

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

Köster, F.W.<sup>1)</sup>; Hinrichsen, H.-H.<sup>1)</sup>; Schnack, D.<sup>1)</sup>; St. John, M.A.<sup>2)</sup>; MacKenzie, B.R.<sup>2)</sup>; Tomkiewicz, J.<sup>1, 2)</sup>;  
Möllmann, C.<sup>1)</sup>; Kraus, G.<sup>1)</sup>; Plikshs, M.<sup>3)</sup> and Makarchouk, A.<sup>3)</sup>

<sup>1)</sup> Institute of Marine Sciences, Düsternbrooker Weg 20, 24105 Kiel, Germany

<sup>2)</sup> Danish Institute for Fisheries Research, Charlottenlund Castle, 2920 Charlottenlund, Denmark

<sup>3)</sup> Latvian Fisheries Research Institute, Daugavgrivas Street 6, 1007 Riga, Latvia

**Abstract**

Relating data for subsequent early life history stages of Baltic cod and sprat, i.e. potential egg production by the spawning stock, realized and surviving egg production as well as larval and 0-group abundance, allowed the identification of critical periods within the recruitment process of both species. Based on an exploratory statistical analysis, variables having significant influence on the survival of critical life stages are incorporated into modified stock-recruitment models, first for single ICES Sub-divisions containing spawning areas with distinct hydrographic regimes and recruitment success and secondly combined for the entire Central Baltic.

Recruitment of cod critically depends on egg survival, with oxygen concentration in dwelling depths and predation by clupeids being major processes affecting egg mortality rates. Surviving egg production and larval abundance are hardly correlated in cod, however, larval abundance is significantly related to year class strength. This indicates either hatching and/or the early larval stage to be a further critical period for cod recruitment. Although sprat eggs are vulnerable to low temperature and cannibalism, the egg stage does not appear to be critical for sprat recruitment. Similarly, the production of late egg stages is significantly related to larval abundance. In contrast year class strength is largely independent of larval abundance, which indicates the main critical period in sprat recruitment to be the late larval and/or early juvenile stage. Potential variables identified to affect this life stage are ambient temperature and wind stress, while no indication for an impact of food availability was derived.

The statistical model obtained for prediction of cod recruitment at age 0 in Subdivision 25 based on the potential egg production explained 69% of the variance. Besides egg production, corrected for egg predation by clupeids, the oxygen condition in the reproductive volume and a larval transport index were introduced as variables. In the more eastern spawning areas the hydrographic regime did in general not allow successful egg development in the prolonged stagnation period throughout the 1980s. Thus, only relatively simple models based on the egg production by the spawning stock and the reproductive volume are required to achieve a reasonable explanation of recruitment variance (55% and 66%). Contrary to cod, sprat reproduces successfully in all major Baltic basins. Preliminary models established for Sub-division 25 and 26 are based on the spawning stock biomass as a measure of egg production, ambient temperature and in the latter area growth anomaly of adult fish throughout the feeding and subsequent winter season. These statistical models explained 45 and 41% of the variance in recruitment, while for Sub-division 28 no significant model could be developed.

## **Introduction**

Throughout the last two decades a shift from a cod- to a sprat-dominated system occurred in the upper trophic levels of the Central Baltic Sea. The cod stock declined, due to recruitment failure and high fishing intensity (Bagge et al. 1994) and resulted via a decrease in predation pressure in combination with high reproductive success and relatively low fishing mortalities in an increased sprat stock (Parmanne et al. 1994). Apart from being the major prey species of cod in pre- and spawning periods (Bagge et al. 1994), sprat has been identified as an important predator on cod eggs (Köster and Schnack 1994). Thus, a dominance of one of either predator may stabilize a cod-dominated or a sprat-dominated system (Rudstam et al. 1994). Destabilization of the system may be caused either by unfavourable hydrographic conditions for reproduction and subsequent recruitment failure of one of the species, or high mortalities caused by the fishery (Schnack 1997).

Besides shifts in upper trophic levels of the Central Baltic, substantial changes in the mesozooplankton community have been described as well (e.g. Vuorinen et al. 1998, Möllmann et al. 2000). They have been addressed to i) decreasing salinity caused by lack of inflows of saline water from the western Baltic (Matthäus and Franck 1992) and exceptionally high rain fall (Bergstöm and Carlsson 1994), and ii) a potential top-down control by planktivorous fish species, i.e. sprat and herring (Möllmann and Köster 1999). Apart from whether fluctuations in clupeid stock size cascade down to the trophic level of mesozooplankton, changes in abundance and species composition of zooplankton will affect the food supply for cod and sprat larvae and pelagic juveniles (e.g. Raid 1989, MacKenzie et al. 1996), and adult sprat (e.g. Möllmann and Köster 1999).

Cod and sprat utilize the same deep Baltic basins as spawning areas (Fig. 1), having also largely overlapping spawning times, i.e. in general within the period March to August (Bagge et al. 1994, Parmanne et al. 1994). However, they utilize their spawning habitat obviously with a pronounced difference in reproductive success, indicating deviating reproductive strategies or significantly different environmental requirements. In the past 10-15 years substantial effort has been allocated to examine the major processes believed to affect the recruitment variability in Eastern Baltic cod (Bagge and Thurow 1993, MacKenzie et al. 1996), with most recent activities addressing also sprat as strong interactions between both species were evidenced (ICES 1999b, Köster and Möllmann 2000a). As a result several new time series are becoming available for variables relating to these processes. We utilize this material to:

- a) improve stock-recruitment relationships, both with respect to spawning stock biomass as a measure of egg production as well as abundance of recruits as a measure of reproductive success,
- b) identify critical periods within the recruitment process by following the success of a year-class during ontogeny from spawner abundance through the egg and larval to the juvenile stage,
- c) investigate whether process-oriented recruitment models incorporating environmental variability can be developed and to identify what information might be lacking to make such a model as reliable as possible.

The first task includes a test on the reliability of spawning stock biomass obtained by the standard stock assessment as a measure of egg production, questioned recently for a number of fish stocks (Marshall et al. 1998, Marteinsdottir and Thorarinsson 1998, MacKenzie et al. 1998), and summarizes which information is available or needed to improve the relationships. Additionally, in order to dis-entangle processes acting on early pelagic and later demersal juveniles (Ulltang 1996), the feasibility of estimating recruitment success

before juveniles recruit to the fisheries is tested by comparing MSVPA derived estimates with recruitment 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 there have been few such attempts at following this approach (walleye pollock in Shelikof Strait, see e.g. Kendall et al. 1996, North Sea plaice, see e.g. Beverton and Iles 1992), as the amount of multi-disciplinary information required is large. In these aforementioned cases, attempts are still ongoing, as indeed it is in the Baltic, with the major problem in all systems being the lack of availability of time series of key processes and the variety and complexity of processes involved.

The third task aims at incorporation of environmental processes and species interaction in stock-recruitment relationships as suggested by Sparholt (1996) and Jarre-Teichmann et al. (2000) for Baltic cod as well as Grauman and Yula (1989) for sprat. Based on an exploratory statistical analysis, variables having significant influence on survival rates of critical life stages are incorporated into modified stock-recruitment models. These were established first for single ICES Subdivisions containing spawning areas (Fig. 1) with distinct hydrographic regimes (Plikshs et al. 1993, MacKenzie et al. 2000), recruitment success and stock development trends (Ojaveer 1989, Sparholt and Tomkiewicz 2000) and secondly combined for the entire Central Baltic.

Region specific stock-recruitment relationships were established on basis of area dis-aggregated Multispecies Virtual Population Analysis (ICES 1999b, Köster et al. submitted). For cod, an analysis of processes explaining variability in these area specific stock-recruitment relationships has been performed by Köster et al. (1999). Here, we extend this exercise with respect to (i) the reliability of SSB as a measure of egg production. (ii) the reliability of MSVPA derived recruitment estimates by comparison with trawl survey results and (iii) the extension of the exploratory analysis using newly available data on mesozooplankton abundance to investigate the influence of prey availability on larval survival. For sprat, the present analyses is a new approach to explain variability in region specific stock-recruitment data and establish environmentally sensitive recruitment models, specifically testing hypotheses on significant environmental factors impacting reproductive success suggested earlier (e.g. Grauman and Yula 1989, Kalejs and Ojaveer 1989, Raid 1989).

## **Material and methods**

Various time series on stock parameters of cod and sprat as well as on processes affecting early life stage survival have been compiled and used in the analysis. Due to the availability of time-series the exploratory analysis for cod is mainly restricted to Sub-division 25 comprising the Bornholm Basin (Fig. 1), the only spawning areas with hydrographic conditions allowing regularly a successful egg development (MacKenzie et al. 2000). For sprat sufficient data for the exploratory analysis was only available for the more eastern spawning areas in Sub-division 26 (Gdansk Deep) and Sub-division 28 (Gotland Basin) (Fig.1).

### **Stock parameters**

**Stock abundance and biomass estimates** for Sub-divisions 25, 26 and 28 were obtained from spatially dis-aggregated MSVPA runs for the period 1977-1996. The time series for cod was extended backwards to include 1976 (Köster et al. submitted), a year with well above average reproductive success at only intermediate spawning stock size. To determine cod **spawning stock biomass values** (SSB) for different

Sub-divisions, region specific sex ratios and proportions of sexually mature individuals at age (Tomkiewicz et al. 1997) were utilized. As far as sufficient sampling was conducted, annual values were applied, i.e. in Sub-division 25 from 1986 to 1996 and in Sub-division 26 from 1993 to 1996. Otherwise 5 year averages were used (Tomkiewicz et al. 1997). In order to demonstrate the effect of an introduction of year and sex specific maturity ogives on SSB estimates as a measure of egg production, two additional options were tested: i) average maturity ogives utilized 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 since 1996. Besides inspection of the variability of age-specific sexual maturation inherent in this data series and its impact on the estimated SSB, a test on the deviation between total and female SSB caused by changes in sex ratios with age was performed.

Estimates of cod and sprat recruitment at age 0 and 1 were also derived from MSVPAs. As cod recruits to the fishery at an age of 2 and cannibalism acting on younger cod makes an assessment of year-class strength at an earlier age more difficult, regular assessments estimate cod recruitment at age 2, being also the basis for constructing stock-recruitment relationships. In the present study, we utilize spatially disaggregated MSVPA runs (ICES 1999b, Köster et al. submitted) to estimate 0- and 1-group abundances, thus considering cannibalism in our estimation procedure explicitly. It should be noted that estimates of cod recruitment at age 0 in 1996 were omitted from the analysis, as they are heavily dependent upon the tuning performed.

For sprat, predation mortalities derived by spatially aggregated MSVPAs (ICES 1999b) are utilized in the standard stock assessment to determine recruitment at age 1 (ICES 1999a). To dis-entangle the impact of predation by cod on young of the year sprat from other processes affecting recruitment, we utilized 0-group estimates as a measure of reproductive success.

Alternative area specific recruitment indices were utilized for validation of MSVPA estimates. For cod age-group 1 and 2, we applied results from international bottom trawl surveys conducted since the early 1980's compiled by CORE (1998). For sprat, estimates of 0- and 1-group abundance from international hydroacoustic surveys performed since 1981 were recompiled and corrected for variation in area coverage (ICES 1997). Survey results in 1993 were excluded, due to technical problems and lack of area coverage (ICES 1994). It should, however, be noted, that data series for cod and sprat age-groups 1 and 2 were incorporated into the tuning procedure of the MSVPAs. Thus they are not strictly independent, but as a tri-cubic down-weighting of historical observations (Mohn and Cook 1993) has been applied, a reduced effect on the outputs back in time can be expected. This feature makes these data valid for a comparison of trends for a major part of the time series.

A further validation of cod age-group 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 1980's. Independent recruitment estimates for sprat are available from the polish young fish survey in Sub-division 26 (ICES 1999a) comprising a geometric mean year-class abundance index based on catch rates of age-group 0 and 1.

To estimate area-specific **potential egg production** of cod, female SSB according to Sub-division were coupled to predicted relative individual fecundity values (Kraus et al. 2000). Utilization of relative instead of absolute age-specific fecundity is justified by the fact, that this measure is independent of body size (Kraus et al. 2000). It should be noted that a significant variability in relative fecundity was detected between years

but not between spawning areas within a specific year (Kraus et al. 2000), hence, relative fecundity was assumed to be similar among areas. Individual fecundity was predicted by utilizing a statistical model relating relative fecundity (with ambient temperature in the 4<sup>th</sup> quarter and average wet weight growth rate anomaly from the 3<sup>rd</sup> to the 1<sup>st</sup> quarter of the years preceding the investigated spawning period (Kraus et al. 2000). As an alternative approach, a time series of relative individual fecundity values (Shapiro 1988; Bleil and Oeberst 1996; Kraus et al. 2000), with missing information derived by linear interpolation, was applied. For sprat, available information on batch fecundity and spawning frequency (Petrowa 1960, Polivaiko 1980, Alekseeva et al. 1997) makes it difficult to construct a reliable series of potential egg productions. Thus, only a proxy of the nutritional condition and the reproductive potential of the population, an index of growth throughout the feeding and subsequent winter period, i.e. the average growth rate anomaly of age-groups 2 to 4 from the preceding 3<sup>rd</sup> to the 2<sup>nd</sup> quarter could be constructed. To characterize the condition of the fish in pre-spawning periods, the weight at age anomaly for the same age-groups in the 1<sup>st</sup> quarter was applied additionally. Basin specific quarterly weight at age of adult fish were compiled for both species by ICES (1999b), but allowed a full analysis only for Sub-division 26.

Mean annual **egg and larval abundance** values are available for the different Sub-divisions from ichthyoplankton surveys in 1976-1996, for cod summarized by Köster et al. (1999) and for sprat compiled by Grauman and Krenkel (1986), Karasiova (1999), Krenkel (1981), Köster and Möllmann (2000a). Cod egg abundance estimates are based on a three-month period encompassing the main spawning period, i.e. April-June up to 1989 and successively shifted to May-June (1990-1992) and June-August (1993-1996) to take into account a shift in the spawning period in recent years (Wieland et al. 2000). Sprat egg abundance estimates refer to the main spawning period May-June (ICES 1976). Cod larval abundance data refer to a period similar to the 3 month period of egg abundance estimates but shifted to account for the 2 to 4 week period of development from egg to larvae (Wieland et al. 1994). Due to a faster egg development in sprat (Thompson et al. 1981), sprat larval abundance data refer to the main spawning period, i.e. to the period May to June.

Estimates of **realized daily egg production** during main spawning periods were established for cod in the Bornholm Basin (Sub-division 25) and for sprat in the Gdansk Deep (Sub-division 26) and the Gotland Basin (Sub-division 28) using stage specific abundance data (sources see above) and egg development-temperature relationships (cod: Wieland et al. 1994, sprat: Thompson et al. 1981). For cod temperatures at the depth of the center of mass of eggs were utilized for the estimation of developmental period, obtained from CTD-casts performed concurrently with the vertically resolving ichthyoplankton sampling in 1986-1996 (Wieland and Jarre-Teichmann 1997) or from predicted vertical distributions in combination with depth specific temperatures obtained from the ICES hydrographic database (Köster et al. 1999).

The vertical distribution of sprat eggs is less intensively studied and appears to be more variable (Müller and Pommeranz 1984, Müller 1988), with a typical spring and early summer situation of deep occurrence and a summer situation with occurrence in more shallow water layers (Grauman 1975, Grimm and Herra 1984). As main sprat spawning normally takes place in May/June, i.e. predominantly in relatively deep water layers, average temperature in the 60-80 m depths layer were applied for estimating developmental periods. Finally, daily egg production rates were calculated by dividing the stage specific abundance of eggs by the development time of each egg stage.

## Environmental factors potentially affecting early life history stages

The low salinity in upper water layers of the Central Baltic does not allow cod eggs to float in surface layers, thus they concentrate in a narrow depths range within and below the permanent halocline (Wieland and Jarre-Teichmann 1997). Here they are exposed to low oxygen concentration, limiting egg survival (Wieland et al. 1994, Nissling 1994). Estimates of the **reproductive volume (RV)**, i.e. the volume of water fulfilling minimum requirements for successful egg development (Plikshs et al. 1993), in the different Sub-divisions were obtained from MacKenzie et al. (2000) for peak spawning periods. However, as this index does not consider the actual oxygen conditions inside the water volume principally sustaining egg development, two modifications of this index were tested for the Bornholm Basin. The first **oxygen related egg survival factor** considers not only the volume potentially sustaining egg development, but gives a measure of the oxygen conditions within the salinity range over which cod eggs are neutrally buoyant. This modification is based on an integration of the mean oxygen concentrations per 1 meter depth interval over the thickness of the spawning layer using similar stations to those employed in the original calculation of the RV (MacKenzie et al. 2000). For the second modification, the integrated **oxygen content in the RV**, the fraction of the egg production surviving in each year was estimated on basis of predicted vertical distributions of cod eggs relative to water density (Köster et al. 1999), measured oxygen concentrations during spawning time and an oxygen concentration-egg survival relationship derived from laboratory experiments (Wieland et al. 1994, Rohlf 1999).

Sprat eggs have on average a higher buoyancy than cod eggs, and hence they float in general in more shallow water layers (Wieland and Zuzarte 1991). Thus, oxygen depletion has a more limited impact on sprat egg survival. However, sprat eggs are sensitive to low temperatures (e.g. Thompson et al. 1981) and due to their higher buoyancy they float at least partly in the intermediate water, a cold water layer between the thermo- and the halocline formed in the Central Baltic in winter. Depending on the strength of the winter cooling, the temperatures may be lethal. Even if the sprat eggs are developing within the halocline, ensuring in general sufficient ambient temperatures, the larvae have to migrate into surface layers with sufficient food supply and light conditions for capture success (Wieland and Zuzarte 1991), a process in principal also described for cod (Grønkjær et al. 1997). To explore the impact of temperature on survival of eggs and larvae, the average **water temperatures at main spawning time** in the 40-60 m depths layer of the Gdansk Deep (Sub-division 26) and the Bornholm Basin (Sub-division 25) and due to the lower halocline the 40-80 m depth layer of the Gotland Basin (Sub-division 28) were determined from the ICES hydrographic database. According to Grauman (1965) sprat egg survival in June/July depends critically on the wind conditions with high wind stress resulting in a high egg mortality of eggs distributed in these months in upper water layers. However, wind conditions impact also on encounter rates of larvae and their prey as well as capture success and hydrodynamic transport. The impact of the first processes was tested by applying anomalies of **weekly-averaged wind speed** in May/June 1977-1994 recorded at Christiansø, a small island 10 nm northeast of the main island of Bornholm.

Jarre-Teichmann et al. (2000) demonstrated, that the cumulative wind energy at peak spawning time impacts on cod recruitment success. The suggested process being a transport of larvae and pelagic juveniles to coastal nursery habitats during periods of high transport and a retention in the central basins during periods of low wind stress of variable wind direction (Hinrichsen et al. 2000). Köster et al. (1999) incorporate 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**). Hydrodynamic modelling studies by Voss et al. (1999) and Hinrichsen et al. (2000) demonstrated that larval drift towards the west and north is caused primarily by winds of westerly and southerly direction, whereas winds of opposite direction result in larval transport to the south and east. Periods of low wind energy or varying directions are in turn causing retention in spawning areas. For sprat larvae preliminary hydrodynamic modelling approaches demonstrated the sensitivity of performed ichthyoplankton surveys to high wind stress resulting in a rapid advection of larvae out of the covered survey area of the Bornholm Basin (Sub-division 25) (STORE 2000). This rapid transport is caused by a concentration of sprat larvae in upper-most water layers after successful completion of their initial vertical migration from hatching depth. To test whether this transport affects the larval abundance estimates, a larval transport index for sprat was developed according to the procedure described for cod considering the deviating vertical distribution and adjusted to the main spawning season of sprat, i.e. May/June. The data set was also applied to Sub-division 26 to resolve a transport from Sub-division 25 to 26 and 28 as described by Grauman (1976), as dominating westerly winds will result on average in a transport of particles in surface layers to eastern basins (Fig. 1).

Consumption of cod eggs by sprat has a significant impact on egg survival in the Bornholm Basin in spring and early summer, while later in the cod spawning season herring replaces sprat as the principal predator (Köster and Möllmann 2000b). Similarly, egg cannibalism by sprat in the Bornholm Basin is a potential compensatory process limiting the reproductive success (Köster and Möllmann 2000a). Predation by sprat decreased throughout the 1990's, while the impact of herring on cod eggs increased, due to a delay in spawning of cod (Wieland et al. 2000). Apart from intra- and inter-annual trends, spatial variation in the intensity of egg predation also occurs, with egg consumption in the Gdansk Deep and Gotland Basin being considerably lower than in the Bornholm Basin. This difference has been attributed to the lack of light for successful feeding on the transparent and motionless eggs at the increased depth of occurrence in these eastern spawning basins (CORE 1998). For this reason, predation on eggs by clupeids was included as a variable in the exploratory analysis for cod in Sub-division 25 only. Existing data on sprat and herring diet composition suggests that the ratio of cod eggs in the stomachs and in the food supply is linearly related to their degree of vertical overlap, mainly driven by the oxygen concentration in the bottom water limiting the vertical distribution of clupeids during the daylight-feeding period, while the density regime determined the vertical distribution of cod eggs (Köster and Möllmann 2000a). This observation led to the development of an index of vertical predator/prey overlap (Köster et al. 1999). Applying a linear relationship between the ratio of hourly consumption and egg abundance with the vertical predator/prey overlap index enabled the prediction of consumption rates by predator populations (Köster and Möllmann 2000b). Predation pressure was introduced into the analysis as a **relative egg predation index** expressing consumption per standing stock of eggs scaled to the potential egg production, setting the maximum predation pressure to result in a 95% egg removal.

A substantial predation by adult herring on young of the year sprat has been reported by Patokina and Feldman (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 (Patokina and Feldman 1998) and may additionally be coupled to the small average size of the sprat due to low growth rates (ICES 1998). To test whether survival from the larval to the 0-group stage is coupled to size, **weight at age anomalies** of 0-group sprat (4<sup>th</sup> quarter) compiled by ICES (1999b) for Sub-division 26 were applied.

Recent studies demonstrated, that the species composition of the Central Baltic mesozooplankton community and, thus potentially the prey availability for larvae and early juveniles, has undergone substantial changes in the last two decades. *Pseudocalanus elongatus* depends strongly on salinity (Ojaveer 1998, Vuorinen et al. 1998) and on low temperature in summer (Möllmann et al. 2000), both features resulting in a reduction of the standing stock throughout the stagnation period of the 1980's. In contrast, copepods *T. longicornis*, *Acartia* spp. and cladocerans show a strong preference for higher temperatures and an affinity to lower salinities in spring (Sidrevics 1984, Möllmann et al. 2000), sustaining increasing standing stocks throughout the late 1980' and early 1990's. It has been hypothesized that the abundance of *T. longicornis* and *Acartia* spp. nauplii and copepodids 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. These hypothesis are tested by utilizing species and stage specific data on **abundance of major mesozooplankton species** in Sub-division 26 during 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). Although the zooplankton data for Sub-division 28 are based as well on a reasonable temporal and spatial coverage, the low occurrence of non-zero larval abundance values does not allow a comparable test for Sub-division 28.

## **Results**

### **Linearity of stock recruitment relationships**

Linear regression analyses revealed significant relationships between spawning stock and recruitment of cod and sprat as determined by the standard stock assessment for the eastern and entire Baltic respectively (ICES 1999a), (Fig. 2). However, the explained variance in recruitment at age 2 and 1 respectively is low, with a significant intercept for cod and high outlying recruitment values for both species. Furthermore there is a clear time trend in residuals for cod, with a high number of positive residuals in the beginning of the time series up to 1981 and only negative residuals afterwards (Fig. 2). The stock-recruitment relationships derived by the area dis-aggregated MSVPA runs show corresponding pattern for cod, with a significant linear relationship in Sub-division 26 and 28, but not in Sub-division 25 (Tab. 1). Again high recruitment success originated from intermediate SSB in the beginning of the time series. Recruitment declined despite high SSB in early 1980's. This pattern results in significant auto-correlation in the residuals. For sprat a significant linear relationship was obtained only for Sub-division 25 (Tab. 1), while in both other areas an outstanding high recruitment of the 1982 year-class originated from a low SSB does not coincide with a linear relationship. Omitting this year-class from the analysis resulted in significant linear relationships (Tab. 1 ).

### **Validation and improvement of stock-recruitment relationships**

#### **Spawning stock biomass as a measure of egg production**

The SSB of cod in Sub-division 25 calculated with the maturity ogive being constant over time is not correlated to the realized daily egg production at peak spawning time, while the SSB determined on basis of yearly or period specific ogives is (Tab. 2). The correlation is further enhanced when utilizing the female SSB and the predicted potential egg production, with largest deviations between potential and realized egg production in the most recent year of the time series. Utilization of the alternative time series of potential egg production rates based on measured relative fecundity values and linear interpolation of years with missing



information results as well in a significant correlation to the realized egg production, however, with a slightly higher unexplained variance ( $r^2 = 0.39$ ,  $p = 0.001$ ).

For sprat in Sub-division 26 and 28, the result of the performed test is different. The SSB calculated with an invariate maturity ogive is significantly correlated to the realized egg production (Tab. 2). Utilizing an age-specific sex ratio invariate with time to compute the female SSB in Sub-division 26 does not enhance the correlation ( $r^2 = 0.42$ ,  $p = 0.003$ ). Female and total SSB are closely correlated in both areas ( $r^2 = 0.98$ ) although the sex ratio is rather skewed to female dominance with increasing age.

#### Abundance of recruits as a measure of reproductive success

MSVPA derived cod recruitment at age 1 and 2 is in all areas significantly correlated with abundance indices from the international bottom trawl survey (BITS), with highest variability in Sub-division 25 (Tab. 3). Here, especially a low abundance index of the year-class 1979 in the survey 1980 does not coincide with high recruitment estimated by the MSVPA. As survey data for Sub-division 26 and 28 are available only from 1981 and 1982 onwards, a validation of the MSVPA derived 1979 year-class strength as age-group 1 is impossible. However, as two year old, the year-class was covered by the 1981 survey in Sub-division 26, again indicating that the MSVPA result is substantially overestimated. Utilizing independent age-group 2 abundance indices from Latvian bottom trawl surveys conducted in the 1<sup>st</sup> and 4<sup>th</sup> quarter revealed as well significant correlations to MSVPA results in Sub-division 28, however, not in Sub-division 26 for the January series (Tab. 3). Here deviations occurred especially in 1976 with high MSVPA estimates and relatively low bottom trawl survey indices in both surveys. It should, however, be noted that in 1981 no trawl surveys were conducted, thus not allowing a further validation of the 1979 year-class strength.

MSVPA derived sprat recruitment at age 0 is highly correlated to abundance estimates from autumn hydroacoustic surveys in Sub-division 25, however, not in both other Sub-divisions (Tab. 4). Here outlying high recruitment values were determined by the MSVPA runs for 1982, while hydroacoustic survey estimates indicate a low year-class strength. Omitting this year-class from the analysis, result in significant correlations for both areas as well. For recruitment at age 1, a corresponding comparison revealed as well outlying 1982 year-class strengths in Sub-division 26 and 28 estimated by the MSVPAs. Apart from this, all correlations were statistically significant (Tab. 4) and excluding the 1982 year-class improved the relationships further. Comparison with independent polish young fish survey estimates in Sub-division 26 revealed a significant correlation to MSVPA derived estimates (Tab. 4), however, with considerable variability and outstanding high MSVPA recruitment again in 1982 and additionally in 1994.

#### **Identification of critical early life history stages**

From correlation analyses of daily production rates of early and late egg developmental stages, abundance estimates of larvae and juvenile fish (Tab. 5), critical periods for cod recruitment in Sub-division 25 appear to be the late egg to the larval stage ( $r = 0.36$ ) and also the correlation between production rates of egg stage I (first development stage) and III indicates a substantial variability in egg survival ( $r = 0.51$ ). Egg production at stage III was utilized as a proxy for the production of the oldest egg stage IV, as the abundance of the latter is highly variable, due to a relatively short stage duration and hatching, which in Baltic cod commences during this stage (Wieland et al. 1994). Lowest egg survival rates were encountered in the 1<sup>st</sup> half of the 1980's (i.e. 1983 and 1985), however, being also the period with most gaps in the egg production data base. Larval abundance per egg stage III production was lowest in 1992 to 1996 indicating extremely low survival

in these years. By far highest survival is in contrast indicated for 1985. Larval abundance in turn is highly correlated to MSVPA derived 0-group recruitment ( $r = 0.80$ ). Recruitment at age 0 and age 1 determined by MSVPA are as well very closely related ( $r = 0.99$ ).

In contrast to cod, correlations between sprat early and late egg stage production as well as late egg stage production and larval abundance estimates in Sub-division 26 and 28 are highly significant, indicating that the egg and early larval stage is less critical for the reproductive success of the clupeid than for cod (Tab. 5). In contrast to cod, larval abundance in sprat is hardly correlated to 0-group abundance, even when excluding the 1982 year-class from the analysis, being most likely overestimated by the MSVPA (Sub-division 26:  $r = 0.40$ , 28:  $r = 0.29$ ). Similar to cod, recruitment at age 0 and age 1 estimated by MSVPA are closely related.

### **Processes affecting critical early life history stages**

As demonstrated in the section on the reliability of the SSB as a measure of egg production, processes affecting the maturation and the fecundity of individual female cod as well as the sex structure of the spawning stock have a significant impact on the realized egg production and, as demonstrated below, also on the reproductive success of the stock. However, resolving processes impacting on the nutritional condition, growth and timing of sexual as well as gonadal maturation in Baltic cod is not covered in the present analyses. Instead we utilize best available data series to estimate the potential egg production as a starting point for investigating processes affecting egg and larval survival. For sprat, variation in sexual maturation, individual fecundity and stock structure appear to have a more limited influence on the realized egg production, however, the relatively high variability in the relationships between SSB and realized egg production clearly demonstrates the potential for improvement, which we try below. Likewise from the variety of processes impacting on the survival of juvenile cod and sprat, only predation by cod is considered in the estimation of recruitment at age 0 as a measure of reproductive success.

#### Cod survival during the egg stage

The two primary mechanisms influencing cod egg survival in Sub-division 25 are the oxygen conditions at the depth of incubation and predation by clupeids. In order to examine the effects of these processes on egg developmental success, the daily production of the egg stage III was related to the total potential egg production by the SSB. A linear regression of this egg survival index vs. the oxygen related egg survival ( $p = 0.005$ ) explains 44% of the variance encountered (Fig. 3), however, with pronounced negative residuals in 1983 and 1985 and positive residuals in 1976, 1978 and 1994. Utilizing the egg consumption index to explain variability in egg survival revealed a negative linear relationship ( $p = 0.078$ ) explaining 21% of the variance. A high scatter in egg survival is obvious for low consumption indices, with highest residuals in outlying years identified above (Fig. 3). Incorporating both processes into the potential egg production (i.e. subtracting the consumed egg consumption and multiplying by the oxygen related relative survival) revealed a significant linear regression (Fig. 3) with egg abundance at stage III ( $r^2 = 0.60$ ,  $p < 0.001$ ), with the potential egg production alone explaining 30% of the variance. Again difficulties in explaining the low observed egg survival in 1983 and 1985, but also 1977 and 1995/96 were encountered, while comparatively high egg survival was determined in 1978, for the period 1986-92 as well as 1994. Utilization 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 less clear the impact of egg predation ( $r^2 = 0.16$ ,  $p = 0.122$ ). However, removing the outlying years 1983 and 1985 results as well in

a significant relationship ( $r^2 = 0.35$ ,  $p = 0.027$ ). Incorporating both processes into the potential egg production resulted in a slightly better linear relationship to the observed egg production at stage III, than when utilizing predicted relative fecundity values ( $r^2 = 0.61$ ,  $p < 0.001$ ).

#### Cod survival until the larval stage

The potential egg production determined on basis of predicted relative fecundities is linearly related to larval abundance (Fig. 4), however, only if the three most recent years are 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 significantly lower than expected. Utilizing the daily production of egg stage III instead of the potential egg production did improve the above relationships somewhat, but as well only if 1994 to 1996 are omitted from the analysis ( $r^2 = 0.32$ ,  $p = 0.043$ ).

Correlating the ratio of larval abundance to the predicted potential egg production by SSB, as a measure of survival to the larval stage, vs. the oxygen related egg survival as well as the consumption index revealed no significant relationships, independent whether the most recent three years are considered or not ( $r^2$  between 0.04 to 0.10). The oxygen content in the reproduction volume behaves better than the oxygen related egg survival factor ( $r^2 = 0.16$ ,  $p = 0.073$ ), however with a pronounced negative residual in 1992/93 and high positive residuals in 1980 and 1981 (Fig. 4). Replacing the potential egg production by the late egg stage production did not improve the relationships, in fact they indicated a negative relationships with oxygen conditions and a positive relationship with predation, being biologically not sensible.

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 and temperature in the intermediate water, Sub-division 26 was used as a test case. The ratio of larval abundance to the potential egg production by the SSB (based on actually measured relative fecundity used due to the slightly better performance in explaining egg survival) is significantly correlated to nauplii abundance in May/June ( $r^2 = 0.33$ ,  $p = 0.020$ ). However, since 1988 larval abundance values are zero independent of the prey availability, most likely due to unfavourable hydrographic conditions. To consider the impact of hydrography, the reproductive volume (RV) in Sub-division 26, as a measure of oxygen conditions allowing egg survival, was incorporated into a multiple linear regression analysis keeping otherwise above variables (Fig. 5). This exercise resulted in 65% explained variance in the ratio of larval abundance to the potential egg production with both independent variables being significant ( $p = 0.002$  for the RV and  $p = 0.027$  for nauplii abundance).

#### Egg production by the adult sprat stock

Although realized egg productions are significantly correlated to SSBs, the relationships do not explain major parts of the variance ( $r^2 = 0.44$  and  $0.39$  in Sub-division 26 and 28). In order to resolve environmental processes affecting the egg production of sprat in Sub-division 26, we applied following proxies for the nutritional condition of the adults: i) average weight at age anomaly in pre-spawning times and ii) growth rate anomalies covering the main feeding period during autumn as well as the winter months. Additionally we tested the impact of low temperatures in the intermediate water in May/June, as there is evidence that spawning activity and survival of early life stages of sprat are affected by unfavourable temperature conditions (Elwertowski 1960, Krenkel 1981, Herra 1988) as well as the survival of the offspring).

As a starting point we related the realized egg production separately to above variables, but did not identify any significant correlation. Incorporating the SSB, the temperature in the intermediate water and either

growth/condition proxies in a multiple regression (Fig. 6), resulted however in significant statistical models explaining 56% with following variables: SSB ( $p = 0.007$ ), temperature ( $p = 0.073$ ) and weight at age anomaly ( $p = 0.102$ ) and 63% with: SSB ( $p < 0.001$ ), temperature ( $p = 0.055$ ) and growth anomaly ( $p = 0.039$ ). The Durban-Watson statistics do not indicate serial correlation in residuals and the intercepts in both statistical models were insignificant. However, both models showed a pronounced negative residual in 1996, i.e. the realized egg production was considerably lower than predicted (Fig. 6).

For Sub-division 28 weight at age prior to 1985 are assumed to be invariable with time and consequently corresponding tests could only be conducted with a shorter time series resulting in no significant explanation of variance in the realized egg production by either growth/condition proxy, independent whether temperature in the intermediate water is included in the multiple regression or not.

#### Sprat survival from the larval to the 0-group stage

The ratio of 0-group recruitment to larval abundance as a measure of survival to the juvenile stage is neither correlated with any potentially important hydrographic variables in a biologically sensible way, i.e. average temperature in the intermediate water in May/June (Sub-division 26:  $r = 0.18$  and 28:  $0.04$ ) and average oxygen concentration in and below the halocline (80-100 m) in May/June ( $r = -0.31$  and  $-0.63$ ), nor with prey availability for sprat larvae (i.e. *Acartia* nauplii and copepodids) in May/June ( $r = -0.05$  and  $-0.06$ ) or July/August ( $r = 0.39$  and  $-0.40$ ). A significant negative relationship exists to wind speed anomaly in May/June in Sub-division 28 ( $r = -0.51$ ), but not in Sub-division 26 ( $r = -0.07$ ). In the latter area high scatter occurred at intermediate wind speed, which may indicate rather a parabolic than a linear function.

As there is a significant correlation between late egg stage production and larval abundance in May/June in both Sub-divisions, it appears to be unlikely that the larval abundance data are grossly erroneous, however, a higher correlation between late egg stage production rates and 0-group recruitment in Sub-division 26 ( $r = 0.36$ ) may indicate a problem in the larval abundance data at least in this area. In fact multiple linear regressions with late egg stage production rates and wind speed anomalies in May/June as independent variables explained 73 and 46% of the variance in larval abundance in Sub-division 26 and 28 (Fig. 7) with the variable wind speed being significant in both areas (Sub-division 26:  $p = 0.011$  and 28:  $0.006$ ). Utilizing the larval transport index developed for Sub-division 25 instead of the wind speed anomaly showed the transport index to be insignificant (Sub-division 26:  $p = 0.242$  and 28:  $p = 0.491$ ). Thus, from the available data a significant impact of wind driven transport on larval abundance is not obvious, however, the wind speed has obviously an effect of survival from the late egg to the larval stage.

Relating the larval abundance and above physical variables as well as temperature in the intermediate water as a potential variable affecting growth and survival of larvae iteratively in a multiple regression to year-class strength revealed only the temperature in the intermediate water in Sub-division 26 to be significant (larval abundance:  $p = 0.062$ , temperature:  $p = 0.043$ ). However, the explained variance in 0-group recruitment is rather limited (27%), with the model significantly underestimating recruitment in 1994 (Fig. 8). Adding further prey availability of *Acartia* 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 in the intermediate water as independent variables does not explain a significant part of the variance in 0-group recruitment ( $r^2 = 0.06$ ). Here the only significant physical variable is the larval transport index explaining together with the

larval abundance 26% in recruitment variability (larval abundance:  $p = 0.104$ , temperature:  $p = 0.032$ ). However, recruitment is negatively related to the transport index suggesting lower recruitment in situations of transport from Sub-division 25 to eastern basins, being biologically not sensible. If recruitment from the hydroacoustic survey is utilized in the above multiple regression analyses instead of MSVPA derived estimates, the wind speed anomaly and the transport index are insignificant, while the temperature in the intermediate water is significant, with the model explaining 30% of the variance in 0-group abundance (larval abundance:  $p = 0.223$ , temperature:  $p = 0.030$ ). Large deviations between model predictions and observed recruitment occurred in 1985 (overestimated by the model) and 1991 (underestimated) (Fig. 8). Independent whether 0-group recruitment from the MSVPA or the hydroacoustic survey is utilized, prey availability or weight anomalies do not explain a significant part of the variance in sprat recruitment in Sub-division 28.

### **Incorporation of environmental variability in stock-recruitment relationships**

Based on significant variables identified in their exploratory analysis, Köster et al. (1999) developed a multiple regression based cod stock-recruitment relationship for the different Sub-divisions in the Central Baltic. The statistical model developed for Sub-division 25 included potential egg production by the spawning stock corrected for the removal by egg predation, the oxygen content in the reproductive volume affecting egg survival and larval viability and the larval transport index determining drift to suitable nursery areas. It explained 69% of the variance in 0-group recruitment, with highest deviations from observed values in 1979 (Fig. 9). In other spawning areas, variable hydrographic conditions did not allow for regular successful egg development. Hence, relatively simple models proved sufficient to predict recruitment of 0-group cod in these areas. They included the potential egg production by the spawning stock and the reproductive volume as significant variables explaining 55 and 66% of the variance in 0-group recruitment. Both regression coefficients were significant ( $p = 0.005$  and  $0.032$ ), and no auto-correlation was indicated. Large positive deviation between observed and predicted recruitment occurred, however, again in 1979 (Fig. 9). The sum of the area-specific predicted recruitment at age 0 compare favourable with the observed recruitment of the cod stock as derived from spatially dis-aggregated MSVPAs (Fig. 10). Recruitment in 1979 was underestimated by the model and overestimated in 1984. Some smaller deviations occurred during the later part of the time series, when the model predicted higher recruitment than observed.

To obtain an indication of the sensitivity of the parameter estimates and the predictive power, the models were re-fitted over different shorter time periods and then model predictions were compared with the excluded year's observations. The exercise clearly demonstrated that the models derived for the different Sub-divisions are not sensitive to the exclusion of periods from the parameter estimation procedure. The models were able to capture the trend of decreasing recruitment during the 1980s and an increase in recruitment success in the early 1990s. However, if all observed high recruitment values were excluded from the time series, not surprisingly a substantial underestimation of recruitment in early years was encountered. As a further validation of the model, predicted 0-group abundance and cannibalism rates acting on 0-group were utilized to predict recruitment at age 1 and compared to corresponding area specific recruitment indices obtained from international bottom trawl surveys. In general, the comparison revealed similar trends with declining recruitment throughout the first half of the 1980s and increasing recruitment in the 1990s (Fig. 10). However, considerable deviations are apparent for some years, i.e. recruitment indices from the trawl survey declined and increased earlier than predicted recruitment, lagging approximately two years.

The conducted exploratory analysis revealed temperature during main spawning time in the intermediate water and the growth condition of adult sprat to be variables potentially affecting the realized egg production and again temperature and wind speed to affect the survival from the late egg to the larval stage. Incorporation of these variables iteratively into linear multiple regression based stock recruitment relationships revealed besides the spawning stock biomass, being significant nearly in all areas and combinations of variables, the growth anomaly and the temperature to enhance the MSVPA based relationship in Sub-division 26, explaining 33% and 38% of the recruitment variance (Tab. 6). Utilizing the recruitment determined by the hydroacoustic survey explained 42% of the variance with the spawning stock and the temperature alone, however, the latter variable not being significant ( $p = 0.104$ ). In Sub-division 25, temperature was the only variable improving stock recruitment relationships, but being insignificant when used to explain variability in hydroacoustic derived recruitment ( $p = 0.646$ ). In Sub-division 28, the vice versa situation occurred, i.e. the temperature being significant in a hydroacoustic based stock recruitment relationship ( $p = 0.021$ ) but not in the MSVPA based ( $p = 0.245$ ).

Incorporation of SSB, temperature and additionally in Sub-division 26 the growth anomaly as variables in multiple regressions resulted in recruitment predictions for single Sub-divisions presented in Fig. 11 and for the entire central Baltic presented in Fig. 12. Clearly the statistical models were able to predict the recruitment development up to 1992 quite reasonably, but failed to predict year-class strength in most recent years, with a considerable overestimation in 1996 and 1993 at least in Sub-division 25 and 28 as well as significantly underestimated recruitment in 1994. This is also obvious for the area aggregated predictions. Considering the recruitment pattern from the hydroacoustic survey to be realistic, indicates that the deviation in 1996 is caused by a model mis-specification or unreliable data utilized for parametrization, while the deviation in 1994 appears to be caused by an overestimation of year-class strength by the MSVPA.

## **Discussion**

The present study investigates 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 tries 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).

Our first work step concentrates on the validation and improvement of spawning stock biomass as a measure of egg production and abundance of recruits as a measure of reproductive success. The second work step addresses the identification of critical periods within the recruitment process from potential egg production to juvenile abundance, while the third task is directed to the identification of major processes and environmental factors impacting on the survival of these critical life stages. Based on this exploratory statistical analysis, identified variables having significant influence on survival are subsequently incorporated into modified stock-recruitment models. Investigation of the link between environmental factors, spawning stock features and reproductive success of Baltic cod (e.g. Jarre-Teichmann et al. 2000; Plikshs et al. 1993; Sparholt 1996) and to a lesser extend also sprat (Grauman and Yula 1989) have previously been performed by several investigators. However, these studies did neither address the first nor the second work step performed in our analysis and apart from Plikshs et al. (1993) did also not consider spatial heterogeneity within the Central Baltic. We, however, utilized their findings for generating our working hypotheses in the

process oriented work (for an overview see Schnack and Köster 1998) as well as in the conducted exploratory analysis (see Köster et al. 1999).

### **Validation and improvement of stock-recruitment relationships**

The comparison of cod SSB and realized egg production clearly demonstrated, that spawning stock biomass is no reliable measure of realized egg production, also if utilizing yearly updated or period-specific maturity ogives. In contrast the female SSB and the predicted potential egg production determined on basis of the female spawning stock and relative fecundity estimates are a significantly better measure of the realized egg production. They explain 61 and 63% of the variance in daily production of the youngest egg stage at peak spawning time, with largest deviations between potential and realized egg production in the most recent year 1996. Here the potential egg production is estimated to be significantly higher than the realized, which 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. submitted). Excluding the year 1996, increased the explained variance in realized egg production to 74%. Apart from methodological problems, the remaining variability may be related to artresia due to unfavourable environmental conditions during spawning (Kjesbu et al. 1991), variable fertilization success in relation to salinity changes (Westin and Nissling 1991) and differences in egg mortality already in the first developmental stage.

For sprat the spawning stock biomass appears to be a better measure of realized egg production, indicating that inter-annual variability in maturation processes, age-dependent sex ratios and individual fecundity is of less importance than in cod. However, linear relationships between SSB and egg production explain only 47% and 39% of the variance in realized daily egg production during main spawning period. Although the sex ratio is rather skewed to female dominance with increasing age in sprat (STORE 2000) similar to cod (e.g. Tomkiewicz et al. 1997), the variability in age-structure of the spawning stock has no major impact on its size, as this is determined predominantly by young age-groups 2 and 3 having still rather even sex ratios. Utilizing yearly maturity ogives available for Sub-division 25 for the period 1977-1987, resulted in pronounced deviations compared to the SSB determined by standard assessment ogives (ICES 1999a) in some years, e.g. 1983. However, this is related to variation in sexual maturity of age-group 1 in combination with high fluctuations in abundance estimates of this age-group. As demonstrated in the exploratory section, the relationship between SSB and potential egg production can substantially be improved by incorporating ambient temperature in the intermediate water during spawning time and growth anomaly from the 3<sup>rd</sup> to the 2<sup>nd</sup> quarter in a linear relationship, explaining 63% of the variance in realized egg production in Sub-division 26. The effect of temperature on realized egg production may have several reasons:

- i) low winter temperature may affect the nutritional condition and growth of sprat (positive correlations between utilized May/June temperature and the growth/nutrition proxies are indicated, but are not significant),
- ii) low temperature in pre-spawning periods may negatively affect the batch fecundity as well as the batch number (Petrowa 1960), by this reducing the total seasonal egg production,
- iii) low temperature during spawning season may delay spawning activity to later month of the year (e.g. Elwertowski 1960, Grimm and Herra 1984), not corrected for in the present time series of egg production.

Largest deviations between SSB as a measure of egg production and the realized egg production occurred in 1996. A correlation of 1<sup>st</sup> quarter average surface temperatures (0-50 m) with the utilized May/June

temperatures ( $r = 0.79$ ) showed 1996 to be one of the years, when winter severity is not fully represented in the intermediate water. This may indicate, that influencing processes act already before the spawning period, i.e. points to i) or ii) as responsible process. However, it should be noted, that especially the most recent stock size estimate is subject to considerable uncertainty caused by the tuning procedure (Köster et al. submitted).

Conducted comparisons between MSVPA derived cod recruitment at age 1 and 2 with trawl survey indices showed an overall good agreement especially in Sub-division 26 and 28, however, with a significant auto-correlation in the residuals. For our test population in Sub-division 25, the variability was in general higher with an explained variance of only 34% for age-group 1 and 52% for age-group 2. Here especially the high year-class strength 1979 estimated by the MSVPA is not confirmed by the trawl survey. Excluding this year-class improved the relationship between MSVPA recruitment at age 1 and corresponding trawl survey abundance indices considerably ( $r^2 = 0.60$ ). Also in Sub-division 26, the 1979 year-class covered in the trawl survey only as 2 year old fish in 1981, appear to be substantially overestimated by the MSVPA. In contrast, most recent year-class strength as estimated by the MSVPA runs fit to the abundance indices obtained from the trawl surveys. This, however, can be explained by the fact, that the survey has been used to tune the MSVPAs. As independent survey information is available for earlier periods only, a validation of most recent recruitment utilized in the exploratory analysis and the subsequent recruitment modelling approach appears to be difficult.

MSVPA derived sprat recruitment at age 0 and 1 is highly correlated to corresponding abundance estimates from international hydroacoustic surveys in Sub-division 25. In both other areas, the year-class strength 1982 does not coincide. Here the MSVPA based estimate is far higher than indicated by the surveys. A similar tendency is obvious from a comparison with an independent sprat recruitment index from the polish young fish survey in Sub-division 26. Removing the 1982 year-class strength from the correlations, yielded significant relationships with the hydroacoustic estimates in both areas. Thus, it can be concluded that the 1982 recruitment is most likely significantly overestimated by the MSVPA runs and was consequently removed from the further exploratory analysis.

### **Identification of critical early life stages**

Apart from egg production by the spawning stock, critical periods for cod recruitment appear to be the egg to the larval stage. In contrast, correlations between these life stages are highly significant for sprat, indicating that these stages are less critical for the reproductive success of the clupeid. However, the correlation breaks down from larval to 0-group abundance, while these life stages are highly correlated in cod.

The importance of hydrographic conditions within and below the halocline for cod egg survival is well known (e.g. Nissling et al. 1994, Wieland et al. 1994, MacKenzie et al. 1996), while the poor correlation between late egg stage production and larval abundance has been identified only recently (Köster et al. 1999). However, already Plikshs et al. (1993) pointed out, that egg survival is highly correlated to the reproductive volume, but year-class strength is not, indicating other processes acting on other life stages affecting recruitment as well. Apart from the total egg production by the spawning stock or corresponding proxies (e.g. Sparholt 1996, Jarre-Teichmann et al. 2000), larval survival in dependence of egg quality characteristics (Nissling et al. 1998, Petersen et al. 1997), egg incubation at low but not lethal oxygen concentrations (Rohlf 1999), food supply for initial feeding (Plikshs et al. 1993) and transport to favourable nursery areas (Hinrichsen et al. 2000) have been suggested as additional processes affecting larval and early juvenile



survival. The close correlation between larval abundance and 0-group recruitment suggest, however, that a major part of the remaining variability in reproductive success is introduced already in the late egg and early larval stage. Recruitment at age 0 and age 1 as determined by MSVPA are very closely related ( $r = 0.99$ ), with some variability in the beginning of the 1980's, i.e. time periods with highest intensity of cannibalism (ICES 1999b). This may indicate that cannibalism is of minor importance for the recruitment success of cod. However, the limited variability in cannibalism rates is to a certain extent artificially created by the estimation procedure implemented in the MSVPA, which utilize constant suitability coefficients throughout time (Neuenfeldt and Köster 2000).

Studies on processes affecting the reproductive success of sprat in the Baltic are considerably more limited than for cod (Grauman and Yula 1989, Kalejs and Ojaveer 1989). The close correlations between early and late egg production as well as between late egg production and larval abundance are somewhat astonishing. Given the higher buoyancy of sprat eggs compared to cod (e.g. Wieland and Zuzarte 1991), we expected a considerable impact of low temperature in the intermediate water on egg survival, as Thompson et al. (1981) demonstrated that sprat egg survival depends on temperature below a threshold of 6°C, seldom reached in this water layer in the Baltic. Furthermore we expected that egg predation by clupeids, in intensity dependent on the vertical overlap between eggs and predators forced by salinity and oxygen concentrations (Köster and Möllmann 2000b), would introduce additional variability into the egg survival. The larval stage has been identified as a critical for sprat recruitment (Grauman and Yula 1989, Kalejs and Ojaveer 1989), suggesting the food supply being the major factor impacting on larval survival, with temperature being a co-variate as meso-zooplankton production depends on the temperature conditions especially in spring. The close correlation identified between the late egg stage production and larval abundance in Sub-division 26 suggests, that shortage in food supply may affect the later larval and early juvenile stage, but probably not first feeding larvae. The correlation determined for Sub-division 28 explains, however, only 23% of the variance in larval abundance. Apart from outlying years 1990 (below average survival) and 1985 and 1994 (above average survival) encountered in both Sub-divisions, a major deviation occurred in 1989 in Sub-division 28, with very low larval abundance originating from relatively high egg production. In the section on processes affecting critical life stages, it was possible to improve this relationship considerably by including the wind speed anomaly as an additional variable explaining 73 and 46% of the variance in larval abundance in Sub-division 26 and 28 respectively. The significant positive impact of the wind speed anomaly on larval abundance may in principal be explained by a wind drift of larvae from the Bornholm Basin into eastern Baltic basins (Grauman 1976). However, the sprat larval transport index specifically designed to test this hypothesis, did not confirm a significant impact. Thus, the processes involved appear to be others than larval drift, e.g. an increase in turbulence enhancing prey encounter rates. The findings do not confirm the hypothesis that high wind stress has a negative effect on egg survival in surface layers (Gauman 1965). It should be noted, however, that in our analysis only the main spawning period in May/June is considered, in which typically a deeper distribution of sprat eggs is encountered (Wieland and Zuzarte 1991).

### **Processes affecting critical early life stages**

#### Cod survival during the egg stage

The performed analysis is an extension of the exploratory analysis conducted by Köster et al. (1999) utilizing newly available data on production of different egg stages. It confirmed a significant impact of oxygen and

predation on egg survival until developmental stage III in Sub-division 25. Inclusion of both survival/mortality indices in the potential egg production increased the explained variance in egg stage III production from 30 to 60%. Egg stage III production was low during the period 1986-92 both according to ichthyoplankton surveys and predicted on basis of the potential egg production corrected for egg mortality. However, a substantial deviation occurred in 1983 and 1985 (with a 1984 value missing) with a relatively high potential egg production and a low survival to egg stage III. A similar deviation occurred in 1995/96, while the observed production of egg stage III was higher than predicted in 1978 and 1994. Oxygen conditions in 1983 and 1985 should have allowed a considerable egg survival, especially as the egg predation index was very low at the same time. The presently only possible explanation for the deviation is an insufficient area coverage by the ichthyoplankton surveys, being in general less intensively carried out in the 1<sup>st</sup> half of the 1980's compared to earlier and later periods. This does, however, not hold as an explanation for the 1990's with a good spatial and temporal coverage in the surveys. The hydrographic regime in 1994 was characterized by higher than average salinities and in the beginning of the spawning season high oxygen concentrations in and below the halocline. However, as the spawning peak was late in the year, eggs were exposed nevertheless to relatively low oxygen levels (MacKenzie et al. 1996), thereby resulting in similar oxygen related survival rates as in 1995 and 1996 (54-60%). Egg predation by sprat was lower since 1993 than in preceding years, caused by i) a continuous shift in spawning time of cod to later month (Wieland et al. 2000) resulting in a limited temporal overlap between sprat as predators and cod eggs as prey (Köster and Möllmann 2000a) and ii) a limited vertical overlap between predator and prey due to the changed hydrographic regime (Köster and Möllmann 2000a). This decrease in predation pressure was partly offset by an increase in consumption by herring in summer. Thus, observed differences in egg survival rates between 1993 to 1994 and subsequent years are not explainable by the considered environmental processes. A validation of the MSVPA results based on independent population estimates revealed an overestimation of the cod spawning population in Sub-division 25 in 1996 (Köster et al. submitted). Consequently, the potential egg production is an overestimation as well, as is also evident from egg production estimates derived by ichthyoplankton surveys. This in turn leads to an underestimation of the observed egg survival rates, hence, partly explaining the discrepancy.

#### Cod survival until the larval stage

As demonstrated by Köster et al. (1999) there is a significant linear relationship between larval abundance of cod and the potential egg production by the SSB, and there is also indication that the sum of oxygen in the reproductive volume impacts on survival to the larval stage. However, both relationships explained only a very limited part of the variance in larval abundance, i.e. 23 and 15%. Köster et al. (1999) were unable to identify other processes affecting the survival to the larval stage, also when using late egg stage production rates instead of potential egg productions. This lead to the conclusion that either i) factors other than oxygen and predation related mortality influence the survival until the larval stage, or ii) the variability in larval abundance (integrated over all developmental stages) is too high to detect a major impact of both mentioned factors, or iii) that the abundance estimates of larvae may be biased by inadequate spatial and temporal sampling strategies.

Behaviour studies conducted with larvae demonstrated that low oxygen concentration has an impact on larval mortality (Nissling 1994) and that egg incubation at low oxygen concentration impacts on larval activity as well (Rohlf 1999). Furthermore, the 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 minimum lethal oxygen concentrations in the egg and larval stage (Rohlf 1999) it appears to be unlikely, that the oxygen related egg survival is a suitable measure of oxygen related survival probability of larvae. In fact the oxygen content in the reproduction volume performed better in the exploratory analysis and was hence included also in the final model configuration for Sub-division 25.

A multiple linear regression of larval abundance and potential egg production as corrected for egg predation and the oxygen content in the reproductive volume exhibited large negative residuals in recent years. This suggested a mis-match in the timing of the plankton surveys and time periods of high larval abundance caused by a delayed spawning (Wieland et al. 2000) in these years. This of course has implications on the use of the larval abundance estimates as a potential predictor of recruitment.

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. 1999). This result is not surprising as the environmental conditions are less favourable for successful egg survival in these areas compared to the Bornholm Basin (MacKenzie et al. 2000). However, a high reproductive volume does not necessarily result in high survival of early life stages. In 1994 an extremely high 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, 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.

A review of information on the abundance of zooplankton, suitable as prey for cod larvae and early juveniles, suggest at least similar if not better feeding conditions in the Central Baltic compared to other spawning areas (MacKenzie et al. 1996). A detailed study based on extensive vertically resolving sampling of zooplankton in different areas of the Central Baltic at various times of the year concluded similarly that the abundance of nauplii and copepodids should be sufficient to ensure that starvation is not a major source of larval and juvenile cod mortality (Krajewska-Soltsy and Linkowski 1994). However, our preliminary test on the impact of prey availability for first feeding cod larvae, i.e. nauplii (Zuzarte et al. 1996) revealed a significant influence on the apparent survival from egg production to the larval stage in Sub-division 26. Considering additionally the reproductive volume (RV) in a multiple linear regression resulted in 65% explained variance in larval abundance. As zooplankton data are not available for the period 1992 to 1995, most of the years in which larval surveys are potentially affected by the shift in spawning time (see above), were excluded from this analysis. As most of the nauplii in May/June are *Pseudocalanus elongatus*, a rather similar statistical model can be established if only *Pseudocalanus* nauplii are incorporated ( $r^2 = 0.63$ ). This may indicate that the prey availability of *Pseudocalanus* has an impact on larval survival. Furthermore it may be concluded that the shift in spawning time to summer month has decreased the prey availability of first feeding cod larvae, as the abundance of *Pseudocalanus* nauplii is by far highest in May, the yearly reproduction period of this copepod (e.g. Line 1979). This may, however, be compensated by a high abundance of *Acartia* spp. and *Temora longicornis* nauplii being most abundant in summer months and showing a trend of increasing standing stocks since the late 1980's (Möllmann et al. 2000). As *Pseudocalanus* depends strongly on salinity (e.g. Ojaveer et al. 1998, Vuorinen et al. 1998) which in turn is

related to the magnitude of Baltic inflows also the major process affecting the oxygen conditions in cod spawning areas, the detected correlation may be spurious and in fact there is a trend of increasing nauplii and specifically *Pseudocalanus* nauplii with increasing RV, however, not being significant. Apart from this, the quantities of available prey that are suitable for larvae are difficult to assess, as much of the available plankton data has been collected at large temporal and spatial scales, which bear little resemblance to prey abundances and distributions required by larval and early juvenile stages (MacKenzie et al. 1996). This holds also for the present zooplankton time series, although it is presently the data set resolving seasonal and spatial variability in meso-zooplankton abundance best in the central Baltic.

#### Sprat survival from the larval to the 0-group stage

The exploratory analysis conducted, identified the temperature in the intermediate water as the only biologically sensible factor impacting sprat survival from the larval to the 0-group stage. Neither physical/chemical variables as the oxygen condition in deep water layers, wind speed anomaly and larval transport index nor biological variables 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 is significantly correlated to larval abundance, especially if incorporating the wind speed anomaly, it appears to be unlikely that the larval data is grossly erroneous. Utilizing larval abundance data from May to July instead from May/June did not improve the relationship between sprat larval abundance and 0-group recruitment either (Sub-division 26:  $r = 0.08$  and 28:  $r = 0.32$  without the year-class 1982). Thus, excluding late born cohorts from the analysis does not explain the deviation in abundance estimates between both life stages. Similarly, significant correlations between MSVPA based recruitment and hydroacoustic survey abundance estimates indicate the utilized data series to be of acceptable quality.

The impact of winter and spring temperature on sprat larval abundance has been described earlier by Grauman and Yula (1989). They identified additionally the solar activity and the spawning stock biomass (as a measure of egg production) as significant factors impacting larval abundance. Other variables as deep water temperature, salinity and oxygen concentration had an intermediate effect on larval abundance. Similar to our results, the availability of nauplii in May did not explain any variability (Grauman and Yula 1989). The impact of temperature on larval abundance is nevertheless in general explained by a coupling to the availability of *Temora longicornis* as a thermophil prey species for sprat larvae (Grauman et al. 1986, Kalejs and Ojaveer 1989). Apart from the fact, that our diet composition analysis of sprat larvae from the Bornholm Basin revealed *Acartia* spp. as the major prey species, introduction of *Temora* juvenile stages into the exploratory analysis did not yield any conclusive result.

Also incorporation of the weight anomaly of 0-group sprat in Sub-division 26 did not increase the explained variance in recruitment. Thus, there is no indication that low weight at age of survivors is coupled to high larval or early juvenile mortality, e.g. caused by a size dependent predation through adult herring as reported by Patokina and Feldman (1998). It should, however, be noted that the weight anomaly is significantly correlated to juvenile *Acartia* abundance ( $r = 0.56$ ,  $p = 0.047$ ), but not to temperature in the intermediate water.

## Applicability of stock-recruitment models

The significant linear relationship between cod larval abundance and recruitment at age 0 in Sub-division 25 (Köster et al. 1999) was not enhanced by inclusion of any additional variable. This identifies the applicability of the simple model for predicting recruitment. In Sub-division 26 a significant relationship between larval abundance and recruitment was also obtained, but the fit of the model was less satisfactory, while for Sub-division 28 no significant relationship could be established (Köster et al. 1999). This can be explained by the fact, that recruitment success occurred in this area despite the lack of larvae in the ichthyoplankton. As recruitment was not only determined by the MSVPA, but also observed in the bottom trawl surveys as age-group 1, this 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. 2000), comparison of trawl survey results and MSVPA output (Köster et al. submitted) and also indicated by the fact that the parameter estimate for the larval transport index is negative in Sub-division 25.

The close correlation between 0- and 1 group recruitment of cod as well as sprat is to a certain extend artificially created by the estimation procedure implemented in the MSVPA (see above), considering additionally only predation by cod as a cause of natural mortality. In fact, inspecting the relationship of cod year-class strength at age 1 and 2 as derived from the international bottom trawl survey revealed significant correlations only for Sub-division 26 and 28 ( $r^2 = 0.65$  and  $0.80$ ). For Sub-division 25, being the only area allowing regular reproductive success, both estimates are not correlated ( $r^2 = 0.10$ ). For sprat, 0- and 1-group estimates of year-class strength derived from the international hydroacoustic survey are significantly correlated in Sub-division 25 ( $r^2 = 0.42$ ), but not in the other areas ( $r^2 = 0.19$  and  $0.23$ ). Even when assuming that survey estimates are noisy, especially for pre-recruits not targeted by the survey, this considerable variability between 1 and 2-group cod as well as 0- and 1-group sprat abundance estimates of year-class strength may indicate that survival during the first and second (cod) year of life is not only dependent on cod predation, but also other processes may modify recruitment success substantially. Apart from these potentially important processes not covered in the present analysis, the stock-recruitment models established here explain a considerable part of the variability encountered in recruitment to the juvenile stage (with a considerably better performance for cod than for sprat). The remaining variability may be due to a number of processes not included in the present analyses such as egg fertilization (e.g. Westin and Nissling 1991) and the influence of parental (age/size structure, condition) on egg and larval characteristics (buoyancy, survival probability, e.g. Marshall et al. 1998; Trippel 1998), 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 from recent studies on these topics are becoming available (e.g. Nissling et al. 1998; MacKenzie et al. 1998, STORE 2000) and potentially they can be incorporated into new generations of recruitment models (Vallin et al. 1999). Apart from these potential improvements, major difficulties in establishing environmentally sensitive stock-recruitment models are to i) incorporate various factors affecting different early life stages (Paulik 1973) in one model relating egg production by the spawning stock to subsequent recruitment and ii) resolve the potential non-linearity and additive 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 been conducted yet. Despite of the shortcomings and uncertainties also in respect to the second problem, the presented stock-recruitment models for cod may be utilized for enhancing short-term recruitment predictions. The predictions could be based on: i) most recent female spawning stock biomass coupled to relative fecundity 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 conducted analysis has to be taken as a first step to resolve key variables impacting stock recruitment only, generating new working hypotheses to be tested in specifically designed process studies and validated by a subsequent analysis of enhanced long-term data bases.

### **Acknowledgement**

This study was carried out within the frame of the EU-projects SAP (FAIR 97 3805) and Baltic STORE (FAIR 98 3959), utilizing process oriented results and databases built up within the former EU-projects Baltic CORE (AIR 94 1226) and BASYS (MAS3 96 0058). All participants of the projects have contributed their experience, knowledge and results to the present study which was a prerequisite for performing the analysis and is thus gratefully acknowledged here.

### **References**

- Alekseeva, E.I., Baranova, M.M., Dmitrieva, M.A., and Ryazantseva, E.F. 1997. Ovaries maturation, batch eggs forming, batch fecundity and distribution during sex cycle of Baltic sprat *Sprattus sprattus Balticus*. ICES C.M. 1997/U:02.
- Bagge, O., and Thurow, F. 1993. The Baltic cod stock: Fluctuations and possible causes. ICES Mar. Sci. Symp. **198**: 254-268.
- Bagge, O., Thurow, F., Steffensen, E., and Bay, J. 1994. The Baltic cod. Dana, 10: 1-28.
- Bailey, K.M., Brodeur, R.D., and Hollowed, A.B. 1996. Cohort survival patterns of walleye pollock *Theragra callogramma*, in Shelikof Strait, Alaska: a critical factor analysis. Fish. Oceanogr. **5**(Suppl. 1): 179-188.
- Bergström, S. & B. Carlsson 1994: River runoff to the Baltic Sea: 1950-1990. Ambio **23**: (4-5): 280-287.
- Beverton, R.J.H., and Iles, T.C. 1992. Mortality rates of 0-group plaice (*Platessa platessa* L.), dab (*Limanda limanda* L.) and turbot (*Scophthalmus maximus* L.) in European waters. III. Density dependence of mortality rates of 0-group plaice and some demographic implications. Neth. J. Sea Res. **29** (1-3):61-79.
- Bleil, M., and Oeberst, R. 1996. The fecundity of cod in ICES Sub-divisions 22, 24 and 25 in the years 1992 to 1995 (preliminary results). ICES C.M. 1996/J:8.
- Campana, S.F., Frank, K.T., Hurley, P.C.F., Koeller, P.A., Page, F.H., and Smith, P.C. 1989. Survival and abundance of young Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) as indicators of year class strength. Can. J. Fish. Aquat. Sci. **46**(Suppl. 1): 171-182.
- CORE 1998. Mechanisms influencing long term trend in reproductive success and recruitment of Baltic cod: Implications for fisheries management. Final Report to the EU Commission, AIR 94 1226.
- Elwertowski, J. 1960. Biologische Grundlagen der Sprottenfischerei in der östlichen und mittleren Ostsee. Fisch. Forsch. **3** (4): 1-19.
- Grauman, G.B. 1965: Changes in the egg size of cod (*Gadus morhua calliarias* L. ) within the spawning period. ICES C.M. 1965/Baltic-Belt Seas Committee Paper No. 47.
- Grauman, G.B. 1975: Ecological peculiarities of reproduction of fishes with pelagic eggs. ICES C.M. 1975/Baltic Fish Committee.
- Grauman, G.B. 1976. On the distribution and passive migration of Baltic sprat eggs and larvae in Bornholm-Slupsk spawning ground. ICES C.M. 1976/P:8.
- Grauman, G.B., and Krenkel, K. 1986. Investigations about the dynamic of spawning processes of the Baltic sprat in 1984. ICES C.M. 1986/J:17.
- Grauman, G.B., and Yula, E. 1989. The importance of abiotic and biotic factors in early ontogenesis of cod and sprat. Rapp. P-v Réunion. Cons. Int. Explor. Mer **190**: 207-210.
- Grauman, G.B., Line, R.Ya., and Sidrevics, L.L. 1986. On the factors determining abundance of Baltic sprat. ICES C.M. 1986/J:8.
- Grimm, S.K., and Herra, T. 1984. Spawning cycles of southern Baltic fishes based on surveys of eggs and larvae. ICES CM 1984/J:30.
- Grønkvær, P., Clemmesen, C., and St. John, M.A. 1997. Nutritional condition and vertical distribution of Baltic cod larvae. J. Fish. Biol. **51** (Suppl. A): 352-369.

- Grønkjær, P., Clemmesen, C., and St. John, M.A. 1997. Nutritional condition and vertical distribution of Baltic cod larvae. *J. Fish. Biol.* **51** (Suppl. A): 352-369.
- Herra, T. 1988. Ichthyoplankton survey in the southern Baltic in August 1987. ICES C.M. 1988/L:23.
- Hinrichsen, H.-H., St. John, M.A., Aro, E., Grønkjær, P., and Voss, R. 2000. Testing the larval drift hypothesis in the Baltic Sea: Retention vs. dispersion due to the influence of the wind driven circulation. *ICES Mar. Sci. Symp.* **209**, no. 2 (in press).
- ICES 1976. Report of the Working Group on Surveys of Fish Eggs and Larvae in the Baltic. ICES C.M. 1976/P:10.
- ICES 1994. Report of the Planning Group for Hydroacoustic Surveys in the Baltic. ICES C.M. 1994/J:4.
- ICES 1996. Report of the Baltic Fisheries Assessment Working Group. ICES C.M. 1996/Assess:13.
- ICES 1997. Report of the Baltic Fisheries Assessment Working Group. ICES C.M. 1997/Assess:12.
- ICES 1998. Report of the Baltic Fisheries Assessment Working Group. ICES C.M. 1998/ACFM:16.
- ICES 1999a. Report of the Baltic Fisheries Assessment Working Group. ICES C.M. 1997/ACFM:15.
- ICES 1999b. Report of the Study Group on Multispecies Model Implementation in the Baltic. ICES C.M. 1999/H:5.
- Jarre-Teichmann, A., Wieland, K., MacKenzie, B.R., Hinrichsen, H.-H., Plikshs, M., and Aro, E. 2000. Stock-recruitment relationships for cod (*Gadus morhua callarias* L.) in the central Baltic Sea incorporating environmental variability. *Arch. Fish. Mar. Res.* **48** (2): 97-123.
- Kalejs, M., and Ojaveer, E. 1989. Long-term fluctuations in environmental conditions and fish stocks in the Baltic. *Rapp. P-v Réun. Cons. Int. Explor. Mer* **190**: 153-158.
- Karasiova, E. 1999. On the possible relation of the cod peak spawning timing with the environmental conditions in the Gdansk Deep of the Baltic Sea. ICES CM 1999/Y:29.
- Kendall, A.W., Schumacher, J.D., and Kim, S. 1996. Walleye pollock recruitment in Shelikof Strait, Alaska. *Fish. Oceanogr.* **5**(Suppl. 1): 4-18.
- Kjesbu, O.S., Klungsoyr, J., Kryvi, H., Witthames, P.R. & M. Greer Walker 1991: Fecundity, Atresia and Egg Size of Captive Atlantic Cod (*Gadus morhua*) in Relation to Proximate Body Composition. *Can. J. Fish. Aquat. Sci.*, **48**: 2333-2343.
- Köster, F.W., and Schnack, D. 1994. The role of predation on early life stages of cod in the Baltic. *Dana* **10**: 179-201.
- Köster, F.W., and Möllmann, C. 2000a. Trophodynamic control by clupeid predators on recruitment success in Baltic cod ? ICES J. Mar. Sci. **57**, no. 2: 310-323.
- Köster, F.W., and Möllmann, C. 2000b. Egg cannibalism in Baltic sprat *Sprattus sprattus*. *Mar. Ecol. Progr. Ser.* **196**: 269-277.
- Köster, F.W., Hinrichsen, H.-H., St. John, M.A., Schnack, D., MacKenzie, B.R., Tomkiewicz, J. and Plikshs, M. 1999. Stock-recruitment relationships of Baltic cod incorporating environmental variability and spatial heterogeneity. ICES CM 1999/Y:26.
- Köster, F.W., Möllmann, C., St. John, M.A., Neuenfeldt, S., Plikshs, M., and Voss, R. submitted. Developing Baltic cod recruitment models I: Resolving spatial and temporal dynamics of spawning stock and recruitment. *Can. J. Fish. Aquat. Sci.*
- Krajewska-Soltys, A. and Linkowski, T.B. 1994. Densities of potential prey for cod larvae in deep-water basins of the southern Baltic. ICES CM 1994/J:17.
- Kraus, G., Müller, A., Trella, K., and Köster, F.W. 2000. Fecundity of Baltic cod: temporal and spatial variation. *J. Fish Biol.* **56**: 1327-1341.
- Krenkel, K. 1981: Über das Vorkommen der Eier und Larven von Sprott (*Sprattus sprattus*) und Dorsch (*Gadus morhua*) in der Ostsee in den Jahren 1977-1980. *Fischerei-Forschung* **19**: 31-36.
- Line, R.J. 1979. Some observations on fecundity and development cycles of the main zooplankton species in the Baltic sea and the Gulf of Riga. In: Fisheries investigations in the basins of the Baltic sea. Riga, Zvaigzne Vol. **14**: 3-10 (in russian).
- MacKenzie, B.R., St. John, M.A., and Wieland, K. 1996. Eastern Baltic cod: perspectives from existing data on processes affecting growth and survival of eggs and larvae. *Mar. Ecol. Progr. Ser.* **134**: 265-281.
- MacKenzie, B.R., Tomkiewicz, J., Köster, F.W., and Nissling, A. 1998. Quantifying and disaggregating the 'spawner' effect: incorporating stock structure, spatial distribution and female influence into estimates of annual population egg production. ICES C.M. 1998/BB:11.
- MacKenzie, B.R., Hinrichsen, H.-H., Plikshs, M., Wieland, K., and Zezera, A.S. 2000. Quantifying environmental heterogeneity: habitat size necessary for successful development of cod *Gadus morhua* eggs in the Baltic Sea. *Mar. Ecol. Progr. Ser.* **193**: 143-156.
- Makarchouk, A. 1997. Abundance and composition of ichthyoplankton in Eastern Baltic in early nineties. Proceedings of the 14<sup>th</sup> Baltic Marine Biologists Symposium, Paernu, Estonia: 149-155.
- Marshall, T.C., Kjesbu, O.S., Yaragina, N.A., Solemdal, P., and Ulltang, Ø. 1998. Is spawner biomass a sensitive measure of the reproductive and recruitment potential of Northeast Arctic cod. *Can. J. Fish. Aquat. Sci.* **55**: 1766-1783.
- Marteinsdottir, G., and Thorarinnsson, K. 1998. Improving the stock-recruitment relationship in Icelandic cod (*Gadus morhua* L.) by including age diversity of spawners. *Can. J. Fish. Aquat. Sci.* **55**: 1372-1377.
- Matthäus, W. & H. Franck 1992: Characteristics of major Baltic inflows - a statistical analysis. *Contl. Shelf Res.* **12**: 1375-1400.
- Möllmann, C., Kornilovs, G. and Sidrevics, L. 2000. Long-term dynamics of main mesozooplankton species in the central Baltic Sea. *Journal of Plankton Research* **22** (11): in press.
- Möllmann, C. and Köster, F.W. 1999. Food consumption by clupeids in the Central Baltic: Is there evidence for Top-down control? *ICES Journal of Marine Science*, **56**: 100-113.
- Mohn, R.K. and Cook, R. 1993. Introduction to Sequential Population Analysis. *NAFO Sci. Counc. Stud.* **17**.
- Müller, A. 1988: Vertical distribution of ichthyoplankton in the Bornholm Basin. *Kieler Meeresforsch. Sonderh.* **6**: 341-347.

- Müller, A. & T. Pommeranz 1984: Vertical distribution of fish eggs in the Bornholm Basin. Int. Symp. Early Life History of Fishes and 8th Annual Larval Fish Conference, Vancouver 1984. 21 pp.
- Neuenfeldt, S., and Köster, F.W. 2000. Trophodynamic control on recruitment success in Baltic cod: the influence of cannibalism. ICES J. Mar. Sci. **57**, no. 2: 300-309.
- Nissling, A. 1994. Survival of eggs and yolk-sac larvae of Baltic cod (*Gadus morhua* L.) at low oxygen levels in different salinities. ICES Mar. Sci. Symp. **198**: 626-631.
- Nissling, A., Larsson, R., Vallin, L., and Frohland, K. 1998. Assessment of egg and larval viability in cod, *Gadus morhua* - methods and results from an experimental study. Fish. Res. **38**: 169-186.
- Ojaveer, E., Lumberg, A. and Ojaveer, H. (1998) Highlights of zooplankton dynamics in Estonian waters (Baltic Sea). ICES Journal of Marine Science, **55**: 748-755.
- Ojaveer, E. 1989. Population structure of pelagic fishes in the Baltic. Rapp. P.-v. Réun. Cons. Int. Explor. Mer **190**: 17-21.
- Parmanne, R., Rechlin, O., and Sjöstrand, B. 1994. Status and future of herring and sprat stocks in the Baltic Sea. Dana **10**: 29-59.
- Patokina, F.A. and Feldman, V.N. 1998. Peculiarities of trophic relations between Baltic herring (*Clupea harengus membras* L.) and sprat in the south eastern Baltic Sea in 1995-1997. ICES CM 1998/CC:7.
- Paulik, G.J. 1973. Studies of the possible form of the stock-recruitment curve. Rapp. P.-v. Réun. Cons. int. Explor. Mer **164**: 302-315.
- Petersen, G.I., Gerup, J., Nilsson, L., Larsen, J.R. & R. Schneider 1997: Body burdens of lipophilic xenobiotics and reproductive success in Baltic cod (*Gadus morhua*). ICES C.M. 1997/U:10.
- Petrowa, E.G. 1960. Fecundity and maturation of sprat in the Baltic. VNIRO, **42**: 99-108.
- Polivaiko, A.G. 1980. Some data on maturation, spawning and fecundity of sprat. Fisch. Forsch. **18**(2): 69-72.
- Plikshs, M., Kalejs, M., and Graumann, G. 1993. The influence of environmental conditions and spawning stock size on the year-class strength of the eastern Baltic cod. ICES C.M. 1993/J:22.
- Plikshs, M., Hinrichsen, H.-H., Köster, F.W., Tomkiewicz, J., and Berzins, V. 1999. Baltic cod reproduction in the Gotland Basin: annual variability and possible causes. ICES C.M. 1999/Y:31.
- Raid, T. 1989. The influence of hydrodynamic conditions on the spatial distribution of young fish and their prey organisms. Rapp. P.-v. Réun. Cons. Int. Explor. Mer **190**: 166-172.
- Rohlf, N. 1999. Aktivität und Vertikalwanderung der Larven des Ostseesardines (*Gadus morhua callarias*) während der Dottersackphase. PhD. thesis, Institute of Marine Sciences, Kiel, 60pp. Ber. Inst. für Meereskunde, Nr. 312.
- Rothschild, B.J. 1986. Dynamics of Marine Populations. Harvard University Press, Cambridge, USA.
- Rothschild, B.J. 2000. "Fish stock and recruitment": the past thirty years. ICES J. Mar. Sci. **57**, no. 2: 191-201.
- Rudstam, L.G., Aneer, G., and Hildén, M. 1994. Top-down control in the pelagic Baltic ecosystem. Dana **10**: 105-129.
- Schnack, D. 1997. Influence of hydrographic gradients and fishery on the biological interaction and balance between sprat and cod stocks in the Baltic Sea. Commented review. ICES CM 1997/S:10.
- Schnack, D., and Köster, F.W. 1998. Baltic Cod Recruitment Project: Summary of results 1994-97. ICES CM 1998/R:21.
- Shapiro, L.A. 1988. Correlation between the quantity and quality of the gonads in the Baltic cod. Fisch.-Forsch. **26** (2): 66-69. (Translated from Can. Transl. Fish. Aquat. Sci. no. 5515).
- Sidrevics, L.L. (1984) The main peculiarities of zooplankton distribution in the South-eastern, Eastern and North-eastern Baltic. In: Articles on biological productivity of the Baltic sea. Moscow, **2**: 172-187 (in russian).
- Sparholt, H. 1996. Causal correlation between recruitment and spawning stock size of central Baltic cod ? ICES J. Mar. Sci. **53**: 771-779.
- Sparholt, H., and Tomkiewicz, J. 2000. A robust method to compile trawl survey data applied in assessment of Central Baltic cod. Arch. Fish. Mar. Res. **48** (2): 125-151.
- STORE 2000. Environmental and fisheries influences on fish stock recruitment in the Baltic Sea. Consolidated Progress Report to the EU Commission, FAIR 98 3959.
- Thompson, B.M. & J.D. Riley 1981: Egg and larval developmental studies in the North Sea cod (*Gadus morhua* L.). Rapp. P.-v. Réun. Cons. int. Explor. Mer **178**: 553-559. Tomkiewicz, J., Eriksson, M., Baranova, T., Feldman, V., and Müller, H. 1997. Maturity ogives and sex ratios for Baltic cod: establishment of a database and time series. ICES CM 1997/CC:20.
- Tomkiewicz, J., Eriksson, M., Baranova, T., Feldman, V. and Müller, H. 1997. Maturity ogives and sex ratios for Baltic cod: establishment of a database and time series. ICES CM 1997/CC:20.
- Trippel, E.A. 1998. Egg size and viability and seasonal offspring production of young Atlantic cod. Am. Fish. Soc. **127**: 339-359.
- Ulltang, Ø. 1996. Stock assessment and biological knowledge: can prediction uncertainty be reduced. ICES J. Mar. Sci. **53**: 659-675.
- Vallin, L., Nissling, A., and Westin, L. 1999. Potential factors influencing reproductive success of Baltic cod, *Gadus morhua*: a review. Ambio Vol. **28**, No. 1: 92-99.
- Vuorinen, I., Hänninen, J., Viitasalo, M., Helminen, U. and Kuosa, H. (1998) Proportion of copepod biomass declines with decreasing salinity in the Baltic Sea. ICES Journal of Marine Science, **55**: 767-774.
- Voss, R., Hinrichsen, H.-H., and St. John, M.A. 1999. Variations in the drift of larval cod (*Gadus morhua* L.) in the Baltic Sea: combining field observations and modelling. Fish. Oceanogr. **8**, 3: 199-211.
- Westin, L., and Nissling, A. 1991. Effects of salinity on spermatozoa motility, percentage of fertilized eggs and egg development of Baltic cod *Gadus morhua*, and implications for cod stock fluctuations in the Baltic. Mar. Biol. **108**: 5-9.
- Wieland, K., Zuzarte, F. 1991. Vertical distribution of cod and sprat eggs and larvae in the Bornholm Basin (Baltic Sea) 1987-1990. ICES CM 1991/J:37.
- Wieland, K., and Jarre-Teichmann, A. 1997. Prediction of vertical distribution and ambient development temperature of Baltic cod (*Gadus morhua* L.) eggs. Fish. Oceanogr. **6** (3): 172-187.



- Wieland, K., Waller, U., and Schnack, D. 1994. Development of Baltic cod eggs at different levels of temperature and oxygen content. *Dana* **10**: 163-177.
- Wieland, K., Jarre-Teichmann, A., and Horbowa, K. 2000. Changes in the timing of spawning of Baltic cod: possible causes and implications for recruitment. *ICES J. Mar. Sci.* **57**, no. 2: 452-464.
- Zuzarte, F., Köster, F.W., Möllmann, C., Voss, R., and Grønkjær, P. 1996. Diet composition of cod larvae in the Bornholm Basin. *ICES C.M.* 1996/J:19.

**Table 1** Linearity of cod and sprat stock-recruitment relationships derived by area dis-aggregated MSVPA runs for different Sub-divisions (SSB in t); parameter estimates and their significance level,  $r^2$ -values and Durban Watson (DW) statistics indicating serial correlation in the residuals (\* significant at 5% level).

Dependent variable	Sub-division	Time series	Parameter	Parameter estimates	p	$r^2$	DW statistics
cod age-group 2	25	1976-96	slope	815.0	0.091	0.16	0.61*
			intercept	$7.521 \cdot 10^7$	0.101		
cod age-group 2	26	1976-96	slope	869.5	0.037	0.23	0.43*
			intercept	$2.825 \cdot 10^7$	0.037		
cod age-group 2	28	1976-94	slope	1097.1	0.003	0.41	0.49*
			intercept	$3.612 \cdot 10^6$	0.810		
sprat age-group 1	25	1977-96	slope	67645	0.003	0.43	1.44
			intercept	$1.167 \cdot 10^{10}$	0.043		
sprat age-group 1	26	1977-96	slope	43017	0.198	0.10	1.93
			intercept	$7.547 \cdot 10^9$	0.163		
sprat age-group 1	26	1977-96	slope	71804	0.003	0.45	1.76
		without 1982	intercept	$1.724 \cdot 10^{10}$	0.047		
sprat age-group 1	28	1977-96	slope	29529	0.197	0.10	2.19
			intercept	$-4.309 \cdot 10^9$	0.197		
sprat age-group 1	28	1977-96	slope	44524	0.008	0.36	2.39
		without 1982	intercept	$5.819 \cdot 10^9$	0.018		

**Table 2** Linear regressions performed to test various SSB estimates (in t) as a measure of realized egg production (daily production rates at main spawning time derived from ichthyoplankton surveys); parameter estimates and their significance level,  $r^2$ -values and Durban Watson (DW) statistics indicating serial correlation in the residuals (\* significant at 5% level).

Dependent variable	Sub-division	Time series	Parameter	Parameter estimates	p	$r^2$	DW statistics
cod SSB based on maturity	25	1976-96	slope	$1.0138 \times 10^{-7}$	0.488	0.03	0.64*
ogive invariate with time		without 1979-82	intercept	98953	<0.001		
cod SSB based on yearly or	25	1976-96	slope	$2.4079 \times 10^{-7}$	0.027	0.30	0.68*
period specific maturity ogives		without 1979-82	intercept	58533	<0.001		
female cod SSB	25	1976-96	slope	$1.8359 \times 10^{-7}$	<0.001	0.61	1.17*
		without 1979-82	intercept	98953	<0.001		
predicted potential egg	25	1976-96	slope	136.12	<0.001	0.63	1.17*
production of cod		without 1979-82	intercept	$2.2064 \times 10^{13}$	<0.001		
sprat SSB	26	1977-96	slope	3193.6	0.002	0.47	1.15*
			intercept	$1.167 \times 10^{10}$	0.043		
sprat SSB	28	1977-96	slope	2071.9	0.004	0.39	0.69*
			intercept	58152	0.031		

**Table 3** Linear regressions performed to validate cod recruitment at age 1 and 2 estimates (dependent variable) derived by area dis-aggregated MSVPA runs for different Sub-divisions; parameter estimates and their significance level,  $r^2$ -values and Durban Watson (DW) statistics indicating serial correlation in the residuals (\* significant at 5% level).

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

**Table 4** Regressions performed to validate sprat recruitment at age 0 and 1 estimates (dependent variable) derived by area dis-aggregated MSVPA runs for different Sub-divisions; parameter estimates and their significance level,  $r^2$ -values and Durban Watson (DW) statistics indicating serial correlation in the residuals (\* significant at 5% level).

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

**Table 5** Identification of critical life stages of cod and sprat by correlation of production and abundance values of different early life history stages; parameter estimates and their significance level,  $r^2$ -values and Durban Watson (DW) statistics indicating serial correlation in the residuals (\* significant at 5% level).

Dependent variable	independent variable	Sub-division	Time series	correlation coefficient	p
--------------------	----------------------	--------------	-------------	-------------------------	---

**cod**

potential egg production by SSB	realized egg production (stage I)	25	1976-96	0.80	<0.001
realized egg production (stage I)	late egg production (stage III)	25	1976-96	0.51	0.044
late egg production (stage III)	larval abundance	25	1976-96	0.36	0.173
larval abundance	0-group recruitment	25	1976-95	0.80	<0.001
0-group recruitment	1-group recruitment	25	1976-95	0.99	<0.001

**sprat**

SSB	realized egg production (stage I)	26	1977-96	0.66	0.002
realized egg production (stage I)	late egg production (stage III)	26	1973-96	0.82	<0.001
late egg production (stage III)	larval abundance	26	1973-96	0.81	<0.001
larval abundance	0-group recruitment	26	1977-96	0.12	0.617
0-group recruitment	1-group recruitment	26	1977-95	0.99	<0.001
potential egg production by SSB	realized egg production (stage I)	28	1977-96	0.63	0.004
realized egg production (stage I)	late egg production (stage III)	28	1973-96	0.90	<0.001
late egg production (stage III)	larval abundance	28	1973-96	0.48	0.020
larval abundance	0-group recruitment	28	1977-96	0.05	0.824
0-group recruitment	1-group recruitment	28	1977-95	0.98	<0.001

**Table 6** Stock recruitment relationships (age-group 0) for sprat in different Sub-divisions with incorporated variables identified to affect critical life stages; parameter estimates and their significance level,  $r^2$ -values and Durban Watson (DW) statistics indicating serial correlation in the residuals (\* significant at 5% level).

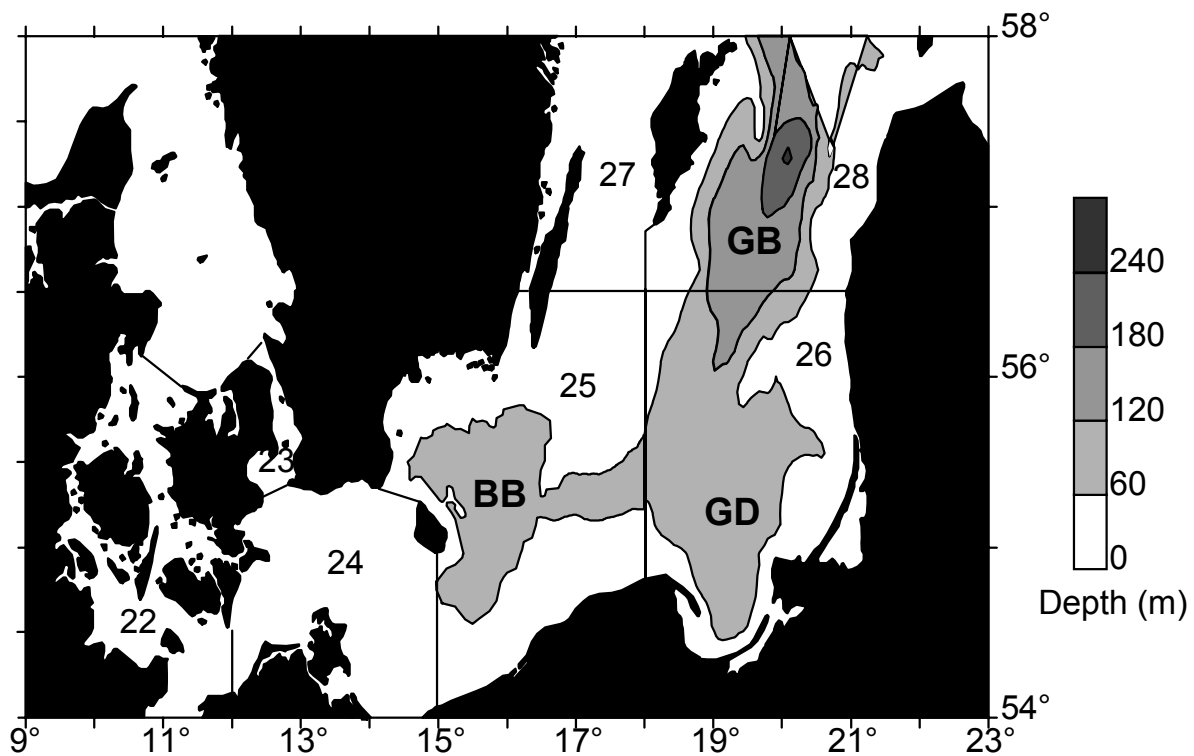
Dependent variable	Sub-division	Time series	Independent variables	Parameter estimates	p	$r^2$	DW statistics
recruitment at age 0	26	1977-96	SSB	57466	0.028	0.33	1.97
MSVPA			temperature in intermediate water	$8.948 \times 10^9$	0.062		
			intercept	$-1.714 \times 10^{10}$	0.313		
recruitment at age 0	26	1979-96	SSB	57632	0.030	0.38	1.87
MSVPA			growth anomaly 3 <sup>rd</sup> to 2 <sup>nd</sup> quarter	$5.629 \times 10^7$	0.045		
			intercept	$1.520 \times 10^{10}$	0.037		
recruitment at age 0	26	1977-94	SSB	81450	0.352	0.25	1.51
MSVPA			wind speed anomaly May/June	$-1.493 \times 10^9$	0.837		
			intercept	$1.086 \times 10^{10}$	0.193		
recruitment at age 0	26	1977-96	SSB	57173	0.035	0.41	1.99
MSVPA			temperature in intermediate water	$6.132 \times 10^9$	0.216		
			growth anomaly 3 <sup>rd</sup> to 2 <sup>nd</sup> quarter	$4.810 \times 10^7$	0.084		
			intercept	$-6.182 \times 10^9$	0.732		
recruitment at age 0	26	1981-96	SSB	39214	0.014	0.42	2.42
hydroacoustic survey			temperature in intermediate water	$4.627 \times 10^9$	0.104		
			intercept	$-1.768 \times 10^{10}$	0.105		
recruitment at age 0	25	1977-96	SSB	62234	0.014	0.45	1.93
MSVPA			temperature in intermediate water	$5.930 \times 10^9$	0.051		
			intercept	$-4.309 \times 10^9$	0.680		
recruitment at age 0	25	1978-96	SSB	74645	0.011	0.28	1.90
MSVPA			weight at age anomaly 1 <sup>st</sup> quarter	$2.046 \times 10^8$	0.557		
			intercept	$1.352 \times 10^{10}$	0.098		
recruitment at age 0	25	1977-94	SSB	70176	0.023	0.38	1.67
MSVPA			wind speed anomaly May/June	$4.504 \times 10^9$	0.541		
			intercept	$1.414 \times 10^{10}$	0.069		
recruitment at age 0	25	1981-96	SSB	7469	0.038	0.22	2.23
hydroacoustic survey			temperature in intermediate water	$1.700 \times 10^8$	0.646		
			intercept	$-1.120 \times 10^9$	0.477		
recruitment at age 0	28	1977-96	SSB	25294	0.196	0.08	2.32
MSVPA			temperature in intermediate water	$4.721 \times 10^9$	0.245		
			intercept	$-9.721 \times 10^8$	0.563		
recruitment at age 0	28	1986-96	SSB	48215	0.120	0.13	2.37
MSVPA			growth anomaly 3 <sup>rd</sup> to 2 <sup>nd</sup> quarter	$3.710 \times 10^7$	0.225		
			intercept	$7.344 \times 10^9$	0.118		
recruitment at age 0	28	1977-94	SSB	52705	0.042	0.16	2.08
MSVPA			wind speed anomaly May/June	$-3.017 \times 10^9$	0.335		
			intercept	$7.249 \times 10^9$	0.033		
recruitment at age 0	28	1981-96	SSB	24865	0.006	0.60	1.92
hydroacoustic survey			temperature in intermediate water	$4.449 \times 10^9$	0.021		
			intercept	$-1.763 \times 10^{10}$	0.191		

## Figure captions

- 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).
- Fig. 2 Linearity of stock-recruitment relationships of eastern Baltic cod (Sub-division 25-32) and Baltic sprat (Sub-division 22-32), data source: standard stock assessment (ICES 1999a).
- 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 egg consumption (b); linear regression of daily egg production at stage III on potential egg production corrected for oxygen related mortality and consumption (c).
- Fig. 4 Linear regressions of **cod** larval abundance on potential egg production by SSB in Sub-division 25 (a); linear regression of larval abundance per unit of potential egg production by SSB on oxygen content in the reproductive volume (RV) (b).
- 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 utilizing nauplii abundance and reproductive volume during main spawning time as independent variables.
- Fig. 6 Realized egg production by **sprat** in Sub-division 26 and predicted by a multiple linear regression model utilizing spawning stock biomass, weight at age anomaly in the 1<sup>st</sup> quarter (age-groups 2-4) and temperature in the intermediate water in May/June as independent variables (a); realized egg production by sprat in Sub-division 26 and predicted by a multiple linear regression model utilizing spawning stock biomass, growth anomaly (increase in weight at age 2-4 from 3<sup>rd</sup> to 2<sup>nd</sup> quarter) and temperature in the intermediate water in May/June as independent variables (b).
- Fig. 7 Larval abundance of **sprat** in Sub-division 26 and predicted by a multiple linear regression model utilizing daily egg production of stage III and wind-speed anomaly in May/June as independent variables (a); same statistical model for Sub-division 28 (b).
- Fig. 8 **Sprat** recruitment at age 0 in Sub-division 26 (determined by MSVPA) and predicted by a multiple linear regression model utilizing larval abundance and temperature in the intermediate water in May/June as independent variables (a); sprat recruitment at age 0 in Sub-division 28 (determined by hydroacoustic surveys) and predicted by a multiple linear regression model utilizing larval abundance and temperature in the intermediate water in May/June as independent variables (b).
- Fig. 9 **Cod** recruitment at age 0 in Sub-division 25 and predicted by a multiple linear regression model utilizing potential egg production by SSB corrected for egg consumption, oxygen content in the reproductive volume and larval transport as independent variables (a); cod recruitment at age 0 in Sub-division 26 and predicted by a multiple linear regression model utilizing potential egg production by SSB and reproductive volume as independent variables (b); same model for Sub-division 28 (c); including time trends of observed (points) and predicted values (lines) for all three statistical models (right panels).
- Fig. 10 **Cod** recruitment at age 0 determined by MSVPA (a) and recruitment at age 1 derived by international bottom trawl survey (b) in combined Sub-division 25, 26 and 28 in comparison to predicted recruitment based on egg production by SSB, environmental factors and species interaction (final model versions).

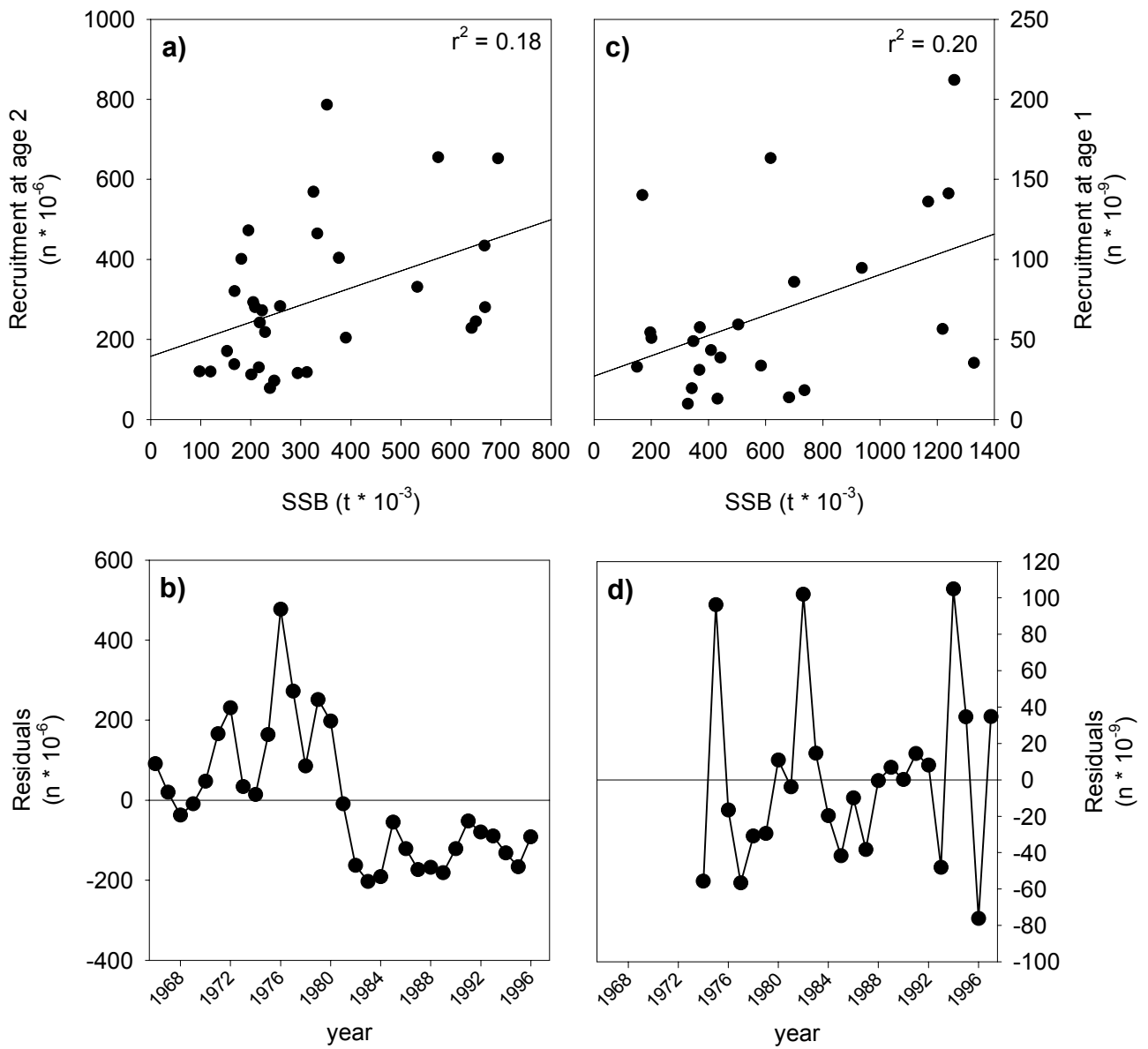
Fig. 11 **Sprat** recruitment at age 0 determined by MSVPA and predicted by a multiple linear regression model utilizing SSB and temperature in the intermediate water as independent variables for Sub-division 25 (a); sprat recruitment as above adding growth anomaly as further independent variable for 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. 12 **Sprat** recruitment at age 0 determined by MSVPA and international hydroacoustic survey in combined Sub-division 25, 26 and 28 in comparison to predicted recruitment based on SSB, temperature and growth anomaly (latter only in Sub-division 26).

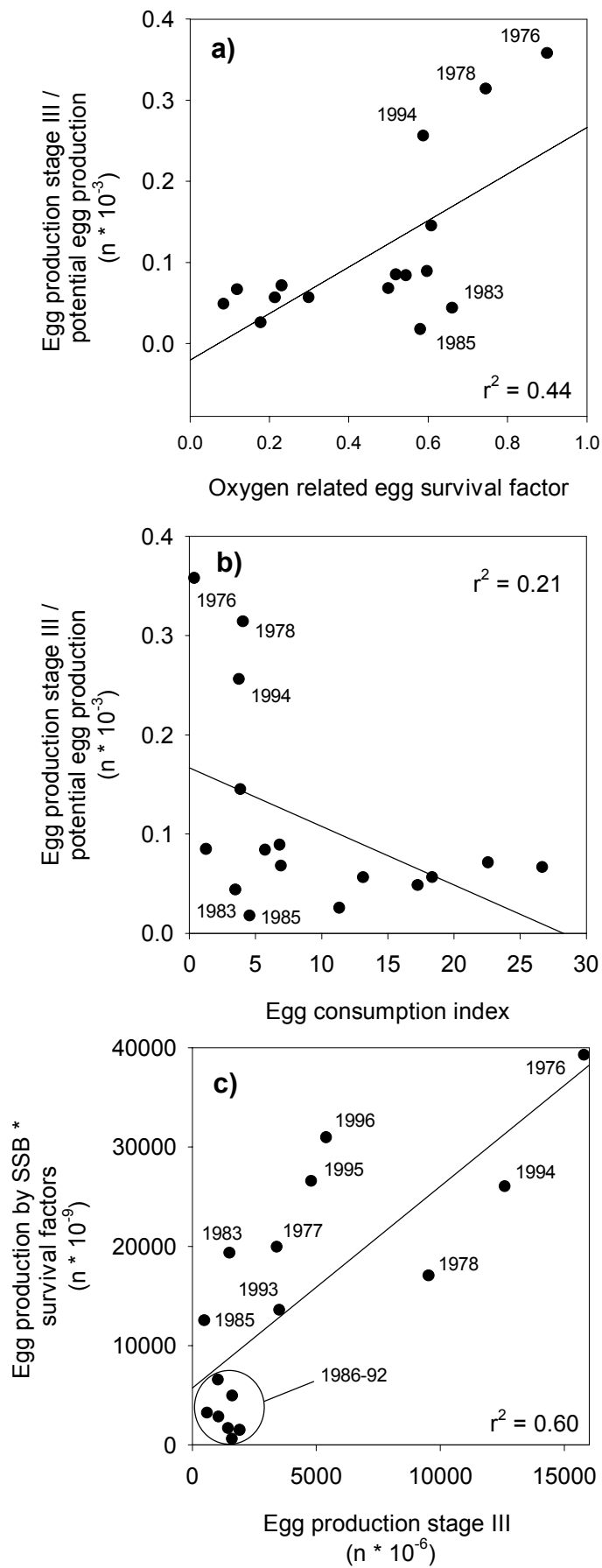


**Fig. 1**

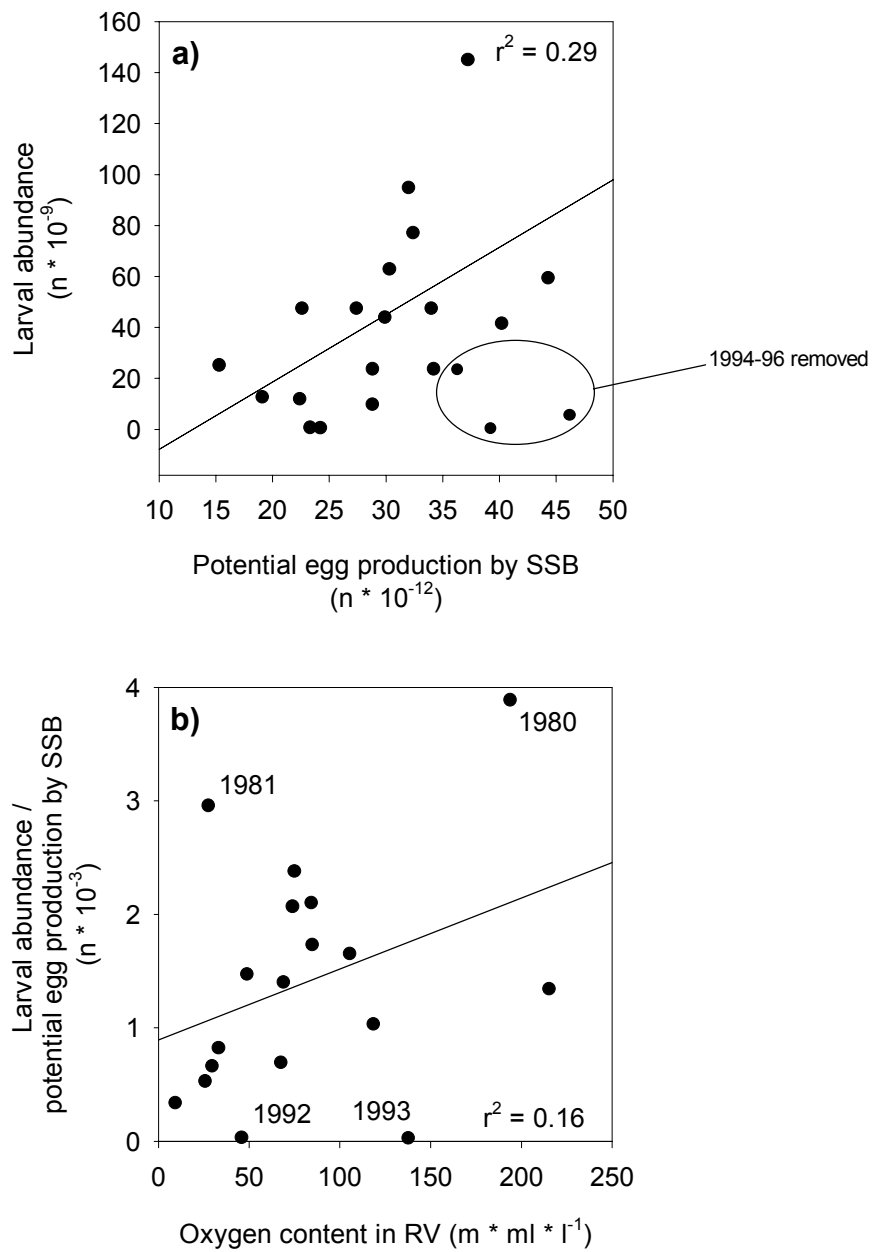




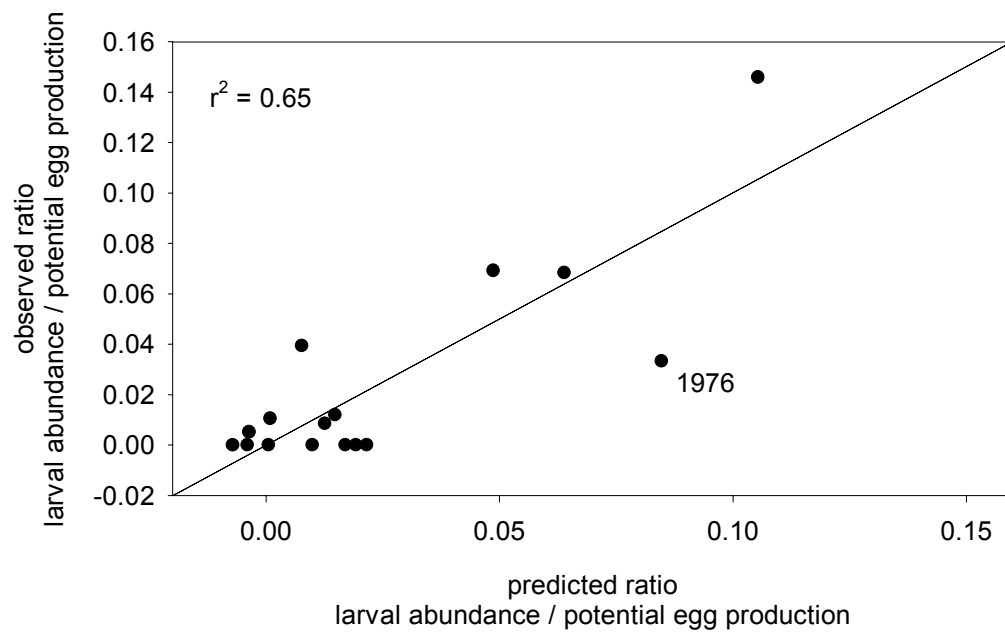
**Fig. 2**



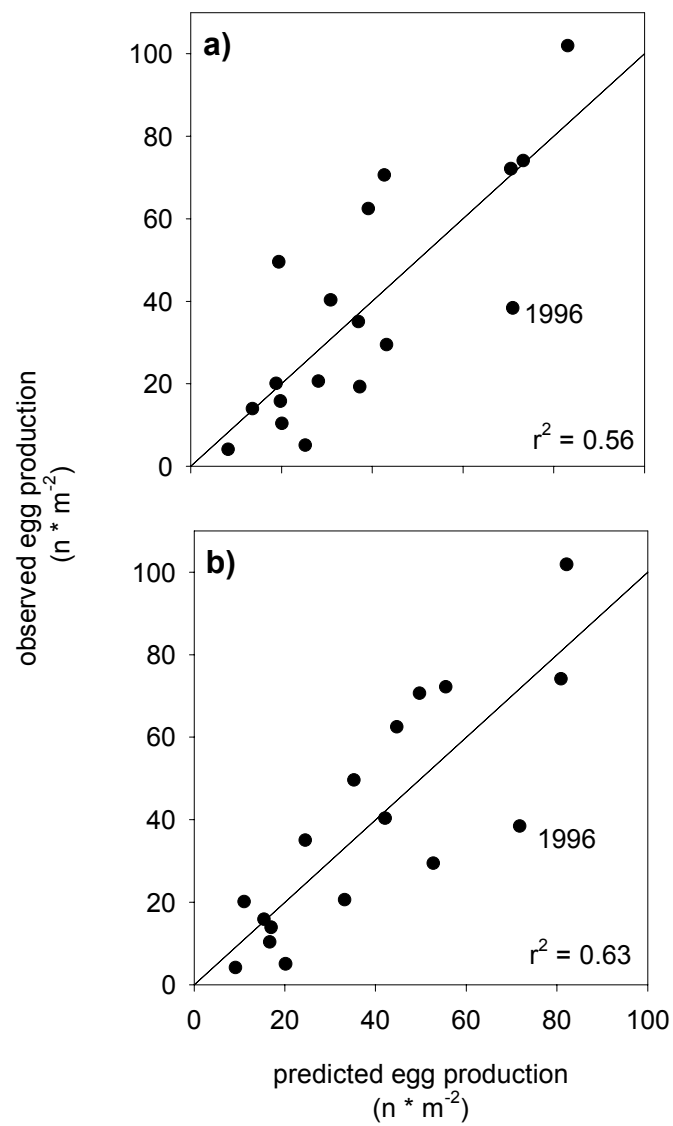
**Fig. 3**



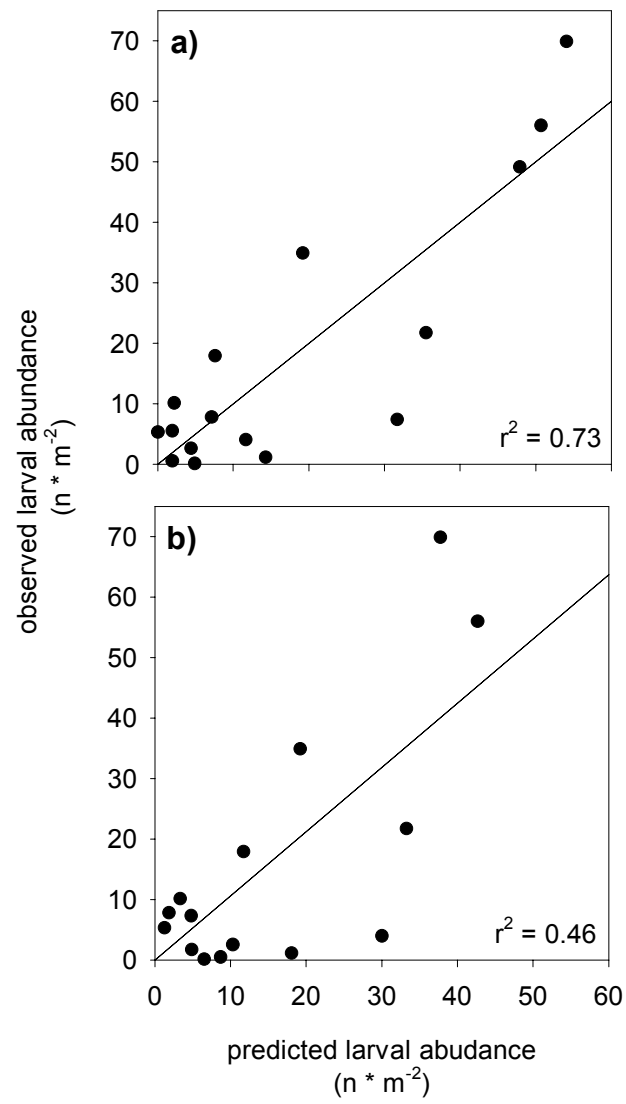
**Fig. 4**



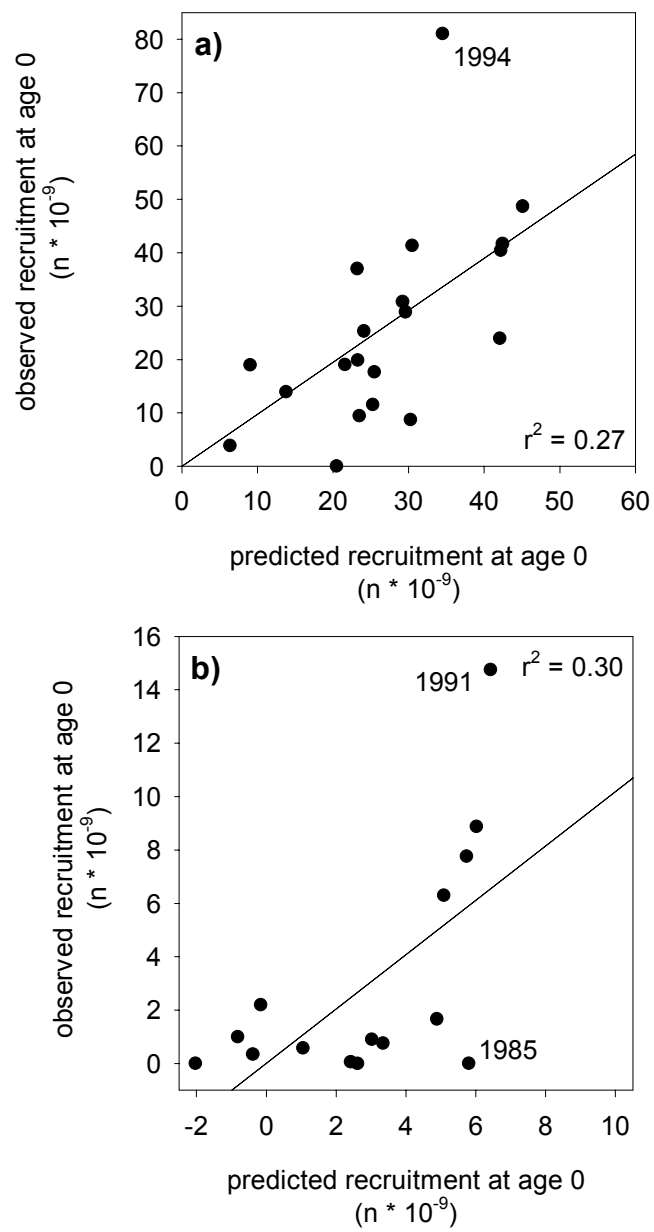
**Fig. 5**



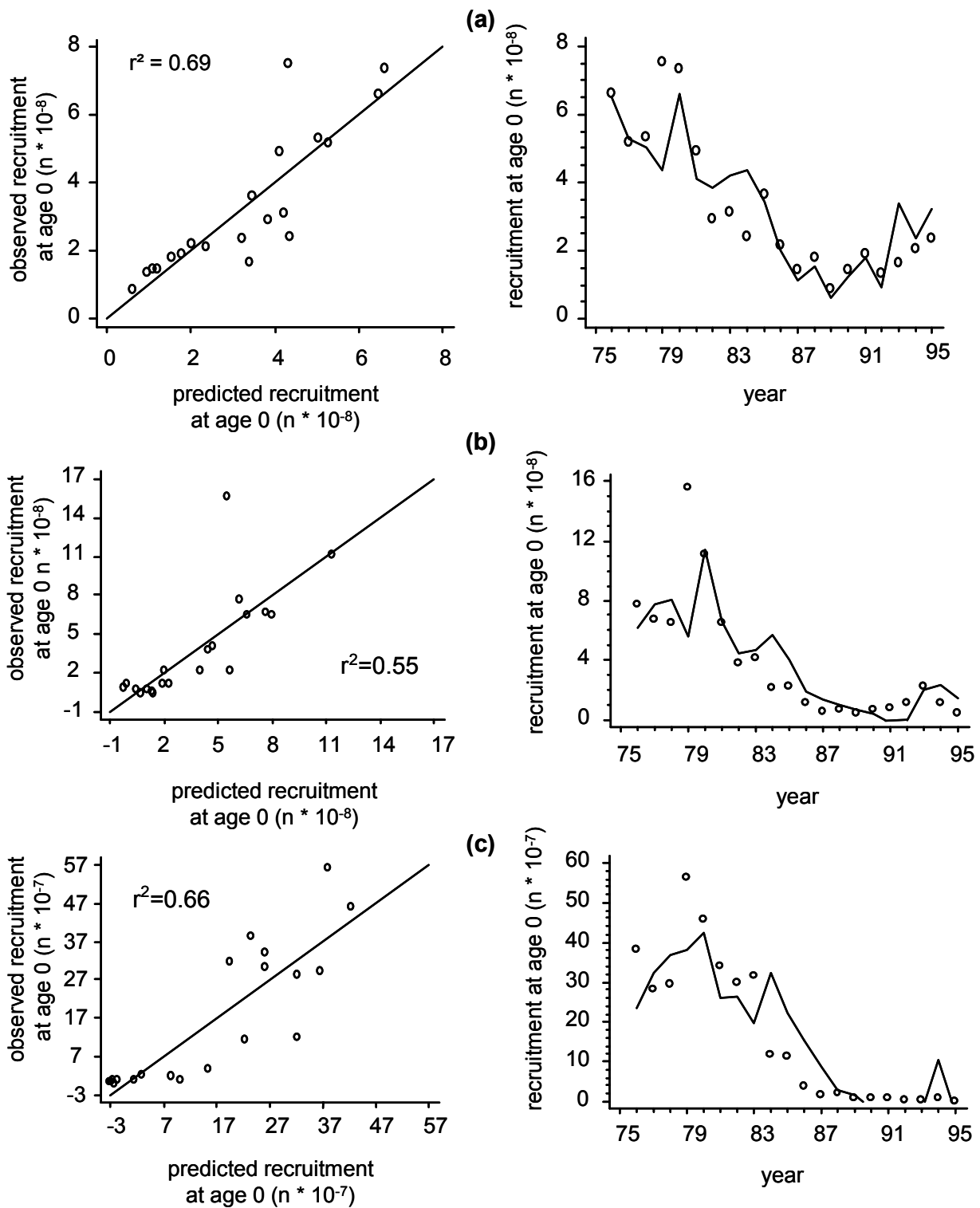
**Fig. 6**



**Fig. 7**

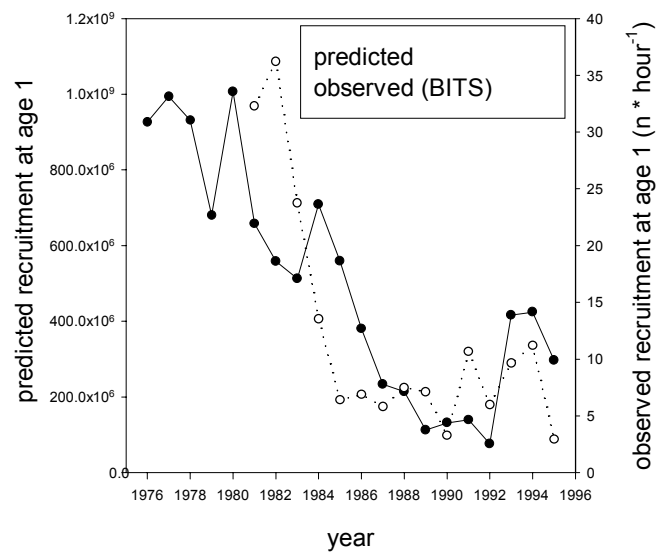
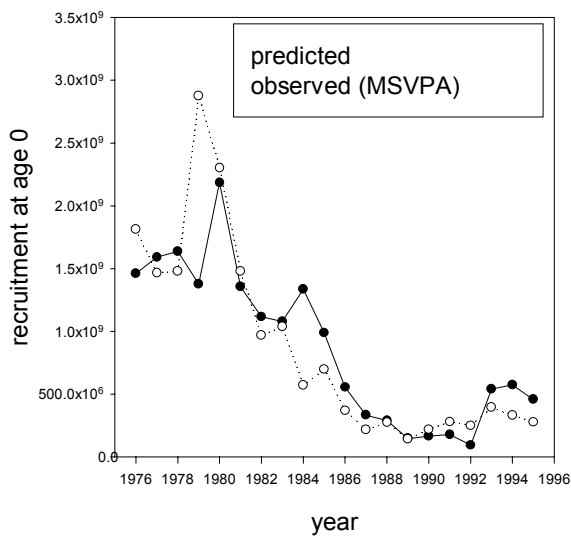


**Fig. 8**

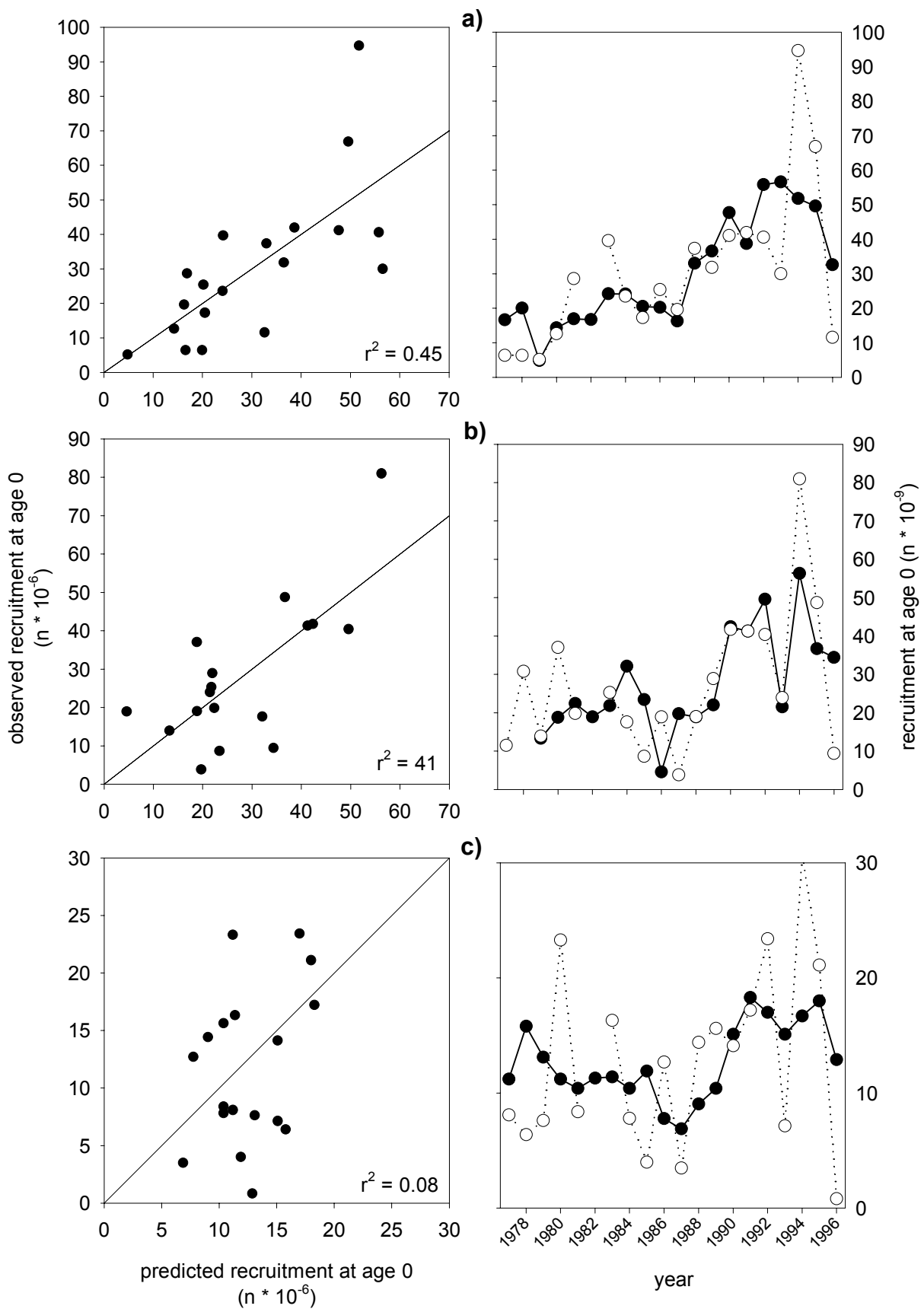


**Fig. 9**

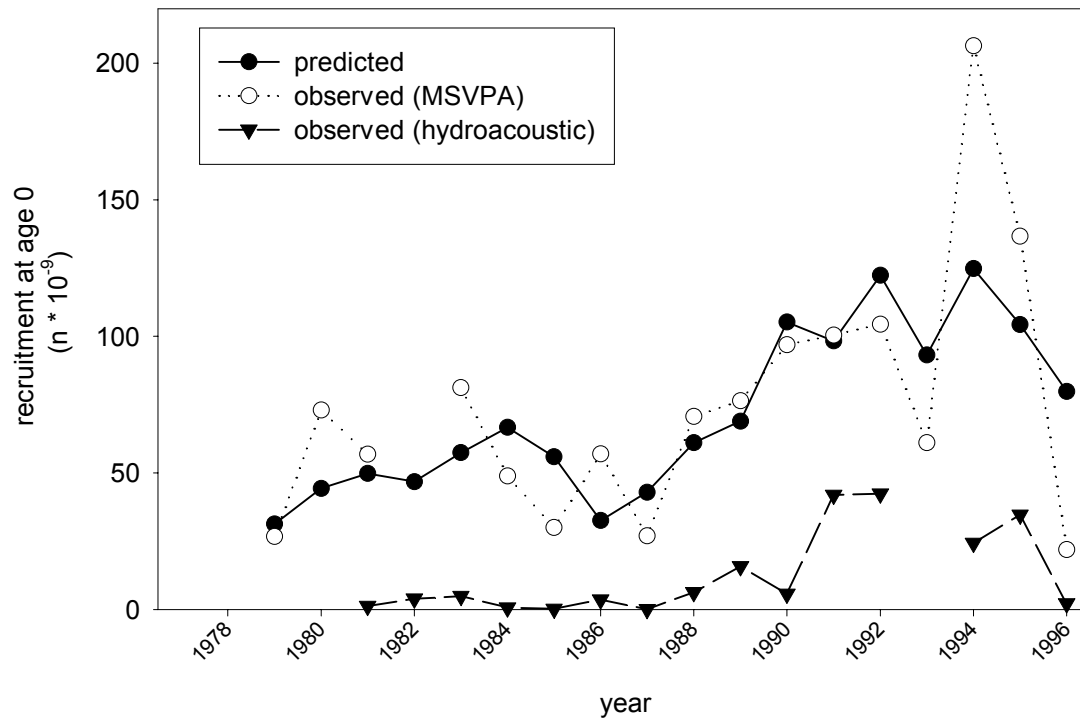




**Fig. 10**



**Fig. 11**



**Fig. 12**