

Recruitment of Baltic cod and sprat stocks: identification of critical life stages and incorporation of environmental variability into stock-recruitment relationships*

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SUMMARY: The recruitment processes of Baltic cod and sprat were analysed and critical periods were identified by addressing the major impact factors on individual early life history stages separately and relating observed abundance data between successive stages. For cod, recruitment appeared to be dependent on egg survival, with low oxygen concentration in dwelling depths and predation by clupeids as the major causes for egg mortality. Surviving egg production and larval abundance were weakly correlated, whereas larval abundance was significantly related to year class strength. This indicated that the period between the late egg and the early larval stage is critical for cod recruitment. A potential variable identified to affect this life stage was prey availability for larvae. For sprat, early and late egg stage production as well as late egg stage production and larval abundance were significantly related. However, year class strength was largely independent of larval abundance. Thus, the period between the late larval and early juvenile stage appeared to be critical for sprat recruitment. Potential variables identified to affect this life stage were ambient temperature and wind stress. Environmental factors showing statistically significant covariance with the survival of one of these critical life stages were incorporated into stock-recruitment models for individual spawning areas separately and for the Central Baltic combined.

Key words: cod, sprat, Baltic, critical life stage, environment, stock-recruitment relationship.

INTRODUCTION

General approach and stock development

The present consensus in fisheries research is that the success of a year class is determined primarily by a series of density independent stochastic

processes acting on the egg, larval and early juvenile stages. These processes, such as co-occurrence with sub-optimal habitats, overlap with predators, reduce the abundance surviving to the juvenile stage. After this period of high mortality, subsequent survival success and recruitment to the fishery is primarily the result of density dependent processes such as competition for optimal habitat and cannibalism (e.g. Myers and Cadigan, 1993; Leggett and

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Deblois, 1994; Heath and Gallego, 1997). Superimposed on these external conditions, parental contributions to the quality (e.g. Trippel *et al.*, 1997; Marteinsdottir and Steinarrson, 1998), quantity (Trippel, 1998; Lambert and Dutil, 2000) and spatio-temporal distribution of reproductive products (e.g. Hutchings and Myers, 1993; Begg and Marteinsdottir, 2000) affect the susceptibility of individuals to environmental conditions and determine the environmental conditions offspring are exposed to (St. John *et al.*, 2000; Vallin and Nissling, 2000). In the present study we examine the reproductive success in two fish species, cod and sprat, characterised by differing life history strategies in a biologically simple but hydrographically complex system, the Central Baltic Sea. The analyses follows the success of a year-class during ontogeny from spawner abundance through the egg and larval to the juvenile stage according to Paulik's (1973) framework, thus considering various endogenous and external processes affecting reproductive success.

During the last two decades, a shift has occurred in the upper trophic level of the Central Baltic Sea Ecosystem, leading from a cod-dominated to a sprat-dominated system. The cod stock declined, due to recruitment failure and high fishing intensity (Bagge *et al.*, 1994). The corresponding decrease in predation pressure on sprat, combined with low fishing mortality and high reproductive success for this species, resulted in a pronounced increase of the sprat stock (Parmanne *et al.*, 1994). Apart from being the major prey species of cod in pre-spawning and spawning periods (Bagge *et al.*, 1994), sprat has been identified as an important predator on cod eggs (Köster and Schnack, 1994). This type of biological interaction may stabilise the dominance of either cod or sprat in the system (Rudstam *et al.*, 1994). A destabilisation of the system or shift in the species dominance may be caused by unfavourable hydrographic conditions for reproduction and subsequent recruitment failure of one of the species, and/or by a high species selective fishing mortality (Schnack, 1997). Cod and sprat utilise the same deep Baltic basins as spawning areas (Fig. 1), though sprat spawning is more distributed and less restricted to the deep parts of the basins. Also, the spawning times are largely overlapping (Bagge *et al.*, 1994; Parmanne *et al.*, 1994). Nevertheless, there is a pronounced difference in reproductive success of the two species, indicating a difference in the environmental requirements.

In the past 10-15 years a substantial effort has been made to examine the major processes assumed to affect the recruitment success of Eastern Baltic cod (Bagge and Thurow, 1994; MacKenzie *et al.*, 1996). The most recent activities are addressing also sprat, in order to adequately consider the strong interactions evidenced between the two species (Köster and Möllmann, 2000a; Köster *et al.*, 2001a). As a result, several new data series of potential relevance for these processes have become available. We utilised this material to address the question whether standard assessment procedures provide estimates of spawning stock biomass, which can be used as a reliable measure of egg production. This has recently been questioned for a number of fish stocks (MacKenzie *et al.*, 1998; Marshall *et al.*, 1998; Marteinsdottir and Thorarinsson, 1998). The present paper presents results for Baltic cod and sprat, and summarises the information available or required to improve the stock-recruitment relationships for these two populations. Additionally, in order to disentangle processes acting on early pelagic and later demersal juveniles (Ulltang, 1996), the feasibility of estimating recruitment success before juveniles recruit to the fisheries was tested by comparing estimates derived from Multispecies Virtual Population Analysis (MSVPA) with abundance indices from research surveys.

The second task follows Paulik's (1973) approach, examining the entire life history process for critical periods and relationships between successive life stages (Rothschild, 1986). To our knowledge, only a few attempts have been made to follow this approach (e.g. Pacific salmon: Larkin and Hourston, 1964; walleye pollock in Shelikof Strait: Kendall *et al.*, 1996; North Sea plaice: Beverton and Iles, 1992). A large amount of multi-disciplinary information is required and in almost all cases, including the Baltic, the major problems are lack of time series data on key processes and the variety and complexity of processes involved.

The third task aims at incorporation of environmental processes and species interaction into stock-recruitment relationships, as suggested by Sparholt (1996) and Jarre-Teichmann *et al.* (2000) for Baltic cod and by Grauman and Yula (1989) for sprat. Based on exploratory statistical analysis, variables were identified which showed significant covariance with survival rates during critical life stages. These variables were incorporated as impact factors into stock-recruitment models, which were established first for individual ICES Sub-divisions (i.e. spawn-

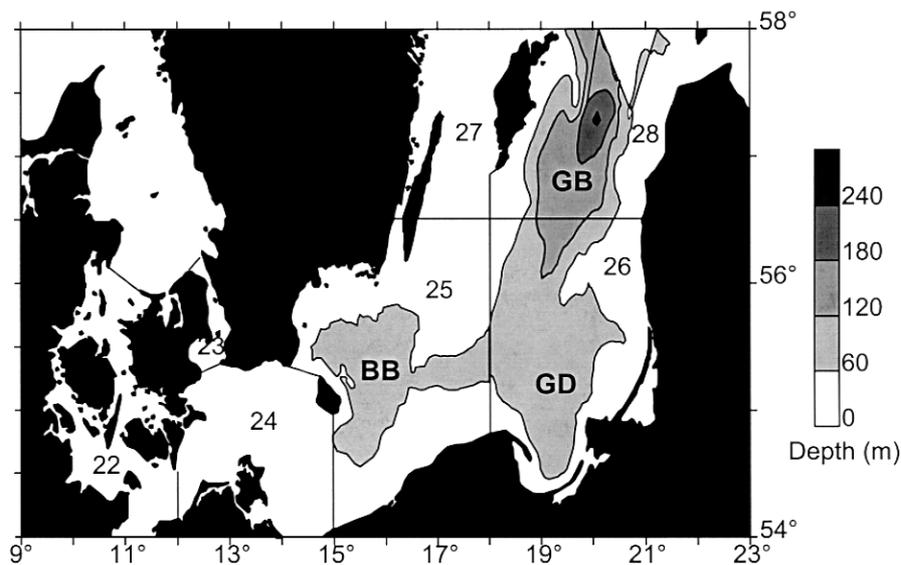


FIG. 1. – Major spawning areas of cod and sprat in the Central Baltic (BB: Bornholm Basin; GD: Gdansk Deep; GB: Gotland Basin; numbers: ICES Sub-divisions).

ing areas, Fig. 1), characterised by distinct hydrographic regimes (Plikshs *et al.*, 1993; MacKenzie *et al.*, 2000) and differences in recruitment success and stock development (Ojaveer, 1989; Sparholt and Tomkiewicz, 2000). These area-specific models were then combined for the entire Central Baltic.

The Sub-division specific stock-recruitment relationships were established on the basis of area disaggregated Multispecies Virtual Population Analysis (Köster *et al.*, 2001a). For cod, a first approach was presented by Köster *et al.* (2001b), in which mechanisms leading to area specific differences were identified. The present approach is an extension of the previous one, addressing the above mentioned aspects and extending the exploratory analysis to data on mesozooplankton abundance as a measure of prey availability for the larvae. For sprat, the present analysis is a new approach to explain differences among areas and establish environmentally sensitive recruitment models, specifically testing hypotheses on the significance of environmental factors suggested earlier (e.g. Grauman and Yula, 1989; Kalejs and Ojaveer, 1989; Raid, 1989).

Environmental factors considered to be critical for year class success

Due to low salinity in upper water layers of the Central Baltic, cod eggs do not float in surface waters, but concentrate in a narrow depth range within and below the permanent halocline (Wieland and Jarre-Teichmann, 1997). At this depth the eggs

are frequently exposed to low oxygen concentration, and survival is largely reduced in these situations (Nissling, 1994; Wieland *et al.*, 1994). Plikshs *et al.* (1993) defined a “reproductive volume” (RV) as an index for potential egg survival, i.e. the volume of water fulfilling minimum requirements for successful egg development. However, as this index does not consider the actual oxygen conditions inside the reproductive volume and the possibility that eggs may float outside the RV, two modifications of this index were employed in the present study.

Sprat eggs have on average a higher buoyancy than cod eggs (e.g. Wieland and Zuzarte, 1991) and by floating in higher ranges of the water column they are less affected by oxygen depletion in the deep water. However, they are sensitive to low temperatures (e.g. Thompson *et al.*, 1981) and may be affected when floating in the cold water layer between the thermo- and the halocline formed in the Central Baltic during winter (Krenkel, 1981; Herra, 1988). Additionally, there is evidence that spawning activity and individual fecundity are affected by unfavourable temperature conditions in pre-spawning periods (Elwertowski, 1960; Petrowa, 1960). According to Grauman (1965), sprat egg survival in summer depends also on the wind conditions, with high wind stress resulting in a high mortality of eggs distributed during these months in upper water layers. Wind conditions also impact encounter rates of larvae and their prey as well as feeding success.

Jarre-Teichmann *et al.* (2000) demonstrated that the cumulative wind energy at peak spawning time

affects cod recruitment. The suggested process is a transport of larvae and pelagic juveniles to coastal nursery habitats during periods of high wind stress and a retention in the central basins during periods of low wind stress of variable wind direction (Hinrichsen *et al.*, 2001). Köster *et al.* (2001b) incorporated these transport processes in their exploratory analysis on cod recruitment processes by modifying the wind energy index to consider explicitly the direction of transport (larval transport index).

For sprat larvae preliminary hydrodynamic modelling approaches demonstrated the sensitivity of results from ichthyoplankton surveys to high wind stress, which may lead to a rapid advection of larvae out of the survey area (STORE, 2001). This rapid transport is caused by a concentration of sprat larvae in the upper-most water layers after successful completion of their initial vertical migration from the hatching depth. Grauman (1976) also described a large-scale wind-driven transport of sprat larvae from Sub-division 25 to 26 and 28 (Fig. 1).

Consumption of cod eggs by sprat has a significant impact on cod egg survival in the Bornholm Basin in spring and early summer, while later in the spawning season herring replaces sprat as a principal predator of cod eggs (Köster and Möllmann, 2000a). Similarly, egg cannibalism by sprat in the Bornholm Basin is a potential compensatory process limiting the reproductive success of the sprat stock (Köster and Möllmann, 2000b). Predation on cod eggs by sprat decreased throughout the 1990s while the importance of herring predation increased, due to a delay in spawning of cod (Wieland *et al.*, 2000). Apart from intra- and inter-annual trends, there is also a spatial variation apparent in the intensity of egg predation which is considerably lower in the Gdansk Deep and Gotland Basin than in the Bornholm Basin. Existing data on sprat and herring diet composition suggest that the ratio of cod eggs in the stomachs and in the food supply is linearly related to the degree of overlap in their vertical distribution. The oxygen concentration in the bottom water limits the vertical distribution of clupeids during the daylight-feeding period, while the density regime determines the vertical distribution of cod eggs (Köster and Möllmann, 2000a). This observation led to the development of an index of vertical predator/prey overlap and enabled the prediction of a relative egg consumption index by the predator populations (Köster *et al.*, 2001b).

A substantial predation by adult herring on young of the year sprat was reported by Patokina and Feld-

man (1998) in Sub-division 26 in autumn 1997. This predation has been related to the outstanding high abundance of young of the year sprat in the area and might be supported by a small average size of sprat due to low growth rates (ICES, 1998).

Recent studies have demonstrated that the species composition in the mesozooplankton community of the Central Baltic, and thus the availability of potential prey for larvae and early juveniles, have undergone substantial changes in the last two decades. *Pseudocalanus elongatus* depends strongly on high salinity (Ojaveer *et al.*, 1998; Vuorinen *et al.*, 1998) and on low temperature in summer (Möllmann *et al.*, 2000). Both factors developed in an unfavourable direction for this species and led to a reduction of the standing stock throughout the stagnation period of the 1980s. In contrast, the copepods *Temora longicornis* and *Acartia* spp. as well as cladocerans show a strong preference for higher temperatures and an affinity for lower salinities in spring (Sidrevics, 1984, Möllmann *et al.*, 2000), and thus developed increasing standing stocks throughout the late 1980s and early 1990s. It has been hypothesised that the abundance of nauplii and copepodid stages of *T. longicornis* and *Acartia* spp. is of importance for the survival of larval sprat (Grauman and Yula, 1989; Kalejs and Ojaveer, 1989), while corresponding juvenile life stages of *P. elongatus* may be of importance for cod larvae.

MATERIAL AND METHODS

According to the availability of time-series data, the exploratory analysis for cod is mainly restricted to Sub-division 25, comprising the Bornholm Basin (Fig. 1), currently the most important spawning ground in the Central Baltic (MacKenzie *et al.*, 2000; Köster *et al.*, 2001b). For sprat the exploratory analysis was restricted to the eastern spawning areas in Sub-division 26 (Gdansk Deep) and Sub-division 28 (Gotland Basin) (Fig. 1).

Stock parameters

Stock size and spawning stock biomass

Stock abundances were obtained from spatially dis-aggregated MSVPA runs for the period 1976-1996 (Köster *et al.*, 2001a). Weight at age in the catch was assumed to be equal to weight at age in the stock, exceptions being age-groups 0 to 2 for

cod. Here, due to size selection by commercial gears, period specific (before 1989 and after 1990) average weights compiled by ICES (1999b) were applied in the different areas. Cod spawning stock biomass values (SSB) were determined for the different Sub-divisions by using area specific sex ratios and maturity ogives (proportions of sexually mature individuals at age) given by Tomkiewicz *et al.* (1997). In cases of adequate sampling, annual values were applied, i.e. for 1986 - 1996 in Sub-division 25 and for 1993 - 1996 in Sub-division 26; otherwise 5 year averages were used (Tomkiewicz *et al.*, 1997). To demonstrate the effect of introducing year and sex specific maturity ogives on SSB estimates as a measure of egg production, two additional options were tested: i) average maturity ogives utilised in former standard stock assessment (ICES, 1996), being invariate over time and ii) temporally and spatially resolved female SSB, based on above described information. For sprat, sex specific maturity ogives and sex ratios were available only for the most recent 5 years in Sub-division 26. This restricted the analysis to a test on the deviation between total and female SSB applying average sex specific maturity ogives and sex ratios.

Abundance of recruits

Cod recruits to the fishery at an age of 2 and year-class strength is difficult to assess at an earlier age due to cannibalism effects. Thus, regular single species assessments of cod cover age 2 as the youngest age-group and presentations of stock-recruitment relationships refer in general to age-group 2. In the present study, spatially dis-aggregated MSVPA runs (Köster *et al.*, 2001a) have been utilised to estimate 0- and 1-group abundances, thus explicitly considering cannibalism in the estimation procedure. The cod 0-group estimate for 1996 was omitted from further analysis, as it depended heavily upon the tuning method employed. For sprat, standard stock assessment procedures estimate recruitment at age 1 (ICES, 1999a), using predation mortalities derived from spatially aggregated MSVPA runs (ICES, 1999b). In the present study, 0-group estimates from area dis-aggregated MSVPA runs have been utilised as a measure of reproductive success, in order to dis-entangle the impact of predation by cod on young of the year sprat from other processes affecting recruitment.

Juvenile abundance estimates derived by MSVPA runs have been validated by area specific

survey indices. For cod age-groups 1 and 2, results from international bottom trawl surveys conducted since the early 1980s have been applied as compiled by the EU-project CORE (1998). For sprat, estimates of 0- and 1-group abundances were recompiled from international hydroacoustic surveys, performed since 1981, and corrected for variation in area coverage (ICES, 1997). Results from the 1993 hydroacoustic survey were excluded, due to technical problems and lack of area coverage (ICES, 1994). It should be noted, that data series for cod age-groups 1 and 2 as well as sprat age-group 1 were utilised for tuning of the MSVPA, thus not being strictly independent. However, the impact is mainly restricted to the later part of the time series, which makes these data valid for a comparison of trends for the major part of the time series. A further validation of cod age 2 recruitment was performed using independent Latvian bottom trawl surveys conducted in Sub-division 26 and 28 in January and November/December. However, these surveys cover only a part of the time series, mainly the 1980s. Independent recruitment estimates for sprat were available from the Polish young fish survey in Sub-division 26 (ICES, 1999a) comprising a geometric mean abundance index, based on catch rates of age-groups 0 and 1.

Potential egg production by the spawning stocks

The area-specific potential egg production has been estimated for cod from female SSB per Sub-division, coupled with predicted relative individual fecundity values (Kraus *et al.*, 2000). The relative fecundity is independent of body size and did not differ among areas though being variable among years. It was predicted as a common value for all Sub-divisions from a statistical model which includes as impact factors: average ambient temperature in the 4th quarter of the year preceding the investigated spawning period and the anomaly in growth of average wet weight from the 3rd quarter of the preceding year to the 1st quarter of the year of spawning (Kraus *et al.*, 2000). As an alternative approach, a time series of observed relative individual fecundity values was utilised (Shapiro, 1990; Bleil and Oeberst, 1996; Kraus *et al.*, 2000), in which missing values were substituted by linear interpolation.

For sprat, available information on batch fecundity and spawning frequency (Petrowa, 1960; Polivaiko, 1980; Alekseeva *et al.*, 1997) hardly allows to

construct a reliable time series of potential egg production values. In this case, a proxy for the nutritional condition and the reproductive potential of the population was obtained from the anomaly in average growth rate over age-groups 2 to 4 from the 3rd quarter of the preceding year to the 2nd quarter of the year of spawning. In addition, the pre-spawning condition of these fish was characterised by the anomaly in weight at age in the 1st quarter of the year of spawning. Basin specific quarterly weight at age values of adult fish have been compiled for both species by ICES (1999b), but a full analysis could be achieved for Sub-division 26 only.

Egg and larval abundance

Mean annual values for egg and larval abundance were available for the different Sub-divisions (water depths > 60m) from ichthyoplankton surveys carried out in 1976-1996. For cod, the data have been summarised by Köster *et al.* (2001b) and for sprat they were compiled from Krenkel (1981), Grauman and Krenkel (1986), Karasiova (1999), Köster and Möllmann (2000a). Abundance estimates for cod eggs were based on sampling during a three-month period encompassing the main spawning season, averaging survey specific mean abundance values. Up to 1989 the sampling period was April-June; thereafter it successively shifted to May-June (1990-1992) and June-August (1993-1996), corresponding to the observed shift in the cod spawning period in recent years (Wieland *et al.*, 2000).

Abundance estimates for sprat eggs refer to the main spawning period, May-June (ICES, 1976). The periods considered for larval abundance estimates were the same as for eggs in the case of sprat, with fast egg development (Thompson *et al.*, 1981), but were shifted for cod to account for a 2 to 4 week period of egg development (Wieland *et al.*, 1994).

Realised egg production

Estimates of the average daily egg production during main spawning periods were based on stage specific abundance data (see above) and temperature related egg development rates (cod: Wieland *et al.*, 1994; sprat: Thompson *et al.*, 1981). For cod, the relevant temperatures were taken from the depth of the centre of mass of egg distribution and were obtained either from direct observations, i.e. CTD-measurements taken concurrently to the vertically resolving ichthyoplankton sampling in 1986-1996

(Wieland and Jarre-Teichmann, 1997), or from the ICES hydrographic database and predicted centre of mass values (Köster *et al.*, 2001b).

The vertical distribution of sprat eggs has been less intensively studied and appears to be more variable (Müller, 1988; Wieland and Zuzarte, 1991), with a typical deep distribution in spring and early summer and a more surface-oriented distribution in summer (Herra and Grimm, 1983; Herra, 1988). As the main spawning season for sprat was May/June it was assumed that the average temperature in the 60-80 m depths layer was most relevant for estimating developmental periods. Finally, stage specific daily egg production rates were calculated by dividing the abundance values for individual egg stages by the development time of the respective stage.

Environmental factors

Oxygen concentration

The relevance of the oxygen condition for cod egg survival was tested by including the reproductive volume (RV), defined by Plikshs *et al.* (1993), in the analysis as an index of potential cod egg survival. RV-values for the different Sub-divisions and for peak spawning periods were derived from MacKenzie *et al.* (2000). As this index is based on minimum oxygen requirements only, two alternative indices were defined and tested in addition for a more complete utilisation of the given information about ambient oxygen conditions in the Bornholm Basin. The first one, the integrated oxygen content in the RV (ORV), is based on an integration of the mean oxygen concentrations per 1 metre depth interval throughout the thickness of the RV (MacKenzie *et al.*, 2000).

The second alternative, the oxygen related egg survival (OES) is based on the fraction of the egg production expected to survive each year when a laboratory established relation of egg survival is applied to oxygen concentration (Rohlf, 1999), using observed oxygen profiles during spawning time and depth stratified abundance data of cod eggs. The depth distribution of eggs was predicted from the observed water density profiles (Köster *et al.*, 2001b).

Temperature

The impact of temperature on survival of sprat eggs and larvae was tested on the basis of average

water temperatures at main spawning time in May derived from the ICES hydrographic database. For the Bornholm Basin (Sub-division 25) and the Gdansk Deep (Sub-division 26) a depth range of 40-60 m was considered, and for the Gotland Basin (Sub-division 28) a range of 40-80 m was considered, corresponding to the deeper location of the permanent halocline. Temperature conditions in the intermediate water and the upper halocline in May were chosen, as they comprise the water layer with lowest temperatures and are closely related to winter temperature in the upper water column, thus representing also an index for the severity of the winter condition that potentially affects sprat condition, maturation and fecundity.

Wind

The impact of wind conditions on transport of cod larvae into suitable nursery areas or retention within the spawning areas has been examined by Köster *et al.* (2001b), who developed a larval transport index as a proxy for this effect. To test whether wind-induced transport affects the sprat larval abundance estimates from ichthyoplankton surveys, a larval transport index was developed corresponding to the one described for cod (Köster *et al.*, 2001b), but adjusted to the differences in vertical distribution and main spawning season of the two species. A potential impact on sprat egg mortality and the effect of turbulence on feeding success of sprat larvae was tested using the anomalies in weekly-averaged wind speed in May/June 1977-1994 recorded at Christiansø (10 nm northeast of the main island of Bornholm).

Predation

Predation pressure on cod eggs was introduced into the analysis as a relative egg predation index, expressing consumption per standing stock of eggs scaled to the potential egg production according to Köster *et al.* (2001b). Predation on sprat by herring during the development from the larval to the 0-group stage was tested in Sub-division 26 for size-dependent effects by relating mortality rates to weight at age anomalies of 0-group sprat during the 4th quarter of the year, using data compiled by ICES (1999b).

Prey availability

The relevance of long term changes in zooplankton species composition for larval and 0-group sur-

vival of cod and sprat was tested by utilising stage-specific data on abundance of major mesozooplankton species in Sub-division 26 and 28 during the main spawning periods, compiled by the Latvian Fisheries Research Institute (LATFRI). For a description of the sampling and analyses procedures see Möllmann *et al.* (2000). Selection of an appropriate prey spectrum according to prey species and stage was conducted on the basis of diet compositions described in Zuzarte *et al.* (1996). For cod, the test was restricted to Sub-division 26, as the number of years in which cod larvae were encountered in Sub-division 28 was too low to conduct any statistical analysis.

Construction and validation of stock-recruitment models

Our stock-recruitment relationships explicitly consider environmental and spatial heterogeneity incorporating causal relationships between survival rates of different critical life stages, environmental factors and species interactions. For cod we tested existing environmentally sensitive stock-recruitment relationships (Köster *et al.*, 2001b) by predicting year-class strength 1996-1999, which was not considered in the parameter estimation, and subsequently comparing it to updated MSVPA results and trawl survey derived recruitment indices. Input data were: i) potential egg production by the spawning stock derived from updated area dis-aggregated MSVPA runs (ICES, 2001a), sex ratios and maturity ogives (ICES, 1998), and relative fecundity values (STORE, 2001), ii) RV and ORV calculated from hydrographic data recorded on ichthyoplankton surveys (STORE, 2000), iii) predation on cod eggs estimated on the basis of the vertical overlap index (Köster *et al.*, 2001b) determined from the above hydrographic data, egg abundance from ichthyoplankton surveys and predator abundance from updated MSVPA according to Köster and Möllmann (2000a), and iv) the updated larval transport index (STORE, 2001). A similar test was conducted for stock-recruitment relationships established for sprat utilising also area disaggregated MSVPA output to determine the SSB (ICES, 2001a) and temperature conditions in the intermediate water in May extracted from the ICES hydrographic database. Predicted recruitment at age 0 was compared to MSVPA output and autumn hydroacoustic survey results (ICES, 1998, 1999a, 2000).

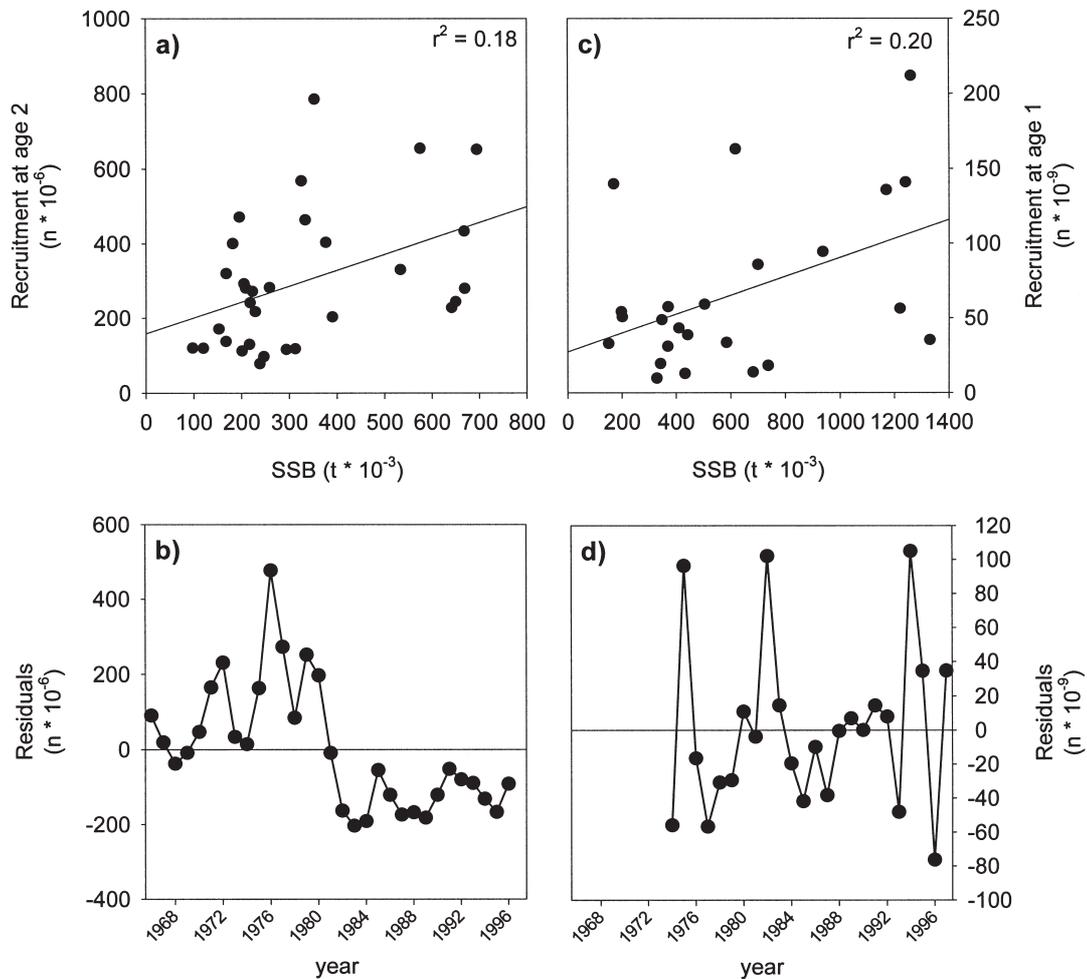


FIG. 2. – Linearity of stock-recruitment relationships of eastern Baltic cod (Sub-division 25-32) (a) and Baltic sprat (Sub-division 22-32) (c) and corresponding residuals (b and d), data source: standard stock assessment (ICES 1999a).

RESULTS

Significance of linear stock-recruitment relationships

Linear regression analyses revealed significant relationships between spawning stock biomass and recruitment of cod and sprat as determined by the standard stock assessment for the eastern and the entire Baltic respectively (Fig. 2). However, the explained variance in recruitment at age 2 and 1 is low, with a significant intercept for cod and high outlying recruitment values for both species. Furthermore, there is a clear time trend in the residuals for cod with a high number of positive residuals at the beginning of the time series up to 1981 and only negative residuals afterwards (Fig. 2). The stock-recruitment relationships derived by the area disaggregated MSVPA runs show a corresponding pattern for cod with a significant linear relationship in Sub-

divisions 26 and 28, but not in Sub-division 25 (Table 1). Again, high recruitment success originated from intermediate SSB at the beginning of the time series. Recruitment declined despite high SSB in the early 1980s. This pattern resulted in a significant auto-correlation in the residuals. For sprat a significant linear relationship was obtained only for Sub-division 25 (Table 1), while in the other areas an outstanding high recruitment of the 1982 year-class originating from a low SSB did not coincide with a linear relationship (Fig. 2).

Validation and improvement of stock-recruitment relationships

Spawning stock biomass as a measure of egg production

When using constant maturity ogives over time, the SSB calculated for cod in Sub-division 25 was

TABLE 1. – Linear regressions of cod and sprat recruitment (in numbers) on SSB (in t) derived by area dis-aggregated MSVPA for different Sub-divisions (SSB in t): parameter estimates and their significance level, r^2 -values and Durbin Watson (DW) statistics indicating serial correlation in the residuals if significant (* =significant at 5% level).

Dependent variable	Sub-division	Time series	Parameter	Parameter estimates	p	r^2	DW statistics
Cod age 2	25	1976-96	slope	815.0	0.091	0.16	0.61*
			intercept	$7.521 \cdot 10^7$	0.101		
Cod age 2	26	1976-96	slope	869.5	0.037	0.23	0.43*
			intercept	$2.825 \cdot 10^7$	0.037		
Cod age 2	28	1976-94	slope	1097.1	0.003	0.41	0.49*
			intercept	$3.612 \cdot 10^6$	0.810		
Sprat age 1	25	1977-96	slope	67645	0.003	0.43	1.44
			intercept	$1.167 \cdot 10^{10}$	0.043		
Sprat age 1	26	1977-96	slope	43017	0.198	0.10	1.93
			intercept	$7.547 \cdot 10^9$	0.163		
Sprat age 1	28	1977-96	slope	29529	0.197	0.10	2.19
			intercept	$-4.309 \cdot 10^9$	0.197		

not linearly related to the daily egg production at peak spawning time, but it was significantly related if based on yearly or periodically adapted maturity ogives (Table 2). The relationship was further enhanced when only the female part of the SSB or the predicted potential egg production were used. The largest deviations between potential and realised egg production were apparent for the most recent years of the time series. Utilising observed instead of predicted relative fecundity values, which included a linear interpolation procedure for missing data, also resulted in a significant relation to the

realised egg production, but with a slightly higher unexplained variance ($r^2 = 0.39$, $p = 0.001$).

For sprat in Sub-divisions 26 and 28, the results were different: the SSB was significantly related to the realised egg production even when it was based on constant maturity ogives over time (Table 2). Utilising an age-specific sex ratio invariate with time to compute the female SSB in Sub-division 26 did not further enhance the relationship ($r^2 = 0.42$, $p = 0.003$). Female and total SSB were closely related ($r^2 = 0.98$), although the sex ratio was rather skewed to female dominance with increasing age.

TABLE 2. – Linear regressions of realised egg production of cod and sprat on different measures of potential egg production. Realised egg production = average production of stage I eggs ($n \cdot \text{day}^{-1}$) during the main spawning season derived from ichthyoplankton surveys. Measures of potential egg production are based on alternative estimates for SSB (in t) and include fecundity information in one option. The table presents parameter estimates and their significance levels, r^2 -values and Durbin Watson (DW) statistics indicating serial correlation in the residuals if significant (* = significant at 5% level).

Independent variable	Sub-division	Time series	Parameter	Parameter estimates	p	r^2	DW statistics
cod SSB based on maturity ogive invariate with time	25	1976-96 without 1979-82 & 1984 ¹⁾	slope	344.74	0.488	0.03	0.63*
			intercept	$4.6970 \cdot 10^{10}$	<0.414		
cod SSB based on yearly or period specific maturity ogives	25	1976-96 without 1979-82 & 1984 ¹⁾	slope	1.256.9	0.027	0.30	0.62*
			intercept	$-1.4979 \cdot 10^{10}$	<0.734		
female cod SSB	25	1976-96 without 1979-82 & 1984 ¹⁾	Slope	3315.5	<0.001	0.61	1.04*
			Intercept	$-8.2145 \cdot 10^{10}$	0.048		
predicted potential egg production of cod	25	1976-96 without 1979-82 & 1984 ¹⁾	Slope	$4.6471 \cdot 10^{-3}$	<0.001	0.63	1.40
			Intercept	$-7.1663 \cdot 10^{10}$	0.054		
sprat SSB	26	1977-96 without 1992 ¹⁾	Slope	$1.3710 \cdot 10^{-4}$	0.002	0.44	2.16
			Intercept	12.334	0.201		
sprat SSB	28	1977-96 without 1992 ¹⁾	Slope	$1.9014 \cdot 10^{-4}$	0.004	0.39	1.36
			Intercept	5.9692	0.492		

¹⁾ No reliable egg production rates from ichthyoplankton surveys available.

Abundance of recruits as a measure of reproductive success

Cod abundances at age 1 and 2, as calculated by MSVPA, were significantly related to abundance indices from the international bottom trawl survey (BITS) in all areas with the highest variability in Sub-division 25 (Table 3). In this area especially the 1979 year-class showed a low abundance index as one-year-old in the 1980 survey, which did not coincide with a high recruitment estimated by the MSVPA. In Sub-divisions 26 and 28 survey data were available only since 1981 and 1982 respectively. Thus, a validation of the MSVPA derived 1979 year-class strength was not possible for age-group 1. However, as two-year-old the year-class was covered by the 1981 survey in Sub-division 26, again indicating that the MSVPA resulted in a substantial overestimation of the 1979 year class size. Independent abundance indices for age-group 2 from Latvian bottom trawl surveys, conducted in Sub-divisions 26 and 28 in the 1st and 4th quarter, also revealed a significant relationship with MSVPA results, with the exception of the 1st quarter series in Sub-division 26 (Table 3).

For sprat, MSVPA derived recruitment estimates at age 0 were highly correlated to abundance estimates from international autumn hydroacoustic surveys in Sub-division 25, but not in the two other Sub-divisions (Table 4). Here outstanding high recruitment values were determined by MSVPA for the 1982 year class, while hydroacoustic survey estimates indicated a low year-class strength. Omitting this one year-class from the analysis resulted in significant relationships for both areas (Table 4). Concerning recruitment at age 1, the MSVPA estimated again an outstanding strength for the 1982 year-class in Sub-divisions 26 and 28. Apart from this, all regressions with survey indices were statistically significant (Table 4). A comparison with independent Polish young fish survey estimates in Sub-division 26 revealed a significant correlation to MSVPA derived estimates (Table 4), but with again considerable residual variability and individual outstanding differences from MSVPA estimates for the 1982 year class.

Identification of critical early life history stages

Regression analyses of daily production rates of early developmental stages on later stages during the

TABLE 3. – Linear regressions of MSVPA based cod recruitment at age 1 and 2 (in numbers) on survey based recruitment estimates for different Sub-divisions (BITS: indices, Latvian survey: n^{*}h⁻¹). The table presents parameter estimates and their significance levels, r²-values and Durbin Watson (DW) statistics indicating serial correlation in the residuals if significant (* = significant at 5% level).

Independent variable	Sub-division	year-class	Parameter	Parameter estimates	p	r ²	DW statistics
age 1 BITS	25	1979-95	Slope Intercept	6.2329*10 ⁶ 1.4396*10 ⁸	0.015 <0.001	0.34	0.68*
age 1 BITS	26	1980-95	Slope Intercept	3.2003*10 ⁶ 9.1831*10 ⁷	<0.001 <0.001	0.73	1.12*
age 1 BITS	28	1981-95	Slope Intercept	8.3191*10 ⁶ 98953	<0.001 <0.001	0.88	0.68*
age 2 BITS	25	1980-94	Slope Intercept	2.0996*10 ⁶ 7.5276*10 ⁷	0.001 0.002	0.52	1.54
age 2 BITS	26	1979-94	Slope Intercept	1.2887*10 ⁶ 5.6251*10 ⁷	<0.001 <0.001	0.64	1.82
age 2 BITS	28	1980-94	Slope Intercept	234797 1.3360*10 ⁷	<0.001 0.011	0.79	1.31
age 2 Latvian trawl survey 1 st quarter	26	1976-89 without 1978-79 & 84 ¹⁾	Slope Intercept	47181 8.0621*10 ⁷	0.030 0.080	0.30	0.68*
age 2 Latvian trawl survey 1 st quarter	28	1976-90 without 1978 & 89 ¹⁾	Slope Intercept	54798 2.8730*10 ⁷	<0.001 0.008	0.74	1.15*
age 2 Latvian trawl survey 4 th quarter	26	1976 & 1980-87 without 1985 ¹⁾	Slope Intercept	125256 6.5177*10 ⁷	0.023 0.076	0.61	2.23
age 2 Latvian trawl survey 4 th quarter	28	1979-87	Slope Intercept	50352 3.1662*10 ⁷	0.001 0.005	0.79	1.23

¹⁾ No surveys performed.

TABLE 4. – Linear regressions of MSVPA based sprat recruitment at age 0 and 1 on survey based recruitment estimates (in numbers) for different Sub-divisions. The table presents parameter estimates and their significance levels, r^2 -values and Durbin Watson (DW) statistics indicating serial correlation in the residuals if significant (* = significant at 5% level).

Independent variable	Sub-division	year-class	Parameter	Parameter estimates	p	r^2	DW statistics
age 0 international hydroacoustic survey	25	1981-96	slope	8.6295	<0.001	0.80	2.06
			intercept	$2.6510 \cdot 10^{10}$	<0.001		
age 0 international hydroacoustic survey	26	1981-96	slope	0.7143	0.349	0.07	2.04
			intercept	$2.8611 \cdot 10^{10}$	0.011		
age 0 international hydroacoustic survey	26	1981-96 without 1982	slope	1.0505	0.037	0.31	2.19
			intercept	$1.9886 \cdot 10^9$	0.007		
age 0 international hydroacoustic survey	28	1981-96	slope	0.8379	0.293	0.08	1.92
			intercept	$1.3592 \cdot 10^{10}$	0.005		
age 0 international hydroacoustic survey	28	1981-96 without 1982	slope	1.1563	0.016	0.40	1.90
			intercept	$9.9201 \cdot 10^9$	<0.001		
age 1 international hydroacoustic survey	25	1981-95	slope	5.4102	<0.001	0.68	1.38
			intercept	$2.1162 \cdot 10^{10}$	<0.001		
age 1 international hydroacoustic survey	26	1981-95	slope	1.3676	0.012	0.42	2.42
			intercept	$1.1497 \cdot 10^{10}$	0.146		
age 1 international hydroacoustic survey	26	1981-95 without 1982	slope	1.2488	0.001	0.65	2.54
			intercept	$9.1156 \cdot 10^9$	0.062		
age 1 international hydroacoustic survey	28	1981-95	slope	0.2798	0.002	0.35	2.12
			intercept	$9.8700 \cdot 10^{10}$	0.024		
age 1 international hydroacoustic survey	28	1981-95 without 1982	slope	0.2925	<0.001	0.79	1.91
			intercept	$7.8830 \cdot 10^9$	<0.001		
year-class index from polish young fish survey	28	1976-96 without 1995	slope	$3.0927 \cdot 10^{10}$	0.009	0.34	2.03
			intercept	$1.2398 \cdot 10^{10}$	0.141		

egg to juvenile development (Table 5) indicated that in Sub-division 25 cod recruitment at age 1 (derived from MSVPA) was closely related to age 0 ($r^2 = 0.98$), and age 0 recruitment was significantly related to larval abundance ($r^2 = 0.64$). Critical periods appeared to be the late egg to larval stage ($r^2 = 0.13$) and somewhat less the egg stage I to III ($r^2 = 0.26$). The oldest egg stage IV was not considered as its abundance is highly variable due to a relatively short stage duration and the hatching process, which in Baltic cod commences during this stage (Wieland *et al.*, 1994). The lowest egg survival rates were estimated for the first half of the 1980s (i.e. 1983 and 1985), though this is a period in which the amount of missing data was greatest. Larval abundance per egg stage III production was lowest in the period 1992 to 1996, indicating extremely low viable hatch or larval survival in these years.

For sprat, the relations between production estimates of early and late egg stages as well as between late egg stage production and larval abundance were highly significant for Sub-divisions 26 and 28. This indicates that mortality during the egg and early larval stage is less critical for the reproductive success

of sprat compared to cod (Table 5). In contrast to cod the 0-group abundance of sprat was hardly related to the larval abundance, even when the 1982 year-class, which was most likely overestimated by the MSVPA (Sub-division 26: $r^2 = 0.16$, 28: $r^2 = 0.08$) was excluded from the analysis. But similar to cod, recruitment at age 0 and age 1 estimated by MSVPA were closely related.

Processes affecting critical early life history stages

Cod survival during the egg stage

The daily production of stage III cod eggs during the main spawning time divided by the total potential egg production from SSB was used as the best estimate of the actual egg survival rate in Sub-division 25. A statistically significant linear regression of this “actual survival rate” on the oxygen related egg survival (OES) index was obtained ($p = 0.005$), and explained 44% of the variance encountered (Fig. 3); however, pronounced negative residuals were apparent for 1983 and 1985 and positive residuals in

TABLE 5. – Linear regression of abundance or production estimates of individual life stages on the abundance or production of the succeeding life stage of cod and sprat. The table presents r^2 -values and significance levels.

Independent variable	Dependent variable	Sub-division	Time series	r^2	p
cod					
realised egg production (stage I)	late egg production (stage III)	25	1976-96 without 1979-82 & 1984 ¹⁾	0.26	0.044
late egg production (stage III)	larval abundance	25	1976-96 without 1979-82 & 1984 ¹⁾	0.13	0.173
larval abundance	0-group recruitment	25	1976-95	0.64	<0.001
0-group recruitment	1-group recruitment	25	1976-95	0.98	<0.001
sprat					
realised egg production (stage I)	late egg production (stage III)	26	1973-96 without 1992 ¹⁾	0.67	<0.001
late egg production (stage III)	larval abundance	26	1973-96 without 1992 ¹⁾	0.66	<0.001
larval abundance	0-group recruitment	26	1977-96	0.01	0.617
0-group recruitment	1-group recruitment	26	1977-95	0.98	<0.001
realised egg production (stage I)	late egg production (stage III)	28	1973-96 without 1992 ¹⁾	0.80	<0.001
late egg production (stage III)	larval abundance	28	1973-96 without 1992 ¹⁾	0.23	0.020
larval abundance	0-group recruitment	28	1977-96	<0.01	0.824
0-group recruitment	1-group recruitment	28	1977-95	0.96	<0.001

1) No reliable egg production rates from ichthyoplankton surveys available.

1976, 1978 and 1994. Utilising the egg consumption index to explain variability in actual egg survival revealed a negative linear relationship explaining 21% of the variance, but it was not statistically significant ($p = 0.078$). A high scatter in egg survival was obvious for low consumption indices with the highest residuals in the outlying years identified above (Fig. 3). When both processes were applied as impact factors on the potential egg production, i.e. subtracting the consumed from the potential egg production and multiplying by the OES similar to the procedure in Köster *et al.* (2001b), the observed daily stage III egg production was significantly related to this combined predictive index ($r^2 = 0.60$, $p < 0.001$, Fig 3). The potential egg production alone explained 30% of the variance in stage III cod egg production. Again, difficulties in explaining the low stage III egg production in 1983 were encountered. Utilisation of the alternative time series of potential egg production based on actual fecundity measurements confirmed the significant impact of oxygen conditions in deep water layers on egg survival ($r^2 = 0.30$, $p = 0.027$), but the impact of egg predation ($r^2 = 0.16$, $p = 0.122$) was less clear. Applying both processes as impact factors on the potential egg production as above, but based on actually measured fecundity values instead of pre-

dicted ones, resulted in the same quality of linear relationship to the observed egg production at stage III ($r^2 = 0.61$, $p < 0.001$).

Cod survival to larval stage

The potential egg production, based on predicted relative fecundity values, was linearly related to larval abundance (Fig. 4a) only if the three most recent years were removed from the regression analysis ($r^2 = 0.29$, $p = 0.022$). Compared to the high potential egg production in these years, the observed larval abundance was much lower than expected. Utilising the averaged daily production of stage III eggs instead of the potential egg production did improve the above relationships somewhat, but again only being significant if 1994 to 1996 were omitted from the analysis ($r^2 = 0.32$, $p = 0.043$).

When the ratio of larval abundance to the predicted potential egg production was used as a measure of survival to the larval stage, no significant linear relation of this survival to the OES index or to the egg consumption index was obtained, regardless of whether the most recent three years were considered or not (r^2 between 0.04 to 0.10). Using the ORV provided a better but still insignificant relationship ($r^2 = 0.16$, $p = 0.073$). Pronounced negative residu-

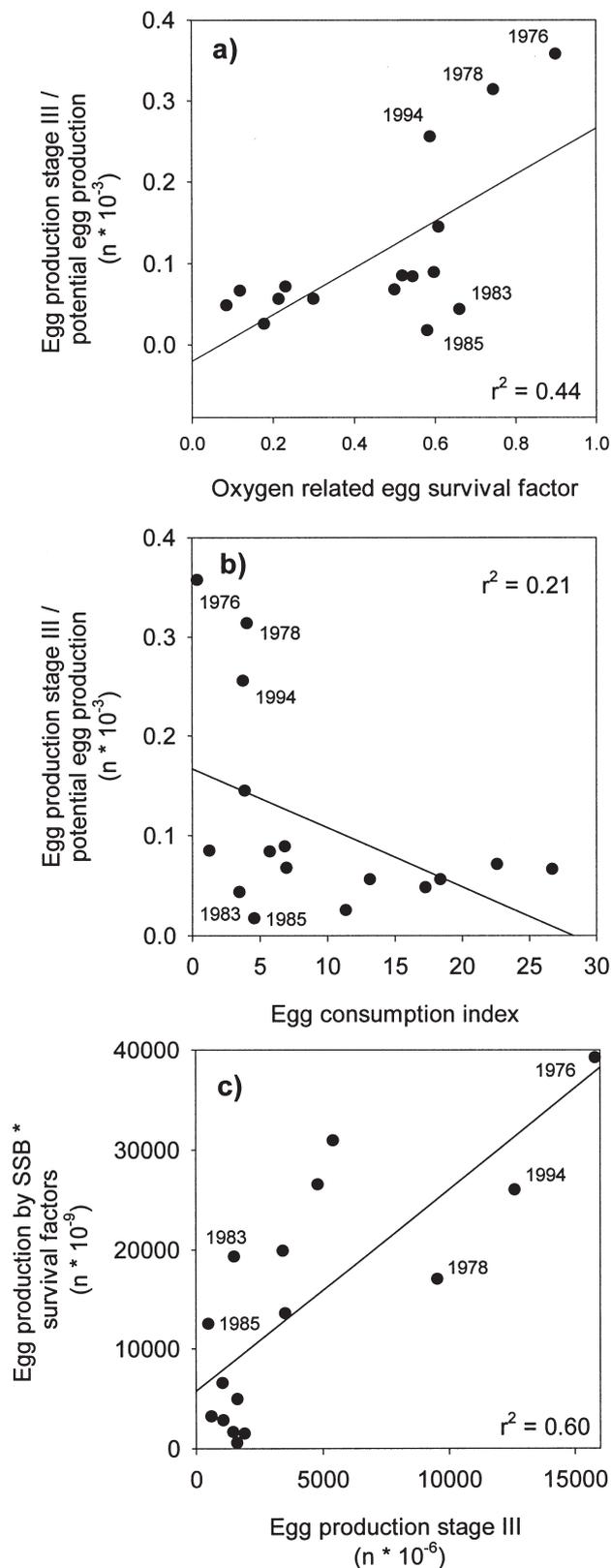


FIG. 3. – Linear regressions of daily cod egg production at stage III in Sub-division 25 per unit of egg production by SSB (as a measure of egg survival) on oxygen related relative egg survival (a) and on an index of cod egg consumption (b); linear regression of daily egg production at stage III on potential egg production corrected for oxygen related mortality and egg consumption (c).

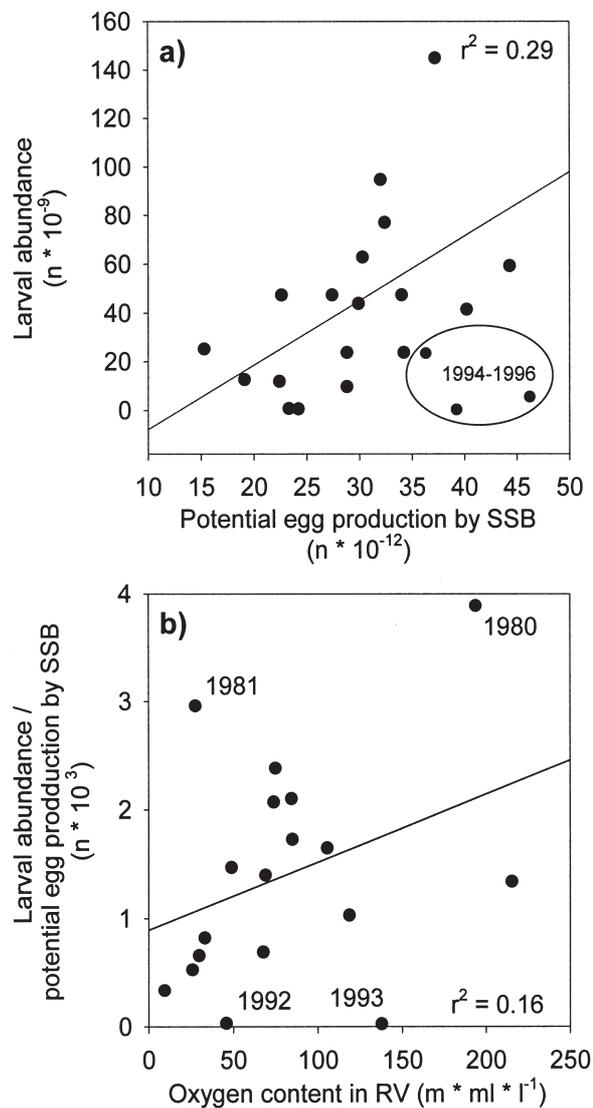


FIG. 4. – Linear regressions of cod larval abundance on potential egg production by SSB in Sub-division 25 (a), indicated data for 1994-1996 removed; linear regression of larval abundance per unit of potential egg production by SSB on oxygen content in the reproductive volume (ORV) (b).

als were apparent in 1992 and 1993 and high positive residuals in 1980 and 1981 (Fig. 4b). Replacing the potential egg production by the late egg stage production did not improve the relationships.

In order to test the impact of food availability for first feeding cod larvae in combination with hydrographic conditions, i.e. oxygen content in the bottom water, Sub-division 26 was used as a test case. The ratio of larval abundance to the potential egg production (based on observed relative fecundity) was significantly related to nauplii abundance in May/June ($r^2 = 0.33$, $p = 0.020$). However, since 1988 larval abundance values were zero indepen-

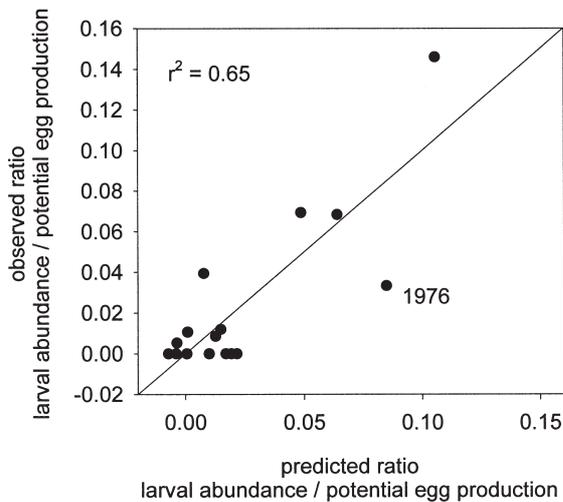


FIG. 5. – Cod larval abundance per unit of potential egg production by SSB in Sub-division 26 and predicted by a multiple linear regression model utilising nauplii abundance and reproductive volume during main spawning time as independent variables.

dent of the prey availability, probably due to unfavourable hydrographic conditions. To consider the impact of hydrography, the reproductive volume in Sub-division 26 was incorporated into a multiple linear regression analysis. This exercise resulted in 65% explained variance in the ratio of larval abundance to the potential egg production (Fig. 5), with both independent variables being significant ($p = 0.002$ for the RV and $p = 0.027$ for nauplii abundance).

Sprat egg production

The relationships between realised egg production and sprat SSB described above did not explain major parts of the variance. Thus, we made an attempt to identify processes influencing the egg production of sprat. For Sub-division 26, the average weight at age anomaly in pre-spawning times and growth rate anomalies covering the period during autumn and winter months were tested as proxies for the nutritional condition of the adults. Additionally, the impact of low temperatures in the intermediate water in May/June was tested. The egg production was not significantly related to any one of these factors alone. However, incorporated into a multiple regression, the SSB, the temperature in the intermediate water and either growth or weight at age anomaly resulted in significant statistical models (Fig. 6). A major proportion (63%) of the variation was explained by the following combination of variables: SSB ($p = 0.003$), tem-

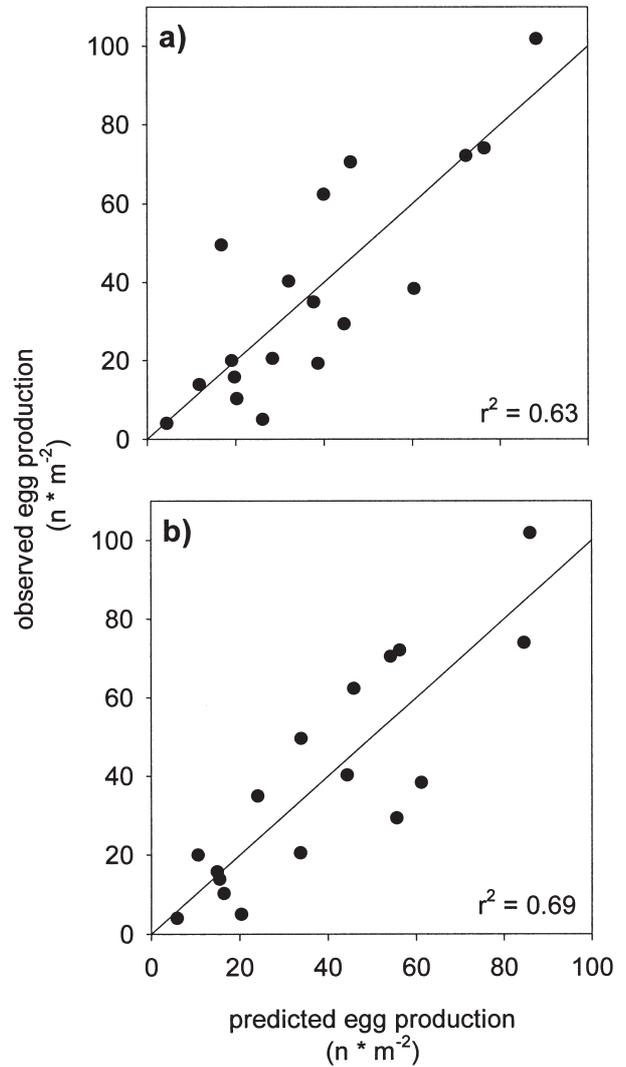


FIG. 6. – Realised egg production of sprat in Sub-division 26 from ichthyoplankton surveys versus predicted by a multiple linear regression model utilising spawning stock biomass, weight at age anomaly in the 1st quarter (age-groups 2-4) and temperature in the intermediate water layer in May/June as independent variables (a); realised egg production by sprat in Sub-division 26 versus predicted by a multiple linear regression model using spawning stock biomass, growth anomaly (increase in weight at age 2-4 from 3rd to 2nd quarter) and temperature in the intermediate water in May/June as independent variables (b).

perature ($p = 0.021$) and weight at age anomaly ($p = 0.053$). Also, 69% was explained by SSB ($p < 0.001$), temperature ($p = 0.013$) and growth anomaly ($p = 0.018$). The Durbin-Watson statistics did not indicate serial correlation in residuals, and the intercepts in both statistical models were insignificant. For Sub-division 28, weight at age prior to 1985 was assumed to be invariate with time and consequently corresponding tests could be conducted with a shorter time series only. No significant relations to temperature and condition proxies were obtained in this case.

Sprat survival from the larval to the 0-group stage

The ratio of 0-group recruitment to larval abundance was used as a measure of survival to the juvenile stage. This index appeared to be related neither to temperature (intermediate water at spawning time) and oxygen (average oxygen concentration in and below the halocline) in a biologically sensitive way nor with prey availability for sprat larvae (*Acartia* spp. nauplii and copepodids). In Sub-division 28, a significant negative linear relationship was identified between this index and wind speed anomaly in May/June ($r^2 = -0.26$), whereas in Sub-division 26 ($r^2 < -0.01$) a high scatter in survival occurred at intermediate wind speed, suggesting rather a parabolic than a linear function. In contrast, multiple lin-

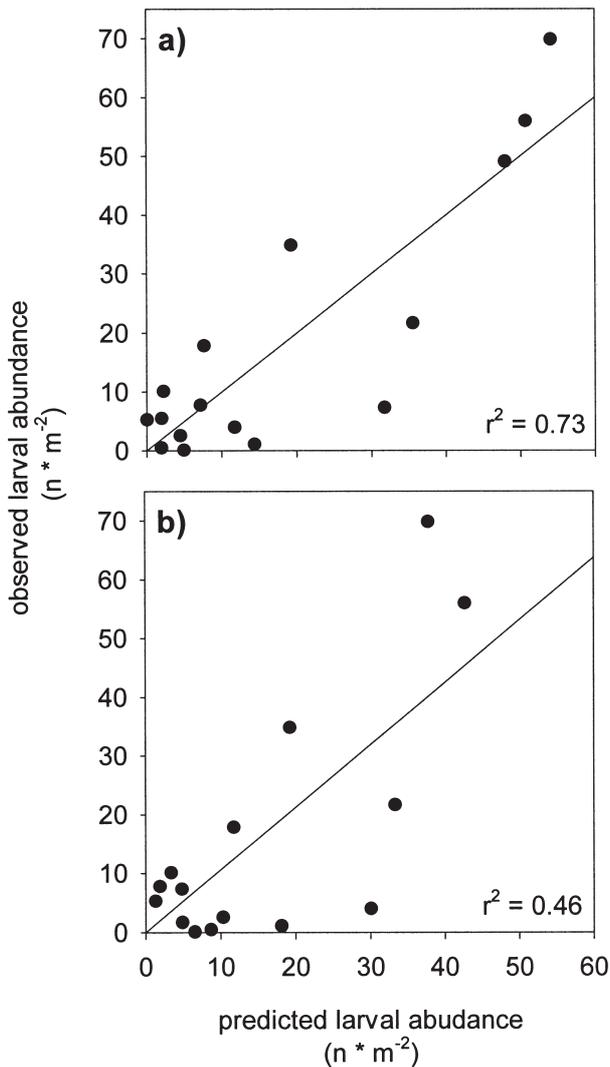


FIG. 7. – Larval abundance of sprat in Sub-division 26 from ichthyoplankton surveys versus predicted by a multiple linear regression model utilising daily egg production of stage III and wind-speed anomaly in May/June as independent variables.

ear regressions with late egg stage production values and wind speed anomalies in May/June as independent variables explained 73 and 46% of the variance in larval abundance in Sub-divisions 26 and 28, respectively (Fig. 7). Wind speed had a statistically significant impact in both areas (Sub-division 26: $p = 0.011$ and 28: $p = 0.006$). The larval transport index developed for Sub-division 25, on the other hand, did not show a significant effect on larval abundance in Sub-divisions 26 ($p = 0.242$) or 28 ($p = 0.491$). Thus, from the available data a significant impact of wind driven transport on larval abundance was not obvious, but the wind speed obviously had an effect on survival from the late egg to the larval stage.

Stepwise multiple linear regression of year class strength on larval abundance and the above-mentioned physical variables revealed a significant effect only for temperature in Sub-division 26 (larval abundance: $p = 0.065$, temperature: $p = 0.028$). The explained variance in 0-group recruitment was rather limited (31%), with the observed recruitment in 1994 being largely underestimated by the model (Fig. 8). Adding further prey availability of *Acartia* spp. or *Temora longicornis* or all copepod juvenile life stages in May/June or July/August as a variable did not enhance the statistical model. Also, incorporation of the weight anomaly of 0-group sprat did not increase the explained variance.

In Sub-division 28, a multiple linear regression with larval abundance and temperature as indepen-

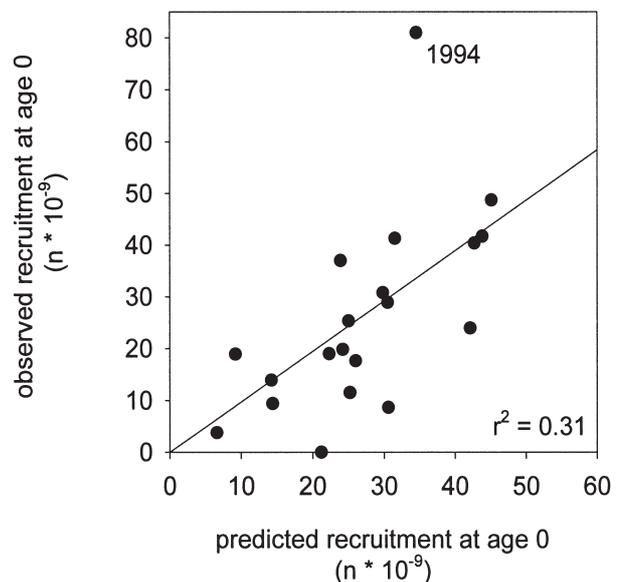


FIG. 8. – Sprat recruitment at age 0 in Sub-division 26 determined by MSVPA versus predicted by a multiple linear regression model utilising larval abundance and temperature in the intermediate water in May/June as independent variables.

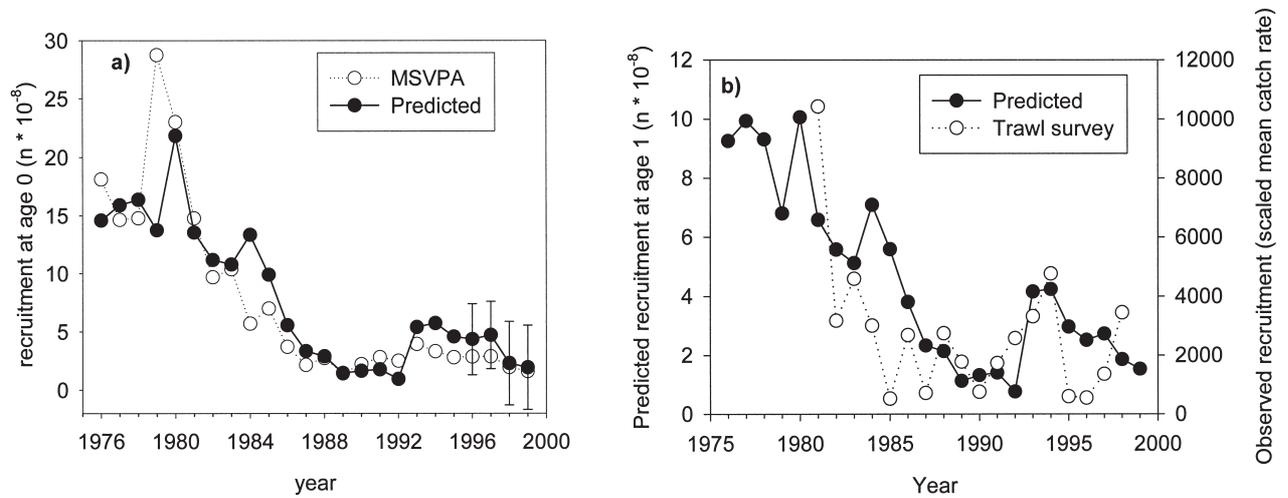


FIG. 9. – Cod recruitment at age 0 in Sub-division 25, 26 and 28 combined (from MSVPA) and predicted by a multiple linear regression model; parameter estimated from data series 1976-1995 and recruitment predicted for 1996-1999 with 95% confidence limits of the predicted means (a); cod recruitment at age 1 in Sub-divisions 25, 26 and 28 from 1st quarter bottom trawl survey (scaled arithmetic mean catch rates) and predicted by above multiple linear regression model and applied predicted 0-group predation mortalities (b).

TABLE 6. – Stock-recruitment relationships for sprat (age-group 0 in numbers, SSB in t) in different Sub-divisions with incorporated variables identified to affect critical life stages. The table presents parameter estimates and their significance levels, r^2 -values and Durbin Watson (DW) statistics indicating serial correlation in the residuals if significant (* = significant at 5% level).

Dependent variable	Sub-division	Time series	Independent variables	Parameter estimates	p	r^2	DW statistics
recruitment at age 0 MSVPA	26	1977-96	SSB	61219	0.014	0.42	2.07
			temperature in intermediate water	$1.0505 \cdot 10^{10}$	0.018		
			intercept	$-2.2977 \cdot 10^{10}$	0.146		
recruitment at age 0 MSVPA	26	1979-96	SSB	57632	0.030	0.38	1.87
			growth anomaly 3 rd to 2 nd quarter	$5.6287 \cdot 10^7$	0.045		
			intercept	$1.5198 \cdot 10^{10}$	0.037		
recruitment at age 0 MSVPA	26	1977-96	SSB	58015	0.031	0.47	2.04
			temperature in intermediate water	$7.9327 \cdot 10^9$	0.087		
			growth anomaly 3 rd to 2 nd quarter	$4.3814 \cdot 10^7$	0.087		
			intercept	$-1.2862 \cdot 10^{10}$	0.446		
recruitment at age 0 hydroacoustic survey	26	1981-96	SSB	41557	0.007	0.49	2.62
			temperature in intermediate water	$5.3867 \cdot 10^9$	0.039		
			intercept	$-2.0634 \cdot 10^{10}$	0.043		
recruitment at age 0 MSVPA	25	1977-96	SSB	62234	0.014	0.45	1.93
			temperature in intermediate water	$5.9304 \cdot 10^9$	0.052		
			intercept	$-4.3085 \cdot 10^9$	0.680		
recruitment at age 0 hydroacoustic survey	25	1981-96	SSB	7469	0.038	0.22	2.23
			temperature in intermediate water	$1.700 \cdot 10^8$	0.646		
			intercept	$-1.1195 \cdot 10^9$	0.477		
recruitment at age 0 MSVPA	28	1977-96	SSB	26514	0.166	0.12	2.37
			temperature in intermediate water	$5.2995 \cdot 10^9$	0.154		
			intercept	$-1.1635 \cdot 10^{10}$	0.428		
recruitment at age 0 hydroacoustic survey	28	1981-96	SSB	26377	0.006	0.63	2.01
temperature in intermediate water	$4.2940 \cdot 10^9$	0.011					
intercept	$-1.7102 \cdot 10^{10}$	0.011					

dent variables only explained a small part of the variance in 0-group recruitment. Here the only significant physical variable was the larval transport index, which together with the larval abundance

explained 26% of the recruitment variability (larval abundance: $p = 0.104$, temperature: $p = 0.032$). However, recruitment was negatively related to the transport index, suggesting lower recruitment in sit-

uations of transport from Sub-division 25 to eastern basins, which appeared to be biologically not sensible. If recruitment from the hydroacoustic survey was utilised in the above multiple regression analyses instead of MSVPA derived estimates, the wind speed anomaly and the transport index were insignificant while the temperature in the intermediate water became significant; the model explained, however, only 27% of the variance in 0-group abundance (larval abundance: $p = 0.274$, temperature: $p = 0.041$). Regardless of the method for estimating 0-group recruitment, prey availability or weight anomalies did not explain a significant part of the variance in sprat recruitment in Sub-division 28.

Environmentally sensitive stock-recruitment relationships

The conducted exploratory analysis on processes affecting critical early life stages of cod confirmed the results of an earlier analysis (Köster *et al.*, 2001b), and additionally revealed new evidence that food availability affects cod larval survival, which was shown only for one Sub-division due to the lack of suitable data. On this basis, a revision of the multiple regression based cod stock-recruitment model established by Köster *et al.* (2001b) was not indicated. However, we performed a test of the models developed for the different Sub-divisions which included the potential egg production corrected for egg predation, the ORV and the larval transport index for Sub-division 25, while relatively simple models for both other Sub-divisions included the potential egg production and the RV. Based on these area specific models, we predicted cod recruitment for the period 1996-1999 and compared the prediction for the entire Central Baltic with 0-group abundance data from updated MSVPA runs (ICES, 2001a) and 1-group abundance indices from the international bottom trawl survey (STORE, 2000). MSVPA derived and predicted recruitment were in good agreement (Fig. 9a), both indicating a decline in the reproductive success in most recent years. The comparison with the survey index showed considerably more variability (Fig. 9b), with a similar declining trend at the beginning of the time series, low year-class strength at the end of the 1980s and beginning of the 1990s followed by an increase up to year-class 1994. However, in most recent years, there was an opposite trend in the observed and predicted recruitment.

For sprat, the multiple regression analysis revealed that the spawning stock biomass had a significant effect on 0-group recruitment in almost all areas and combinations of variables. Considering either growth anomaly ($p = 0.045$) or temperature ($p = 0.018$) in addition led to 38% or 42% explained variance in Sub-division 26 respectively, when recruitment estimates were based on MSVPA; both variables added in combination resulted in 47% explained variance (Table 6). When utilising recruitment estimates from hydroacoustic surveys, the combination of spawning stock and temperature as independent variables explained 49% of the variance with the temperature effect ($p = 0.039$). In Sub-division 25, temperature was the only variable improving stock-recruitment relationships ($p = 0.051$), but the effect was insignificant when recruitment estimates were derived from hydroacoustic surveys ($p = 0.646$). In Sub-division 28, the opposite occurred: the temperature effect was statistically significant in a hydroacoustic based stock recruitment relationship ($p = 0.011$) but not in the MSVPA-based relationship ($p = 0.154$). Other variables, such as wind speed or growth anomaly were insignificant in any other variable/area combination, regardless of whether recruitment from MSVPA or hydroacoustic survey was utilised.

The best recruitment predictions are presented in Figure 10 for Sub-divisions separately and in Figure 11 for the entire Central Baltic. They are based on multiple regression models including SSB and temperature as independent variables in all three areas, and growth anomalies in addition for Sub-division 26. These statistical models were able to predict the general trends in recruitment success fairly well (Fig. 10), but failed to mirror the large fluctuation in the observed recruitment values in most recent years, with a considerable overestimation of recruitment in 1996 and a significant underestimation in 1994 when compared to MSVPA estimates. This was also obvious for the area aggregated model output (Fig. 11a). Similarly the model predicted recruitment too low in 1997 and too high in 1998, both MSVPA derived recruitment estimates being outside the 95% confidence limit of the predicted means. Comparing the model with independent recruitment estimates from hydroacoustic surveys showed agreement in both time trends (Fig. 11b), but with substantially lower recruitment indices from the survey in 1990 and again in 1996 and 1998, but not in 1994.

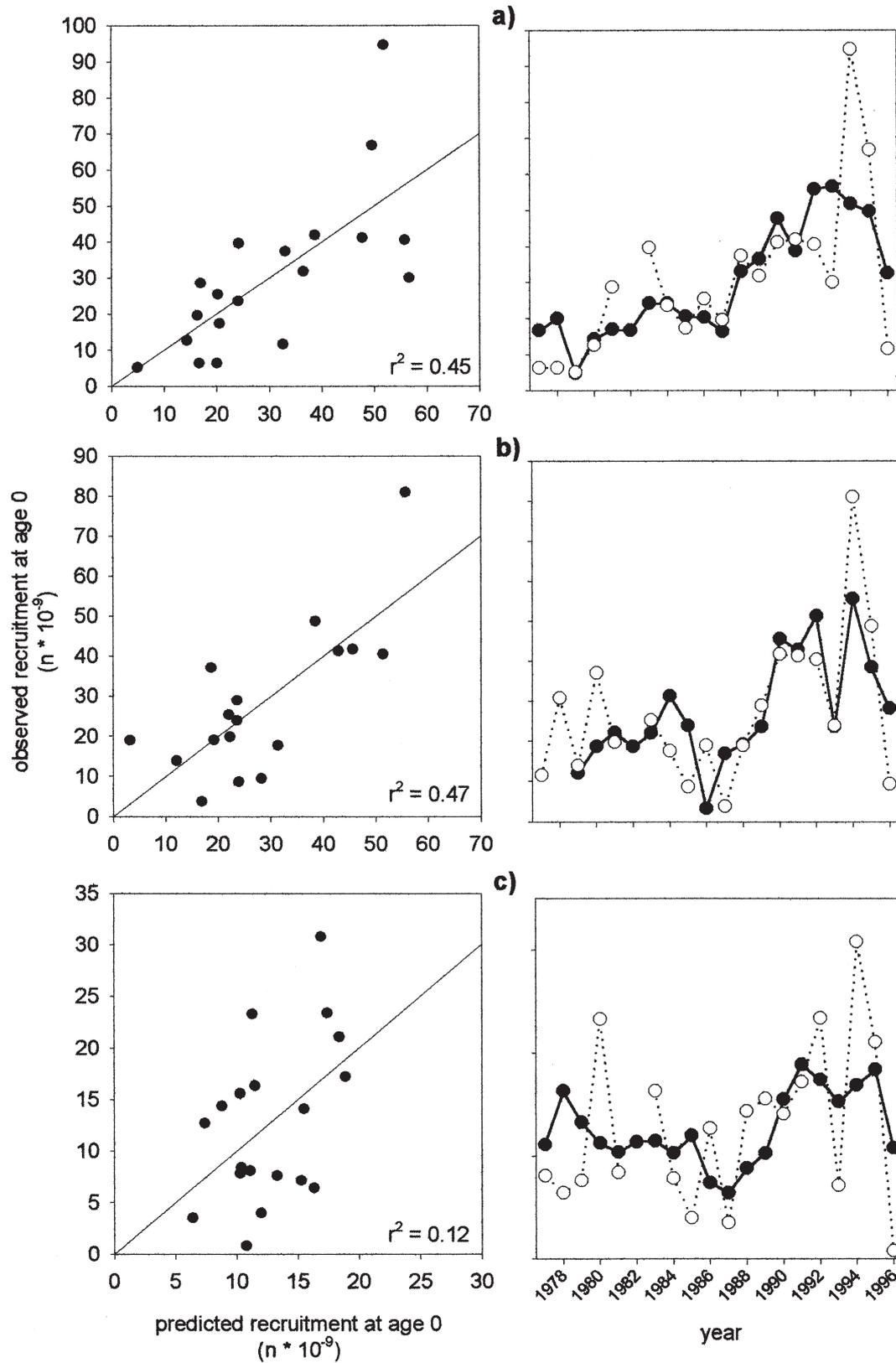


FIG. 10. – Sprat recruitment at age 0 determined by MSVPA and predicted by a multiple linear regression model utilising SSB and temperature in the intermediate water as independent variables for Sub-division 25 (a); sprat recruitment as above adding growth anomaly (available since 1979) as further independent variable for Sub-division 26 (b); sprat recruitment predicted as in Sub-division 25 for Sub-division 28 (c); including time trends of observed (dotted lines and open circles) and predicted values (solid lines and circles) for all three statistical models (right panels).

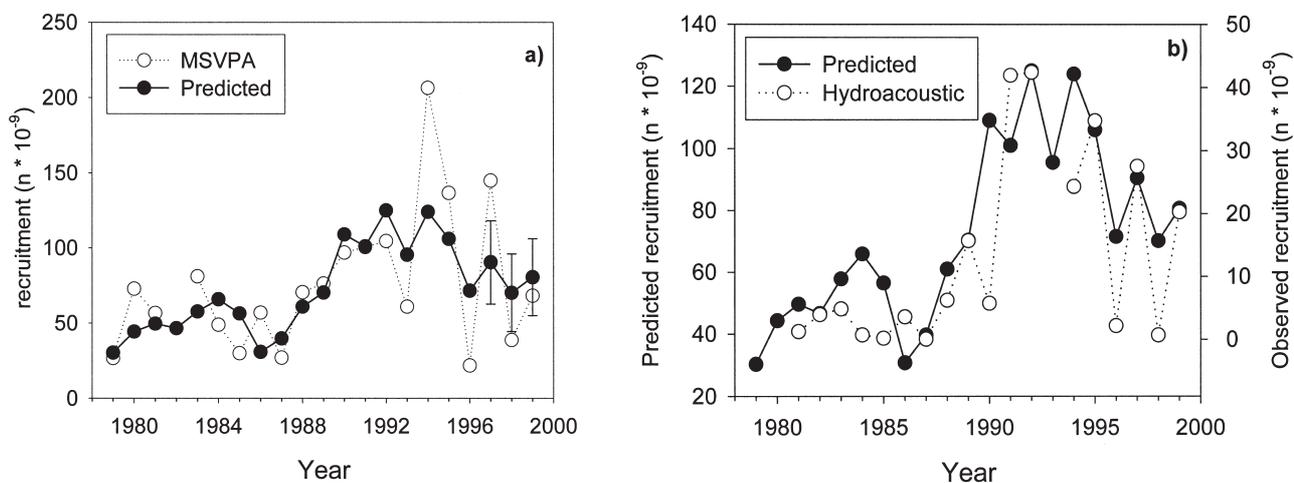


Fig. 11. – Sprat recruitment at age 0 in Sub-divisions 25, 26 and 28 combined, predicted by multiple linear regression models established for separate Sub-divisions and observed recruitment from MSVPA (a) and from autumn hydroacoustic surveys (b).

DISCUSSION

The present study investigated whether a process-oriented approach based on the results of extensive field, laboratory and modelling studies can be used to develop environmentally sensitive stock-recruitment models, and tried to identify what information might be lacking to make such models as reliable as possible. Our approach attempts to follow the success of a year-class during ontogeny from spawner abundance through the egg and larval to the juvenile stage according to Paulik's (1973) framework for examining the entire life history process, a concept broadly accepted but not really implemented yet (Rothschild, 2000). Investigation of the link between environmental factors, spawning stock features and reproductive success of Baltic cod (e.g. Plikshs *et al.*, 1993; Sparholt, 1996; Jarre-Teichmann *et al.*, 2000) and to a lesser extent also sprat (Grauman and Yula, 1989), have previously been performed by several investigators. However, these studies did not consider the problems inherent in the estimates of egg production based on spawning stock biomass and in the recruitment estimates. Also, they did not attempt to identify specific critical periods within the recruitment process, and apart from Plikshs *et al.* (1993) did not consider spatial heterogeneity within the Central Baltic. The earlier findings were utilised in the present study to generate the working hypotheses for the process oriented work (for an overview see Schnack and Köster, 1998).

Validation and improvement of stock-recruitment relationships

The comparison of cod SSB and realised egg production clearly demonstrated that spawning stock biomass is no reliable measure of realised egg production, even if yearly or periodically updated maturity ogives are used. It turned out that the female SSB and the predicted potential egg production determined on the basis of the female spawning stock and relative fecundity estimates provide significantly better measures of the realised egg production. They explain 61 and 63% of the variance in daily production of the youngest egg stage during peak spawning time. The largest deviations between potential and realised egg production, apparent in the most recent year 1996, can be explained by an overestimation of the adult stock size by the MSVPA for Sub-division 25 due to tuning problems (Köster *et al.*, 2001a). Apart from methodological problems, the remaining variability may be related to atresia due to unfavourable environmental conditions during spawning (Kjesbu *et al.*, 1991), variable fertilisation success in relation to salinity changes (Westin and Nissling, 1991) and variation in egg mortality already during the first developmental stage.

For sprat, however, the total spawning stock biomass appeared to be a better measure of realised egg production, indicating that inter-annual variability in maturation processes, age-dependent sex ratios and individual fecundity are of less importance. Although the sex ratio becomes increasingly skewed to female dominance with increasing age in

sprat (ICES, 2001b), similar to cod (e.g. Tomkiewicz *et al.*, 1997), the observed variability in age-structure of the spawning stock had no major impact on the proportion of females in the stock as the generally dominating age-groups 2 and 3 have rather balanced sex ratios. Variation in sexual maturity of age-group 1 (ICES, 2001b) in combination with high fluctuations in the abundance of this age-group (Köster *et al.*, 2001a) will, however, result in deviations in SSB estimates derived from yearly maturity ogives as compared to constant standard assessment ogives for individual years. It has been shown that the relationship between SSB and potential egg production of sprat can be improved substantially by incorporating ambient temperature in the intermediate water during spawning time and growth anomaly from the 3rd to the 2nd quarter in a multiple linear regression. The effect of temperature on realised egg production may be due to several reasons: i) low winter temperatures may affect the nutritional condition and growth of sprat (positive relationships between May/June temperature and the growth/nutrition proxies are indicated, but are not statistically significant), ii) low temperature in pre-spawning periods may reduce the batch fecundity as well as the batch number (Petrowa, 1960), and thus the total seasonal egg production, and iii) low temperatures before and during the spawning season may cause a delay in the onset and the peak of spawning activity (e.g. Elwertowski, 1960; Grimm and Herra, 1984). This effect has not been corrected for in the present time series of egg production. The largest deviations between SSB as a measure of egg production and realised egg production occurred in 1996. In this year, specifically low winter temperatures at the surface (0-50 m) were not fully represented by the May/June temperatures in the intermediate water considered in the model. This may underline the importance of the pre-spawning period for the above mentioned processes.

MSVPA derived cod recruitment at age 1 and 2 compared in general fairly well to trawl survey indices, especially in Sub-divisions 26 and 28. However, the residuals of the linear regression showed a significant auto-correlation over time and the very high year-class strength 1979 estimated by the MSVPA was not confirmed by the trawl surveys. In contrast, most recent year-class estimates from MSVPA fitted well to the surveys indices, which for age-group 2 may be explained by the fact that the survey abundance was been to tune the MSVPA.

MSVPA derived sprat recruitment at age 0 and 1 was highly correlated to corresponding abundance estimates from international hydroacoustic surveys. An exception was the strength of the 1982 year-class in Sub-divisions 26 and 28 being substantially higher in the MSVPA than indicated by the surveys. A similar tendency was obvious from a comparison with an independent sprat recruitment index from the Polish young fish survey in Sub-division 26. Thus, it was concluded that the 1982 recruitment was substantially overestimated by the MSVPA and was consequently removed from the further exploratory analysis.

Identification of critical early life stages

Difference in the covariance of abundance estimates for successive developmental stages indicated that critical periods for cod recruitment in the Baltic are mainly passed from the egg to the larval stage. The importance of hydrographic conditions within and below the halocline for cod egg survival is well known (e.g. Nissling, 1994; Wieland *et al.*, 1994; MacKenzie *et al.*, 1996), while a poor correlation between late egg stage production and larval abundance has been reported only recently (Köster *et al.*, 2001b). However, Plikshs *et al.* (1993) pointed out that egg survival is correlated to the reproductive volume but not to year-class strength, indicating that unidentified processes acting on other life stages are important as well. Egg quality characteristics (Petersen *et al.*, 1997; Nissling *et al.*, 1998), low but not lethal oxygen concentrations during egg incubation (Rohlf, 1999), food supply during initial feeding (Plikshs *et al.*, 1993) and transport to favourable nursery areas (Hinrichsen *et al.*, 2001) have been suggested as additional variables with substantial impact on the larval and early juvenile survival. The close correlation between larval abundance and 0-group recruitment suggested, however, that a major part of the remaining variability in reproductive success is already introduced in the egg and early larval stage.

Recruitment at age 0 and 1 determined by MSVPA was very closely related. Increased variability at the beginning of the 1980s, i.e. a time period with the highest intensity of cannibalism (Köster *et al.*, 2001a). This may indicate that cannibalism is usually of minor importance for the recruitment success of Baltic cod. However, the limited variability in cannibalism rates was to a certain extent artificially created by the estimation procedure imple-

mented in the MSVPA, which uses constant suitability coefficients over the whole time series, regardless of the size and distribution of the adult and juvenile stock (Neuenfeldt and Köster, 2000).

For sprat, studies on processes affecting the reproductive success in the Baltic are scarce compared to cod. The strong positive linear relationships between production values of early and late egg stages as well as between the late egg stage and larval abundance were unexpected. Given the higher buoyancy of sprat eggs compared to cod (e.g. Wieland and Zuzarte, 1991), a considerable impact of low temperature on egg survival could be expected. Thompson *et al.* (1981) demonstrated that sprat egg survival decreases at temperatures below 6°C, which is seldom reached in intermediate water layers of the Baltic. Furthermore, it could be expected that egg predation by clupeids is dependent on the vertical overlap between eggs and predators forced by salinity and oxygen concentrations (Köster and Möllmann, 2000b); this should result in additional variability of egg survival. However, in the given range of variation both temperature and predator-prey overlap seem to have only a limited regulatory impact on egg survival.

The larval stage has earlier been identified as critical for sprat recruitment (Grauman and Yula, 1989; Kalejs and Ojaveer, 1989), suggesting that food supply could be a major impact factor, with temperature being a co-variate, as meso-zooplankton production depends on the temperature conditions, especially in spring (e.g. Möllmann *et al.*, 2000). However, the close relation identified in the present study between the production of the late egg stage and larval abundance in Sub-division 26 suggests that food supply may not vary to a large extent for first feeding larvae in this area, but may do so in Sub-division 28 where a large portion of the variance in larval abundance remains unexplained (77%). However, it was possible to improve the relationship in both areas considerably by including the wind speed anomaly as an additional variable. The significant positive impact of wind speed may in principal be caused by a wind induced drift of larvae from the Bornholm Basin into the eastern Baltic basins (Grauman, 1976). However, the sprat larval transport index specifically designed to test this hypothesis did not confirm a significant transport. Thus, other processes like enhanced prey encounter rates at increased turbulence may be involved. The present results also did not confirm the hypothesis that high wind stress has a negative

effect on egg survival in surface layers (Grauman, 1965). It should be noted, however, that in this analysis only the main spawning period in May/June was considered, in which typically a deeper distribution of sprat eggs is encountered (Wieland and Zuzarte, 1991).

Processes affecting critical early life stages

The exploratory regression analysis confirmed a significant impact of oxygen and predation on cod egg survival for Sub-division 25. However, these regressions were not specifically convincing. Most observed egg survival rates vary within a certain range, rather independently of the oxygen related survival factor (OES) and the predation index. There were three years (1976, 1978, 1994) in which the egg survival rates ranged at an obviously higher level. These years were in fact characterised by favourable oxygen supply and low predation rate, but under the same conditions low survival rates were also obtained. By including the information on oxygen and predation in the recruitment model, the potential for a high egg survival is considered but some causal relation is still missing, so estimates for individual years remain uncertain though trends may be represented reasonably well.

The average annual abundance values for cod larvae were to some extent related to the potential egg production, and a part of the remaining variance could be explained by an impact of oxygen on the survival from spawning to the larval stage. Both regressions were statistically significant, but explained only a very limited part of the observed variance in larval abundance. The high residual variance may be due to some additional major impact factor affecting survival during the larval phase or part of it, but it may also be due to sampling problems leading to high variation or bias in larval abundance estimates. As in the most recent years of the time series a delay in cod spawning occurred (Wieland *et al.*, 2000), this may have caused a mismatch in the timing of the plankton surveys and the occurrence of peak larval abundance, and thus may have led to an underestimation of larval abundance (Köster *et al.*, 2001b).

Behavioural studies of cod larvae demonstrated that low oxygen concentration has an impact on larval mortality (Nissling, 1994) and that egg incubation at low oxygen concentration also has an effect on larval activity (Rohlf, 1999). Furthermore, these experiments revealed that vertical migration into

upper water layers is not started before day 4 after hatch. Hence, a significant impact of the environment within and below the halocline on larval survival can be expected. Due to differences in buoyancy and in the minimum lethal oxygen concentrations in the egg and larval stage (Rohlf, 1999), it appears to be unlikely that the OES is a suitable measure of oxygen related survival probability of larvae. In fact, the ORV performed better in the exploratory analysis and was therefore included in the final model configuration in Sub-division 25.

In the more eastern spawning areas, variability in larval abundance was more easily explained as a highly significant impact of the hydrography is obvious (Köster *et al.*, 2001b). This result was expected as the environmental conditions were less favourable for successful cod egg survival in these areas compared to the Bornholm Basin (MacKenzie *et al.*, 2000). However, a large reproductive volume does not necessarily result in high survival of early life stages. In 1994, an extremely large reproductive volume was encountered in the Gotland Basin due to an inflow into this basin. This inflow displaced the anoxic bottom water upwards (Plikshs *et al.*, 1999), resulting in an intermediate layer with insufficient oxygen concentration but densities sufficient to keep cod eggs floating, and hence creating conditions detrimental to the development of cod eggs. Situations like these clearly demonstrate the potential for index improvement through the development of models for predicting the vertical distribution of cod eggs in all spawning areas relative to oxygen conditions.

One additional factor to be considered for larval survival may be the food supply. Information on the abundance of zooplankton, suitable as prey for cod larvae and early juveniles, has been reviewed by MacKenzie *et al.* (1996), suggesting that the Central Baltic provides at least similar if not better feeding conditions compared to other spawning areas. Also, from a detailed study based on extensive vertically resolving sampling of zooplankton in different areas of the Central Baltic at various times of the year, Krajewska-Soltys and Linkowski (1994) concluded that the abundance of nauplii and copepodites should be sufficient to ensure that starvation is not a major source of larval and juvenile cod mortality. However, our preliminary test on the impact of the supply of nauplii as suitable prey for first feeding cod larvae (Zuzarte *et al.*, 1996) revealed a significant influence on the apparent survival from egg to larval stage in Sub-division 26. Multiple linear regression including food abundance and reproduc-

tive volume (RV) as independent variables explained the variance in larval abundance reasonably well (65%). Zooplankton data were not available for the period 1992 to 1995. Thus, most of the years in which larval surveys were potentially affected by the shift in spawning time (see above) were excluded from this analysis.

For sprat survival from the larval to the 0-group stage, the exploratory analysis identified the temperature in the intermediate water as the only biologically sensible factor with a marked influence. Neither physical/chemical variables such as the oxygen condition in deep water layers, wind speed anomaly and larval transport index nor biological variables such as food availability or 0-group weight anomaly explained a significant part of the variance encountered in 0-group recruitment. This may lead to the question of the reliability of larval abundance and 0-group recruitment data series used in the analysis. As the late egg stage production was significantly related to larval abundance, with a significant improvement when incorporating the wind speed anomaly, it appears to be unlikely that the larval data are grossly erroneous. Using larval abundance data averaged from May to July instead of May to June did not improve the relationship between sprat larval abundance and 0-group recruitment either. Thus, the exclusion of late born cohorts from the analysis did not explain the deviation in abundance estimates between the two life stages. Similarly, significant relationships between MSVPA based recruitment and hydroacoustic survey abundance estimates indicated an acceptable quality of the data series we used in this analysis.

The impact of winter and spring temperature on sprat larval abundance has been described earlier by Grauman and Yula (1989). They identified the solar activity and the spawning stock biomass (as a measure of egg production) as additional significant factors regulating larval abundance. Other variables such as deep water temperature, salinity and oxygen concentration had an effect of intermediate strength on larval abundance. Similar to our results, the availability of nauplii in May did not explain any major portion of the variability (Grauman and Yula, 1989). The impact of temperature on larval abundance was nevertheless explained by a temperature related development of the *Temora longicornis* population as a thermophil prey species for sprat larvae (Grauman *et al.*, 1986; Kalejs and Ojaveer, 1989).

Also, there was no indication that low weight at age of survivors is coupled to high larval or early

juvenile mortality, which could be caused by a size-dependent predation of adult herring reported by Patokina and Feldman (1998). It should, however, be noted that the weight anomaly is significantly correlated with the juvenile *Acartia* spp. abundance in May/June, but not with temperature in the intermediate water.

Applicability of recruitment models

In Sub-division 25, a significant linear relationship between cod larval abundance and recruitment at age 0 has been described (Köster *et al.*, 2001b), which could not be enhanced by the inclusion of any additional variable. Thus, the simple model appears to be applicable for predicting recruitment. The corresponding relationship in Sub-division 26 was also statistically significant, but the fit of the model was less satisfactory, while for Sub-division 28 no significant relationship could be established. Recruitment success occurred in the latter area in a series of years despite an absolute lack of larvae in the plankton. The occurrence of recruitment estimated by the MSVPA was also confirmed by bottom trawl surveys catching age-group 1 cod. Thus, the lack of larvae indicates either i) a problem in sampling efficiency of the gear at low larval abundance, or ii) a transport of larvae and pelagic 0-group out of the Bornholm area into the more eastern Baltic basins. The latter hypothesis is supported by hydrodynamic modelling (Hinrichsen *et al.*, 2001), comparison of trawl survey results and MSVPA output (Köster *et al.*, 2001a), and also by the fact that the parameter estimate for the larval transport index in the recruitment model is negative in Sub-division 25 (Köster *et al.*, 2001b).

The close linear relation between 0- and 1 group recruitment of cod as well as sprat is to a certain extent artificially created by the estimation procedure implemented in the MSVPA (see above), considering only predation by cod as an additional cause of natural mortality. In fact, on inspecting the cod year-class strength at age 1 and 2, as derived from the international bottom trawl survey, it appeared that regressions were significant only for Sub-division 26 and 28, but not for Sub-division 25, which was the only area allowing regular reproductive success. For sprat, a regression of 1-group on 0-group estimates, derived from the international hydroacoustic survey, was significant in Sub-division 25 but not in the other two areas. Even assuming that survey estimates

are noisy, especially for pre-recruits not targeted by the survey, this considerably decoupled variation in the abundance estimates of 1 and 2-group cod and 0- and 1-group sprat may indicate that survival during the first years of life is not only dependent on cod predation, but that other processes also may modify recruitment success substantially.

The recruitment models established here explain a considerable part of the variability encountered in survival to the juvenile stage with a considerably better performance for cod than for sprat. Sprat exhibited high recruitment fluctuations in the most recent years, which the established recruitment model was not able to predict. Remaining variability may be due to a number of processes not included in the present analyses such as egg fertilisation (e.g. Westin and Nissling, 1991) and the influence of parental characteristics (age/size structure, condition) on egg and larval characteristics (buoyancy, survival probability, e.g. Marshall *et al.*, 1998; Trippel, 1998; Vallin and Nissling, 2000), but also uncertainties in the way variables are assumed to represent processes of interest (e.g. reproductive volume effect on cod egg survival, temperature effect on sprat larval survival). Results on these topics have recently become available (e.g. MacKenzie *et al.*, 1998; Nissling *et al.*, 1998; Vallin and Nissling, 2000), and potentially they can be incorporated into new generations of recruitment models (Vallin *et al.*, 1999).

Apart from this potential for improvements, major difficulties in establishing environmentally sensitive stock-recruitment models are i) to incorporate various factors affecting different early life stages (Paulik, 1973) in one linear model relating egg production to subsequent recruitment, and ii) to resolve the potential non-linearity and interdependent effects of different factors on subsequent early life stages. The first problem has been described in detail before (Rothschild, 1986; Ulltang, 1996). Bailey *et al.* (1996) and Campana *et al.* (1989) considered it explicitly when constructing survival curves of walleye pollock as well as Nova Scotia cod and haddock cohorts relative to their physical and biological environment. For the Baltic, however, this type of approach has not yet been conducted.

Despite the remaining shortcomings and uncertainties also with respect to the second problem, the stock-recruitment models presented for cod may be utilised for improving short-term recruitment predictions. They could be based on: i) most recent female spawning stock biomass and relative fecun-

dity estimates (Kraus *et al.*, 2000), ii) hydrographic conditions during spawning periods and at spawning sites, which would enable prediction of the egg and larval survival in relation to ambient oxygen concentrations and larval transport from spawning areas, and iii) predator population sizes as well as spatial overlap between predator/prey, both forced by hydrographic processes. For sprat, the presented analysis should be taken as a first step resolving towards key variables regulating recruitment success, and generating new work hypotheses to be tested in specifically designed process studies and to be validated by subsequent analysis of further extended long-term data bases.

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