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RESEARCH ARTICLE

The influence of temperature on the development of Baltic Sea sprat (*Sprattus sprattus*) eggs and yolk sac larvae

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Abstract In spring 2004 and 2005 we performed two sets of experiments with Baltic sprat (*Sprattus sprattus balticus* Schneider) eggs and larvae from the Bornholm Basin simulating ten different temperature scenarios. The goal of the present study was to analyse and parameterise temperature effects on the duration of developmental stages, on the timing of important ontogenetic transitions, growth during the yolk sac phase as well as on the survival success of eggs and early larval stages. Egg development and hatching showed exponential temperature dependence. No hatching was observed above 14.7°C and hatching success was significantly reduced below 3.4°C. Time to eye pigmentation, as a proxy for mouth gape opening, decreased with increasing temperatures from 17 days post hatch at 3.4°C to 7 days at 13°C whereas the larval yolk sac phase was shortened from 20 to 10 days at 3.8 and 10°C respectively. Maximum survival duration of non-fed larvae was 25 days at 6.8°C. Comparing the experimental results of Baltic sprat with existing information on sprat from the English Channel and North Sea differences were detected in egg development rate, thermal adaptation and in yolk sac depletion rate (YSDR). Sprat eggs from the English Channel showed significantly faster development and the potential to develop at temperatures higher than 14.7°C. North Sea sprat larvae were found to have a lower YSDR compared to larvae from the Baltic Sea. In light of the predictions for global warming, Baltic sprat stocks could experience improved conditions for egg development and survival.

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Introduction

The stocks of many marine fish species are widely distributed and therefore experience different hydrographic conditions. For example, flatfishes such as turbot (*Psetta maxima*), plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*) or other fishes like cod (*Gadus morhua*), sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) are distributed in the North Sea in an almost fully marine environment as well as in the brackish waters of the Baltic Sea. For this reason, stocks of the same species are specialised and adapted to prevailing hydrographical conditions in their habitat (Von Westernhagen 1970; Nissling and Westin 1991, 1997; Karås and Klingsheim 1997) and these adaptations are considered specific for the respective population as a result of long-term selection.

Early life stages are most susceptible to mortality and therefore affect recruitment success (e.g. Hjort 1914; Rothschild 1986, 2000; Chambers and Trippel 1997; Houde 2002). The early ontogenetic stages, i.e. eggs and larvae, are strongly influenced by abiotic factors such as temperature, salinity, oxygen or wind forcing (Grauman and Yula 1989; Blaxter 1992; Köster et al. 2003). Temperature plays a central role due to its importance in controlling physiological processes (Blaxter 1992; Fuiman 2002). The exact timing of critical transitions during early life history is extremely important for larval survival and

thus the success of a cohort. For example, the duration of early development during stages not requiring food (eggs and endogenously feeding yolk-sac larvae) can vary by a factor of 2–5 depending on the species (e.g. Bisbal and Bengtson 1995; Buckley et al. 2000). The speed of yolk depletion depends on the surrounding water temperature. As soon as endogenous reserves have been consumed and morphological changes, such as a functional visual system, functional jaw formations and mouth gap opening allow successful foraging (Lasker 1964), prey availability is essential for the larvae. Therefore, knowledge about the duration and timing of early life stages is a prerequisite for understanding and interpreting match and mismatch situations between larval predators and their prey (Cushing 1972).

Temperature can mediate differences in timing and duration of critical life stages both between and within species. Due to the strong temperature influence on metabolism and ontogenetic development, phenotypic plasticity is frequently observed in ectotherms. Consequently, differences in thermal environments during life history evolution could lead to a change in the optimal set of phenotypes expressed by a genotype (i.e. reaction norm: Pritchard et al. 1996; and references therein). In a study on the effect of temperature on the development of aquatic insect eggs, the slope of the average reaction norm was used as an index of adaptation, with positive slopes indicating cold-adapted species, negative slopes indicating warm-adapted species, and slopes around 0 indicating generalist species (Pritchard et al. 1996). The slope of this reaction norm can be taken as an indicator of thermal sensitivity. Within the present study, we calculated this index for thermal sensitivity for different sprat stocks to clarify whether a specific adaptation in accordance to temperature exists between North Sea and Baltic sprat. Possible consequences of these adaptations concerning a climate warming are discussed.

While sprat are of high ecological and commercial value, little is known about temperature effects on their early life stages. Sprat are multiple batch spawners releasing several thousand pelagic eggs per spawning season, which lasts from late March to July in the Baltic and from April to August in the North Sea. Due to the low salinity in the Baltic, egg buoyancy is restricted to the more saline, deeper and colder water layers (e.g. 40–65 m in the Bornholm Basin, one of the important spawning areas in the Baltic Sea). As the spawning season progresses the eggs were found higher in the water column. Alternately in the North Sea sprat eggs float in the surface layers (5–20 m, Conway et al. 1997). Historic observations of egg and larval development are limited to a few temperature regimes and the majority of studies use field caught sprat eggs and larvae which causes variation due to the difference in age (e.g. Ehrenbaum 1936; Morawa 1953). Experimental data on sprat egg and larval development from the English Channel and the North Sea are provided by Thompson et al. (1981) and Alshuth (1988). Shields (1989) investigated larval growth in feeding experiments with field caught sprat eggs from the Irish Sea. For the Baltic Sea information is even less abundant. Nissling (2004) provides information on egg developmental times, larval length at hatch, yolk sac depletion and mortality, originating from either strip spawned or field caught eggs from the Gotland Basin and the Gdansk Deep, respectively.

The aims of this study were the parameterisation of the timing of important ontogenetic milestones of sprat eggs and early larval stages from the Bornholm Basin, Baltic Sea, under different temperature scenarios. Such information can be used for example as input parameter for Individual Based Models (e.g. Kühn et al. 2008). To our knowledge this is the first study in this specific spawning area, which (1) investigates in a comprehensive experimental approach Baltic sprat egg stage duration and mortality, as well as time to hatch, hatching rates and size at hatch, growth during yolk sac phase, eye pigmentation, and yolk sac depletion under a broad range of temperature conditions from 1.8 to 16°C. (2) Results of the present study are compared to corresponding data on sprat early life history from the English Channel, North Sea and other regions of the Baltic Sea in order to assess whether possible population specific differences occur and if so, (3) what implications this might have for the respective population under climate warming scenarios.

Material and methods

Four experiments were conducted within the present study using material from the Bornholm Basin of the Baltic Sea. Figure 1 shows a map of hydrographic areas from which data on sprat early life history is available for comparison. Table 1 provides an overview on the methods and parameters measured in each trial. Sprat eggs were obtained from the Bornholm Basin either by stripping of running ripe sprat (female sprat with hydrated, fully mature eggs ready to be fertilised) or by in situ sampling using a 'Helgoländer larval net' (143 cm in diameter; mesh size 300 µm) towed vertically through the water column. For trial 1 and trial 2 hand stripped sprat eggs were obtained during one cruise with RV Alkor in March/April 2004 whereas experiments 3 and 4 were run with field caught eggs in April and June 2005, respectively. Sprat used for stripping experiments were caught at night with a pelagic trawl (Engel Kombi-Trawl, codend mesh size: 10 mm).

Trial 1 consisted of eggs from one single female which were fertilised with a mixture of sperm from six males for

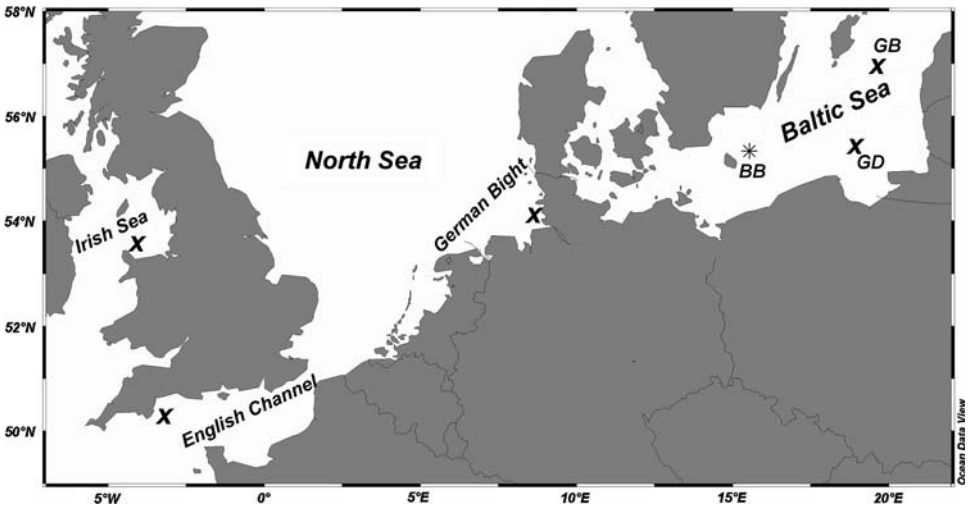

Fig. 1 Map of hydrographic areas from where data on sprat early life history are available (*crosses*). *From left*: Irish Sea, English Channel, North Sea (German Bight), Baltic Sea [*GD* Gdansk Deep (ICES Subdivision, SD 26)], Baltic Sea [*GB* Gotland Basin (SD 28)]. The *asterisk* marks the origin of early life stages used for experiments in this study [Baltic Sea (*BB* Bornholm Basin (SD 25)]

Table 1 Time and origin of biological material, experimental setups, conditions, methods used and parameters measured for each trial

Trial	1	2	3	3a	4
Month/year	March 2004	April 2004	April 2005	April 2005	June 2005
Method used to obtain fertilised eggs	Stripping	Stripping	Helgoländer larval net	Helgoländer larval net	Helgoländer larval net
Position of sampling	φ: 55° 30.78′N; λ: 016° 13.46′E	φ: 54° 59.82′N; λ: 015° 35.91′E	φ: 55° 17.86′N; λ: 015° 44.88′E	φ: 55° 17.86′N; λ: 015° 44.88′E	φ: 55° 17.51′N; λ: 015° 45.01′E
Date of sampling	29th March	1st April	27th April	27th April	8th June
Eggs (*n*)	2,906	287	1,125	64	165
Incubation temperatures (°C)	1.8; 3.4; 5.2; 6.8; 8.4; 10.0; 11.6; 13.1; 14.7; 16.0	8.4 and 10.0	3.8; 5.7; 7.6	3.8; 7.6	7.5; 9.4; 11.1; 12.9
Salinity	14.8	14.8	13.4	13.4	14.0
Light regime light/darkness (hours)	12/12	12/12	14/10	14/10	14/10
Replicates (beakers per temperature)	4	3	5	1	4
Image software	Image Tool 3.0	Image Tool 3.0	Image Pro-Plus 5.0	Image Pro-Plus 5.0	Image Pro-Plus 5.0
Imaged: alive/frozen	Alive	Alive	Frozen	Frozen	Frozen
Egg phase: stage development	+	−	−	−	−
Egg phase: egg mortality	+	+	−	−	−
Egg phase: hatching success	+	+	−	−	−
Yolk sac larvae: yolk depletion	−	+	+	+	−
Yolk sac larvae: growth	−	+	+	+	−
Yolk sac larvae: eye pigmentation	−	+	+	+	+
Yolk sac larvae: mouth gape opening	−	+	+	+	+
Larvae: starvation 100% mortality	+	+	−	−	−

30 min in unfiltered surface seawater at ambient salinity of 7.1. Trial 2 followed the same procedure with eggs from another single female and mixture of sperm from another six males. Subsequently eggs were transferred into a 500 ml plastic box containing 1.0 µm filtered Baltic seawater with a salinity of 18, which keeps fertilised eggs floating (Nissling et al. 2003; Nissling 2004). Unfertilised eggs were negatively buoyant and consequently eggs which had sunk to the bottom were removed (Nissling 2004). Subsamples of the remaining floating eggs were checked under a stereo microscope after 12 h to ensure fertilisation success. The fertilised eggs were stored in darkness and cooled to 6°C in a climatic exposure test chamber (fluctuation max. ±0.5°C). All eggs were transported within 38 h to the Leibniz-Institute of Marine Science in Kiel and upon arrival separated into 150 ml beakers filled with 6°C and 5 µm filtered water with a salinity of 14. The salinity of 14 kept the eggs at all temperatures floating. Each beaker containing 30–156 eggs was placed into a temperature gradient table. This incubation table was made of aluminium and was heated on one side and cooled on the other side, which created a stable temperature gradient. Up to ten different temperatures could be held at high accuracy (0.08–0.17°C standard deviation) in six replicates. A functional diagram of such an incubation table can be found in Thomas et al. (1963) and a similar table was used for experiments with sprat eggs conducted by Thompson et al. (1981). After the beakers were placed into the table, they were gently acclimated to the chosen temperature by approximately 1°C per hour. Experiment 1 was performed with ten different temperatures in four replicates (8.4 and 10.0°C in three replicates) whereas trial 2 was restricted to 8.4 and 10.0°C in three replicates due to the low egg numbers obtained for this trial (Table 1). Before incubation sub-samples of eggs were checked again under a stereo microscope to determine the developmental stage at the start of the incubation. Egg stages were determined based on a modified scale developed by Thompson et al. (1981) for English Channel sprat. All eggs in trial 1 were added to the temperature gradient table at the development stage IA. Since the eggs for experiment 2 were obtained 1 day prior to start they had developed further and had already reached the development stage II. The light regime was chosen to be 12L:12D. Egg mortality was checked daily and dead eggs were removed from the beakers via pipetting (pipette with 5 mm diameter). Every 24 h, digital images of randomly chosen sub-samples (one to two eggs/beaker) of eggs were recorded with a NIKON CoolPix 995 camera (3.4 megapixel) under a stereo microscope (WILD M3 Z). Eggs were gently removed from the beakers with the pipette, carefully released in a drop of sampling water (with the same temperature and same salinity) on a petri dish and photographed. Due to the overall low numbers, photographed eggs were immediately and carefully replaced in the respective beaker. Egg developmental stages were determined from the images.

The duration of the egg stages I–IV was defined as days until the last egg of a temperature group reached the next stage. Egg development rate (EDR, percentage/day) until hatch was calculated, with hatching being defined as the time interval (T) from fertilisation, until the first larvae within a temperature had hatched.

$$\mathrm{EDR} = \frac{1}{T} \times 100 \quad (1)$$

Additionally, daily sprat egg survival was determined.

Sub-samples of hatched larvae were photographed daily and morphometric measurements were taken using image analysis software Image Tool 3.0 (UTHSCSA; http://ddsdx.uthscsa.edu/dig/itdesc.html). The time to yolk sac depletion was expressed as yolk sac depletion rate (YSDR, percentage/day) and was calculated from the time interval (T) from hatch to depletion of the yolk sac.

$$\mathrm{YSDR} = \frac{1}{T} \times 100 \quad (2)$$

Larval standard length (SL) of each larva was measured from the tip of the mouth to the end of the notochord. In addition, timing of completed eye pigmentation was recorded as a proxy for mouth gap opening and first feeding (Alshuth 1988; Fukuhara 1990). Occurrence of 100% larval mortality was noted.

For experiments 3 and 4 sprat eggs were obtained by tows with the 'Helgoländer larval net' in the Central Bornholm Basin (ICES Subdivision 25) during two cruises with RV Alkor in April and June 2005, respectively (Table 1). Eggs of both trials were sorted into 500 ml plastic containers and stored at 6°C. The fertilised eggs were transported within 48 h to the Leibniz-Institute of Marine Science in Kiel. In the laboratory, eggs were transferred individually into 800 ml beakers containing 5 µm filtered Baltic Sea water using a syringe (5 mm diameter). The different development stages of the in situ sampled eggs were separated into early (egg stage I and II) and late (egg stage III and IV) development stages and treated as two distinct trials. The beakers were transferred to the temperature gradient table and again temperatures were gently adjusted as was done for the first set of experiments. The photoperiod was adjusted to the time of the year at 14L:10D (Table 1). Corresponding to trial 1 and 2 eye pigmentation was recorded and dead eggs and larvae were removed and counted daily. Larvae of the late developmental stage group of experiment 3 were sampled on day 1, 2, 7 and 10 post hatch (dph). Larvae of the early stage group were sampled every 2–3 dph to analyse yolk sac area decrease and larval growth. Sampled larvae were immediately frozen at −70°C in seawater and digital

images were recorded under a stereo microscope within 2 month of sampling. Morphometric measurements were taken as in experiment 1 and 2.

Larval growth

In order to determine the effect of freezing and thawing on the length measurements of larvae, one shrinkage experiment was conducted. At total of 42 larvae was measured alive, frozen at −24°C for 540 days and were measured following thawing.

The growth curves for yolk sac larvae at different temperatures were estimated by fitting Laird-Gompertz growth equations:

$$L_t = L_0 \times e^{\left[a \times \left(1 - e^{(-b \times t)}\right)\right]} \quad (3)$$

where L_t is the length (mm) at age t (in days); L_0 is length (mm) at hatch; and a and b are model parameters. This function has previously been used to model larval growth rates of clupeoid fish larvae (Munk 1993; Gaughan et al. 2001; Llanos-Rivera and Castro 2006).

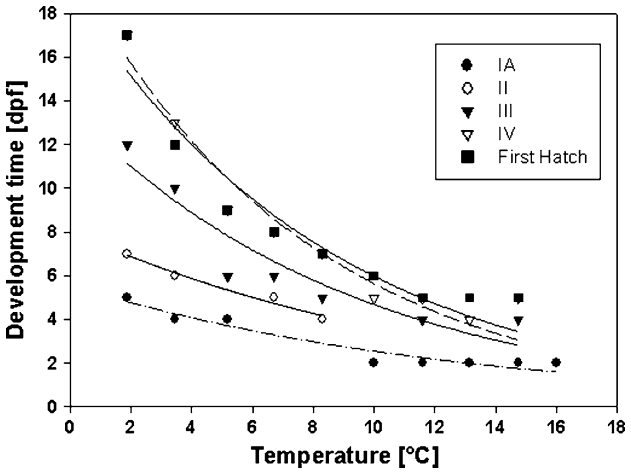

Fig. 2 Stage specific egg developmental times in days post fertilisation (*dpf*) for Baltic sprat eggs incubated under different temperature regimes. Shown are values of the last observed occurrence of a specific development stage and the first occurrence of hatched larvae

Results

Egg phase

Depending on temperature the time to first hatch varied between 5 days post fertilisation at 14.7°C and up to 17 days at 1.8°C (Fig. 2). As expected, the duration of each developmental stage decreased with increasing temperature (Table 2). Above 14.7°C no successful egg development was observed. At the lowest temperature 1.8°C only two eggs survived, one larva having a malformed yolk sac and the other hatching successfully. EDR until first hatch rose from 5.9 to 20% per day with increasing temperature (Fig. 3). Egg survival varied between the experiments and showed no significant differences between the temperatures (Fig. 4). In trial 1 survival until hatch was generally low

Table 2 Results of the parameterisation during the egg stage of sprat egg incubation experiments from the present study and from literature sources

Stage duration	Stage/area	Equation	Coefficients		Standard error	r^2	*P* value
This study	IA	Exponential	a	5.5739	0.3759	0.93	<0.0001
			b	0.0763	0.0093		0.0002
This study	II	Exponential	a	8.0628	0.3500	0.98	0.0019
			b	0.0763	0.0092		0.0131
This study	III	Exponential	a	13.6062	1.2366	0.89	<0.0001
			b	0.1068	0.0149		0.0002
This study	IV	Exponential	a	20.3280	1.4337	0.95	<0.0001
			b	0.1285	0.0126		<0.0001
This study	First hatch	Exponential	a	19.0949	1.4707	0.93	<0.0001
			b	0.1163	0.0131		<0.0001
Egg development rate							
This study	Baltic Sea	Potential	a	3.9255	0.4101	0.97	<0.0001
			b	0.6296	0.0446		<0.0001
Nissling (2004)	Baltic Sea	Potential	a	2.3657	0.1579	0.99	<0.0001
			b	0.8320	0.0284		<0.0001
Thompson et al. (1981)	English Channel	Potential	a	1.5133	0.1713	0.98	<0.0001
			b	1.2353	0.0413		<0.0001

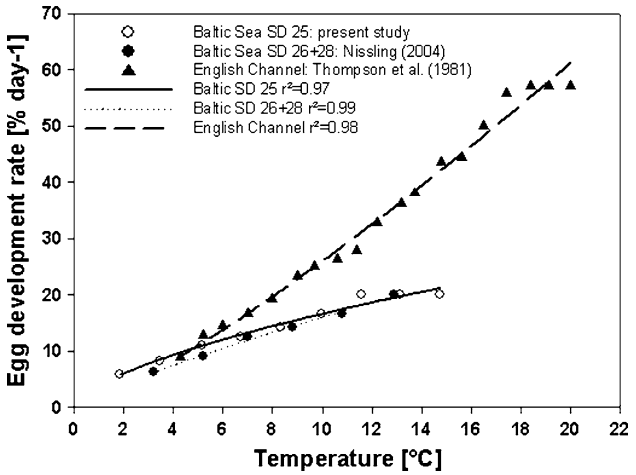

Fig. 3 Shown are egg development rates in percent per day versus temperature for egg incubation experiments from different areas. Literature values from Nissling (2004) represent 50% hatch data whereas Thompson et al. (1981) and this study reflect first hatch data for each temperature. Potential equations are fitted to the data

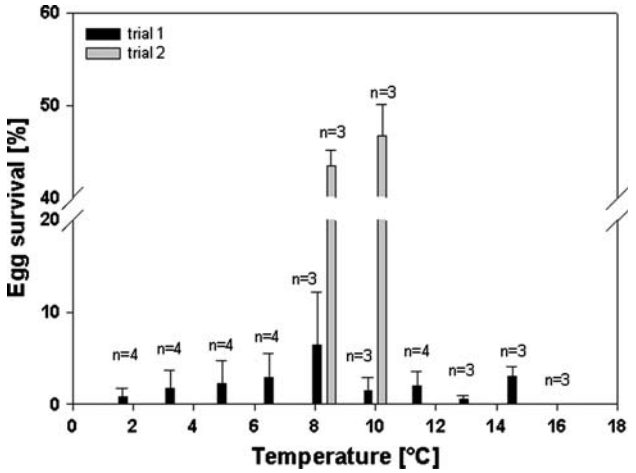

Fig. 4 Temperature dependent egg survival for two different experimental trials at different incubation temperatures. No survival was observed at 16°C. Same temperatures (8.4 and 10.0°C) were used for trial 1 and trial 2. Shown are mean (+SD) values of three to four replicates (*n*)

1–6.5% compared to 43 and 47% survival in trial 2. However, survival showed an increasing but not significant trend from the lowest temperature to 8.4°C in trial 1, while in trial 2 higher survival was observed at 10°C compared to 8.4°C.

Larval phase

In the preservation experiment, no significant differences in frozen SL versus alive SL were found. An analysis of covariance showed no significant difference in slope ($P > 0.05$) or intercept ($P > 0.05$) from a 1:1 ratio and residuals were normally distributed and showed no trend. Thus it was assumed that the morphometric measurements conducted on frozen material were comparable to live measurements and no correction was applied.

Laird-Gompertz curves were fitted to larval growth data (Fig. 5). The calculated length at hatch of 3.4 and 3.5 mm at 10.0 and 8.4°C, respectively, agreed well with the observed measured values of 3.5 mm for both temperatures (Fig. 5a, b). For these temperatures eggs were obtained by fertilising eggs of a single ripe female. The slopes of the growth curves at 10.0 and 8.4°C were not statistically different (*F*-test, $P > 0.05$). Larvae from the third trial hatched from eggs obtained by in situ sampling. The fitted growth curves for 3.8, 5.7 and 7.6°C are shown in Fig. 5c–e. For these data length at hatch was not observed directly but estimates based upon fitted Laird-Gompertz functions. Neither growth curves nor lengths-at-hatch showed a temperature effect in this trial (Table 3).

The timing of total yolk sac depletion, marked by a dashed line within the growth curve plots (Fig. 5), ranged from 10 days up to 20 days from 10.0 to 3.8°C. In accordance with these results the observed YSDR increased with increasing temperature (Fig. 6 and Table 3). Baltic sprat larvae showed a higher depletion rate at the same temperature compared to North Sea sprat larvae within the analysed temperature range. The linear regression of the data obtained within the present study for the Bornholm Basin showed no significant difference to the data published by Nissling (2004) for the Gdansk Deep and the Gotland Basin, and an analysis of covariance revealed significant differences in the slopes of linear regression lines between the Bornholm Basin (Baltic Sea) and the North Sea data on YSDR ($P < 0.001$).

For every temperature examined, the time to complete eye pigmentation coincided well with the timing of mouth gap opening (Fig. 7). Time to pigmentation decreased exponentially with increased temperature. Between 3.8 and 10.0°C larval development was accelerated by a factor of 2.3 from 16 to 7 dph for Baltic sprat larvae.

Although the survival of starving sprat larvae showed high variability between different temperatures, a maximum survival was observed at 6.8°C with a mean of 24 dph (Fig. 8). Temperatures above and below 6.8°C lead to earlier mortality.

Discussion

Egg phase

Sprat egg development was temperature dependent. With increasing temperature, the incubation period from

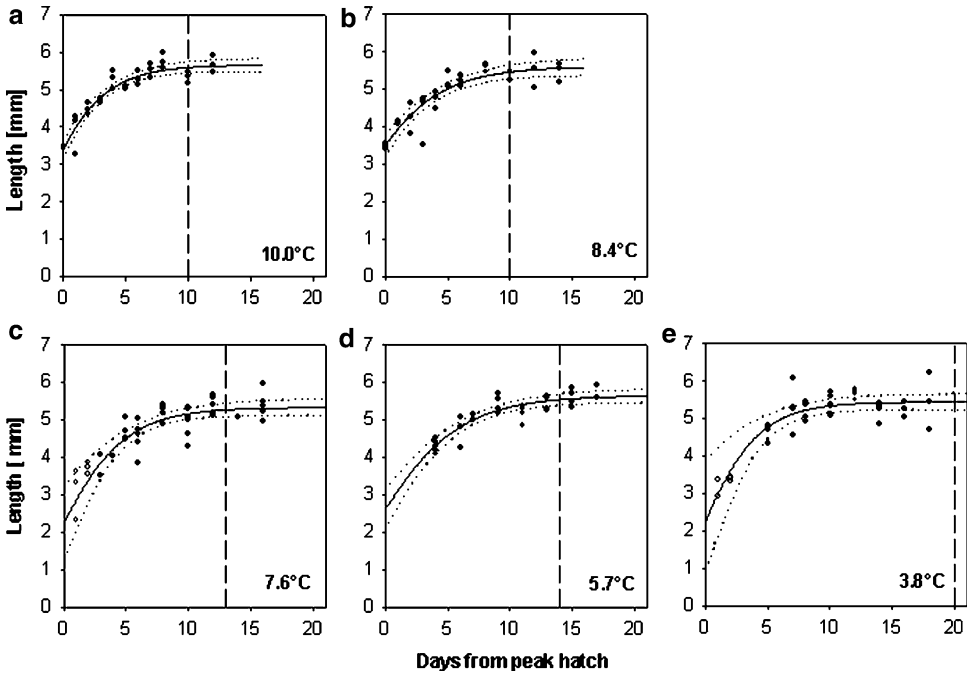

Fig. 5 Individual length measurements of sprat yolk sac larvae incubated at 10.0°C (**a**), 8.4°C (**b**), 7.6°C (**c**), 5.7°C (**d**) and 3.8°C (**e**). Laird-Gompertz growth curves are fitted to the data. Open dots represent measurements from one single replicate only and were not included in the regression analyses. *Dotted lines* indicate 95% confidence interval of the nonlinear regression. *Dashed vertical lines* represent age in days at total yolk depletion

fertilisation to hatch was reduced. For temperatures above 5°C, time to hatch was similar to data published by Nissling (2004) for Baltic sprat eggs. Differences between the studies were found at colder incubation temperatures (1–5°C), with Nissling obtaining a 2.5-day longer incubation period to hatch. This could be the result of the different definitions of the periods considered. While Nissling defined the period as the duration from fertilisation to 50% hatch, we defined the hatch date where first hatching larvae were observed. By applying first hatch as indicator for the duration of the egg development period the results were shifted in the direction to the fastest developing embryos. Consequently, our model predicts the minimum time required for sprat larvae to hatch after fertilisation. Additionally, we had to account for the first 38 h post fertilisation, where all eggs experienced 6°C temperature conditions (transport/acclimatisation) which biased our 1.8 and 3.4°C treatments and caused faster development of the eggs compared to conditions with low constant temperatures from the time of fertilisation.

Furthermore, colder temperatures increased the intraspecific variability of hatching, resulting in some eggs still being at stage IV while other larvae already had hatched. No successful egg development was observed at the lower and upper end of the tested temperature range. The lack of successful hatching at the temperature extremes agreed with results from experiments conducted by Nissling (2004). He found a significantly lower survival of sprat eggs at temperatures below 5°C. However, survival was generally low (0.6–6.5%) in trial 1 compared to trial 2 (43–46%). Since, in both experiments, eggs incubated were gently transferred to waters of higher salinity shortly after fertilisation during the hardening phase of the egg membrane, differences in egg volume due to water loss through the membrane could not be excluded. Whether this had a potential effect on development or viability could not be assessed, but results from further experiments under different salinity regimes during incubation suggested the effect to be non-significant (C. Petereit et al., unpublished data). Since eggs from only one female were used for each trial, the different survival rates might have reflected differences in egg quality due to maternal effects (Brooks et al. 1997; Chambers 1997; Trippel et al. 1997, 2005).

Thompson et al. (1981) performed experiments on sprat egg development from the English Channel using 19 different temperatures from 4.5 to 20°C and found successful development over all temperatures, although from 17.4 to 20°C hatching occurred prematurely before many eggs reached stage IV. The authors stated that it was doubtful whether the larvae were sufficiently well developed to survive. Egg survival until hatch between 6 and 18.5°C ranged from 36 to 67%, with higher mortality at the extremes of the used temperatures. These findings of successful egg development above 14.7°C are in contradiction to the findings of the present study and may be related to possible genetic differences, non-genetic adaptations or just differences in incubation salinity between the two populations.

Baltic sprat and English Channel sprat showed obvious differences in EDR. Baltic sprat EDR increased from 5.9 to 20% per day depending on temperature (Fig. 3) whereas this rate for English Channel sprat eggs increased by a

Table 3 Results of the parameterisation during the larval stage of sprat egg incubation experiments from this study and from literature sources

Yolk sac larval growth	Temperature (°C)	Equation	Coefficients		Standard error	r^2	P value
Trial 2 (this study)	10.0	Laird-Gompertz	a	0.5046	0.0366	0.89	<0.0001
			b	0.3713	0.0592		<0.0001
			L_0	3.4158	0.1274		<0.0001
Trial 2 (this study)	8.4	Laird-Gompertz	a	0.4723	0.0432	0.82	<0.0001
			b	0.2886	0.0609		<0.0001
			L_0	3.4964	0.1515		<0.0001
Trial 3 + 3a (this study)	7.6	Laird-Gompertz	a	0.7172	0.0910	0.78	<0.0001
			b	0.2886	0.0579		<0.0001
			L_0	2.6174	0.2609		<0.0001
Trial 3 + 3a (this study)	5.7	Laird-Gompertz	a	0.7762	0.2304	0.79	0.0023
			b	0.2621	0.0773		0.0022
			L_0	2.6019	0.6411		0.0004
Trial 3 + 3a (this study)	3.8	Laird-Gompertz	a	0.8952	0.1300	0.81	<0.0001
			b	0.3710	0.0677		<0.0001
			L_0	2.2970	0.3051		<0.0001
Completed eye pigmentation							
This study	Baltic Sea	Exponential	a	23.2675	2.0871	0.91	<0.0001
			b	0.1157	0.0119		<0.0001
Alshuth (1988)	North Sea	Exponential	a	40.3277	7.0769	0.97	0.0047
			b	0.1709	0.016		0.0004
Yolk sac depletion rate							
This study	Baltic Sea	Potential	a	1.7621	0.4212	0.94	0.0139
			b	0.7688	0.1132		0.0025
Nissling (2004)	Baltic Sea	Potential	a	1.0143	0.218	0.98	0.0187
			b	1.0462	0.0911		0.0014
Alshuth (1988)	North Sea	Potential	a	0.2705	0.0773	0.98	0.0249
			b	1.4951	0.1061		0.0001
Starvation induced mortality							
This study	Baltic Sea 100%	Normal distribution	a	23.0473	1.1308	0.74	<0.0001
			b	4.6151	0.5437		<0.0001
			X_0	6.1449	0.4378		<0.0001

factor of 5 from 9 to 44% per day (temperature range 4.3–14.8°C; Thompson et al. 1981). An analysis of covariance between the two linearised data sets of development rates revealed significant differences in the slopes ($P < 0.001$) and intercepts ($P < 0.001$).

At temperatures exceeding 5°C, Baltic sprat eggs developed more slowly compared to North Sea sprat eggs. This may have been the result of different salinities during incubation. Increased embryonic development rate at higher salinity has been demonstrated for other species e.g. turbot by Karås and Klingsheim (1997) who also reported a wider temperature range for optimal survival of North Sea turbot eggs (9–18°C) compared to Baltic turbot eggs (14–17°C). Egg survival rates were highest between 20 and 35 salinity in the North Sea stock and very low at 15 and below, whereas eggs from the Baltic population had high survival rates at salinities between 10 and 15 (Kuhlmann and Quantz 1980; Karås and Klingsheim 1997). For herring Holliday and Blaxter (1960) found a negative effect of low salinities on hatching. No significant effect of incubation salinity from 26 to 36 on 50% hatch was found for Atlantic cod eggs by Laurence and Rogers (1976). Additionally, results from a meta analysis of the ontogeny of yolk-feeding fish by Kamler (2002) reported no decelerating effects of salinity on ontogenetic rates in the majority of the analysed studies. However, no experiments examining the effects of salinity on the development rate of Baltic or North Sea sprat eggs have been published, which would have the potential to assess the magnitude of the factor salinity on time to hatch for this species.

The index of thermal sensitivity for Baltic sprat eggs was calculated to be 0.63, (Parameter b of power Function-

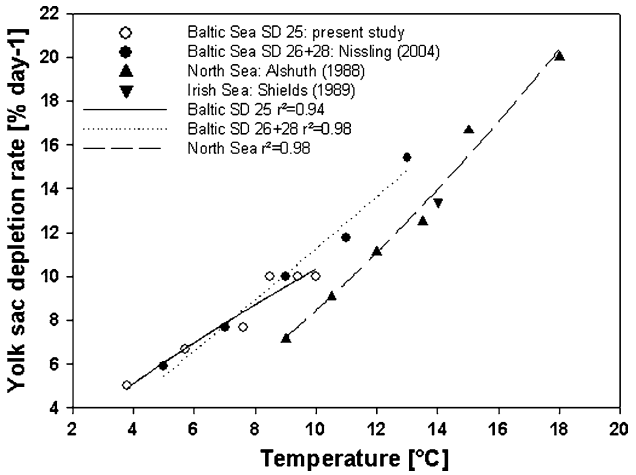

Fig. 6 Yolk sac depletion rate for yolk sac larvae from different areas incubated at different temperatures. Potential equations are fitted to the data. Data from the North Sea, Irish Sea as well as from Subdivisions (SDs) 26 and 28 from the Baltic Sea are extracted from the literature

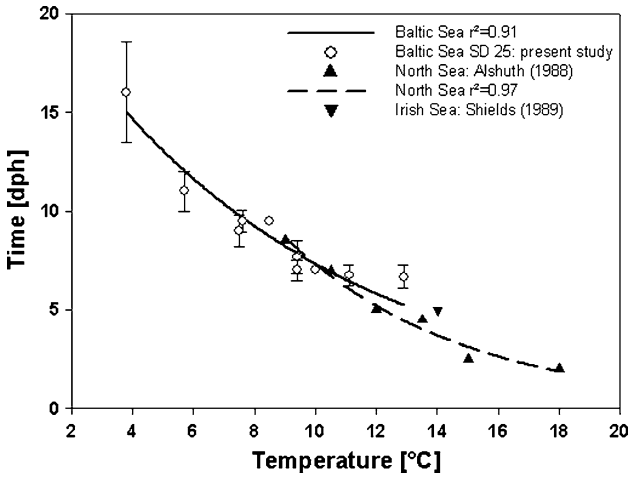

Fig. 7 Time period from hatch to eye pigmentation of yolk sac larval sprat. Exponential functions were fitted to the data. North Sea and Irish Sea data were extracted from the literature. For Baltic sprat larvae, shown are mean (±SD) values of three to six replicates

slope of reaction norm, Table 2), which reflected cold-adaptation according to the gradient of the slope (Pritchard et al. 1996). Similarly, the temperature-dependent time-to-hatch data (50% hatch) reported by Nissling (2004) were used, fitted to the power function to obtain 0.83 for the parameter b (Table 2), which also reflected cold-adaptation. It can therefore be concluded, that the experimentally derived egg data from individuals from the three major spawning areas (Bornholm Basin, Gdansk Deep, Gotland Basin) in the Baltic have a cold-adapted egg development.

In comparison, English Channel sprat eggs (first hatch data) showed a thermal sensitivity of 1.23 (Parameter b of power Function, Table 2) which reflected warm-adaptation

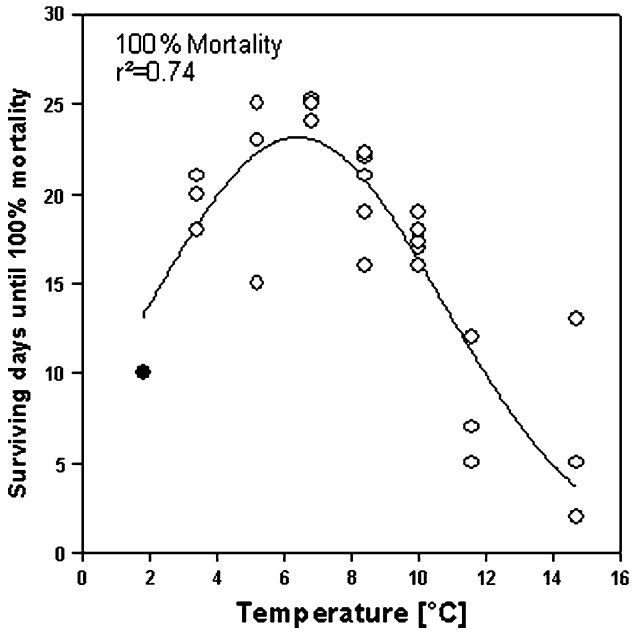

Fig. 8 Starvation induced 100% mortality of sprat larvae in days after hatching. Shown is the fitted normal distribution curve for mortality (*solid line*). *Each circle* represents the time, until the last larvae within a single replicate (beaker) survived. At some temperatures (6.8, 8.4 and 10°C) two replicates were terminated on the same day. Therefore, dots were offsetted graphically, which had no influence on the curve fitting. The single observation (*black circle*) was not included in the analysis

indicating thermal adaptation differences between the two populations.

According to Peck et al. (Prof. Myron Peck, University of Hamburg; unpublished data), no such thermal population differences were found for Gadiformes and Clupeiformes. They compared thermal sensitivity of six populations of Atlantic cod and stated that population specific differences may exist (specifically Baltic Sea) but in this case did not correlate with differences in latitudes. For Atlantic herring populations (Irish Sea/Baltic Sea; spring and autumn spawners) the thermal sensitivity did not differ much (Parameter b from 1.08 to 1.31), and always exceeded the b value of 1, which reflected more rapid egg development with increasing temperature. All considered Clupeiformes showed warm-adaptation except for the sprat population in the Baltic.

Fox et al. (2003) conducted temperature dependent development experiments with plaice (*Pleuronectes platessa* L.) eggs from the Irish Sea. They found more rapid EDRs under similar temperature conditions in Irish Sea plaice populations compared to eggs from species from the North Sea. Larvae hatched up to 2 days earlier from Irish Sea plaice eggs. The authors suggested that known genetic differences between the two stocks could lead to the inter-stock differences in EDRs. Also, maternal effects (egg size and spawning season) should be taken into consideration as

EDRs were shown to be affected by egg size. Since the application of incorrect EDRs clearly has the potential to bias the assessment of spawning stock biomass using egg production methods, Fox et al. (2003) recommended that egg development relationships should be evaluated separately for each stock.

Larval phase

Larval size at hatch is generally influenced by incubation temperature (Chambers 1997; Blaxter 1992) and larval length at hatch is an important parameter which influences initial locomotion performances such as swimming speed, escape response and predator avoidance (Blaxter 1992). However, in some cases larger larvae experienced higher vulnerability to predation pressure compared to conspecifics at the same age with smaller body size (Litvak and Leggett 1992).

Eye pigmentation is essential for the developing larvae as it enables spatial orientation and allows control navigation. This event coincided well with mouth gap opening (this study; Alshuth 1988; Shields 1989). A functional visual system is also a prerequisite for successful feeding and improved predator avoidance (Blaxter 1992; Fuiman 2002). This ontogenetic event is positively related to increasing temperature. As a consequence, eye pigmentation occurs sooner under warmer conditions and vulnerability to predation may be reduced. No prominent differences could be detected between sprat larvae from the Baltic Sea and the North Sea. The literature on North Sea sprat concurs with the results of this study and extend the temperature range at which eye pigmentation was completed within 3.5 dph up to 18.0°C (Alshuth 1988). However, the ambient hydrographical conditions for the early life stages of sprat are not the same in both areas. Mean water temperatures during the time when early life stages of sprat occur are lower in the Baltic Sea (>3–7°C, ICES Oceanographic Database; http://www.ices.dk/ocean/) compared to that of the North Sea (mean monthly temperatures 6.7–12.1°C April–June; Loewe et al. 2005). Our results clearly indicate that the lower ambient temperatures in the Baltic may extend the pre-visual phase, and hence protract the period of non targeted swimming and feeding behaviour of sprat larvae in this area.

For anchoveta (*Engraulis ringens*) from two different populations (13° latitude apart) from the coast off Chile, Llanos-Rivera and Castro (2006) found no differences in the duration of the yolk sac phase, yolk consumption rate and larval growth rate until yolk exhaustion when larvae were reared at the same temperature in the range between 12 and 20°C. The opposite was found for sprat larvae in this study. YSDRs were differently affected under identical temperature conditions for Baltic and North Sea larvae. A higher depletion rate leads to an earlier demand for exogenous food resources and thus increases the risk of starvation.

For the YSDR, we have seen the same thermal adaptation pattern as for the egg development. The parameters b were 0.76 (present study), and 1.04 (Nissling 2004) for the Baltic and 1.49 for the North Sea. The slopes of the regression lines were statistically different between Baltic Sea and North Sea. Therefore, it may be possible that different thermal adaptations on population level exist indicating that North Sea sprat larvae could cope better with warmer water than Baltic sprat larvae.

Population specific future implications

In this study we have shown the close coupling of temperature and the timing and duration of important ontogentic events during the egg and yolk sac larval stages of sprat from the Bornholm Basin (Baltic Sea). Our results suggest that increased temperatures predicted due to global climate change (IPCC 2002) would impact early life stages of sprat in the North Sea and Baltic Sea in different ways.

Assuming an increase of at least 2°C for the ambient water layers where sprat eggs and larvae occur, we would expect differences in the viability of Baltic and North Sea sprat eggs.

Alheit et al. (2005) compared temperature time-series for the Bornholm Basin from 1970 to 1987 and 1988 to 2003 and found an increase in the spring and autumn surface mixed layer temperature by about 1.5°C. On shorter time scales temperatures in the upper halocline, i.e. the water layer where sprat eggs occur (Nissling et al. 2003) may be affected further due to the inflow of warm summer surface waters from the Kattegatt (Mohrholz et al. 2006). This may be advantageous (MacKenzie et al. 2007) as present average ambient conditions in the water layer where sprat eggs occur (45–65 m; ~4°C) range well below the optimal survival temperature (8.4°C) found in this study and (5–13°C) as described by Nissling (2004). Additionally, low temperatures do not only directly influence survival but, as shown in the present study, also prolong the development time thus increasing the susceptibility to predation or malformation of the embryos (Nissling 2004).

Contrary to the Baltic Sea, in the North Sea sprat eggs and larvae are distributed in the upper 5–20 m of the water column (Conway et al. 1997). Wahl and Alheit (1988) report the peak spawning time for North Sea sprat to be in May/June. Mean May temperatures from 1968 to 2005 were 9.1°C with a maximum of 10.9°C in 1990, whereas in June the mean temperature was 12.08°C with the maximum

temperature of 14.2°C in 1992 (Loewe et al. 2005). Even for this temperature range lethal thermal values for successful egg development are unlikely, but a further warming would move temperature related survival rates further towards the descending leg of the curve.

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