Recruitment variability in Baltic Sea sprat (*Sprattus sprattus*) is tightly coupled to temperature and transport patterns affecting the larval and early juvenile stages

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Abstract: Recruitment patterns of Baltic Sea sprat (*Sprattus sprattus*) were correlated to time series of (*i*) month- and depth-specific temperature conditions and (*ii*) larval drift patterns inferred from long-term Lagrangian particle simulations. From the latter, we derived an index that likely reflected the variable degree of annual larval transport from the central, deep spawning basins to the shallow coastal areas of the Baltic Sea. The drift index was significantly ($P < 0.001$) correlated to sprat recruitment success and explained, together with sprat spawning stock biomass, 82% of the overall variability between 1979 and 2003. Years of strong larval displacement towards southern and eastern Baltic coasts corresponded to relative recruitment failure, while years of retention within the deep basins were associated with relative recruitment success. The strongest correlation between temperature and recruitment occurred during August in surface waters, explaining 73% of the overall variability. Together, the two approaches advocate that new year classes of Baltic sprat are predominantly composed of individuals born late in the season and are determined in strength mainly by processes acting during the late larval and early juvenile stages. However, prior to be included in recruitment predictions, the biological mechanisms underlying these strong correlations may need to be better resolved.

Résumé : Nous avons mis en corrélation les patrons de recrutement du sprat (*Sprattus sprattus*) de la Baltique avec des séries chronologiques (*i*) de conditions de température en fonction du mois et de la profondeur et (*ii*) de patrons de dérive des larves obtenus à partir de simulations de Lagrange à long terme de particules. D'après ces simulations, nous avons élaboré un indice qui représente vraisemblablement le degré variable de transport annuel des larves depuis les bassins de fraye centraux et profonds vers les zones côtières peu profondes de la Baltique. L'indice de dérive est en corrélation significative ($P < 0{,}001$) avec le succès du recrutement du sprat; combiné à la biomasse du stock reproducteur du sprat, il explique 82 % de la variabilité globale entre 1979 et 2003. Les années de fort déplacement des larves vers les côtes du sud et de l'est de la Baltique correspondent à des insuccès relatifs du recrutement, alors que les années de rétention dans les bassins profonds sont associées à un succès relatif du recrutement. La corrélation la plus forte entre la température et le recrutement s'observe en août dans les eaux superficielles, ce qui explique 73 % de la variabilité globale. Ensemble, les deux approches indiquent que les nouvelles classes d'âge annuelles des sprats de la Baltique se composent principalement d'individus nés tard dans la saison et que la force des classes est déterminée par des processus qui agissent à la fin de la vie larvaire et durant les stades juvéniles. Cependant, il faut mieux élucider les mécanismes sous-jacents à ces fortes corrélations avant de les inclure dans les prédictions du recrutement.

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Introduction

Explaining and predicting recruitment variability are perennial goals in fisheries science (Sissenwine 1984). In sprat, *Sprattus sprattus*, currently the most abundant, commercially exploited fish species in the Baltic Sea, recruitment variability has increased considerably at the beginning of the 1990s (ICES 2005*a*), thereby coinciding with other profound changes in the Baltic ecosystem that affected all trophic levels (Alheit et al. 2005).

Previous studies have found significant but weak correlations between recruitment strength and (*i*) spawning stock biomass (SSB) and (*ii*) temperature conditions experienced during the egg and early larval stages of Baltic Sea sprat (Köster et al. 2003; MacKenzie and Köster 2004). However, Köster et al. (2003) noted that estimates of egg and larval abundance are generally well correlated, whereas larval production poorly predicts recruitment levels. It has been argued, thus, that year-class strength in Baltic Sea sprat may rather be determined by environmental influences during the late larval and early juvenile stages (Voss et al. 2005). Thus, to improve current sprat recruitment models, potential environmental effects may need to be considered throughout all pre-recruit life stages.

Feeding sprat larvae predominantly occur in surface waters (Voss et al. 2003), where variable, wind-driven circulation patterns may transport them either to suitable or unsuitable nursery areas (Sinclair 1988). Previously, we followed this rationale by using a hydrodynamic circulation model in combination with Lagrangian particle tracking to simulate 23 years of larval sprat drift patterns (Baumann et al. 2004). Our retention index, defined as the annual proportion of drifters collected within predefined rectangles in and outside of the Bornholm Basin, a major sprat spawning area (Köster et al. 2001), was significantly related to the number of age-0 sprat recruits in the central Baltic. The relationship suggested that retention within the deep basin would be beneficial for recruitment, while dispersion and transport to southeastern Baltic shores would lead to relative recruitment failure. Shortcomings of the previous approach were that the index (*i*) did not explain the full recruitment time series but only the most recent 12 years, (*ii*) was restricted to sprat from the Bornholm Basin, and (*iii*) relied on the definition of arbitrary rectangles in the model domain (Baumann et al. 2004).

Here we present an improved drift index to explain sprat recruitment variability within the entire Baltic Sea and over the whole, extended time series of 25 years (1979–2003). The index was again based on hydrodynamic modelling in conjunction with Lagrangian particle simulations, but instead of final horizontal drifter positions (previous approach), we now integrated the entire drift period by considering the average water depth across all daily particle positions to be a proxy of larval transport from the deep spawning basins to the coast. The underlying rationale was that years of predominant larval retention or coastal transport should result in anomalously deep or shallow particle distributions, respectively.

In a second line of investigation, we evaluated the relationship between recruitment variability and month- and depth-specific temperature conditions based on 30 years of observations. In contrast with previous studies, our approach did not make any a priori assumptions regarding the time and the water depth (and thus the life stage affected) of such potential temperature–recruitment correlations, thereby encompassing possible effects prior, during, and after the main spawning season of Baltic Sea sprat.

## Materials and methods

Hydrodynamic circulation model

A comprehensive description of the hydrodynamic model and the Lagrangian particle-tracking technique has recently been published by Hinrichsen et al. (2005). Briefly, the three-dimensional, baroclinic circulation model of the Baltic Sea (Lehmann 1995; Lehmann and Hinrichsen 2000) is an adaptation of the free surface Bryan–Cox–Semtner model (Killworth et al. 1991), with a model domain that encompasses the entire Baltic Sea, including the Gulf of Bothnia, Gulf of Riga, the Belt Seas, Kattegat, and the Skagerrak, with a realistic bottom topography. The horizontal resolution is 5 km, and 60 vertical levels are specified with a thickness chosen to best represent the different sill depths in the Baltic Sea. The model is forced by atmospheric data provided on a $1° \times 1°$ grid (i.e., geostrophic wind, 2 m air temperature, 2 m relative humidity, surface pressure, cloudiness, and precipitation; Swedish Meteorological and Hydrological Institute, Norrköping) and river runoff taken from a mean runoff database (Bergstrøm and Carlsson 1994). The model was run for a time series of 25 years (1979–2003). Three-dimensional velocity fields extracted from the circulation model were used to predict the trajectories of passive Lagrangian drifters using a 4th order Runge–Kutta scheme (Hinrichsen et al. 1997), which allowed particles to be tracked independently from the resolution of the hydrodynamic circulation model. Along each particle's drift path, corresponding bottom depths (i.e., the water depth at the current position of each particle) were initially stored in 6 h intervals, but later averaged to obtain daily estimates.

Particle releases and indices

Initial horizontal drifter positions were based on average sprat egg distributions in the Baltic Sea (Köster 1994; A. Makarchouk, Latvian Fisheries Research Institute, Daugavgrivas St. 8, Riga, LV-1007, Latvia, unpublished data), assumed to be a proxy for the spatial distribution of first-feeding sprat larvae. The vast majority of particles was released inside the 40 m isobath of the four major Baltic spawning grounds: Arkona Basin, Bornholm Basin, Gdansk Deep, and Gotland Basin (Fig. 1*b*). All drifters were seeded and forced to remain within the 5–10 m depth layer, because feeding sprat larvae predominantly occur in surface waters and appear not to exhibit clear vertical migration patterns (Voss et al. 2005). Each year, particle cohorts representing batches of first-feeding, passively drifting sprat larvae were released on 21 April (day 111) and then every 10 days until 10 July (day 191) to cover the entire average spawning season of Baltic Sea sprat (Köster and Möllmann 2000; Karasiova 2002). Each of these nine larval pulses per year consisted of 2671 particles that were seeded in regular spatial intervals of about 5 km (Fig. 1*b*).

Fig. 1. Distributions of 2671 Lagrangian particles (black dots) released on 10 July (day 191) within areas of Baltic Sea sprat (*Sprattus sprattus*) spawning effort and tracked for 50 days in (*a*) 1997 and (*b*) 1998. The bathymetry of the study area is shown in panel *a*; the particle seeding pattern (grey dots) is depicted in panel *b*. Water abbreviations: AB, Arkona Basin; BB, Bornholm Basin; GB, Gotland Basin; GD, Gdansk Deep. Land abbreviations: DK, Denmark; Ger, Germany; Lat, Latvia; Li, Lithuania.
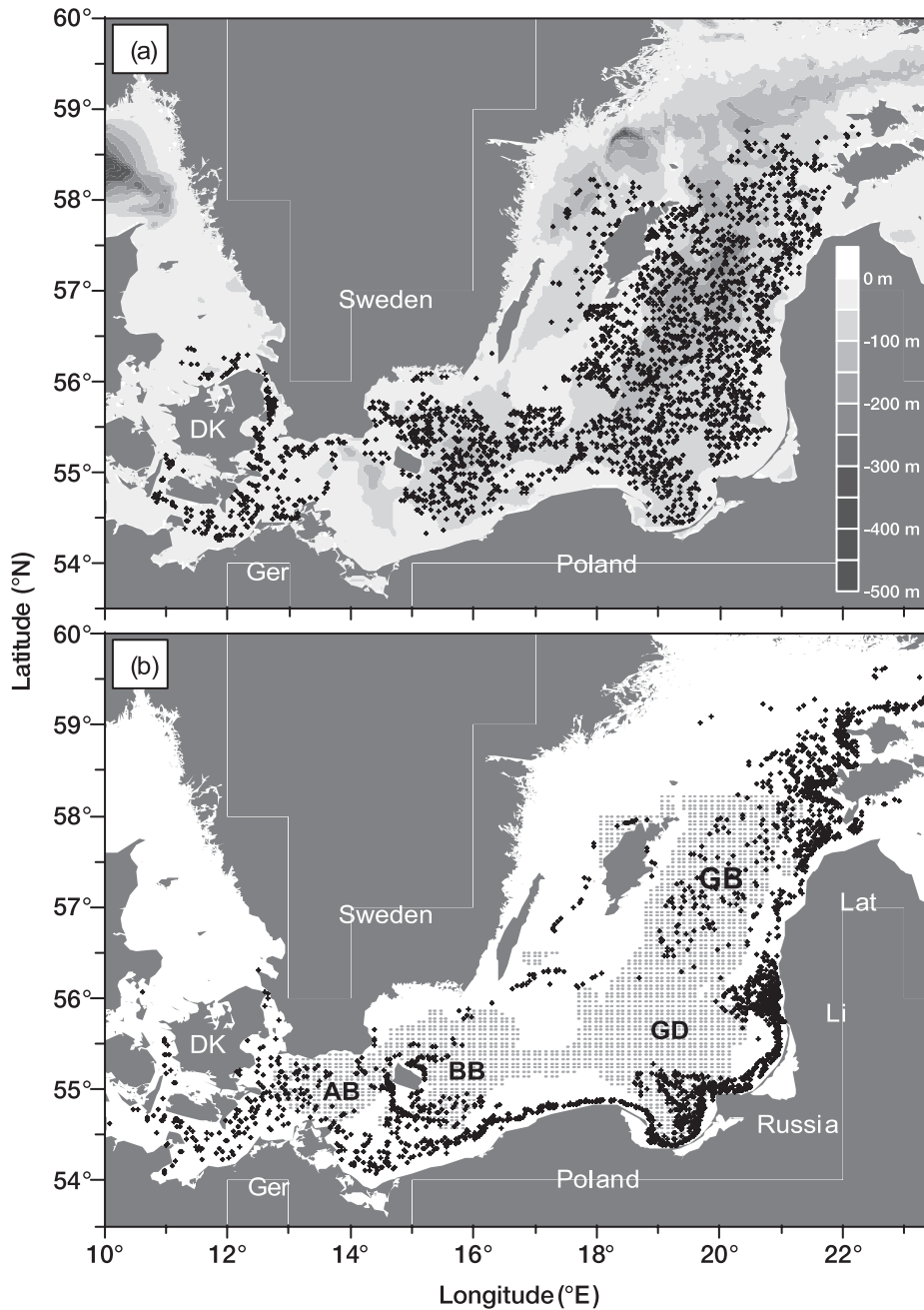
Two different approaches were tested regarding the end of the simulations. First, particles were tracked through the model domain for variable drift periods of 50–130 days, until a common collection date on 28 August (day 240). This arbitrary date was chosen to compromise sufficient drift times for late-released larval batches while avoiding too long drift periods for oldest larvae, because active swimming for the latter becomes likely. In a second approach, drifters were tracked for fixed periods of 50 days, entailing nine different collection dates (9 June to 28 August).

For an integrated view of annual drift patterns, daily bottom depths were averaged by year and release date across all 2671 particles, regardless of their individual positions in model domain. Then, because we were interested in anomalies rather than absolute values, average daily bottom depths (D_{ikl}) were standardized to zero mean and unit deviation across all 25 years modelled (i.e., $S_{ikl} = (D_{ikl} - m_{kl})SD_{kl}^{-1}$, where S_{ikl} is the standardized bottom depth of the *i*th year, the *k*th release, and the *l*th day; and *m* and SD are the day- and release-specific mean and standard deviation of bottom depth across all 25 years, respectively). Finally, daily standardized bottom depths were averaged over the considered simulation period (i.e., either over 50 days after release (fixed drift periods) or over release-specific variable drift

periods (fixed collection date)). Annual, mean, standardized bottom depths are hereafter referred to as bottom depth anomalies (BDAs).

Temperature, recruitment, and larval abundance

Temperatures in the Baltic Sea were compiled from the International Council for the Exploration of the Sea (ICES) Oceanographic Database (http://www.ices.dk/ocean/), containing two main data sets of (*i*) surface temperatures (0–10 m) and (*ii*) depth-specific CTD (conductivity–temperature–depth) and bottle measurements. From the combined data, we selected all available temperatures between 1974 and 2003 within the area of the major Baltic Sea sprat stock abundance (53°–60°N, 13°–23°E, ICES 2005*b*). Data were subsequently aggregated to obtain monthly means per year and 10 m depth stratum down to a water depth of 70 m (i.e., 0 to <10, 10 to <20, …, 60 to <70 m). Temperature means were derived from, on average, 223 observations available per month, depth stratum, and year.

Both temperature and BDA time series were correlated to the abundance of age-0 sprat during the 3rd quarter of each year in the entire Baltic Sea (ICES subdivisions 22–32). The abundance estimates (1974–2003) were taken from the most recent area-aggregated, multispecies virtual population analysis (MSVPA; ICES 2005*b*), which also provided the updated time series of sprat SSB. Data on larval sprat abundance were available from various ichthyoplankton surveys in the Bornholm Basin, Gdansk Deep, and Gotland Basin between 1979 and 1999 (stations deeper than 60 m), as described by Köster et al. (2003).

Baltic Sea Index (BSI)

To obtain a general impression of how atmospheric conditions over the Baltic Sea influence transport and temperature patterns, we applied the BSI (Lehmann et al. 2002), which is defined as the difference of normalized sea level pressure anomalies between Oslo (Norway) and Szczecin (Poland). Positive indices correspond to anomalous sea level pressures associated with westerly winds, whereas negative indices indicate predominantly easterly winds over the Baltic Sea. BSIs were recorded in 3 h intervals, but later averaged over the desired periods of larval drift simulations.

Correlations between time series of BDA, temperature, BSI, and sprat recruitment were studied using Pearson's bivariate, two-sided correlation coefficient (SPSS 13.0.1, SPSS Inc., Chicago, Illinois).

Results

Transport (BDA) and recruitment

For all nine drifter cohorts per year, final particle positions on day 240 (28 August) were indicative of considerable interannual differences in Baltic circulation patterns. Two main scenarios could be distinguished: (*i*) years of predominant particle retention within the central deep basins, likely induced by prevailing weak to variable easterly winds in summer (e.g., 1997; Fig. 1*a*), and (*ii*) years of large-scale particle displacement and dense accumulation along southern, southeastern, and eastern Baltic coastlines, probably as a consequence of prevailing strong to variable westerly winds in summer (e.g., 1998; Fig. 1*b*). Particle displacement

Fig. 2. Release-specific bottom depth anomalies (BDAs) derived from long-term Lagrangian particle simulations. Shaded lines correspond to BDAs derived from releases 1–8 (day 111 – day 181), while BDAs based on the last release 9 (day 191) is shown by the dash-dotted line. BDA$_9$ was best correlated to Baltic Sea sprat (*Sprattus sprattus*) 0-group abundance (solid dark line), which was estimated by area-aggregated multispecies virtual population analysis (MSVPA).
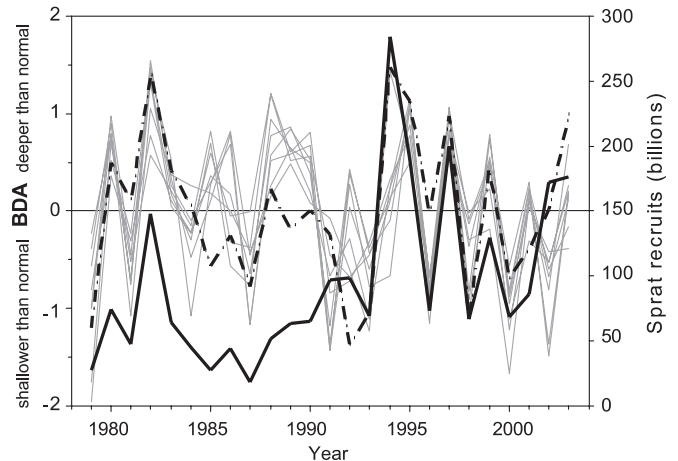
towards Swedish coastlines (westward drift) was generally negligible.

Release-specific BDAs (BDA$_{1–9}$) reflected these interannual differences well, with positive and negative BDAs indicating years when the majority of sprat larvae likely drifted over deeper-than-normal or shallower-than-normal waters, respectively, (Fig. 2). Indices derived from variable drift periods (fixed collection on 28 August) were all significantly cross-correlated ($P < 0.05$), in contrast with indices based on fixed 50-day drift periods, where significant cross-correlations did not exceed two subsequent release dates (e.g., BDA$_3$ was correlated to BDA$_2$ and BDA$_{4–5}$, but not to BDA$_{6–9}$). Within a given drift period, the coefficient of variation (CV) of daily average bottom depths ranged between 4% and 32% (temporal transport variability).

Drift indices based on early release dates 1–7 (BDA$_{1–7}$) were not significantly correlated to sprat age-0 abundance ($P > 0.05$), irrespective of fixed or variable simulation periods. In contrast, highly significant positive correlations occurred between sprat recruitment and BDA$_8$ (release 30 June, $P = 0.003$, $r^2 = 0.32$) and BDA$_9$ (release 10 July, $P < 0.001$, $r^2 = 0.50$). For the latter, an exponential function of the form $y = ab^x$ best fitted the data ($r^2 = 0.64$). However, the residuals of the fitted BDA$_9$–recruitment curve showed a clear decadal pattern; residuals between 1979 and 1990 were all negative, in contrast with all positive residuals between 1991 and 2003 (except 1996). If separate exponential curves were fitted to these two periods, BDA$_9$ explained 92% of the variability between 1979 and 1990 and 84% between 1991 and 2003 (Fig. 3). The shift in the relationship between BDA$_9$ and recruitment coincided with the strong increase in Baltic Sea sprat SSB at the end of the 1980s (Fig. 4).

Temperature and recruitment

Out of 84 correlations (12 months × 7 depth strata), temperature was significantly ($P < 0.05$) and positively corre-

Fig. 3. Relationship between bottom depth anomaly 9 (BDA$_9$) and Baltic Sea age-0 sprat (*Sprattus sprattus*) recruitment (*R*). Exponential curves ($R = a \cdot b^{\text{BDA}_9}$) best fitted the periods 1979–1990 ($r^2 = 0.92$, squares) and 1991–2003 ($r^2 = 0.84$, circles).
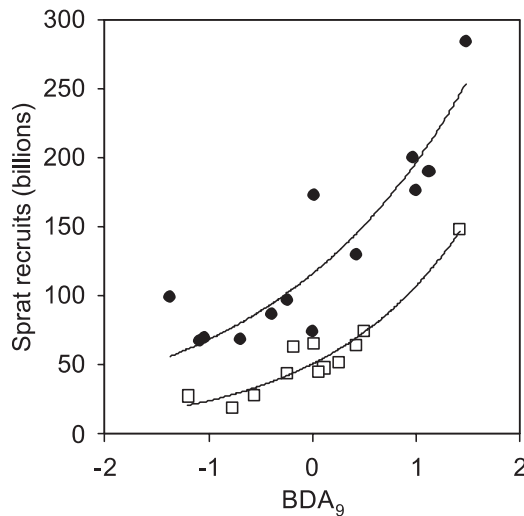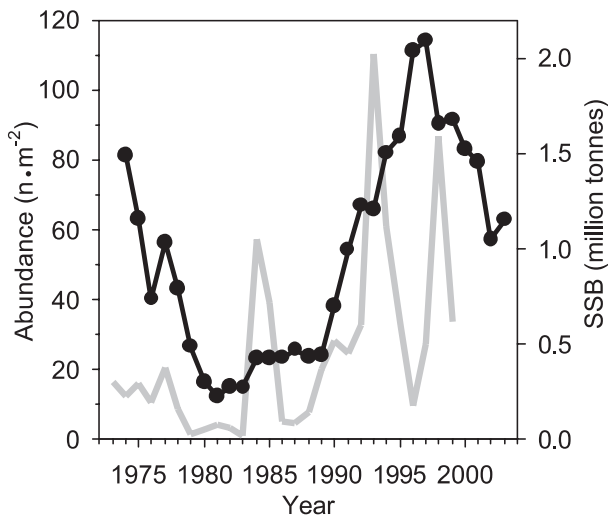

Fig. 4. Time series of Baltic Sea sprat (*Sprattus sprattus*) spawning stock biomass (SSB, solid line) and mean larval abundance (shaded line) in the main Baltic spawning grounds Bornholm Basin, Gdansk Deep, and Gotland Basin between May and July.

lated to Baltic Sea sprat recruitment success in 31 cases, thereby showing a characteristic month- and depth-specific pattern (Fig. 5). Significant temperature–recruitment correlations were already observed in January and in depths between 40 and 70 m ($r^2_{\text{max}} = 0.34$). February temperatures were uncorrelated to recruitment. Between March and July, significant but weak correlations to recruitment developed mostly in midwater depths (20–60 m, $r^2_{\text{max}} = 0.21$), with April correlations having the broadest depth range. From July to August, correlations shifted notably to surface waters, with August temperatures in 0–10 m explaining 66% of sprat recruitment variability between 1974 and 2003 (Fig. 5). A quadratic fit to the data, however, explained 73% of the overall recruitment variability. A shift in the relation-

Fig. 5. Summarizing the month- and depth-specific temperature–recruitment correlations of Baltic Sea sprat (*Sprattus sprattus*) based on 30 years of observations (1974–2003). Shading and isolines correspond to r^2 and P values, respectively, while crosses refer to the data grid points used to create the contour plot (i.e., Kriging).
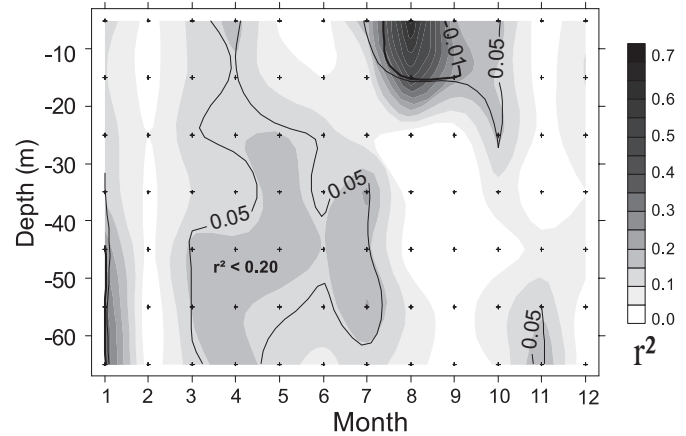
ship between decades, as observed for BDA$_9$, was not apparent for temperature. Surface temperatures were still significantly correlated to recruitment strength in September and October ($r^2_{\text{max}} = 0.22$), whereas in November, a weak but significant correlation reappeared in deeper water layers (50–70 m, $r^2_{\text{max}} = 0.20$; Fig. 5).

The BSI averaged between 10 July and 28 August (days 191–240) was found to be significantly and negatively correlated to the corresponding drift index (BDA$_9$, $P = 0.001$, $r^2 = 0.38$) and surface temperature in August ($P = 0.003$, $r^2 = 0.35$; Fig. 6). The relationships indicated that differences in sea level pressure associated with westerly winds (positive BSIs) induced both coastal particle transport and relatively cold surface temperatures, while negative BSIs and easterly winds were conducive to warm years and particle retention.

Recruitment models

The strong cross-correlation between surface temperature in August and BDA$_9$ ($P < 0.001$, $r^2 = 0.46$) precluded the inclusion of both variables in a common recruitment model. SSB alone explained 28% of the recruitment variability ($P = 0.007$) and was significantly cross-correlated to August temperature ($P = 0.023$) but not to BDA$_9$ ($P = 0.75$). We therefore constructed two different models, the first using BDA$_9$ and SSB and the second using only August surface temperature (*T*) as independent variables to predict the MSVPA estimates of sprat age-0 abundance (Table 1). The used model functions were

(1)   age 0 sprat $= a^{\text{BDA}_9} + b \cdot \text{SSB}$

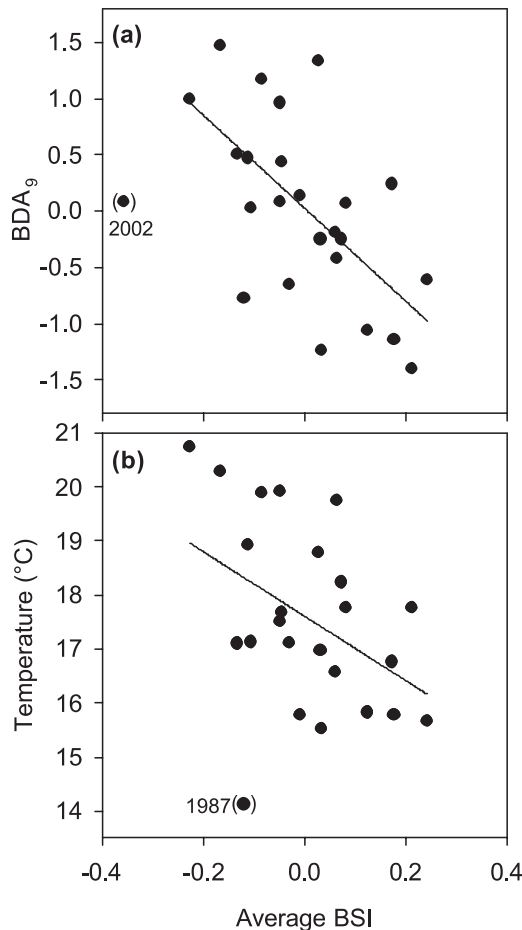(2)   age 0 sprat $= a \cdot T^2 + b \cdot T$

The explained variability in the BDA$_9$+SSB model was 82% (1979–2003; Fig. 7a) and therefore slightly better than the recruitment prediction using August temperature only (1974–2003, $r^2 = 0.73$; Fig. 7b). However, both models predicted different years of sprat recruitment success differently and with a differing quality of prediction. While sprat recruitment was considerably underestimated by the

Table 1. Parameter estimates and their 95% confidence limits, significance levels, and r^2 values for the two recruitment models using bottom depth anomalies plus spawning stock biomass (BDA$_9$+SSB) (abundance (R) = a^{BDA_9} + $b \cdot$SSB) and August surface temperature (R = $a \cdot T^2$ + $b \cdot T$ + constant) to predict the multispecies virtual population analysis (MSVPA) estimates of age-0 sprat, *Sprattus sprattus*, in the entire Baltic Sea.

Dependent variable	Time series	Independent variable(s)	Parameter	Parameter estimate	95% confidence limits Lower	95% confidence limits Upper	P	r^2_{adj}
R'	1979–2003	BDA′, SSB (entire Baltic)	a	4.478	4.177	4.779	<0.001	0.82
			b	5.47×10^{-5}	4.26×10^{-5}	6.69×10^{-5}		
R	1974–2003	August temperature (0–10 m)	Constant	1.33×10^{12}	-9.99×10^{10}	2.77×10^{12}	<0.001	0.73
			a	5.84×10^{9}	1.26×10^{9}	1.04×10^{10}		
			b	-1.74×10^{11}	-3.37×10^{11}	-1.14×10^{10}		

Note: Transformed variables were used to fit the BDA+SSB model (i.e., BDA′ = BDA$_9$ + 2 and R' = $R \times 10^{-9}$).

Fig. 6. Relationship between the Baltic Sea Index (BSI) and (*a*) bottom depth anomaly (BDA, 1979–2003, r^2 = 0.38) and (*b*) surface temperature in August (1974–2003, r^2 = 0.35). Data indicated with parentheses were years that were not included in the regression.

Fig. 7. Time series of observed (triangles, shaded line) and predicted (circles, solid line) Baltic Sea sprat (*Sprattus sprattus*) recruitment. (*a*) BDA+SSB (bottom depth anomaly plus spawning stock biomass) model explaining 82% of the recruitment variability between 1979 and 2003. (*b*) Temperature model (August, 0–10 m) explaining 73% of recruitment variability between 1974 and 2003.
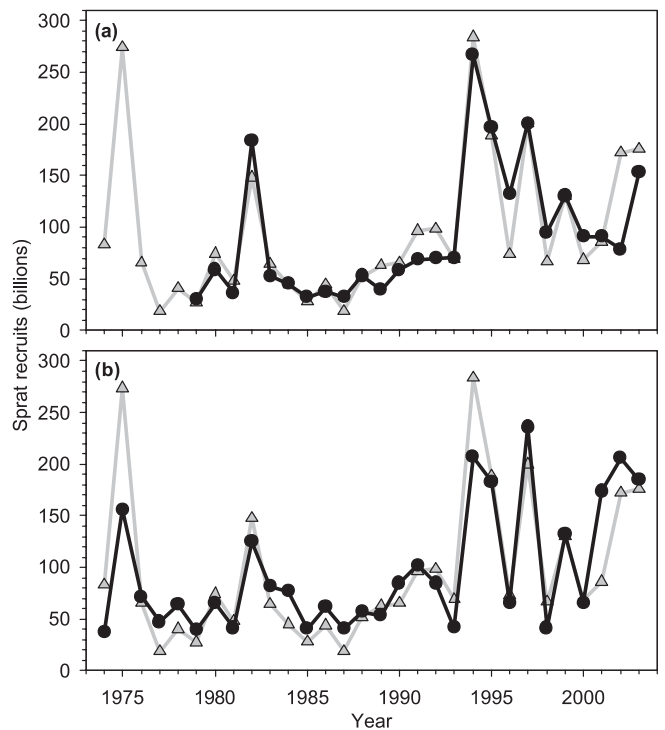

variability around BDA$_9$ (P = 0.02, r^2 = 0.36), indicating that years of highly variable transport patterns increasingly led to recruitment overestimation (Fig. 8).

BDA$_9$+SSB model in 1996 and 2002, the quadratic temperature model yielded much closer estimates. Conversely, temperature-based predictions were considerably poorer than the BDA$_9$+SSB model in 1994 and particularly in 2001 (Fig. 7).

Interestingly, residuals scaled by observed recruitment numbers were significantly and negatively correlated to the

Discussion

BDA as a drift proxy

We found BDAs a meaningful way to condense and quantify the large amounts of information produced by long-term Lagrangian simulations. BDAs reflected well the variable degree of annual particle transport from the central deep

Fig. 8. Relative deviations of recruitment predictions made by the BDA+SSB (bottom depth anomaly plus spawning stock biomass) model as a function of BDA_9 variability (SD BDA_9; i.e., standard deviation of standardized bottom depths between days 191 and 240), showing increased recruitment overestimation for years of high drift variability ($P = 0.02$, $r^2 = 0.36$).
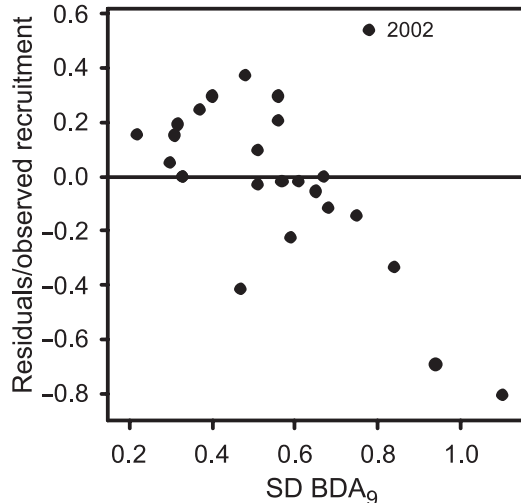
spawning basins of the Baltic Sea to shallower coastal waters. In addition, averaging daily standardized bottom depths along particle trajectories effectively integrated the drift information over the entire simulation period, which was advantageous over our previous approach using only the final horizontal particle positions (Baumann et al. 2004). This did not affect the key results, though, which were similar for both studies and indicated that years of relative particle retention or coastal displacement corresponded to relative sprat recruitment success or failure, respectively. Both studies were also consistent in finding the strongest correlations to recruitment for particles released late in the season.

However, when moving from particles to living organisms, inferences drawn from Lagrangian simulations rely on the assumption that passive drifter trajectories reflect the average transport patterns of the planktonic species or life stage studied. In demersal fish like cod or flatfish, juvenile settlement concludes the susceptibility to ocean circulation and thus sets a natural limit to drift studies (e.g., 65 days; Hinrichsen et al. 2003). Such a limit is not as readily defined in pelagic species like sprat. The onset of active swimming behaviour or schooling may not necessarily preclude Lagrangian drift simulations if late larvae or early juveniles keep moving randomly within a water body that is subject to predictable physical forcing. For example, Allain et al. (2003) successfully used a hydrodynamic model to infer likely origins of approximately 100-day-old and 80 mm long (Cermeno et al. 2003) juvenile European anchovy, *Engraulis encrasicolus*, in the Bay of Biscay. For the Baltic Sea, Hinrichsen et al. (2005) compared average Lagrangian drifter distributions with field data on 0-group sprat abundance, as determined by annual hydroacoustic surveys. They found model and field distributions in generally good accordance, with the highest mean October abundance of sprat juveniles along the southern and eastern Baltic coasts. The authors also reported that the inclusion of simulated larval

vertical migration did not produce contradictory results. It may, therefore, be justified to assume that average transport patterns of sprat larvae and early juveniles were generally reflected by the present drift model.

Still, longer simulation periods increase uncertainty, which could have been a contributory but not the only reason for the lack of correlation between early released particles and recruitment strength, because fixed and variable drift periods produced similar results. Furthermore, both approaches did not show a gradual but a very sudden shift from nonsignificant to highly significant BDA–recruitment correlations from early- (April–June) to late-released particles (July), possibly reflecting the seasonally different contribution of larval production to recruitment. In other words, sprat larvae born early in the season may play a negligible role in the recruitment process, while new sprat year classes appear to consist predominantly of individuals born relatively late in the season. The hypothesis is supported by recent findings of Voss et al. (2005), who studied larval sprat survival and condition in relation to food availability in the central Baltic Sea during 2002. The authors presented evidence that the late larval stages critically relied on the abundance of larger copepodites and adult copepods, which were scarce in April–May but significantly more abundant in June–July 2002. In addition, Baumann et al. (2006*a*) inferred distributions of days-of-first-feeding (DFF, a proxy for hatch date) from otolith microstructure analyses in newly recruited 0-group sprat caught in October 2002 in the Baltic Sea. Depending on the Baltic region, DFF distributions of sprat survivors peaked between the end of June and mid-July 2002, which is consistent with the present conclusion.

If recruitment levels are mainly determined by variable survival patterns of individuals born late in the season, what potential mechanisms could cause the observed dependence on circulation variability? Previous studies on other species and different marine systems (reviewed by Sissenwine 1984; Leggett and Deblois 1994) have mostly attributed the coupling between recruitment success and advective processes to food availability (e.g., Borja et al. 1998; Skogen 2005; Zeldis et al. 2005) or feeding success (Crecco and Savoy 1987). For Baltic Sea cod (*Gadus morhua*) larvae, Hinrichsen et al. (2003) showed that retention to but also advection out of the central Bornholm Basin could have beneficial effects to survival, depending on the season and the abundance of the calanoid copepod *Pseudocalanus acuspes*. For Baltic Sea sprat, stock size and 0-group numbers (Kornilovs. et al. 2001; Alheit et al. 2005) appear to be correlated to long-term trends in abundance of the two most important prey species, *Acartia* spp. and *Temora longicornis*, which showed significant, temperature-related increases during the 1990s (Möllmann et al. 2000). However, these observations did not resolve potential differences between Baltic basins and coastal areas. The latter normally support a higher primary and secondary production, which appears contradictory to our findings of poor recruitment levels associated to years of high larval onshore transport.

Apart from influencing transport, variable forcing conditions also affect turbulence, which is potentially important for larval feeding success (MacKenzie et al. 1994). On the population level, however, this mechanism is not unequivocally supported by field studies and appears to be of less im-

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Fig. 9. Relationship between sprat (*Sprattus sprattus*) recruitment success and the number of Lagrangian drifters (out of 2671) that had at least one next neighbour within a 0.5 km radius of their final position. A significant (r^2 = 0.62, P = 0.001) logarithmic relationship was found only for the period 1991–2003 (solid circles, solid line). The nonsignificant relationship between 1979 and 1990 (open circles) is shown by a broken line. Particles were released on 10 July (release 9) and tracked for 50 days.
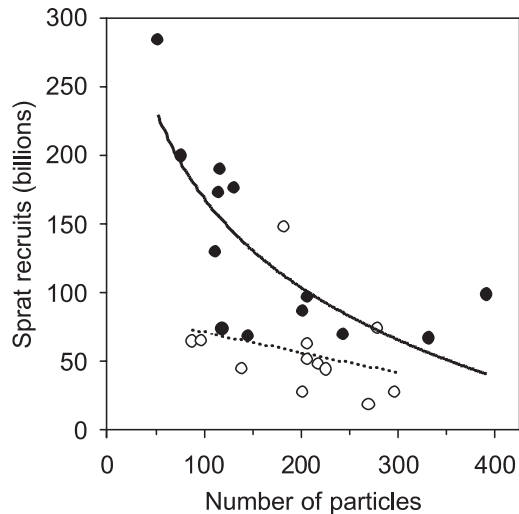
portance for older larvae and early juveniles, where turbulence levels probably need to be unnaturally high to hamper feeding success (MacKenzie 2000).

It has also been suggested that density-dependent processes operating during the late larval – early juvenile stages may substantially modify recruitment levels (Cushing 1974; Leggett and Deblois 1994). To test this hypothesis with our drift model, we calculated the distance between each particle and its next neighbour on 28 August (end of simulation). During years of large-scale coastal transport (e.g., 1998), particles were found in much denser aggregations than during retention years (e.g., 1997), with particle density being significantly (P < 0.05) and inversely related to recruitment strength (Fig. 9). The fact that such a relationship was only apparent throughout the last decade may be explained by the, on average, higher larval abundance during the 1990s. In addition, Baumann et al. (2006b) compared otolith-based growth rates of sprat recruits caught in October 2003 in the western Baltic Sea with those of pre-recruits caught at the end of August in very shallow coastal waters. The authors presented evidence that a sudden growth decline observed exclusively in pre-recruit otoliths likely resulted from severely depleted food resources. It could thus be argued that coastal areas may not always comprise the most suitable nursery grounds for Baltic Sea sprat, particularly if high summer temperatures in shallow waters lead to increased energetic demands and thus food requirements (Houde 1989) of post-larvae and early juveniles.

The strong increase of the sprat spawning stock at the end of the 1980s may have increased the potential impact of transport-related, density-dependent processes. This is supported by the fact that over a similar range of BDA values, the magnitude of recruitment fluctuations almost doubled from the 1980s to the 1990s. It does not imply a greater sen-

sitivity of recruitment to transport, since BDAs during the 1980s were more closely related to recruitment variability than during the 1990s. However, although SSB may have been the most important factor responsible for the shift in the drift–recruitment relationship, it co-occurred with a whole suite of changes in the Baltic ecosystem that affected all trophic levels (Alheit et al. 2005). Particularly, the unknown effects of pronounced shifts in Baltic zooplankton composition and dynamics (Möllmann et al. 2000) could have increased unexplained variability around the drift–recruitment relationship.

Temperature and recruitment

As with transport, studies that show significant temperature–recruitment correlations are numerous across species and marine systems (e.g., Campana 1996; Fowler and Jennings 2003; Zeldis et al. 2005), but often a multitude of interrelated mechanisms, acting on different life stages, are proposed to have caused these relationships. Temperature-enhanced growth rates certainly appear to reduce cumulative predatory losses in early larval populations (Pepin 1991; Heath 1992), as formulated by the "bigger-is-better", the "stage-duration", or "growth-selective predation" hypotheses (Takasuka et al. 2004). In many cases, the temperature effect of enhanced survival through higher growth rates is probably augmented by temperature-dependent zooplankton dynamics (Limburg 1996). For Baltic Sea sprat, significant temperature effects on recruitment strength have so far been attributed to the limited tolerance of sprat eggs and early larvae to low midwater temperatures after severe winters (Nissling 2004).

The present analysis of month- and depth-specific temperature–recruitment relationships has broadened our perception of when and where ambient temperature conditions interact with recruitment variability. Three main cores of such temperature–recruitment relationships were found: the first is in January and at depths below 40 m, which may reflect positive effects on the gonad development of prespawning adults, which are known to overwinter in the deep Baltic basins (Stepputtis et al. 2003). The second core encompassed correlations in midwater depths between March and July and is consistent with the body of published work on temperature-dependent sprat egg and early larval survival (Karasiova and Zezera 2000; Köster et al. 2003). However, the third core has not previously been reported and occurred between July and October in Baltic surface waters, with August relationships having a much higher explanatory power than all temperature correlations earlier in the year. This indicates that temperature-related survival processes during the late summer months, and therefore throughout or after metamorphosis (Baumann et al. 2005, 2006a), explain most of the recruitment variability in Baltic Sea sprat. Furthermore, the fact that August and September correlations occurred only in surface waters may reflect the predominant vertical distribution of pre-recruit sprat late in summer.

Although Houde (1992) found survival until metamorphosis to be 45 times lower in marine than in freshwater fish, and consequently suggested that "in marine species larval stage dynamics will have a greater influence on recruitment success", studies concluding just the opposite have become numerous. Bradford (1992) analysed abundance data of fish

eggs and larvae compiled from the literature and suggested that "recruitment levels are fixed after the early-larval period", while Leggett and Deblois (1994) more explicitly proposed that "interannual variability in survival during the juvenile life stage is the most important contributor to recruitment variability". Small pelagic clupeoids appear to fit into this concept, as indicated by the present and other recent studies (e.g., by Wilhelm et al. 2005 on Cape anchovy, *E. encrasicolus*, and Takahashi and Watanabe 2005 on Japanese anchovy, *Engraulis japonicus*).

In the case of post-larval Baltic Sea sprat, we need to reconsider the mechanisms responsible for the apparently strong temperature–recruitment relationship. It is noteworthy that all of the established temperature–growth–survival hypotheses for fish larvae imply size- or growth-rate-selective predation to act as the ultimate mortality agent. Following this rationale, years of high surface temperatures in August would increase population growth and thus body size at the end of summer, which then somehow confers a survival advantage with respect to predation. However, the only major predator of Baltic sprat was assumed to be Baltic cod (Köster et al. 2003), before stocks dramatically declined because of a combination of climate-induced recruitment failures and overfishing (Bagge and Thurow 1993). This has caused an estimated fivefold decrease in predation mortalities of 0-group sprat from the mid 1970s to the early 1990s and thereafter (ICES 2005b), which did not affect the persistently strong temperature–recruitment relationship. Recent studies on Atlantic cod in the North Sea also suggested that relatively small prey size differences (e.g., due to temperature) have very limited consequences for the total predation mortality (Floeter and Temming 2003). Whether other Baltic piscivores, particularly in shallow coastal areas, can significantly prey on 0-group sprat remains to be demonstrated (e.g., Patokina and Feldman 1998). We argue that the predation by Atlantic cod on post-larval and juvenile sprat cannot be regarded as the major mechanism underlying the observed strong coupling between recruitment and late summer surface temperature.

However, bigger sizes due to accelerated growth in summer may not necessarily grant immediate survival benefits but could also lead to lower mortality throughout the subsequent first winter (e.g., Henderson et al. 1988). Smaller fish have lower energy reserves than bigger conspecifics and could therefore be physiologically less tolerant against low temperatures during overwintering (Sogard 1997). This may be particularly important in a species like sprat, for which the Baltic Sea comprises the northern extreme of its geographical distribution (MacKenzie and Köster 2004). We note that our approach of considering sprat age-0 estimates does not rule out this possibility, because MSVPAs are predominantly driven by catch-at-age data starting at age 1 and are therefore insensitive to potential interannual variations in age-0 overwinter mortality. To assess the magnitude of this potential mechanism, future studies should compare independent abundance time series of sprat recruits prior to and after their first winter.

The strong correlations among long-term data of surface temperature, modelled transport patterns, and sprat recruitment variability advocate that new year classes of Baltic Sea sprat are (*i*) mainly composed of individuals born late in the season and (*ii*) determined in strength by processes acting during the late larval and early juvenile stages. Furthermore, recruitment and atmospheric processes appear to be tightly coupled in the Baltic Sea. The significant relationships between both recruitment proxies and the BSI suggested that temperature and transport have a combined and coherent influence on sprat recruitment. Positive BSIs are characteristic for prevailing westerly winds (Lehmann et al. 2002), which cause eastward and southeastward larval transport and result in lower summer surface temperatures because of increased cloud cover and precipitation (i.e., maritime weather). Conversely, larval retention and high summer surface temperatures appear to be linked through prevailing weak easterly winds (negative BSIs; i.e., continental weather). For these two scenarios, the temperature and the drift model were reliably consistent, suggesting that recruitment levels can be predicted with relatively high confidence. However, a potential decoupling of temperature and transport may happen and will result in inconsistent and therefore less confident predictions (e.g., 2001 and 2002). The drift model may presently be advantageous to the temperature model, given (*i*) that it explicitly includes SSB as a biologically sensible variable, (*ii*) that it is based on a reasonable and testable mechanism (i.e., density-dependent processes in coastal areas), and (*iii*) because of its higher explanatory power.

Correlational studies are useful means to detect long-term trends and general relationships between environmental variables and fish recruitment, which are instrumental for hypothesis generation (e.g., MacKenzie and Köster 2004; Ottersen et al. 2006). Process-oriented field and laboratory studies including all pre-recruit life stages are inevitable for hypothesis testing and exploration of the mechanisms driving such environment–recruitment correlations, which will contribute to improved recruitment models less prone to postpublication failure. The intended revenue of such efforts may be an increased readiness of fisheries managers to include environmentally based projections into regular assessment procedures.

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