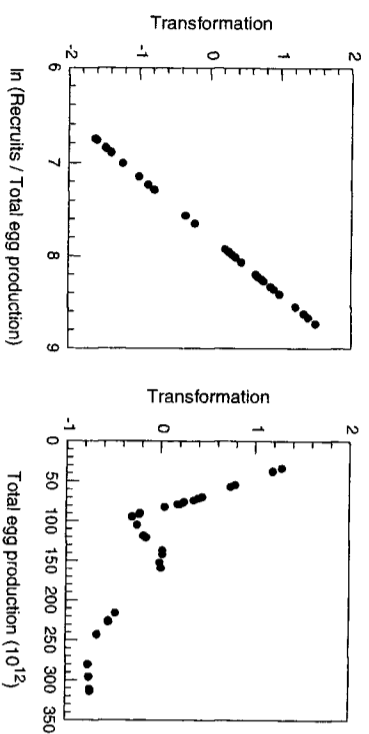


Figure 9. ACE transformations of the variables that contribute significantly to the multiple regression of cod recruitment in the central Baltic Sea, 1966 to 1994, based on total egg production.

The trajectories of observed recruitment and recruitment predicted by the model based on total egg production (Figure 11) follow each other quite well. The strongest deviations occurred in 1979/1980.

When focusing on the present regime of low recruitment, corresponding to the period of low reproductive volume (1982 to 1994), the same independent variables explained the variance in recruitment for total egg production (Figure 12) as well as for egg production by females of age 5+ (Figure 13). The relationship between recruitment per unit egg production and egg production is negatively curvilinear, and smoother than in the entire time series (Figures 9, 10). A logarithmic relationship is suggested from the transformation of reproductive volume. Cumulative wind energy shows the same breakpoint at approximately  $60 \text{ kW} \cdot \text{m}^{-2}$ , and improved recruitment with increasing southerly or westerly winds ( $70$  to  $250 \text{ kW} \cdot \text{m}^{-2}$ ). The transformation also leads to a much smoother trajectory than that of the entire time series. The multiple linear regression based on total egg production explained 97 % of the observed variance, where egg

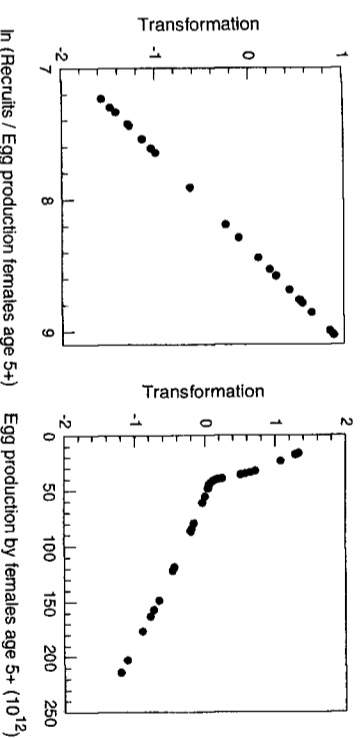


Figure 10. ACE transformations of the variables that contribute significantly to the multiple regression of cod recruitment in the central Baltic Sea during 1966 to 1994, based on egg production by females of age 5+.

production contributed 87 %, and the difference was shared roughly equally by reproductive volume and wind. All variables were significant at  $P < 0.01$ . When using egg production by females of age 5+, the explained variance was slightly higher (98 %), and all variables were significant at  $P < 0.001$ , as expected from the smoother transformations.

Neither sprat nor herring biomass, nor total clupeids, contributed significantly to the regression, and their transformations were inconclusive, depending on what other variables were used. The same applied to zooplankton abundance.

The trajectory of observed and predicted recruitment (Figure 14) shows a very close fit, as expected from the high coefficient of determination. There was no evidence of autocorrelation in the residuals for any of models based on transformed or untransformed data, neither for the entire time series nor for the recent period of low recruitment. Therefore, the ACE transformation process does not appear to have induced a spurious relationship.

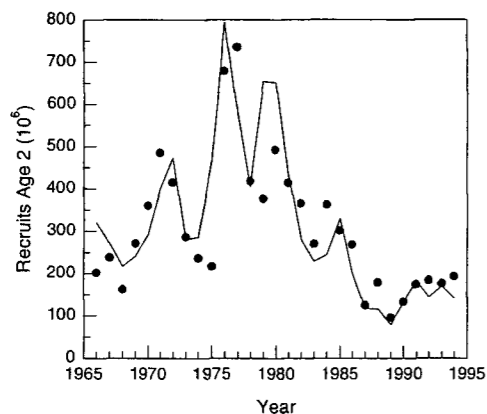


Figure 11: Observed (line) and predicted (points) recruitment of central Baltic cod at age 2 (R), 1966 to 1994. Predictions are based on multiple regression of recruitment per unit of egg production on total egg production, reproductive volume, and cumulative wind energy.

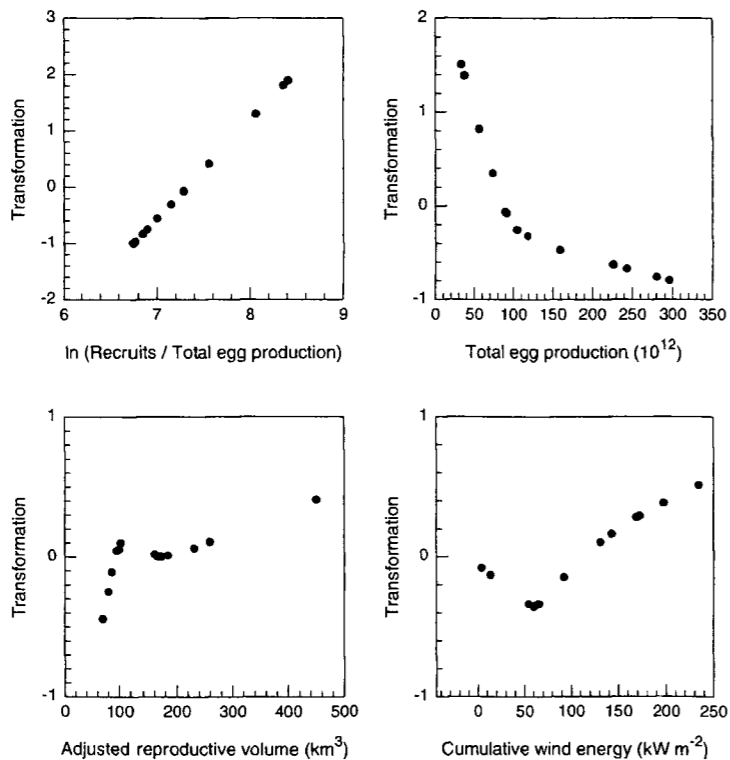


Figure 12: ACE transformations of the variables that contribute significantly to the multiple regression of cod recruitment in the central Baltic Sea, based on total egg production, 1982 to 1994.

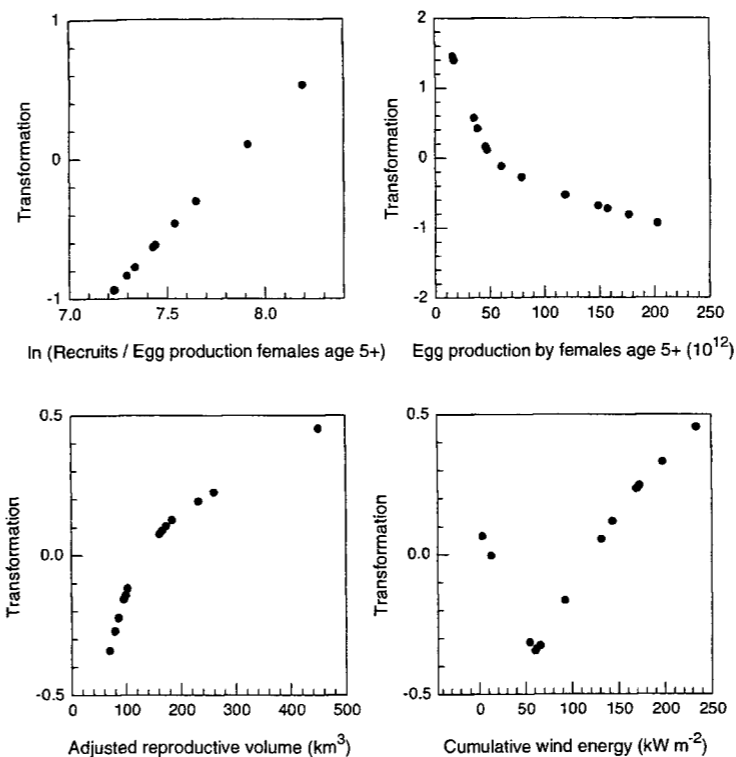
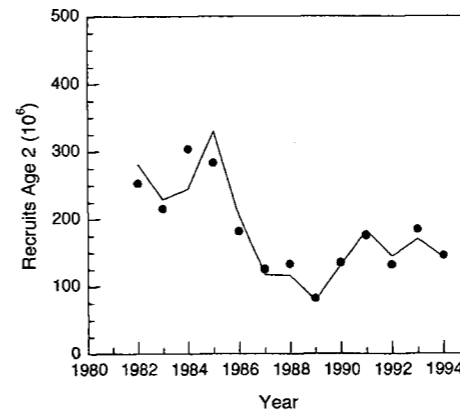


Figure 13: ACE transformations of the variables that contribute significantly to the multiple regression of cod recruitment in the central Baltic Sea, based on egg production by females of age 5+, 1982 to 1994.

Figure 14: Observed (line) and predicted (points) recruitment of central Baltic cod at age 2 (R), based on total egg production, 1982 to 1994. Predictions are based on multiple regression of recruitment per unit of egg production on total egg production, reproductive volume, and cumulative wind energy.



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## Discussion

### *Data series on fish biomass and recruitment*

We used data series from routine stock assessment based on VPA, which provide the basis for current scientific advice on fisheries management. Shortcomings of the methodology have been discussed elsewhere, and shall not be repeated here. In principle, multispecies assessment bears the advantage that predation is explicitly accounted for and the variable natural mortality is expected to result in more realistic biomass estimates for fish prey (in the Baltic basically sprat, herring and juvenile cod). The data sets underlying MSVPA for the central Baltic are at present undergoing revision, and the tuning methodology is being refined (ICES 1997b), which makes it difficult to obtain consistent time series. Only after this task has been completed should stronger differences in the fish estimate in the Baltic be expected, than are now revealed from comparison of the single- and multi-species approaches.

### *Cod egg production*

Estimates of total egg production were compiled based on available data on stock numbers, maturity ogives, sex ratios, distribution, and weight-specific fecundity estimates, and represent our best knowledge at present. Nevertheless, the available information may not always be adequate. Spatial distributions as presented in ICES (1997a) were obtained from annual research vessel surveys conducted in February-March, and may not reflect stock distribution at peak spawning time. For maturity ogives, sex ratios as well as stock distribution, observations for 1980 to 1984 were extrapolated to all previous years. In view of density-dependent effects such as observed changes in condition (Baranova 1989, 1995) and of existing theories of habitat use (MacCall 1990), it seems unlikely that these parameters have remained the same over a large range of biomass estimates. The distribution area of cod extended into the northern Baltic during the period of high stock abundance, but contracted to the southern Baltic at low stock levels. Homing behaviour to the spawning grounds has also been observed (Aro 1989). Available weight-specific fecundity estimates do not provide full temporal and spatial coverage, and the error introduced by assuming a randomly varying relationship cannot be evaluated. Thus, the estimates of total egg production may not reflect the true range of variation, especially for the years before 1980.

Not all eggs spawned in a given year have the same chance to survive until hatch. The specific gravity of cod eggs implies that they sink to deeper water (Nissling and Vallin 1996), and the distribution of viable eggs is narrowed by oxygen deficiency and/or cold temperature (Wieland and Jarre-Teichmann 1997). Oxygen concentrations usually decrease from spring to summer (MacKenzie *et al.* 1996b), and hence, egg mortality due to oxygen deficiency is likely to be higher in years of late spawning. We accounted for part of this variability by adjusting the reproductive volume by season. However, reduced viability of the eggs may be expected under conditions close to the required minimum (Wieland *et al.* 1994), and the present knife-edge assumption may overestimate the true reproductive volume. Repeat spawners spawn earlier in the year than recruit spawners (Berner 1960, Baranova 1995), and eggs of large females are larger and more buoyant than those of smaller ones (Nissling and Vallin 1996). Large eggs float at lower salinity which reduces their risk of being subjected to low oxygen concentrations, and eggs spawned early can

develop during a time of the year, when oxygen conditions are generally more favorable. Although about 60 % of the female spawning stock consist of first-time spawners on the average, the fraction can vary by 25 % (from about 45 % to 70 % of the total spawning stock, Figure 3). Repeated spawners vary in opposite direction, and the fraction of older females (age 5+) even varies more strongly, between about 15 % and more than 45 % of the spawning stock.

Factors such as these should be reflected in estimates of viable egg production. However, our knowledge is presently insufficient to make reliable estimates, although recent efforts to improve historical data sets (*e.g.* Tomkiewicz *et al.* 1997) and new studies (*e.g.* Nissling and Vallin 1996; Kraus 1997) may make this possible in future (Trippel 1998; MacKenzie *et al.* 1998). We used the close correlation between the mean age of the female spawning stock and the fraction of age 5+ females in the stock as an argument to consider egg production by 5+ females as a proxy for an age-structured measure of egg production. The smoother variable transformations of recruitment estimates based on egg production by spawners of age 5+ (Figures 10, 13) in comparison with those based on total egg production (Figures 9, 12) indicate that we are on the right track.

### *Reproductive volume*

Whereas a smooth intercalibration was generally possible between the time series presented by Pliksh *et al.* (1993) and Hinrichsen and Wieland (1996), their summer estimates were made either for August or July. No attempt was made to adjust the July estimates to August values. Feldman *et al.* (1996) presented the area occupied by water with salinity > 10 psu for the Gdansk Deep, rather than the area > 11 psu as in the other series. It appeared realistic to assume that the areas occupied by 10 and 11 psu do not differ by too much, because the halocline is rather steep in the area (Zezera and Zezera 1997). Although the true reproductive volume will in fact be somewhat overestimated, the error is probably minor compared to the error in other variables (*e.g.* fish abundance, spatial distributions, egg production), and is not likely to affect the results to a large extent. Furthermore, the definition of the present threshold levels refer to minimum conditions required by the eggs. But egg mortality, *e.g.* related to oxygen deficiency, is not a knife-edge effect (Wieland *et al.* 1994). In addition, larvae hatched at oxygen levels close to the minimum may have a reduced viability, and thus the reproductive volumes used here are likely to represent overestimates to an unknown extent.

Our wind data represent the conditions for the Bornholm Basin. Whereas wind direction should be expected to be much the same over the entire central Baltic, wind speeds may differ between Basins. However, distances in the central Baltic Sea are not large and indeed, stronger events such as storms are noted even over the entire Baltic in the course of only a few days. Taking the integral over 60 days around peak spawning should therefore account for short delays between the basins.

Species evolve so as to make optimal use of their habitat. Thus, Baltic cod may be expected to have adapted to the prevailing summer conditions of overall weak to moderate westerly winds which ensure transport of eggs and larvae to coastal waters for settling (Hinrichsen *et al.* 1999). The general importance of turbulence and transport for recruitment of different fish species has been demonstrated for upwelling ecosystems (Cury and Roy 1989, Bakun 1996), with emphasis on moderate conditions under steady wind forcing

from a constant direction (Cury and Roy 1989; Cury *et al.* 1995). Werner *et al.* (1993, 1995) pointed out the importance of advection and turbulence for cod and haddock.

### Zooplankton

Total zooplankton abundance was not significant in our regressions. This did not come as a major surprise, as larvae are not food limited in the Baltic (Graumann 1973; Krajewska-Soltys and Lingowski 1994; Zuzarte *et al.* 1996). Transport to shallow areas, as reflected in the wind effect, may therefore be more important to their survival than food availability.

The most important cause of the changes in zooplankton during recent decades is related to the general increase of organic matter in the zooplankton trophic layer, but also to the stronger inflow events of North Sea water into the Baltic during the winters of 1969/70, 1975/76, 1980, 1993/94. Especially short-lived forms of zooplankton are favoured by upwelling of nutrient-rich water from the deep basins along the coast (Kostrichina and Yurkovskis 1985; Kostrichina *et al.* 1990). Therefore, total zooplankton may not be an appropriate indicator of the limiting impact resulting from particular species or size classes. A more detailed analysis of the effect of single zooplankton groups was beyond the scope of this study.

### Stock-recruitment relationships

The fits of the Ricker curves to the two regimes of high and low cod stock-recruitment, respectively (Figure 7), explained a fair part of the variance in the entire time series, but even more so for the recent period of low reproductive volume, which is also characterized by better data. A break into two regimes, as indicated in the trajectory in Figure 6, is made plausible by the strong change in the level of the reproductive volume after 1981, representing the carrying capacity of the environment for cod reproduction. When the environmental conditions were favorable for cod spawning, optimal recruitment was estimated at 800 000 to 900 000 t of SSB (Figure 6, Table 2). During the past decade up to present, the reproductive volume was limited, and the Ricker curve suggests optimal recruitment at a SSB of approximately 400 000 to 550 000 t. For management purposes, the present situation must be taken into account. The curves further suggest that the probability of low recruitment increases strongly at biomass levels below 250 000 to 300 000 t.

According to the theory, an asymptotic curve should be expected when plotting recruitment per unit parent stock over parent stock. The transformations of egg production (Figures 9, 10), suggest that this relationship holds even for the entire period. The relationship emerges very nicely for the recent period of low recruitment, which is also characterized by better data availability.

The reproductive volume enters the multiple regression using ACE in a straightforward way. Following these results, recruitment is exponentially related to reproductive volume. Whether recruitment is proportional to a term  $e^{x \cdot (\text{Reproductive Volume})}$ , or a relationship of the form  $(\text{Reproductive Volume})^y$  is more appropriate, can currently not be decided. The former relationship is suggested from the entire series 1966 to 1994 (Figures 10, 12), whereas the latter is suggested from the most recent years (Figure 13). In any case, there is no doubt that an increasing reproductive volume benefits cod recruitment in the central Baltic Sea.

The transformation of wind energy indicates a strongly nonlinear correlation with recruitment rate per unit egg production. A minimum was observed for cumulative wind energies around  $60 \text{ kW} \cdot \text{m}^{-2}$ , corresponding to relatively little wind under prevailing westerly wind conditions, as is usually the case for the area. Strong northerly to easterly and in particular moderate to strong southerly to westerly winds favour recruitment, as these transport cod larvae towards shallower areas. Two wind optima should also be expected from possible drift towards either southern Sweden or Poland. Under the recent unfavourable hydrographic conditions in the spawning basins, it may have been particularly important that the larvae were transported into shallow water areas as fast as possible. This could explain the steady increase of recruitment along with increasing southerly or westerly winds during recent years (Figures 12,13).

The effects of reproductive volume and wind energy interact. Egg (Wieland *et al.* 2000) and larval (Grønkvær *et al.* 1995) abundance was high in the Bornholm Basin in 1994 under favourable hydrographic conditions (Figure 6A, C). However, due to missing wind forcing (Figure 8), the larvae were retained in the basin, and year-class strength was far below what could be expected (Figures 2, 4), but estimated correctly (Figure 14).

### Clupeids

Time series of clupeid stock estimates were not available as long back in time as those for cod. Hence, it was impossible to investigate their influence on cod recruitment for the entire data series. During the most recent years, clupeids did not significantly contribute to the regressions, regardless of whether single- or multispecies estimates, only sprat, only herring, or the combined biomass were considered. As cod prey on size-classes of sprat and herring that are potential predators of cod eggs (ICES 1997b), we did not consider it appropriate to distinguish between total and spawning biomass of clupeids.

The predator-prey interactions between clupeids and cod, herring and sprat representing the bulk of the diet of cod (Uzars 1989) while themselves consuming large numbers of cod eggs, are well documented (*e.g.* Sparholt 1994; Köster and Schnack 1994; Rudstam *et al.* 1994; Köster and Möllmann 2000). It is, therefore surprising that no significant effect of their biomass could be established. Apparently, the positive effect that clupeid biomass may have on condition, and consequently on maturation and viable offspring (Baranova 1989; Nissling and Westin 1996) and the negative effects of cod egg predation remain hidden in the time series.

### Estimates of recruitment

The multiple regression of recruitment per unit egg production on egg production, reproductive volume and wind energy explained 80 % to 85 % of the variance for the entire time series, depending on the measure of parent stock. The relationship between observed and predicted variables is accordingly good, with the possible exception of the second half of the 1970s (Figure 11) when recruitment was underestimated. This period was characterized by a series of high recruitment (1975 to 1980), and the biomass of adult cod increased accordingly, with a time lag of about three years. Cod prey on cod juveniles if they are abundant (Uzars 1995), and the underestimates may be due to

an above-average mortality of small (0- and 1-group) cod during this period, which is not adequately represented in the single-species VPA.

This line of reasoning is supported by the trajectory of the current MSVPA, which indicates a higher ratio between recruitment and SSB during the late 1970s and early 1980s. Accounting for cod cannibalism by using MSVPA estimates of stock and recruitment, as also suggested by Sparholt (1996a), is therefore likely to account for the discrepancy in our recruitment model without introducing a new variable into the regression.

The period since 1982 is characterized by low cod recruitment and high abundance of clupeids, and consequently, low cannibalism of cod. Consequently, neglecting cannibalism on 0- and 1-group cod did not have a marked effect, and more than 95 % of the variance was explained by parent stock, and the two variables relating to egg and larvae mortality (adjusted reproductive volume and cumulative wind energy).

#### *Other models of recruitment of central Baltic cod*

Sparholt (1996a) related recruitment of 0-group to cod spawning stock biomass (SSB) estimated from MSVPA, reproductive volume, and sprat SSB. He considered it biologically plausible that 0-group recruitment would be proportional to cod SSB, assuming that recruitment was not determined at the larval stage (Graumann 1973). SSB showed a weak effect in the model. In an alternative model, which allowed for non-proportionality of 0-group recruits to cod SSB, only reproductive volume was significant as additional variable, whereas sprat SSB was not. Sparholt (1996b) also estimated 2-group recruitment based on the alternative model, but the agreement between observed and predicted values was poor for years with low recruitment.

The approaches of Sparholt (1996a, b) and ours are comparable, and in fact complementary. The estimates of a parent stock size of about  $500 \times 10^3$  t for optimal cod recruitment under the present conditions are similar. Our study has confirmed the importance of accounting for cod cannibalism. Large discrepancies exist in the stock assessments for sprat and herring for different years. This clearly needs further investigations. Notwithstanding these uncertainties, egg and larvae mortality vary between years, and cumulative wind energy during the period of larval drift appears to represent an appropriate but non-linear variable to account for the annual differences. It would follow that the assumption of proportionality between spawning stock and 0-group recruitment is inappropriate.

Solari *et al.* (1997) proposed a nonlinear stock-recruitment model for Baltic cod, based on the assumption of multiple steady-states, characterized by a different carrying capacity for young cod and by density-independent transitions between the steady-states.

The widely accepted concept of variable carrying capacity of the environment for a given species forms the basis for our emphasis on reproductive volume. Different density-dependent effects may tend to stabilize stocks around different equilibria, but for a specific set of environmental conditions at one particular point in time cannibalism can only explain a single equilibrium, related to the (higher local) maximum in the stock-recruitment function of Solari *et al.* (1997). We are not aware of any other density-dependent mechanism, which would lead to an additional equilibrium under particular biotic and abiotic conditions.

The goal of parameterizing the function of Solari *et al.* (1997) is ambitious because the six parameters have to be estimated from a relatively short time series. Also, the bio-

logical interpretation of the parameters is not straightforward, partly due to their mathematical interdependence. Following this approach, the cod spawning stock may develop in an unpredictable way due to the high sensitivity to initial values and coefficients of the function. The phenomenon of chaos in a mathematical sense, i. e., a small disturbance in any parameter at a given instant may be enhanced in such a way that the behaviour of the system depends substantially on the nature of the disturbance, may be conceptually appealing. However, it is inconsistent with the ecological context, where the parameters are not only estimated inaccurately but also exhibit a stochastic variation.

A modelling approach that is aimed at making predictions based on empirical information needs to fulfill minimum requirements of robustness consistent with the amount of uncertainty in the available data and in the processes. In that light, the use of the Ricker function as a starting point appears to be more adequate, particularly because it allows for a clear distinction between two coefficients integrating density-dependent and density-independent effects, respectively. The approach still allows to model the dynamics of cod recruitment explicitly including environmental variability, as exercised here.

Alternating periods of high and low abundance of fish stocks have been investigated in shelf (Cushing 1980; Steele and Henderson 1984) and pelagic ecosystems (Lluch-Belda *et al.* 1989; Jarre-Teichmann 1998; Francis *et al.* 1998). These have generated lively discussion on how much change was due to environmental variability and to fishing activities. Both environmental conditions (through limiting successful egg development and larvae transport) and exploitation (through influencing the age structure of the stock) are relevant to the stock size of central Baltic cod. Whereas top-down control of the stock generated through fishing is well accepted (ICES 1997c), the implications of the underlying environmental regime are not yet explicitly used in producing scientific management advice. While future regime shifts may not be predicted, we feel that management advice may be improved significantly by integrating the available knowledge on environmental variability in the Baltic in routine stock assessment procedures.

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