

# Investigating the selective survival of summer- over spring-born sprat, *Sprattus sprattus*, in the Baltic Sea

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## Abstract

To better understand recruitment variability in small pelagic fish like sprat, it is important to know when during the extended spawning season the successful recruits are predominantly produced and which environmental factors determine potential survival windows. Here, we inferred the temporal origin of 2-year classes (2002–2003) of western and central Baltic sprat by means of otolith microstructure analysis, and found that in both years recruits mainly originated from the summer months June and July. In both years, this period coincided with temperature conditions in the surface layer of >12 °C and peak seasonal abundance of the largest copepod stages of *Acartia* spp., the major prey item of sprat larvae. The peaks in seasonal sprat egg abundance, however, occurred in April 2002 and March 2003 and therefore about 1–2 months earlier than the long-term mean spawning peak of sprat in this area (end of May/beginning of June). We hypothesize that increased temperatures in the bottom layer of the Baltic, where the pre-spawning sprat stock concentrates during winter months, potentially caused this shift in sprat spawning patterns, although early spring temperatures and feeding conditions in upper water layers were still unfavourable for larval survival. Sprat recruitment, however, was comparatively strong in both 2002 and 2003, suggesting that summer born individuals had high enough survival rates to compensate for the spawning shift, possibly due to high summer temperatures, limited dispersion, and low predation mortalities by Baltic cod as the major predator of sprat. Recruits were on average younger in 2003 than 2002, yet length distributions in October were almost identical, likely because a period of substantially higher temperatures in July/August 2003 promoted faster initial (larval) growth of survivors. Given the strength of the 2003 year class, in spite of lower overall prey concentrations in 2003 than 2002 in the study area, our findings appear to emphasise the paramount importance of summer temperatures as the recruitment determinant in Baltic sprat.

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## 1. Introduction

Research efforts on Baltic sprat have intensified over the past decade, arguably in recognition of the regime shift that has changed the state of the Baltic ecosystem from a formerly cod-dominated to a now sprat- or clupeid-dominated one (Parmanne et al., 1994; Köster et al., 2003). After cod stocks declined at the end of the 1980s, sprat stock abundance and recruitment variability reached both unprecedented levels in the 1990s (ICES, 2007), which challenged some of the hypotheses regarding recruitment determining processes and environmental influences on sprat

growth and reproduction. For example, recent studies have questioned the recruitment relevance of factors affecting the egg and first-feeding stages of Baltic sprat, because recruitment variability was found to be generated primarily later in ontogeny, during the larval and early juvenile stages (Köster et al., 2003; Baumann et al., 2006a; Voss et al., 2006).

To study recruitment-relevant processes, it is necessary to know during which period of the year the successful recruits, i.e. the survivors of the larval and juvenile stages, are predominantly produced. This is particularly important in a species like Baltic sprat, which is a batch spawner (Alheit, 1988) with a protracted spawning season from March to August (Grimm and Herra, 1984; Elwertowski, 1960). During this period, surface warming leads to increasing ambient temperatures with concurrent increases in primary and secondary production. Thus,

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the two most important factors affecting larval growth (Heath, 1992) change substantially throughout the sprat spawning season, which implies a high potential for seasonally varying growth patterns of sprat offspring. Given that growth and survival in larval fish populations are positively related (Houde, 1987; Anderson, 1988; Leggett and Deblois, 1994; Sogard, 1997), it is likely that sprat larvae produced throughout the season generally experience non-random survival probabilities. For a given year, thus, the temporal origin of successful survivors may differ fundamentally in shape and extent from the seasonal distribution of sprat reproduction effort.

Apart from seasonal variations, inter-annual variability in temperature and feeding conditions may cause year-to-year differences in sprat growth and survival patterns and ultimately recruitment strength. In 2003, the summer months July and August were much warmer ('century-summer') than in 2002, while the fall 2003 (September) was generally colder (Lefebvre, 2003). Variable weather systems encompass different precipitation and air temperatures, which would directly affect ambient temperatures in surface waters. Given that feeding sprat larvae and early juveniles predominantly occur in surface waters (Voss et al., 2003), these inter-annual temperature differences might have played an important role in determining the time windows of predominant sprat survival.

Furthermore, salinity and oxygen conditions in the deep Baltic Basins changed between 2002 and 2003 due to an unusual sequence of major Baltic inflows that introduced exceptional amounts of highly saline, oxygenated North Sea water into the Baltic proper (Grygiel and Grelowski, 2003; Feistel et al., 2003). While the warm summer inflow waters were 'sandwiched' (Meier et al., 2006) into the halocline of the Bornholm basin, the major Baltic inflow in January 2003 completely replenished the 'old', oxygen-depleted water masses below the permanent halocline. Such inflows may not directly affect conditions for sprat offspring in the upper water layer, but they could have indirect effects, like altering the conditions for the pre-spawning sprat stock that concentrates in deep Baltic waters during winter and early spring (Stepputtis, 2006).

To determine the window of predominant recruit survival, otolith microstructure analysis can be used to infer the day of first feeding in the young-of-the-year (Baumann et al., 2006b), given that sprat usually form readily discernible, daily otolith increments approximately from the time of first feeding (Alshut, 1988; Shields, 1989) until their first winter. In addition, the positive isometric relationship between otolith and fish size (Kamal, 2004; Baumann et al., 2006c) allows to reconstruct individual growth histories that can be used to back-calculate length distributions of survivors prior to catch and investigate potential relationships between growth and environmental conditions.

The first goal of the present study was to compare the seasonal reproduction of sprat in 2002 and 2003 with the temporal origin of the successful recruits from these 2 years. Stage-resolved sprat egg abundance was measured throughout the entire spawning season in the major sprat spawning ground in the central Baltic Sea (Bornholm Basin, Köster et al., 2001). Otolith microstructure analysis was applied to the young-of-the-year and used to infer day-of-first-feeding distributions as a proxy for the recruits

temporal origin. Our null hypothesis was that both distributions were similar in timing and extent, which would indicate random mortalities of sprat offspring produced throughout the spawning season. If selective mortality occurred, our second goal was to try and explain the found survival windows by seasonal differences in temperature and prey abundance, known as the two most important growth and survival determinants in larval fish (Heath, 1992). Finally, we asked whether inter-annual differences in recruit temporal origin, growth patterns, and recruitment success could be explained by inter-annual differences in these environmental conditions.

## 2. Methods

### 2.1. Field sampling and otolith analysis

Age-0 sprat recruits were sampled in October 2002 and 2003 during the annual Baltic international acoustic survey (BIAS). Two research vessels conducted pelagic trawls (Fig. 1) in Baltic subdivisions 22 (hereafter the "western Baltic") and 24+25 (hereafter the "central Baltic") with similar types of fishing gear (20 mm stretched mesh in the codend). From each haul, approximately 20 randomly selected individuals smaller than 110 mm TL were stored at  $-20^{\circ}\text{C}$ .

In the laboratory, up to 10 specimens per haul were randomly selected and measured for TL (nearest mm). This was followed by the extraction of both sagittal otoliths, which were then individually mounted on microscopic slides with a drop of thermoplastic glue (Crystallbond<sup>®</sup> 509). Otoliths were polished from both sides with a 3  $\mu\text{m}$  lapping film (266 $\times$  Imperial PSA 3 M<sup>®</sup>) until all micro-increments were sufficiently visible along the core-postrostrum axis (Baumann et al., 2006b). An image analysis software (ImagePro 4.5.1) was used to count and measure ( $\mu\text{m}$ ) individual increments in multi-frame digital images, which were taken under 400 $\times$  magnification with a high-resolution digital camera (Leica<sup>®</sup> DC300). Sufficient ageing precision has previously been confirmed via within- and across-reader comparisons as reported by Baumann et al. (2006b). A total of 383 individuals from 59 hauls were available for the present analysis (Table 1).

To estimate the temporal origin of recruits, we assumed that sprat start to form daily otolith increments around the time of first feeding, based on the two existent laboratory calibrations by Alshut (1988) and Shields (1989). Unfortunately, these experiments were conducted at relatively high temperatures (14–15  $^{\circ}\text{C}$ ) characteristic for Baltic surface waters only in summer but not in spring, leading some to believe in a later onset of increment formation in Baltic sprat. However, the core diameters in the present otolith material were similar to those reported by Alshut (1988) and Shields (1989) for 6 mm first feeding larvae ( $\sim 15 \mu\text{m}$ ), we thus assume that recruits started to form increments around the same first-feeding size. We also observed a very consistent shift from weak and indistinct to sharp and well-defined increments in the otoliths after the innermost four increments (range three to five). These first four increments were excluded from analysis, because they may have corresponded to the yolk-sac stage and thus not been formed daily.

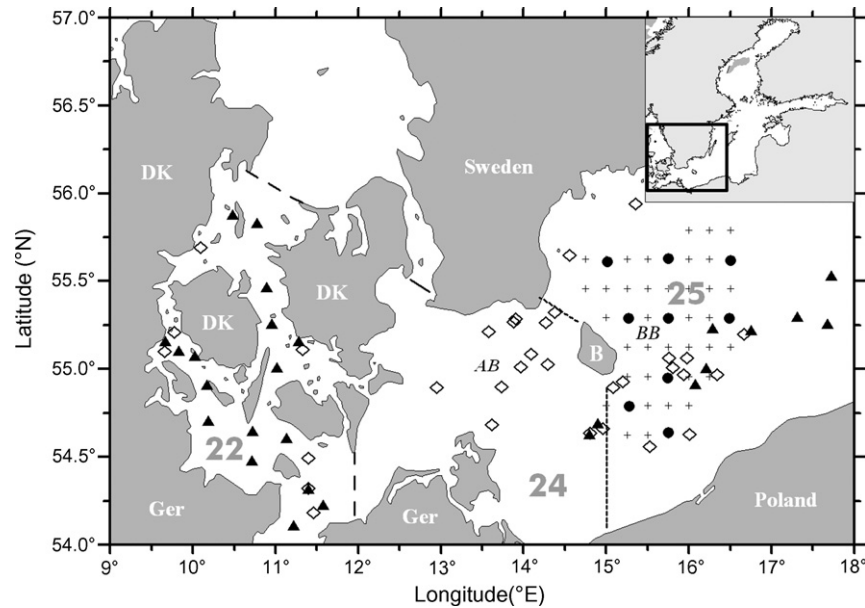


Fig. 1. Study area of the western (subdivision 22) and central Baltic Sea (subdivisions 24+25). (Inlet: whole Baltic Sea), with sampling sites of sprat recruits in October 2002 (diamonds) and 2003 (triangles). Crosses depict the GLOBEC-Germany station grid surveyed bi-weekly/monthly between April 2002 and August 2003 (black circles = focus stations). AB = Arkona Basin, B = Bornholm island, BB = Bornholm Basin, DK = Denmark, Ger = Germany.

While back-calculating first-feeding distributions of sprat recruits, we assumed the bias due differences in age and thus cumulative mortalities of early vs. late born individuals to be negligible. This is justified, because larval instantaneous mortalities decline exponentially with age, thus, the further the sampling and the end of the hatching (first-feeding) period are separated in time (mid-July to mid-October in this case), the smaller the effect of differential cumulative mortalities becomes (Campana and Jones, 1992).

Despite being randomly chosen, some length classes appeared over- or underrepresented in the otolith analysis when compared to the length distributions observed during the surveys. To remove the resulting bias in age-, back-calculated TL, and day-of-first-feeding distributions (DFF), a weighing factor was assigned to each specimen according to the length class and Baltic area (western or central Baltic), where it was caught in October 2002 or 2003. Weighing factors ranged between 0.24 (too many otoliths read in a particular length class) and 2.23 (too few otoliths read, average weighing factor = 1.03). In 2002, random sub-samples in the western Baltic did not

include specimens from the two largest length classes of the assumed yoy catch (100–110 mm TL, ~10% of the TL distribution). In 2003, for the same reason, ~2% of the assumed yoy catch in the central Baltic between 105 and 110 mm TL were not represented by otolith analyses. However, due to the small contribution of the 100–110 mm TL fraction, which likely contained both large age-0 recruits and small 1-year-old fish, the bias resulting from this underrepresentation was assumed to be negligible.

We further accounted for potential bias due to the slightly different sampling periods between years and areas (Table 1). Given that the first haul was done on 5 October, all individual fish lengths were back-calculated to the 4th of October using the biological intercept method (Campana, 1990). The otolith radius at first feeding was set as the distance between the core and the 4th increment, and TL at first feeding was set at 5 mm (Alshut, 1988; Shields, 1989; Voss et al., 2003). The biological intercept method is independent of the slope in the overall otolith–fish size regression, but assumes linearity in individual otolith–fish size trajectories (Campana, 1990).

Table 1

Number of pelagic hauls conducted in 2002 and 2003 in the western (subdivision 22) and central Baltic Sea (subdivisions 24+25), sampling times, individuals analysed for their otolith microstructure, and basic information on TL (mm), age (days after DFF) and DFF (day of first feeding)

	2002		2003	
	Western Baltic	Central Baltic	Western Baltic	Central Baltic
Hauls ( <i>n</i> )	7	26	17	9
Sampling time	14–16 October and 22–24 October	7–8 October and 16–23 October	5–14 October	6 October and 17–23 October
Otoliths ( <i>n</i> )	45	192	77	69
TL, mean (S.D.)	81.5 (8.8)	86.9 (5.1)	79.5 (6.1)	87.6 (5.5)
Age, mean (S.D.)	97 (21.0)	104 (13.1)	86 (10.0)	100 (12.7)
DFF, mean (S.D.)	30 June (21.0)	23 June (13.1)	11 July (10.0)	27 June (12.7)

Note that TL and age correspond to the same day in both 2002 and 2003 (4 October).

Given that the mean and variance of increment widths vary strongly with individual age (Pepin et al., 2001), the comparatively small influence of environmental variability may only be detected in reconstructed growth histories, if the statistical effect of age on increment widths is removed. By standardizing increment widths to zero mean and unit variation (i.e.,  $z_{ij} = (x_{ij} - x_j) / s_j^{-1}$ , where  $x_{ij}$  is the increment width ( $\mu\text{m}$ ) of the individual  $i$  at age  $j$ , and  $x_j$  and  $s_j$  are the mean and standard deviation of increment widths at age  $j$ , respectively, for all specimens observed), the growth anomaly of a given individual was obtained for any given day relative to the population.

## 2.2. Temperature conditions

Daily average water temperatures in 0–10 m were used as a proxy for the conditions experienced by feeding sprat larvae and early juveniles. Temperatures were taken from a three-dimensional, hydrodynamic circulation model of the Baltic Sea (Lehmann, 1995; Lehmann and Hinrichsen, 2000). The models 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 by Swedish Meteorological and Hydrological Institute in Norrköping on a  $1^\circ \times 1^\circ$  grid (i.e., geostrophic wind, 2 m air temperature, 2 m relative humidity, surface pressure, cloudiness, and precipitation) and river runoff taken from a mean runoff database (Bergström and Carlsson, 1994). Over the last decade, the model has been used in a wide range of studies (e.g., Voss et al., 1999; Hinrichsen et al., 2003; Barz et al., 2006; Baumann et al., 2006a) because its simulated physical properties agree well with known Baltic circulation features and observed physical conditions (Hinrichsen et al., 2005).

Modelled water temperatures within 54–56°N, 9–18°E, and 0–10 m were averaged to yield one daily temperature value for 2002 and 2003. Doing so implied two assumptions, first that sprat recruits originated from and stayed in the study area (combined western + central Baltic). This is supported by a previous modelling study, showing that western/central and eastern Baltic sprat offspring have only limited mixing probabilities (Hinrichsen et al., 2005). Secondly, we focused on seasonal temperature effects to explain recruit growth patterns, because the spatial temperature variability within the study area was very small (S.D.( $T_{\min}$ ) – S.D.( $T_{\max}$ ), May–October: 0.4–3.1 °C) compared to the temporal fluctuations ( $T_{\min}$  –  $T_{\max}$ , May–October: 6.5–21.9 °C).

## 2.3. Zoo- and ichthyoplankton sampling

Between March 2002 and August 2003, 17 monthly or bi-weekly research cruises were conducted by the German GLOBEC project in the central Baltic Sea. On each of 45 regular grid-stations a combined Baby-Bongo ( $\varnothing = 20$  cm)/Bongo ( $\varnothing = 60$  cm) sampler with mesh sections of 150 and 335  $\mu\text{m}$ , respectively, and General Oceanics® flowmeters was double-obliquely towed at a ship speed of three knots (Fig. 1). In addition, a multi-net with an opening of 0.25 m<sup>2</sup> and a mesh size

of 50  $\mu\text{m}$  was deployed at 9 out of 45 stations (termed ‘focus stations’) in 10 m depth strata from the bottom to the surface. Zoo- and ichthyoplankton samples were immediately preserved in a 4% buffered formaldehyde/seawater solution. Sprat eggs were subsequently collected from the 335  $\mu\text{m}$  Bongo section, counted, and distinguished into four stages based on morphological criteria (Thompson et al., 1981). Counts were finally scaled to 1 m<sup>2</sup> sea surface based on the filtered water volume and the maximum depth of the tow ( $\sim 2$  m above the ground). Zooplankton was collected from the 150  $\mu\text{m}$  Baby-Bongo and 50  $\mu\text{m}$  multi-nets, subsequently identified to the species level and developmental stage, and counts were scaled to individuals per m<sup>3</sup>.

Given that feeding sprat larvae occur in surface waters (Voss et al., 2003) and appear to feed predominantly on all stages of *Acartia* spp. copepods (Dickmann et al., 2007), the abundance of this copepod genus (consisting of *A. biflosa* and *A. longiremis*) in the upper 20 m was used as a proxy for the feeding conditions of sprat larvae in 2002 and 2003. Copepod stages were combined into three developmental classes, being nauplii (N), stages I–III copepodites (C1–C3), and stage IV copepodites to adult copepods (C4–adult). While the abundance of nauplii was directly taken from multi-net samples, estimates for copepodites and adults were derived from Bongo samples. Those numbers had to be scaled to the upper 20 m by taking into account the vertical distribution of *Acartia* spp. at each of the nine corresponding multi-net stations.

## 3. Results

### 3.1. Temporal origin of sprat recruits

Otolith-derived DFF-distributions indicated that the majority of western and central Baltic sprat recruits originated from the summer months June and July (Fig. 2). In both areas, recruits were on average older and had a broader range of first feeding dates in 2002 than in 2003. In the western Baltic, mean DFF's significantly shifted from 30 June in 2002 to 11 July in 2003 ( $t$ -test,  $df = 48.6$ ,  $P = 0.03$ ), and the corresponding standard deviation decreased from 21 days to 10 days (Fig. 2). In central Baltic recruits, mean DFF in 2002 (23 June) significantly ( $t$ -test,  $df = 260$ ,  $P = 0.03$ ) preceded the mean DFF in 2003 (27 June), but the difference was less pronounced (Table 1) and there was no significant change in variability (Levene-test for variance homogeneity,  $P = 0.67$ ). In contrast to a single DFF peak in 2002, the central Baltic DFF-distribution had two peaks in 2003 (Fig. 2), a minor one during the first week in June 2003 and a second, major one at the beginning of July 2003. In both years, western Baltic sprat recruits were significantly ( $t$ -test,  $P < 0.05$ ) younger than their conspecifics in the central Baltic Sea (Table 1).

### 3.2. Seasonal sprat reproduction

The abundance of sprat eggs was always very heterogeneous between stations in the Bornholm basin and differed seasonally between 2002 and 2003 (Fig. 3). In 2002, earliest egg stages Ia + b showed a main peak in mid-April (max = 500 eggs m<sup>-2</sup>)

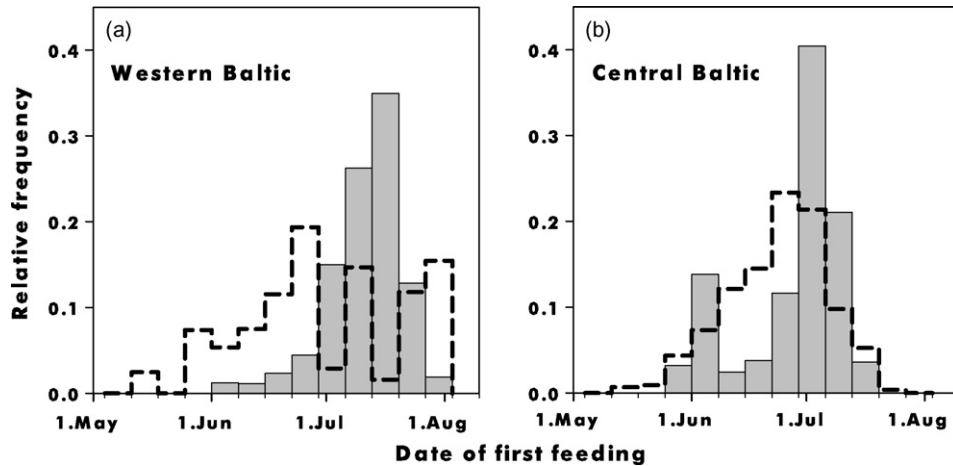


Fig. 2. Back-calculated day-of-first-feeding distributions (DFF) for sprat recruits caught in 2002 (dashed lines) and 2003 (grey bars) in the western and central Baltic Sea. Distributions were corrected for over- or underrepresented length classes in the otolith analysis relative to the catch.

and a minor peak early in June (max = 220 eggs m<sup>-2</sup>). In 2003, a single peak in stage Ia + b eggs appeared around mid-March (max = 750 eggs m<sup>-2</sup>), but the seasonal egg distribution was much broader than in 2002 (Fig. 3a). In 2002, timing and

extent of the major spring peak in April and the minor summer peak in June were similarly apparent in the latest pre-hatching egg stage Iv (max = 71/17 eggs m<sup>-2</sup>, respectively). In contrast, abundance of Iv egg stages in 2003 suggested two similarly

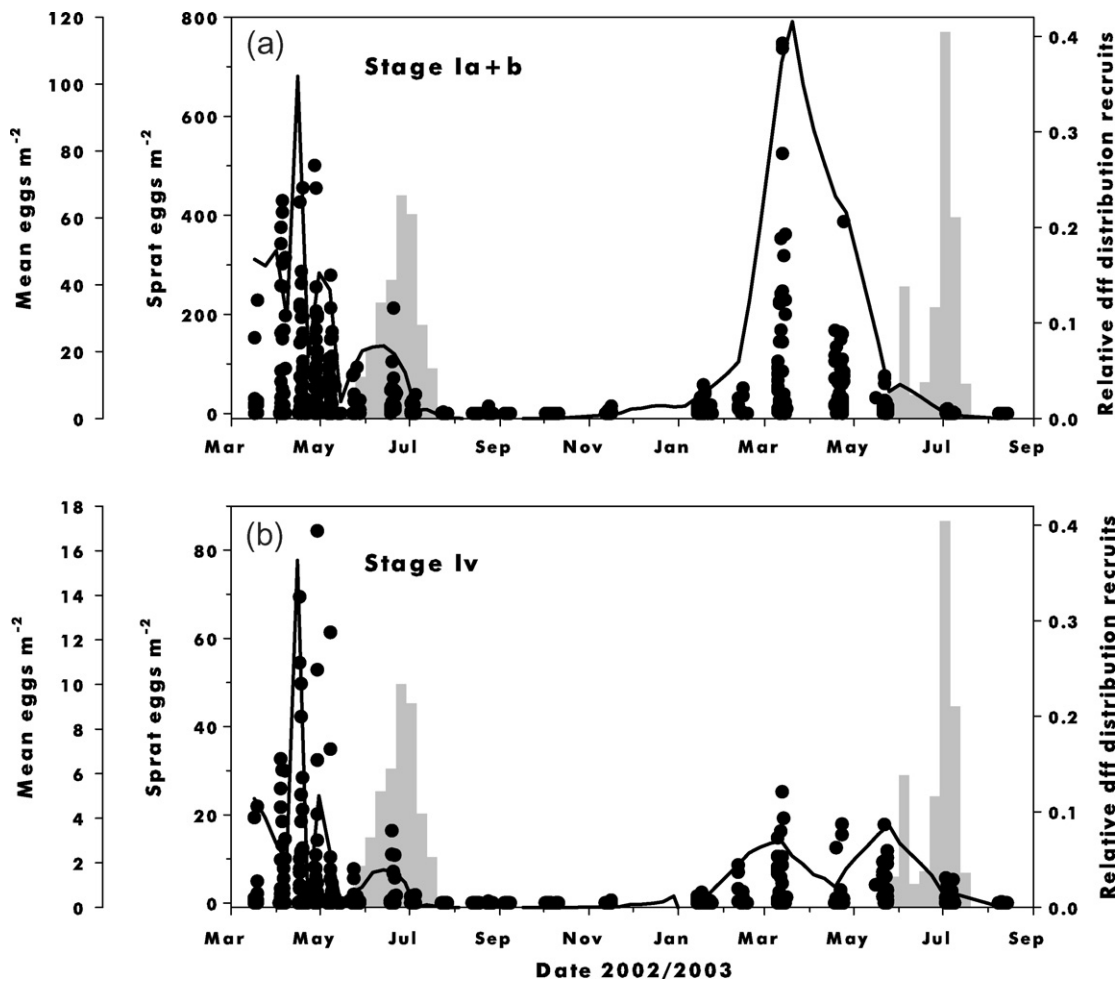


Fig. 3. Temporal origin of central Baltic sprat recruits (DFF, grey bars) in relation to the seasonal abundance of earliest egg stages Ia + b (a) and latest, pre-hatching egg stage Iv (b) in the Bornholm basin between April 2002 and August 2003. Each dot represents one station. A local Loess smoother (tricube weighting with polynomial regression, Sigma Plot.10.0) was used to show the trends in seasonal egg abundance (10% of the data points used to calculate each smoothed value).

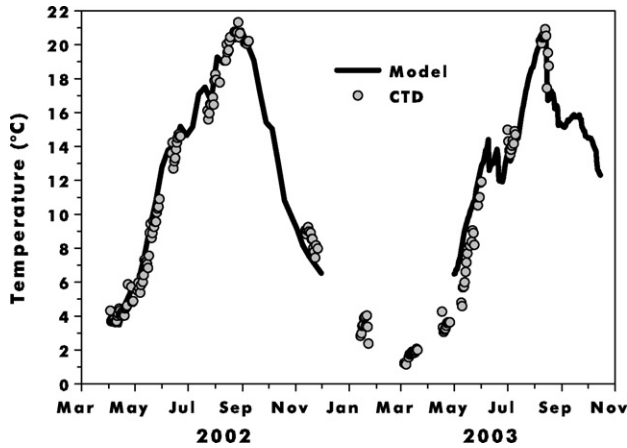


Fig. 4. Temperature conditions between 0 and 10 m in the western in central Baltic Sea between April 2002 and November 2003, estimated from a 3D hydrodynamic model (black line), and average temperatures between 0 and 10 m depth measured by CTD-casts in the Bornholm Basin (grey dots).

high maxima at the beginning of March and the end of May (max = 25/19 eggs  $m^{-2}$ , Fig. 3b). Particularly in 2003, this indicated a considerably higher egg mortality from egg stages Ia + b to Iv in March than at the end of May.

In both 2002 and 2003, the temporal origin of central Baltic sprat recruits was rather coinciding with the secondary, smaller May/June peaks in stage Iv egg abundance, but was offset by more than 1–2 months from the major egg peaks in April 2002 and March 2003 (Fig. 3).

### 3.3. Temperature and feeding conditions

In both years, surface temperatures in the western and central Baltic Sea were consistently below 5 °C between January and the beginning of May (Fig. 4). Surface warming resulted in temperatures of approximately 12 °C at the beginning of June. Until the last week in July, temperatures in the study area showed little inter-annual differences, and further increased to 17.9 °C on 22 July (Figs. 4 and 9). Then, between July 22nd and August 13th, surface temperature rapidly increased in 2003, reaching a maximum of 21.2 °C, whereas conditions in 2002 almost stagnated during this period. However, due to a rapid temperature decline on 15 August 2003 but continuously increasing temperatures in 2002 until the beginning of September, late summer/early fall conditions became reversed between both years. In other words, the period of maximum temperature conditions was relatively short and occurred earlier in 2003, whereas in 2002 the temperature maximum was delayed but lasted longer into the fall (Figs. 4 and 9).

Abundance of all *Acartia* spp. developmental stages varied strongly between seasons and years, and notably also across stations in the Bornholm Basin (Fig. 5). In 2002, nauplii abundance showed a small peak in mid-April, followed by a larger peak at the end of May (Fig. 5a). A third nauplii peak was apparent in November 2002. Nauplii concentrations decreased only slightly throughout the winter and spring 2002–2003, after which they only slightly increased again towards August 2003. C1–C3 copepodites showed similar peaks in May and Novem-

ber 2002, but contrary to nauplii, abundances remained at very low levels throughout 2003 with only a very small peak in May 2003 (Fig. 5a). For C4-adult copepods, peak abundances were observed at the end of May 2002 and the beginning of October, but generally remained at relatively high levels throughout June–August (Fig. 5b). In 2003, abundance of C4-adult copepods only slightly increased at the end of May to a small peak in July, but compared to 2002, the 2003 abundance was substantially lower. In fact, our main observation was that the overall abundance of all *Acartia* spp. developmental stages was about three times higher in summer 2002 than in 2003 (Fig. 5).

In both years, the temporal origin central Baltic recruits occurred after the peaks in nauplii abundance, but coincided with the seasonal abundance maxima of C4-adult *Acartia* copepods (Fig. 5).

### 3.4. Length and growth of sprat recruits

Within areas, length distributions of sprat recruits showed only small inter-annual size differences (Fig. 6). On 4 October 2002, average size of western Baltic sprat recruits was 81.5 mm TL ( $\pm 8.8$  mm S.D.) vs. 79.5 mm TL ( $\pm 6.1$  mm S.D.) on the same day in 2003. In both years, central Baltic recruits were significantly bigger on 4 October ( $t$ -test,  $P < 0.001$ ,  $df_{2002} = 230$ ,  $df_{2003} = 144$ ) than their conspecifics in the western Baltic, with 86.9 mm TL ( $\pm 5.1$  mm S.D.) in 2002 and 87.6 mm TL ( $\pm 5.5$  mm S.D.) in 2003.

Back-calculation of recruit lengths to the 4th of August, 4th of September, and 4th of October revealed that early in summer (August) distributions in both the central and western Baltic still showed considerable inter-annual size differences, likely in reflection of the differences in DFF between 2002 and 2003 (Fig. 7). However, the length ogives became more similar to each other over the course of August and September, until on 4 October only minor inter-annual differences remained in each area (stated above). The spatial differences in TL between western and central sprat recruits, however, persisted in all back-calculated length ogives (Fig. 7).

Average growth trajectories showed significantly faster initial growth in 2003 than 2002 in both western and central Baltic areas (ages 3–28 and 11–28 days post-DFF, respectively,  $t$ -test per increment,  $P < 0.05$ ), but during the following juvenile stage the pattern was reversed (consistently from 40 days post-DFF onward, Fig. 8).

### 3.5. Growth patterns in relation to temperature

To study how seasonal temperature differences affected growth patterns, specimens from both areas were pooled and re-grouped into five bi-weekly DFF-intervals according to their back-calculated day of first feeding. For each 14-day cohort, the age-detrended growth rates (i.e., mean standardized increment widths) were plotted against the day of their formation (Fig. 9). In both years, the oldest two recruits cohorts (DFF between 25 May and 21 June, Fig. 9a-b) had rather similar patterns and exhibited consistently below-average growth until approximately mid-July, which was then followed by a period

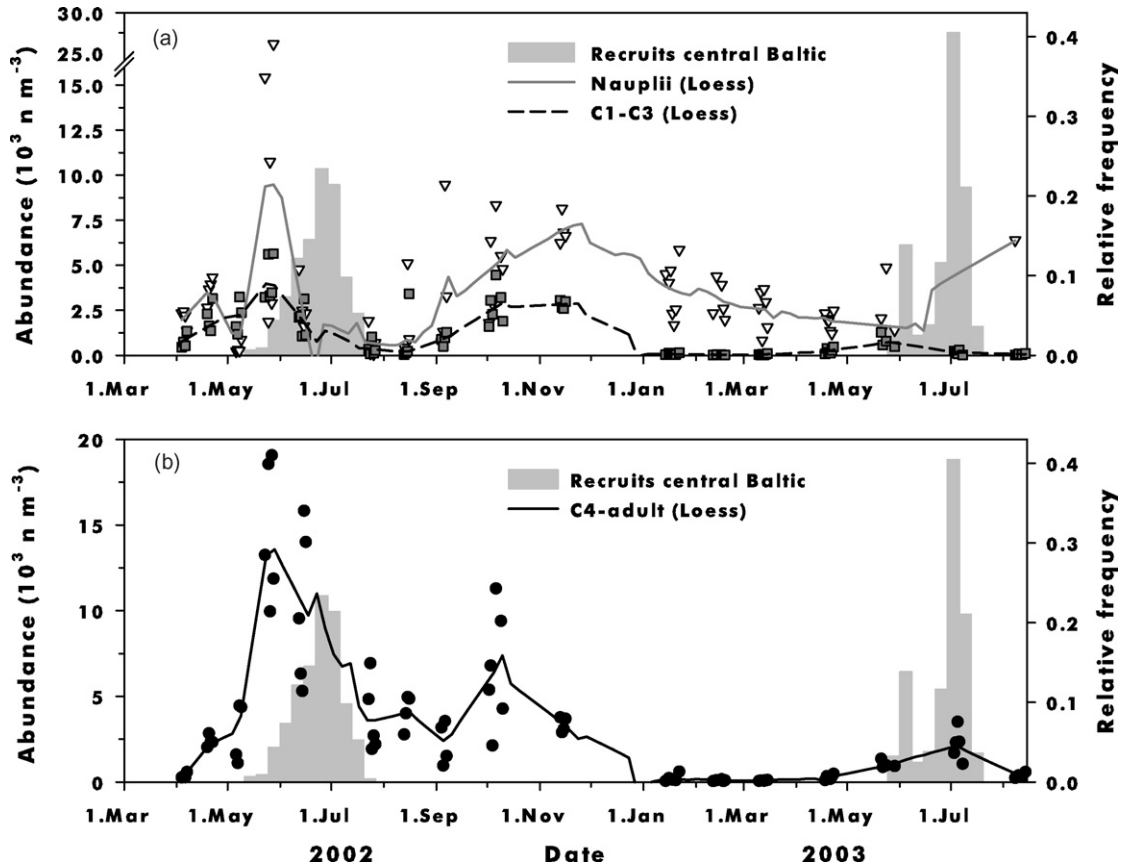


Fig. 5. Temporal origin of central Baltic sprat recruits (DFP, grey bars) in relation to seasonal prey abundance between April 2002 and August 2003 in surface waters (0–20 m) of the Bornholm Basin (stations >60 m). (a) *Acartia* spp. nauplii (triangles) and copepodid stages 1–3 (squares). (b) Copepodite stages 4–adults (circles). A local smoother (Loess, 16% of the data points used to calculate each smoothed value) was chosen to depict seasonal trends in *Acartia* abundance.

of above-average growth until sampling in October. In contrast, age-detrended growth patterns of the youngest three cohorts (DFP between 22 June and 2 August, Fig. 9c–e) appeared to closely reflect the temperature differences between 2002 and 2003. Particularly in the youngest two cohorts, growth between mid-July and mid-August was much higher in 2003 than 2002, virtually mimicking the period of higher 2003 than 2002 surface

temperatures. Around mid-August, the patterns of temperature and age-detrended growth reversed simultaneously, and from then on the 2002 specimens grew better until October than their similarly old conspecifics in 2003.

The daily differences in temperature between 2002 and 2003 were linearly correlated (Pearson, two-sided correlation) to the corresponding daily differences in mean standardized incre-

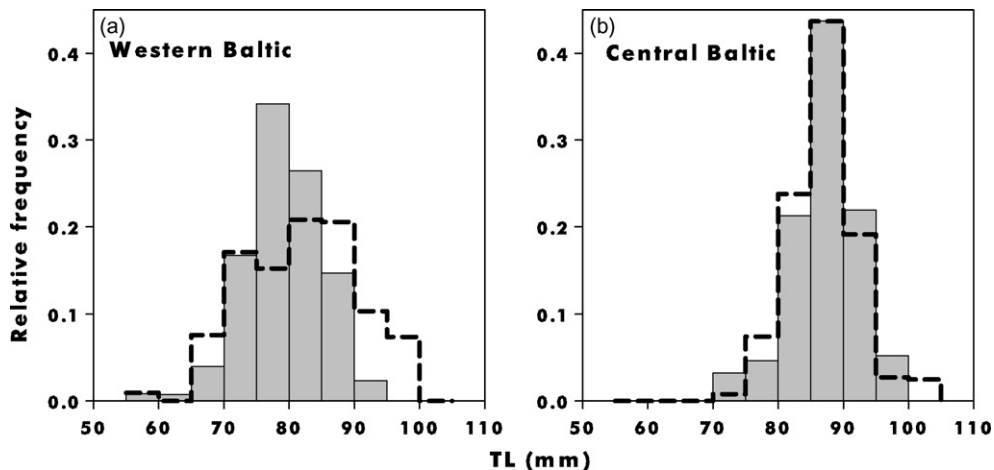


Fig. 6. Back-calculated distributions of total length on 4 October for sprat recruits caught in 2002 (dashed lines) and 2003 (grey bars) in the western and central Baltic Sea. Distributions were corrected for over- or underrepresented length classes in the otolith analysis relative to the catch.

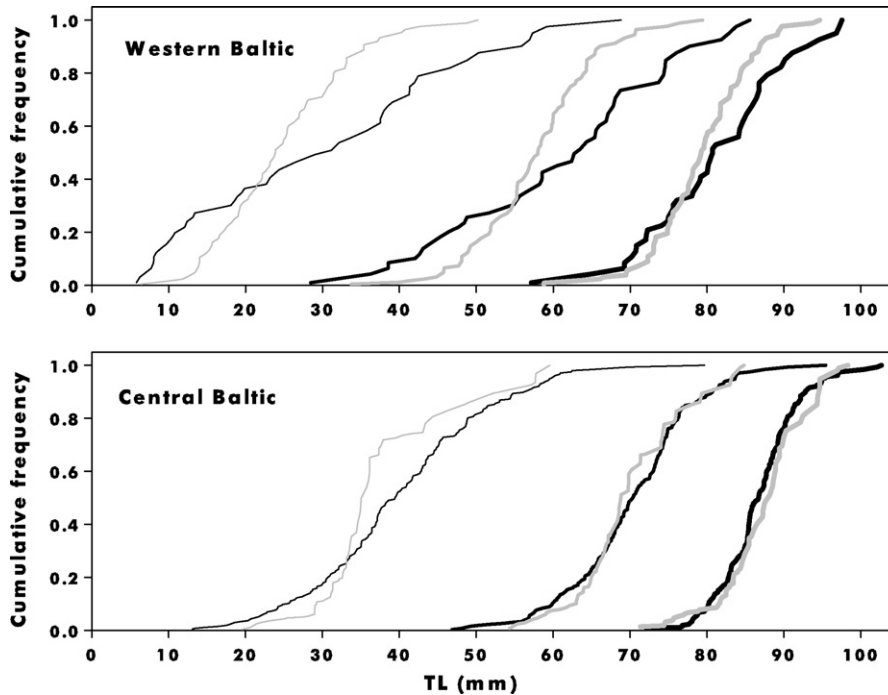


Fig. 7. Cumulative frequency distributions of back-calculated TL of western (upper panel) and central Baltic sprat recruits (lower panel) in 2002 (black lines) and 2003 (grey lines) on 4 August (thin lines), 4 September (medium lines), and 4 October (thick lines).

ment widths for each of 9 weekly recruit cohorts (i.e., which had DFF's within the same 7-day period). Except for individuals with DFF's between 8 and 21 June (DFF-intervals 2 and 3), all correlations were significant ( $P < 0.05$ ) and indicated that inter-annual growth differences were largely attributable to differences in temperature conditions. The coefficient of correlation ( $r^2$ ), however, increased steadily from the oldest to the youngest cohorts. For example, inter-annual temperature differences explained 14% of the variability in age-detrended growth differences for specimens originating from the last week in June, but 73% in the cohort from the 3rd week in July. On 22 July, when temperature patterns first started to diverge

substantially between years, the former cohort was on average 27 days of age and had a back-calculated TL  $\pm$  S.D. of  $24.6 \pm 3.5$  mm in 2002 and  $22.2 \pm 3.3$  mm in 2003. The latter, most temperature-sensitive cohort, was only 7 days of age and measured  $8.3 \pm 1.4$  and  $7.9 \pm 1.6$  mm on 22 July in 2002 and 2003, respectively.

For each weekly DFF-cohort in 2002 ( $n = 12$ ) and 2003 ( $n = 10$ ), back-calculated somatic growth rates (SGR,  $\text{mm day}^{-1}$ ) and temperature ( $T$ ,  $^{\circ}\text{C}$ ) were averaged over the initial 30 days after DFF. A quadratic relationship ( $\text{SGR} = -1.69 + 0.24T - 0.0054T^2$ ,  $n = 22$ ) fitted the data best, explained 90% of the variability, and suggested a temperature

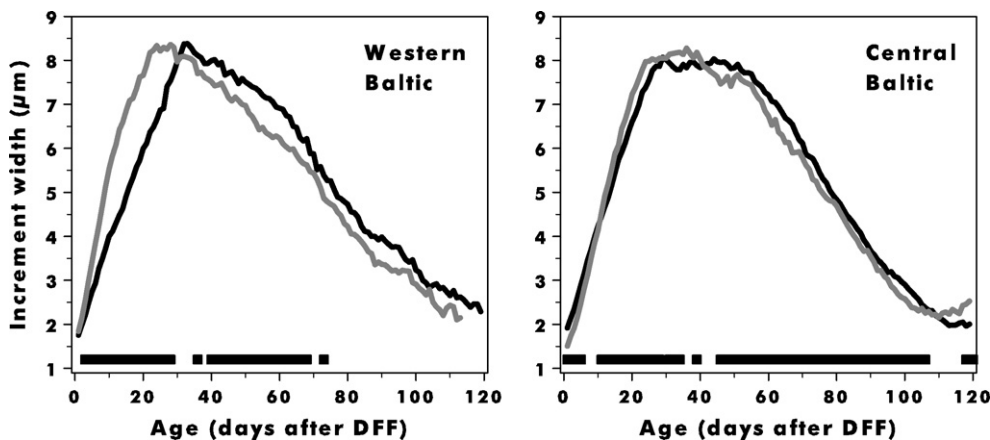


Fig. 8. Mean reconstructed growth-trajectories of sprat recruits caught in 2002 (black line) and 2003 (grey line) in the western and central Baltic Sea. Means were weighed to adjust for over- or underrepresented length classes in the otolith analysis relative to the catch. Black bars indicate significant differences between means ( $P < 0.05$ ).



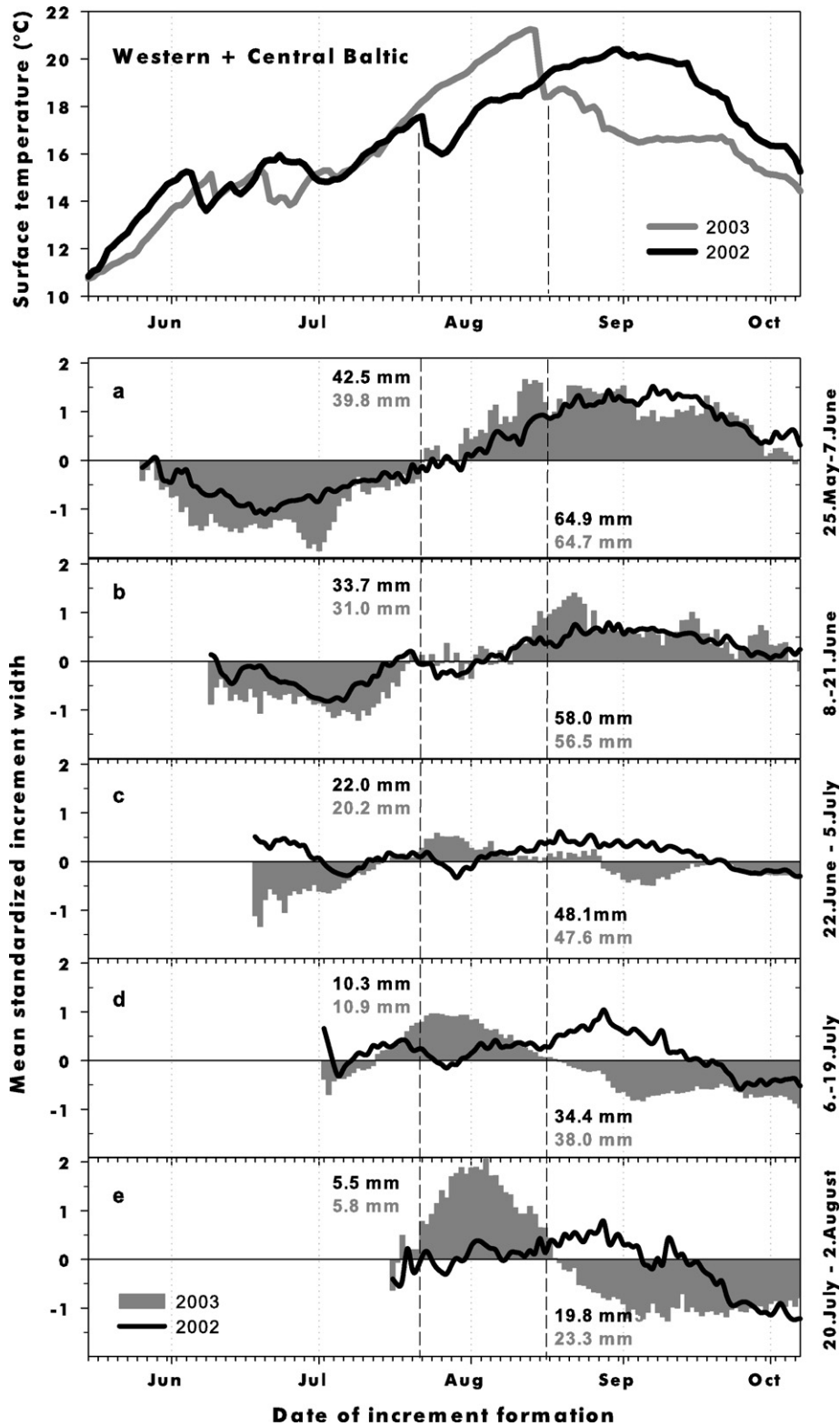


Fig. 9. Age-detrended growth patterns (i.e., mean standardized increment widths) of sprat recruits caught in the western and central Baltic Sea in 2002 (grey bars) and 2003 (black line) in relation to mean sea surface temperature in the study area, derived from a 3D hydrodynamic circulation model. Growth patterns were analysed for each of five cohorts (a–e), discerned based on their back-calculated day of first feeding (DFE, periods given right to each panel). Mean back-calculated lengths are given for each cohort (black = 2002, grey = 2003) next to the dashed lines corresponding to the 22 July and 15 August.

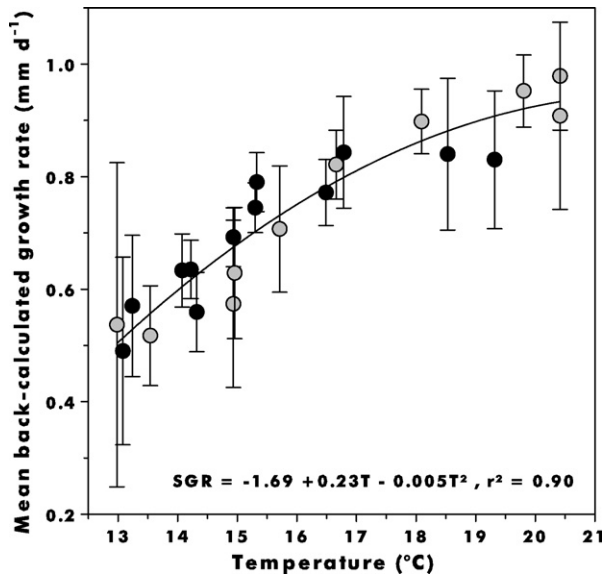


Fig. 10. Quadratic relationship between mean temperature (0–10 m) and mean back-calculated somatic growth rate during the first 30 days after first feeding for sprat recruits sampled in 2002 (black dots) and 2003 (grey dots) in the western and central Baltic Sea. Means and standard errors are based on weekly DFF-intervals.

optimum of 22.0 °C for the larval stage of successful sprat recruits (Fig. 10).

## 4. Discussion

### 4.1. Windows of survival

By applying otolith microstructure analysis to young-of-the-year sprat from the central and western Baltic Sea, estimates for the temporal origin of successful recruits were obtained for the two consecutive year classes 2002 and 2003. The approach assumed that recruits originated from those Baltic areas where they were caught, which is supported by Hinrichsen et al. (2005), who showed that offspring from eastern Baltic spawning grounds have a limited mixing probability with central or western Baltic individuals.

One element of uncertainty inherent to the comparison between latest-stage egg and recruit first-feeding distributions was that both distributions were offset by an unknown number of days that corresponded to the yolk-sac stage of sprat larvae. At temperatures of 14–15 °C, sprat larvae are known to start first-feeding approximately 6 days after hatching (Alshut, 1988; Shields, 1989), but for temperatures <10 °C experiments have so far always been hampered by severe pre-feeding mortalities. However, Petereit et al. (unpublished data) found that the time to total yolk-sac depletion ranged from 16 days at 5 °C to 6 days at 13 °C, therefore the maximum uncertainty related to the temperature-dependent development was 10 days.

Our analyses suggested that in both years, recruits that survived until October originated mainly from the summer months June and July. This is supported by two previous studies that inferred a similar ‘summer’ window of survival for Baltic sprat without using direct otolith increment counts (Reglero, 2004;

Baumann et al., 2006a). In both years, the summer period was characterized by favourably high temperatures above 12 °C in Baltic surface waters, where feeding sprat larvae predominantly occur (Voss et al., 2003, 2007; Dickmann et al., 2007). Furthermore, in both 2002 and 2003 the seasonal abundance of larger stages of *Acartia* spp. copepods, the dominant prey species of sprat larvae (Arrhenius, 1996; Voss et al., 2003; Dickmann et al., 2007) was consistently highest in June/July. Voss et al. (2006) argued that the critical period for larval sprat survival may not occur at the transition between endo- and exogenous feeding, but during the following stages, when larvae rapidly increase their niche breadth (Dickmann et al., 2007) and soon rely on the availability of larger prey items to maintain high growth rates. High temperatures in combination with sufficient concentrations of larger copepod stages are conducive to fast growth and hence high survival of summer born sprat (stage duration hypothesis, Leggett and Deblois, 1994), thereby providing an explanation for the predominant summer origin of successful recruits.

Cushings (1990) match–mismatch hypothesis proposed that spawning patterns in temperate fish populations have evolved to match the average onset of the most favourable conditions for offspring survival. For sprat, long-term data sets of spawning effort in the Bornholm Basin (1973–2002, Baumann et al., 2006c) and the seasonal egg abundance during the 1999 spawning season (STORE, 2003) show that over the extended spawning season from March to August (Elwertowski, 1960; Grimm and Herra, 1984) peak spawning effort traditionally occurred around the beginning of June, which is consistent with the summer window of survival.

During the years of this investigation, however, a notable shift from the long-term average in sprat reproduction was apparent. Egg abundance in May/June was low compared to the large quantities of sprat eggs that were sampled as early as in April 2002 and March 2003 in the central Baltic Sea. During this time, the summer thermocline is not yet established in the upper water layer, and surface temperatures are representative of the conditions, sprat eggs and yolk-sac larvae likely experienced in intermediate water depths (Voss, 2002; Nissling et al., 2003). Earlier work has revealed the high sensitivity of sprat eggs to low temperatures (Köster et al., 2001). Specifically, experiments by Nissling (2004) showed a significantly reduced viability of sprat egg and yolk-sac stages below a temperature threshold of 5 °C. Given that surface temperatures in March/April were consistently below 5 °C, we conclude that such unfavourable conditions likely induced substantial mortality rates in spring-born sprat offspring. Low temperatures are thus one potential explanation for the lack of spring-born individuals among successful October recruits.

Furthermore, measurements of *Acartia* spp. seasonal abundance suggested that spring-born sprat larvae would have encountered prey fields consisting predominantly of small copepod nauplii. These may be sufficient for first-feeding larvae but not for larger individuals that appear to rely on larger prey items (Voss et al., 2006), which were only abundant between May and July. In addition, Dickmann et al. (2007) showed that feeding success in sprat larvae from March and April 2002 was indeed very low, in contrast to larvae sampled in July that had a pro-

nounced peak in gut fullness. We conclude that the small prey sizes in combination with low temperatures would have been conducive only to very slow larval growth rates, which prolonged the period of high larval vulnerability. This likely led to increased cumulative mortalities (Anderson, 1988; Leggett and Deblois, 1994; Meekan et al., 2006) and thus to poor survival until recruitment in fall.

#### 4.2. Sprat early spawning and the recruitment problem

The observed shift of the traditional summer spawning peak (May/June) into spring (March/April) during this investigation is paralleled by similar trends in other Baltic areas. Karasiova (2002) analysed historical sprat spawning patterns in the Gdansk Deep adjacent to the Bornholm Basin and found that during the periods 1947–1955 and 1968–1977, main sprat spawning activity was centred in June, whereas during the most recent years of her study (1998–1999) a shift to earlier peak spawning (May) was apparent. However, increased spawning effort in spring likely leads to higher overall egg mortality due to very low temperatures and exposes sprat offspring to a reduced prey size spectrum (Voss et al., 2006; Dickmann et al., 2007), all of which seem to be disadvantageous for sprat reproductive success. In other words, if conditions are on average most conducive to offspring survival in summer, why would any species ‘choose’ to spawn earlier?

We suggest that an explanation might be found in the vertical separation between maturing, overwintering sprat and the eggs/larvae that are subsequently released. Baltic sprat eggs and larvae generally occur in upper water layers above the permanent halocline (Voss et al., 2003; Nissling et al., 2003). In winter, the pre-spawning adults appear to be distributed mainly below the permanent halocline in the deep Baltic basins, presumably to avoid the very low winter temperatures in upper waters (Stepputtis, 2006). For the Bornholm basin, long-term data clearly show a significant increase in average (January–March) bottom water temperatures over the last 15 years (Fig. 11), possibly because of more frequent warm summer inflows from the North Sea into the Baltic (Alheit et al., 2005). In addition, an exceptionally strong inflow event was recorded in summer 2002 in the Baltic Sea, which increased the temperature in bottom waters by several degrees Celsius (Mohrholz et al., 2006). Assuming that sprat reproduction is cued by temperature (MacKenzie and Köster, 2004), this recent temperature increase may have erratically caused sprat to ripen and spawn earlier, in spite of the apparently unchanged ‘summer’ window of survival.

Intuitively, one might expect early spawning patterns to have led to relative recruitment failure, given the considerable mismatch between reproductive effort and the onset of favourable conditions for survival. However, sprat recruitment success was above average in 2002 (Age-1<sub>2003</sub> = 116 × 10<sup>9</sup> fish, ICES, 2007) and exceptionally high in 2003 (Age-1<sub>2004</sub> = 262 × 10<sup>9</sup> fish, mean<sub>1991–2006</sub> = 105 × 10<sup>9</sup> fish, ICES, 2007), although that does not account for potential differences between Baltic sprat sub-populations. We argue that the negative effects of early spawning could be outweighed by very high survival rates of summer born individuals, because of (i) high egg survival late in the season

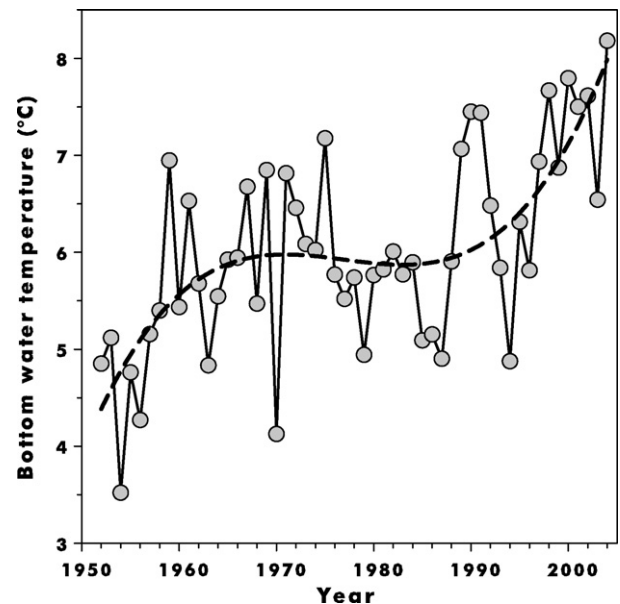


Fig. 11. Time series of mean temperature between January and March in the bottom water of the Bornholm Basin, measured by the permanent measuring station K2 (Alheit et al., 2005). The bottom water was defined by salinities ranging from 8.95 to 14.3 psu, corresponding to the average depth stratum of 50–70 m.

(particularly in 2003, Voss, unpublished data), (ii) high summer temperatures in the surface layer (e.g., in August 2003), (ii) weak coastal transport of early life stages, and (iii) low predation mortalities. Both temperature and transport have previously been shown to be positively related to recruitment strength in Baltic sprat (Baumann et al., 2006a). The relative absence of Baltic cod, *Gadus morhua*, as the major predator of sprat (Köster et al., 2003) may contribute to high young-of-the-year survival, because the decline of the Baltic cod stock has caused an estimated fivefold decrease in predation mortalities on 0-group sprat from the mid 1970s to the early 1990s and thereafter (ICES, 2005).

The strength of the 2002 and 2003 sprat year classes was inconsistent with the observed patterns in prey availability. This is particularly true for 2003, when all developmental stages of *Acartia* spp. were substantially less abundant in the central Baltic than in 2002, thereby indicating overall poorer feeding conditions. Sprat larvae and juveniles might have switched to other planktonic organisms instead of *Acartia*, for example to the second most important prey item of larval sprat, Cladocerans (Dickmann et al., 2007). However, the seasonal abundance of this prey group was similar in 2002 and 2003 and thus inconclusive with respect to recruitment strength (unpublished data, Globan database). It has also been argued that prey concentrations inside the central Baltic basins may not reflect the – so far unresolved – prey environments in the more productive, shallow coastal areas (Fennel and Neumann, 2003), where particularly the early juvenile stages of sprat seem to temporarily aggregate.

The strong recruitment despite similar Cladocerans and lower *Acartia* spp. concentrations in 2003 suggests that prey resources may not be a limiting factor for pre-recruit growth and survival in Baltic sprat, at least not for individuals originating from

the summer months. In the presence of sufficient food (Houde, 1989), ambient temperature comprises the most important determinant of larval fish growth and hence survival (Heath, 1992; Meekan and Fortier, 1996; Fortier et al., 2006). Supportingly, the present study has demonstrated how closely temperature patterns are reflected by otolith-based growth histories of Baltic sprat recruits, and thus argues that the substantial temperature differences between mid-July and mid-August in 2002 vs. 2003 led to pronounced growth differences, which may explain the strength of the 2003 sprat year class.

#### 4.3. Temperature as the key to growth and recruitment

First, it was shown that initial somatic growth rates, inferred from otolith increment widths, were significantly related to sea surface temperature. The positive quadratic relationship indicated a temperature optimum of 22.0 °C, which should be considered with caution because it was predicted outside the observed temperature range, and modelled 0–10 m temperatures were only proxies for the unknown temperature experience of the individuals. Recent laboratory experiments on Baltic sprat early juveniles revealed a somewhat lower temperature optimum (~18 °C, unpublished data), but similar values of 21–22 °C have been reported as thermal growth optima for other clupeid larvae like Japanese anchovy, *Engraulis japonicus* (Takasuka and Aoki, 2006). We note that thermal optima found for average larvae or early juveniles are probably lower than those for prospective survivors, because the latter likely have the higher average growth potential and more efficient feeding capabilities (e.g., Titus and Mosegaard, 1991; Meekan and Fortier, 1996; Vigliola and Meekan, 2002), which are necessary for exploiting high temperatures (Houde, 1989).

Secondly, evidence for the temperature-growth coupling in sprat recruits was found in the patterns of age-detrended otolith growth rates, analysed for recruit cohorts with similar DFFs (weekly/bi-weekly DFF-intervals). The overall patterns well reflected the seasonal fluctuations in surface temperature. Older recruits born earlier in the season and thus at lower ambient temperatures (e.g., June) showed below-average initial increment widths, while later-born conspecifics (e.g., late July) had initially above-average increment widths corresponding to the higher temperatures experienced during their larval stage. Conversely, early (late) born recruits experienced the progressively colder autumn temperatures later (earlier) in ontogeny, and therefore exhibited above (below) average growth rates as juveniles.

Age-detrended otolith growth patterns revealed further that mostly recruits that were still at their larval stage in July benefited from the strong temperature increase between mid-July to mid-August 2003 relative to 2002. Daily temperature differences and corresponding differences in standardized increment widths were strongly correlated only in recruits with DFFs in July but not for recruits born in June. In the latter, growth rates on 21 July, when surface temperature started to increase in 2003, were already very high and perhaps close to their physiological limit (mean  $\pm$  S.D. on 21 July =  $0.98 \pm 0.13$  mm day<sup>-1</sup>). Another possibility is that older survivors actively avoided high

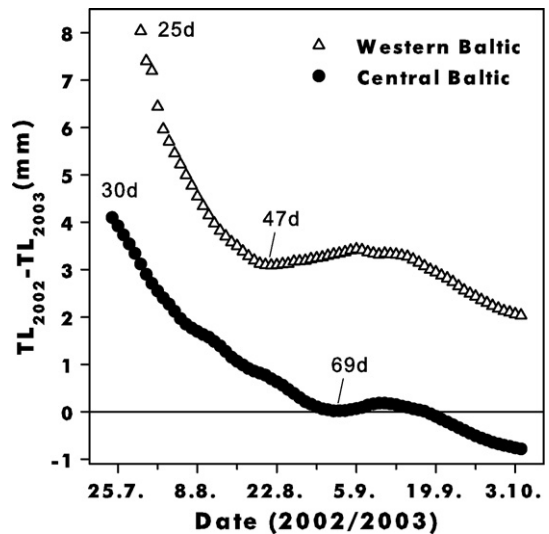


Fig. 12. Daily difference in mean back-calculated TL between sprat recruits from 2002 and 2003 in the western and central Baltic Sea. The figure illustrates how later born survivors in 2003 “catch-up” in length mostly in August relative to their conspecifics of 2002.

summer surface temperatures by seeking a deeper (colder) vertical distribution during their juvenile stage.

Finally, evidence for the strong temperature effect on Baltic sprat growth was found in the converging length distributions. We observed that both western and central Baltic sprat recruits were on average younger in 2003 than in 2002, yet in October the length distributions were almost identical between the 2 years. This entailed that faster growth in 2003 relative to 2002 somehow compensated for the later temporal origin of most Baltic sprat recruits. Specifically, otolith microstructure analysis provided the means to back-calculate previous length ogives of sprat recruits, which clearly indicated that this growth compensation did not happen continuously over time but mostly already in August, i.e., relatively early in the ontogeny of sprat recruits. It was shown that mean otolith-derived size differences between 2002 and 2003 recruits diminished rapidly early in August, and thus coincided with the period of substantially higher surface temperatures in 2003 than 2002. Size-differences increased only slightly and temporarily again at the end of August/early September, and diminished then even further until sampling in October (Fig. 12).

On the other hand, the consistently smaller mean size of western compared to central Baltic recruits appeared not to be growth-related but the result of a broader range in temporal origin, i.e., more smaller and younger individuals survived until October in the western compared to the central Baltic Sea. If growth patterns were contrasted between individuals of similar age, then area differences became small compared to the inter-annual growth variations.

## 5. Conclusion

This study indicated that the traditional survival window of Baltic sprat is restricted mainly to the summer months, during which larvae encounter favourably high ambient temperatures

and a sufficiently wide prey size spectrum. Faster larval growth in 2003, elicited by the notably higher July/August temperatures in 2003 vs. 2002, likely compensated for the later temporal origin of October recruits in 2003. Faster growing larval cohorts likely have better average swimming, preying, and escaping capabilities than slower growing conspecifics (Houde, 1987; Takasuka et al., 2004; Meekan et al., 2006). This has been shown to result in lower cumulative mortalities in fast growing larval cohorts, because they outgrow the period of highest vulnerability to predation and starvation faster than slow growing conspecifics (Leggett and Deblois, 1994; Takasuka et al., 2004). We argue that both timing and strength of the high temperature period in summer 2003 was optimal to promote larval growth, thus conveyed size advantages and shortened the duration of the larval stage, which ultimately led to more individuals surviving until recruitment and produced a strong 2003 year class. This is consistent with our previous analyses of long-term sprat recruitment patterns. Compared to other months and depth strata, August surface temperature explained by far the most variability (73%) in sprat recruitment success between 1974 and 2002 (Baumann et al., 2006a). We therefore suggest that temperature conditions, particularly in summer, comprise the most important environmental determinant of Baltic sprat recruitment success.

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