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Laboratory calibration of optimal growth to deduce *in situ* feeding conditions of early juvenile sprat *Sprattus sprattus* from otoliths

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ABSTRACT: We performed an ad libitum experiment over 30 d to generate otolith growth reflecting optimal fish growth for use in estimation of *in situ* food availability via otoliths in post-larval sprat (*Sprattus sprattus* L.). Between 16 and 22°C, no difference in length or wet mass growth was detected in contrast to a significant and direct increase from 5.5 to 7.9 µm d^{-1} in otolith and 8.7 to 10.5 mg d^{-1} in dry mass growth. The different responses in length/wet mass growth and otolith growth were likely caused by the onset of lipid storage, which we assume to be triggered ontogenetically. We estimated a 10-fold increase in food demand from metamorphosed sprat (30 mm length) to juveniles (50 mm length). According to a bioenergetic approach, juveniles needed a concentration of 3 and 5 individuals l^{-1} assuming ad libitum feeding on *Acartia* sp. at 16 and 22°C, respectively. We described increment width as a function of temperature ($IW = -0.0326T^2 + 1.6472T - 12.506$) and compared this reference with increment widths of Baltic Sea recruits at corresponding temperatures. On average, increments in 2007 were smaller than the laboratory reference, suggesting sub-optimal feeding conditions. In 2003, mean increments were larger, except for early born survivors which exhibited poorer growth. These early born sprat encountered high temperatures after metamorphosis, leading to a higher food demand. Our findings highlight the importance of food availability in near-shore nursery areas and the impact of the right seasonal timing of the juvenile stage on recruitment strength in Baltic sprat.

KEY WORDS: Otolith · Growth · Food availability · Temperature · Sprat · Baltic Sea

INTRODUCTION

Growth during the first year of a fish's life influences its survival (e.g. Hovenkamp 1992, Meekan & Fortier 1996, Sogard 1997) and subsequently the recruitment of young fish to the parental generation (e.g. Martino & Houde 2010, Joh et al. 2013, Payne et al. 2013). Hence, growth studies of early life-stages have received much attention during recent decades. Generally, growth during early life-stages of fish is determined by 3 main factors: 2 exogenously controlled factors (temperature and food availability) and an endogenously controlled factor (ontogeny; Hare & Cowen 1995, West et al. 2001). The first 2 primarily define the environmental habitat and exhibit pronounced variability in their characteristics. In contrast to temperature, prey availability is much more difficult to examine in field studies as it can vary on much smaller temporal and spatial scales. For zooplanktivorous fish, patchiness of zooplankton causes inhomogeneous prey fields. Consequently, standard measurements of plankton density by net samples can be strongly influenced by patchiness (Folt & Burns 1999, Franks 2005). The sampling problem in shallow coastal waters is even larger as standard plankton nets, integrating the density of planktonic organisms over the water column, cannot be operated (Barnett et al. 1984, Nagao et al. 2001,

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Gutkowska et al. 2012). Due to this sampling problem, the average prey abundance may appear to be high, whereas stomach contents of zooplanktivorous fish are lower than expected — or vice versa. Alternatively, the frequency and temporal occurrence of successful feeding events can be estimated from natural tags such as otoliths (Meekan et al. 2003, Kurita et al. 2004, Pecquerie et al. 2012). In otoliths, growth increments are deposited on a daily basis in many fish species (Pannella 1971). A correlation between increment growth on the otolith and somatic growth enables the retrospective analysis of individual growth histories (Campana & Neilson 1985, Campana 1990). However, before using otolith microstructure as a proxy for growth, the correlation between otolith and somatic growth needs to be examined in detail, as uncoupling between otolith and somatic growth has previously been observed (Templeman & Squires 1956, Mosegaard et al. 1988, Takasuka et al. 2008). If uncoupling can be excluded or its mechanism is understood, feeding histories can be deduced from otolith growth. When assuming a linear (or monotone) relationship between otolith and somatic growth, a wide increment depicts a day of strong somatic growth, while a narrow increment represents a day of low somatic growth. Consequently, when comparing fishes of the same life-stage at the same ambient water temperatures, an individual with narrow increments experienced sub-optimal feeding conditions, while an individual with broad increments ingested more or better food. Thus, if the influences of temperature and life-stage are known and uncoupling of somatic growth from otoliths can be excluded, daily increment pattern can be used to uncover the realized feeding conditions on an individual basis.

Baltic sprat form large populations and, together with herring, occupy a central trophic position in the Baltic Sea food web, transferring energy from zooplankton (Kornilovs et al. 2001) to higher trophic levels such as cod, salmon, sea birds and harbour porpoise (Bagge et al. 1994). During the late 1980s, the upper trophic level of the Baltic ecosystem shifted from a cod- to a clupeid-dominated system (Alheit et al. 2005), as a consequence of high fishing pressure and the recruitment failure of cod (Bagge et al. 1994, Casini et al. 2008). Due to the decrease in cod predation, the sprat stock increased to an overall higher biomass compared to the early 1980s (ICES 2012). Recently, the cod stock started to recover in the south-western part of the Baltic Sea, whereas the biomass of forage fish (sprat and herring) decreased to historic low levels (Eero et al. 2012). As a consequence, the body mass and nutritional condition of cod drastically declined, complicating the recovery of this fish stock. This highlights the importance of understanding the processes that control the recruitment of the sprat stock. Previous studies on sprat biology and recruitment were concentrated on the spawning grounds (e.g. Köster & Möllmann 2000, Voss et al. 2006, Peck et al. 2012) and concluded that processes acting during the post-larval, early juvenile stage are finally critical in determining year-class strength (Baumann et al. 2006b, Voss et al. 2012). However, the mechanisms influencing survival in this stage are not well understood, as late larvae and juveniles inhabit near-coastal areas where research during recent decades has been underrepresented. However, otolith microstructures from surviving individuals caught at the end of the first growing season offer the opportunity of investigating growth during early life-stages (e.g. Baumann et al. 2006a). Baumann et al. (2007) transferred young sprat from coastal nursery areas to the laboratory and fed them ad libitum rations; the subsequent increase of growth rates under laboratory conditions indicated that food availability in coastal areas may be sub-optimal and limiting the growth of young sprat. However, it is difficult to judge to what extent this finding can be generalised. There are hardly any data on prey fields available from these very shallow coastal habitats, where standard plankton sampling gear cannot be operated. Here, we expanded the approach of Baumann et al. (2007) in a more systematic way. We likewise transferred sprat from juvenile habitats into the laboratory, but exposed them to 4 different temperatures representing the ambient range. In all trials fish were fed ad libitum, to generate a reference set of otoliths representing optimally growing post-larval sprat. In a second step, we then compared these increment patterns with those of young sprat sampled in 2 field studies (Baumann et al. 2008, Günther et al. 2012) and examined *in situ* feeding conditions in 2 years with contrasting year-class strengths.

MATERIALS AND METHODS

Laboratory experiment

Post-larval sprat were caught on 27 July 2010 in the Kiel Fjord (western Baltic Sea). Fishing gear was a cubical net with the top side open and a mesh size of 3 mm. The base area was 6 m^2, and the height of the side walls was 2.5 m. About 1500 post-larval sprat

were caught and transported to the laboratory. One month before sampling, a marine temperature data logger (Onset® Optic StowAway Datalogger) was deployed at a water depth of 1 m next to the catch site. Additionally, temperature profiles from the nearby measurement station 'Kiel Lighthouse' were obtained (BSH 2013). In the laboratory, fish were transferred to an 800 l flow-through tank connected to a water recirculation system filled with artificial seawater. Fish were kept at a salinity of 15.0 ± 0.5 psu, similar to the natural environment (~16 psu) and a light regime of 14 h light:10 h dark. Before the start of the experiment, water temperature was maintained at 16 ± 0.5°C and sprat were fed with a mixture of live brine shrimp nauplii (*Artemia salina*; Inve, SepArt®), and dry pellets (Larviva, Dana Feed).

The aim of the experimental set-up was to investigate growth at different temperatures (16, 18, 20 and 22°C), while the effect of feeding on growth was minimised by constant and ad libitum food rations. In total, 12 identical circular 150 l tanks (diameter: 0.8 m; water column: 0.3 m) were equipped with aeration and a temperature probe (DS 1820, Hygrosens Instruments). For each temperature, 3 of these tanks were installed on a 700 l source tank that was connected to the re-circulating system. In the source tanks, the water was preheated to the respective temperature (16, 18, 20, or 22°C) and pumped up to the 3 smaller tanks. Thus, 3 replicate tanks per temperature treatment were applied. Before stocking, all tanks were regulated at 16°C to avoid abrupt temperature changes at transition. On 1 August 2010, each tank was loaded with ~60 specimens randomly selected from the 800 l flow-through tank (Table 1). The remaining specimens were sacrificed as an initial sample (hereafter: starter group) to evaluate body length, otolith length and mass at the start of the experiment. Finally, regulated heaters in the source tanks were switched on. Pre-set temperatures in the tanks were reached after 24 h. During the experiment deviations from the pre-set temperature were not larger than 0.2°C.

The diet during the experiment was composed of two-thirds pellets (Larviva, Dana Feed) and one-third live brine shrimp nauplii (Inve, SepArt®). The daily amount of food offered was calculated assuming maximal food consumption (C_{max}) of 15 to 25% dry mass per individual and day for 16 to 22°C, respectively. To assure ad libitum feeding throughout the experimental period taking into account the growth in body mass, a gross conversion rate of 33% fish^{-1} was assumed. Until Day 9 of the experiment, fish were fed on 6 occasions equally distributed over the 14 h light period of the day (dry diet and *A. salina* nauplii were alternated). Feeding started 30 min after the onset of light with pellets and ended 2 h before the end of the light period with live *A. salina* nauplii. Periods between feeding times were equally distributed. From Day 10 of the experiment onwards, sprat were fed 8 times d^{-1} to ensure ad libitum food conditions. On 1 September 2010, all specimens were killed with an anaesthetic overdose (MS-222, >0.2 g l^{-1}).

Thereafter, we distinguished between 5 phases in the life of experimental fish (see also Fig. 3): (1) the field period until catch on 27 July 2010, (2) the maintenance period in the laboratory until the start of the experiment, (3) the experimental period comprising the (4) acclimation period of the experiment until Day 10 and (5) the 'period of interest' when sprat were fed 8 times d^{-1}. The period of interest does not include the last day of the experiment when individuals were killed.

For all fish, standard length, body height at half standard length (relative body height) and wet mass were measured. The dataset which comprises all individuals in the experimental set-up is called Dataset 1. According to the modes of length-frequency distributions per temperature treatment and replicate tank, 21 to 30 individuals were selected for microstructure analysis of the otoliths. This subset of data used for otolith analysis is termed Dataset 2 and

Table 1. Numbers of individuals (n) per tank and temperature at the beginning of the experiment, and mortality and accidental mortality during the experiment

Temperature (°C)	Replicate tank number	n	Absolute mortality	Absolute accidental mortality
16	1	61	5	2
	2	62	2	8
	3	61	2	1
	Mean		3	4
18	1	60	5	7
	2	66	2	2
	3	59	5	10
	Mean		4	6
20	1	60	5	3
	2	59	4	3
	3	60	11	3
	Mean		7	3
22	1	61	8	7
	2	59	3	12
	3	62	8	7
	Mean		6	9

does not contain the small number of poorly growing fish (see 'Statistics' and Fig. 2). However, a few otoliths (n = 11) in the group with poor growth performance were also analysed and used for the establishment of a relationship between length growth and otolith growth (see 'Comparing otolith growth of laboratory and wild sprat' and Fig. 6). Muscle tissues and guts of individuals used for otolith analysis (Dataset 2) were frozen for a subsequent study, and hence this subset could not be used for the determination of dry mass. Therefore Dataset 3, a further subset of Dataset 1, was analysed to estimate the increase in dry mass of well-growing individuals (see 'Statistics' and Fig. 2). Dry mass was measured after 48 h of drying at 70°C, when constant mass was reached.

Otolith analysis

Otolith microstructure analysis was performed for individuals of Dataset 2, the smallest fish in the tanks (n = 11) and a subset of 15 sprat from the starter group. Individual sagittal otoliths were dissected and deposited on microscopic slides with a drop of thermoplastic glue (Crystalbond® 509), the convex side facing upwards. Irrespective of left and right, the otolith with the clearest microstructure was used. Otoliths were polished wet using a grinding machine (Presi Mecapol P260) equipped with a lapping film (Silicon Carbid 1200/4000). The degree of the polished surface was controlled with a light microscope. When the polished surface intersected the core of the otolith, it was turned upside down by reheating the thermoplastic glue on the microscopic slide. Then, the otolith was ground from the other side until the outermost increments were clearly visible along the post-rostral axis of the otolith. Each otolith was photographed with a digital camera (Leica®DC300, 3132 × 2328 pixels) connected to an image analysis system (ImagePro® Plus 6.0) at 400× magnification. Increments were measured along the post-rostrum axis from the core to the edge. We started with the first clearly visible increment outside the core which we defined as day of first increment formation (DFIF). Every otolith was read once by the same experienced reader.

Statistics

To test differences in standard length, relative body height (body height as percentage of standard length), wet mass, relative dry mass (dry mass as percentage of wet mass) and otolith growth between the temperature treatments and replicate tanks we used 2-factorial analyses of variances (ANOVA). Additionally, a post hoc Scheffè test was applied to detect which temperatures and/or tanks differed significantly. As data were slightly skewed to the left in Dataset 1, a Levene test (car-package in R) for homogeneity of variances between all tanks was performed, because homogeneity is the most important assumption when applying an ANOVA. We further fitted a generalized linear model (GLM) using a gamma distribution to account for non-normality in the distributions of the response variable. However, as gamma distributions can only account for positively (right) skewed data and not for negatively (left) skewed data, we inverted the standard length data before applying the GLM.

For the statistical investigations of otolith growth and dry mass, we excluded the exceptional small individuals that existed in each tank. We justified the exclusion of these poorly growing individuals because length distributions of wild young-of-the-year sprat follow a normal distribution in the western Baltic Sea (Baumann et al. 2008). The lack of small individuals in field data suggests that poorly growing individuals like those in the laboratory do not contribute to surviving juveniles at the end of the summer. Additionally, we suggest that the exceptional small individuals at the end of the experiment did not feed and were thus not suitable for an analysis assuming ad libitum feeding rations. To exclude poorly growing individuals, we defined a length (L_c) that separates poorly growing from faster growing individuals (see Fig. 2). For this purpose, we calculated a mean length (L_m) using the 3 most frequent 1 mm length classes (at the end of the experiment) per temperature treatment and replicate tank. Including only the length classes which are larger than L_m, we established an artificial normal distribution by mirroring the right side of the distribution to the left side of L_m. Lastly, the 2-fold standard deviation of this distribution was subtracted from L_m to define L_c.

Comparing otolith growth of laboratory and wild sprat

To deduce *in situ* feeding conditions during the early juvenile stage of wild sprat, we compared increment growth of wild sprat with the ad libitum increment growth reference generated during the

experiment. We investigated increment growth patterns of individuals caught in the growth seasons of 2003 (n = 75) and 2007 (n = 66) in the western Baltic Sea (Baumann et al. 2008, Günther et al. 2012).

First of all, we established a laboratory reference. The rate of otolith accretion in the laboratory was described by a quadratic equation using the mean increment width (IW) per investigated temperature treatment. Here, we included only increments from the period of interest (last 20 d of the experiment).

Subsequently, we identified the 20 increments formed in the life-stage of wild sprat, which matches the life-stage that was investigated in the laboratory reference. These increments start 17 d after the widest increment, which corresponds to the point of metamorphosis (Günther et al. 2012).

In a first step, we assigned daily temperature values to each field increment using surface water temperatures at Kiel Lighthouse in 2003 and 2007 as ambient temperatures. All daily increment widths (field data) that were formed at the same temperature (1°C classes) were averaged and finally compared to the laboratory ad libitum reference of the same temperature. This contrast should reveal whether field individuals were growing optimally at the different temperatures.

In a second step, we tried to disentangle a possible relationship between the different seasonal cohorts and the subsequent growth performance in the post-metamorphic life-stage. For this purpose we estimated for each individual day of the year of first increment formation (DFIF) a proxy for the season in which the individual was spawned. We then calculated an average day of first increment formation (DFIF) for each temperature class. Individuals contributed to these temperature-specific means of DFIF according to the number of increments observed in the respective temperature class. For instance, an individual which formed many increments in a specific temperature class had a stronger influence on the mean DFIF than an individual which formed only a few increments in the same temperature class.

Finally, to convert increment widths to differences in fish length growth we established a relationship between increment width and length growth rate during the experiment. Here, we also included poorly growing individuals (see Fig. 2) to encompass the whole range of growth rates. We applied a random intercept model with increment width as a response and length growth rate as an explanatory variable, where the intercept of the linear regression was allowed to change per temperature treatment but the slope remained constant.

Estimation of the food amount required for laboratory growth

The experimental set-up used to evaluate temperature effects on otolith and length growth was not designed to estimate the amount of food finally ingested. To ensure optimal growth we fed a mixture of live food (brine shrimp) and pellets to cover the widest range possible of the chemical components necessary for growth. Because pellets partly dissolve in water, the consumed amount of food is difficult to quantify. Therefore, we roughly estimated the food intake from a simple bioenergetic budget approach. Such approaches for relating food consumption and growth of fishes are well established (e.g. Winberg 1960, Kitchell et al. 1977, Arrhenius & Hansson 1993).

In a first step, we calculated the daily average energy gain per fish in each temperature treatment based on the mean relative dry mass (dry mass as a percentage of wet mass) of the starter group and the final experimental samples. In accordance to Pedersen & Hislop (2001), the relative dry mass of a fish can be used to estimate its energy density. We used the reciprocal value of the mean relative dry mass as the relative water content (WC) and calculated the energy content (EC) in Joules per gram dry mass. EC was computed for the starter group (index: ST) and for each temperature treatment of the final sample (index: T) using the following linear equation:

$$\begin{gathered} EC = -28964 \cdot WC + 46153 \\ (df = 503,\ p < 0.001,\ F = 456.7) \end{gathered} \quad (1)$$

This equation was derived from a comprehensive dataset from the North and Baltic Seas sampled between 2002 and 2004. Samples covered all seasons and contained standard length classes from 3 to 13 cm. Energy contents in Joules per gram dry mass were estimated using an adiabatic bomb calorimeter (IKA C4000). EC values were used to calculate the total energy amount (TE) in Joules for the starter group and for each temperature treatment of the final sample by multiplication with the respective mean dry mass values. Using TE values we calculated the specific energy gains (g) per day for each temperature treatment, assuming an exponential increase in dry mass over the experimental period according to the equation:

$$g_T = \frac{[\ln(TE_T) - \ln(TE_{ST})]}{t} \quad (2)$$

where t is the experimental period in days. Lastly, energy gains (EG) in Joules per day were derived by

temperature treatments for the first day of the experiment (index: First) using the TE of the starter group such that:

$$EG_{First_T} = TE_{ST} \cdot (e^{g_T} - 1) \quad (3)$$

and for the last day of the experiment (index: Last) using the TE values from each temperature treatment of the final samples:

$$EG_{Last_T} = TE_{Last_T} \cdot (e^{g_T} - 1) \quad (4)$$

In total, 8 values of energy gains result; these correspond to the energy gain for the 4 temperatures at the beginning (first day) and at the end (last day) of the experiment.

In a second step, we estimated the mean consumption (C) in Joules per day using the bioenergetic equation with EG as the growth term. In general, this equation follows the energy balance equation of Winberg (1960). However, the respiration term (R) was extended. Again, we calculated 4 consumption values corresponding to each temperature treatment at the first day of the experiment:

$$C_{First_T} = R_{routine} + R_{feedact} + R_{SDA} + E + F + EG_{First_T} \quad (5)$$

and 4 consumption values corresponding to each temperature at the last day of the experiment:

$$C_{Last_T} = R_{routine} + R_{feedact} + R_{SDA} + E + F + EG_{Last_T} \quad (6)$$

Here, $R_{routine}$ is the respiration term for the routine metabolism, $R_{feedact}$ is the respiration term for feeding metabolism which is caused by feeding-induced swimming activity and R_{SDA} is the respiration term for specific dynamic action. E is the term for excretion, and F is the term for faeces. We assumed that $R_{feedact}$ accounts for 10% of the consumption following Meskendahl et al. (2010) and that R_{SDA}, E and F each also account for 10% of the consumption (Andersen & Riis-Vestergaard 2003, Temming & Herrmann 2009). Routine metabolism ($R_{routine}$) is highly dependent on fish species, fish size and temperature. We applied respiration rates which were established for the same species, life-stages and temperatures as in our experiments (Meskendahl et al. 2010). As routine metabolism is expressed in milligrams of oxygen consumed per hour, we used the oxy-caloric factor (13.72 J mgO_2^{-1}) of Elliott & Davison (1975) for the conversion into Joules per day. We calculated values for routine metabolism for each temperature treatment using the mass at the first and at the last day of the experiment.

In a third step, we converted the total energy intake into the equivalent number of *Acartia* spp. copepods. We chose *Acartia* spp. as it is an important prey item of Baltic sprat during summer (Möllmann et al. 2004). For *Acartia* spp. we used the energy contents for C5/C6 stages (17 920 J g^{-1}) of *A. clausii* as determined by Kerambrun (1987) and a dry mass of *A. tonsa* (9.454×10^{-6} g) published by Durbin et al. (1983).

Finally, we calculated the biting rates (BR) as number of prey items ingested per second assuming light-dependent feeding and thus 14 h of feeding per day according to the experimental conditions. Corresponding to the relationship between biting rate and prey concentration (PC) in juvenile sprat (Brachvogel et al. 2013), we calculated the mean prey concentration required for the biting rate at the first day:

$$PC_{First_T} = \frac{(BR_{First_T} \cdot 25.42)}{(BR_{First_T} \cdot 1.06)} \quad (7)$$

and at the last day of the experiment:

$$PC_{Last_T} = \frac{(BR_{Last_T} \cdot 25.42)}{(BR_{Last_T} \cdot 1.06)} \quad (8)$$

RESULTS

Mortality during the experiment

During the experiment, sprat mortality was differentiated between mortality inside and mortality outside of the tank, as some individuals jumped out of the tank (hereafter: accidental mortality). On average, mortality increased with temperature (Table 1). Mortality in the tanks varied between 3 and 18%, and accidental mortality varied between 3 and 20%.

Effect of temperature on growth

The starter group had a mean (±SD) standard length of 29.1 ± 2.0 mm, a mean body height of 4.2 ± 0.6 mm and mean wet mass 147.2 ± 42.3 mg.

For Dataset 1 (Fig. 1a–c) we found variance homogeneity in all tanks for standard length, wet mass and relative body height (Levene test, $p > 0.1$). On average, relative body height data were normally distributed (Shapiro-Wilk test: $p > 0.1$). We performed a 2-factorial ANOVA and found an effect of temperature, but no effect of replicate tank (Table 2). Relative body height in the 18 and 20°C temperature treatments (Fig. 1c) was significantly lower than at 16°C, but not significantly lower than at 22°C. In contrast, distributions of standard length and wet mass were significantly different from normal distributions

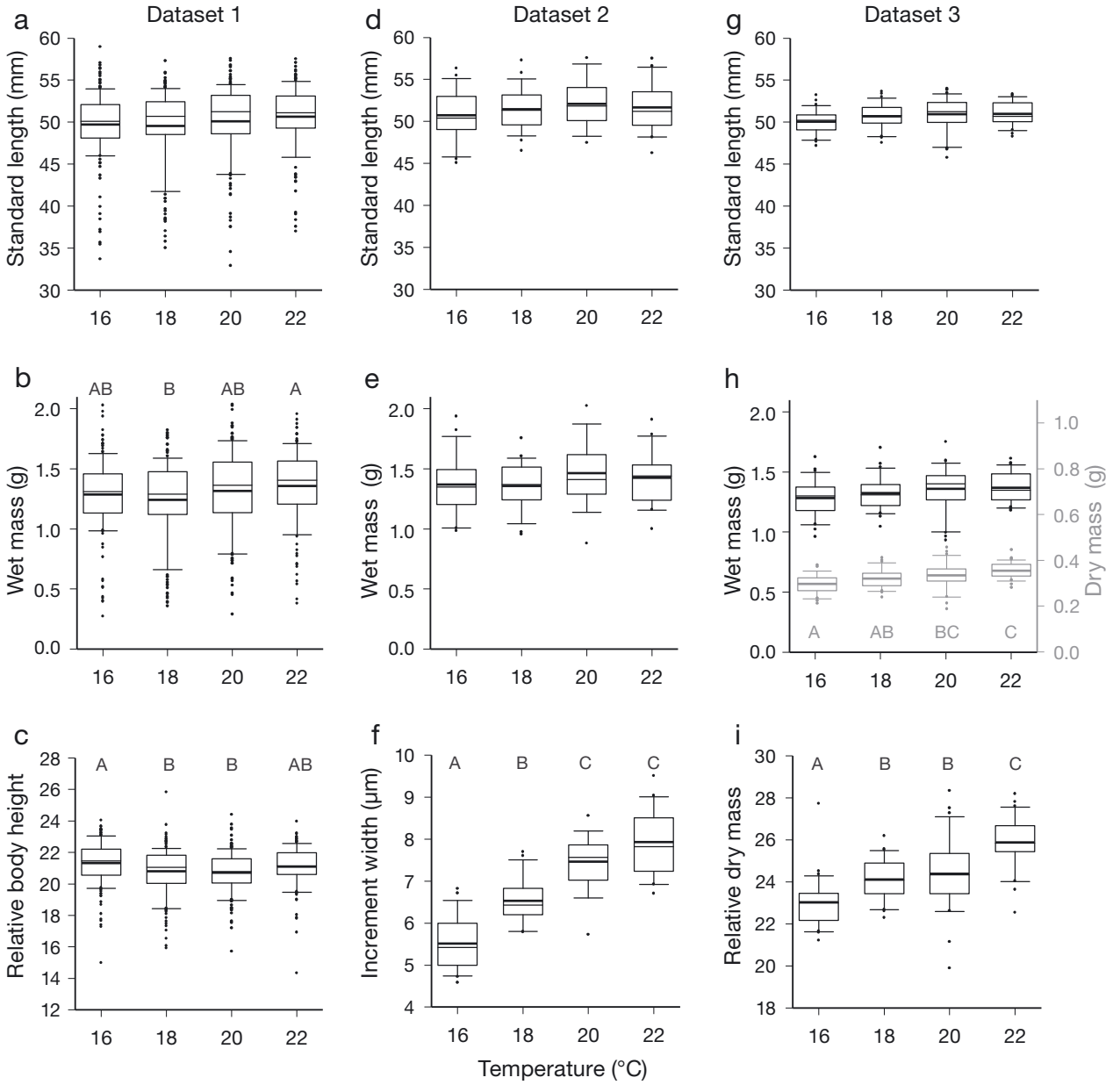

Fig. 1. Temperature-dependence of (a,d,g) standard length, (b,e,h) wet mass, (h) dry mass (grey boxplots), (c) relative body height (as a percentage of standard length), (f) increment width and (i) relative dry mass (as a percentage of wet mass). Thick/thin lines: mean/median; box: 25th–75th percentiles, whiskers: 10th–90th percentiles; dots: outliers. (a,b,c) Dataset 1 comprises all individuals at the end of the experiment; (d,e,f) Dataset 2 contains individuals used for otolith analysis; (g,h,i) Dataset 3 comprises data from the dry mass estimation. Capital letters above/below boxplots (b,c,f,h,i) show results of the Scheffè post hoc significance test: identical letters within a panel indicate no significant differences between temperature treatments

(Shapiro-Wilk test: $p < 0.05$) and (negatively) skewed to the left (Fig. 2 for standard length), with few poorly growing individuals in all tanks. An ANOVA indicated neither a replicate tank nor a temperature effect for standard length ($p > 0.1$). To consider the effect of a non-normally distributed response variable, we additionally performed a GLM with gamma distribution on inverted standard length data. However, neither the GLM (Table 2) nor an ANOVA ($p > 0.1$) on inverted data detected a temperature or replicate tank effect. For wet mass, we found a slight effect of temperature ($p = 0.029$) and no tank effect ($p > 0.1$) using a 2-factorial ANOVA. As data of wet mass were also negatively skewed, we performed the same procedure as for standard length. A GLM (Table 2) and an ANOVA on inverted wet mass data

Table 2. Summary of statistical analyses investigating effects of replicate tanks and temperature treatments on body morphometrics and otoliths. Poorly growing fish were excluded from the analyses (see 'Results'). Dataset 1: all individuals at the end of the experiment; Dataset 2: sprat from otolith analysis only; Dataset 3: individuals from dry mass estimation. RV: response variable; EV: explanatory variable; T: temperature; R: replicate tank; SL: standard length; RelBH: relative body height (body height as a percentage of standard length); WM: wet mass; Invert: inverted data; Mean IW: mean increment width during the last 20 d of the experiment (period of interest); RelDM: relative dry mass (dry mass as a percentage of wet mass); SumSq: sum of the squares; MeanSq: mean squares; ResidDev: residual deviance

RV	Method	EV	SumSq	MeanSq	*F*-value	p-value (*F*)	ResidDev	Deviance	p-value (Chi)
Dataset 1									
SL Invert	GLM (gamma)	T					5.772	0.059	0.129
		R					5.765	0.007	0.715
RelBH	ANOVA	T	38.100	12.699	6.756	<0.001			
		R	4.530	2.263	1.204	0.301			
WM Invert	GLM (gamma)	T					18.360	0.300	0.024
		R					18.317	0.043	0.508
Dataset 2									
Mean IW	ANOVA	T	70.850	23.617	55.936	<0.001			
Dataset 3									
RelDW	ANOVA	T	125.59	41.863	25.968	<0.001			
DW	ANOVA	T	0.056	0.019	9.495	<0.001			

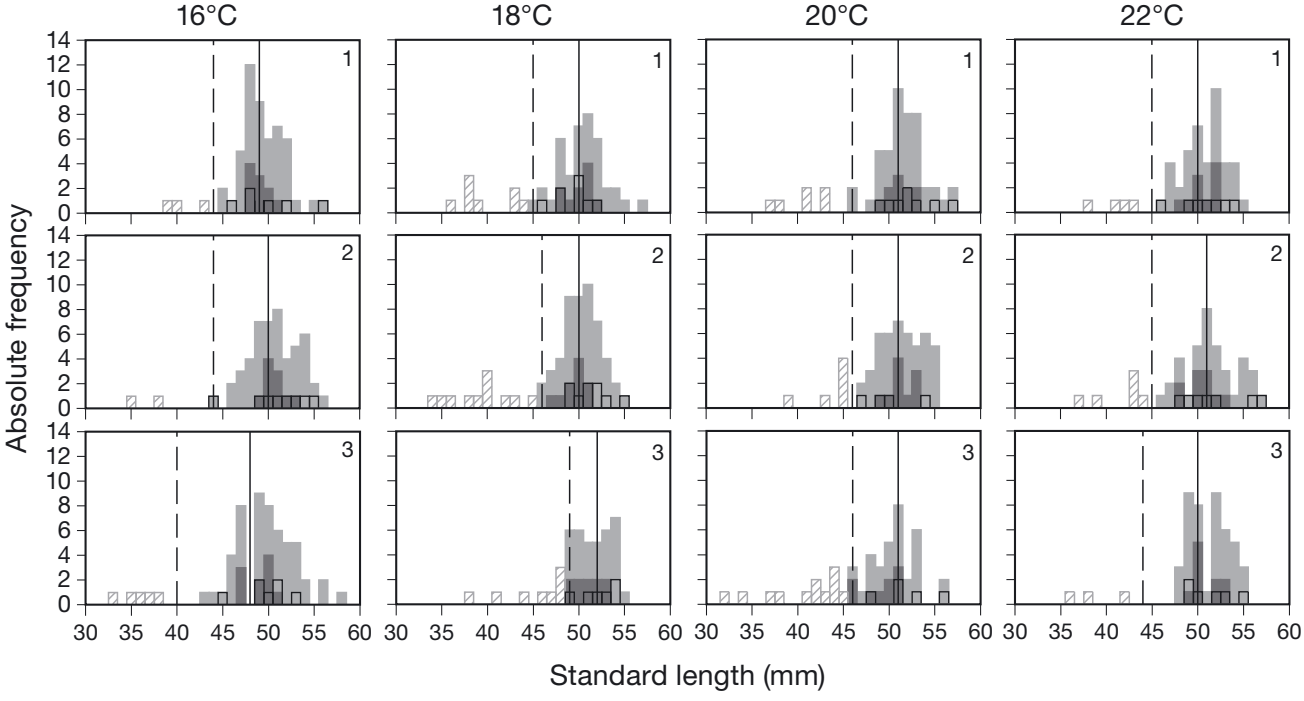

Fig. 2. Distribution of standard length frequencies per replicate tank (numbered 1 to 3). Panels in each column represent 1 temperature treatment with the lowest temperature (16°C) on the left and the highest temperature (22°C) on the right side. The number in each panel indicates the number of the replicate tank. Filled light grey bars (faster growing individuals) and striped light-grey bars (poorly growing individuals) represent all fishes from the experimental setup (Dataset 1). The vertical black lines illustrate the means of the 3 most frequent length classes (L_m), and the dashed lines, the cut-off lengths (L_c) which divide poorly growing fish from the bulk of individuals. Black empty bars show individuals used for otolith analysis (Dataset 2), and dark grey filled bars, individuals used for dry mass estimation (Dataset 3)

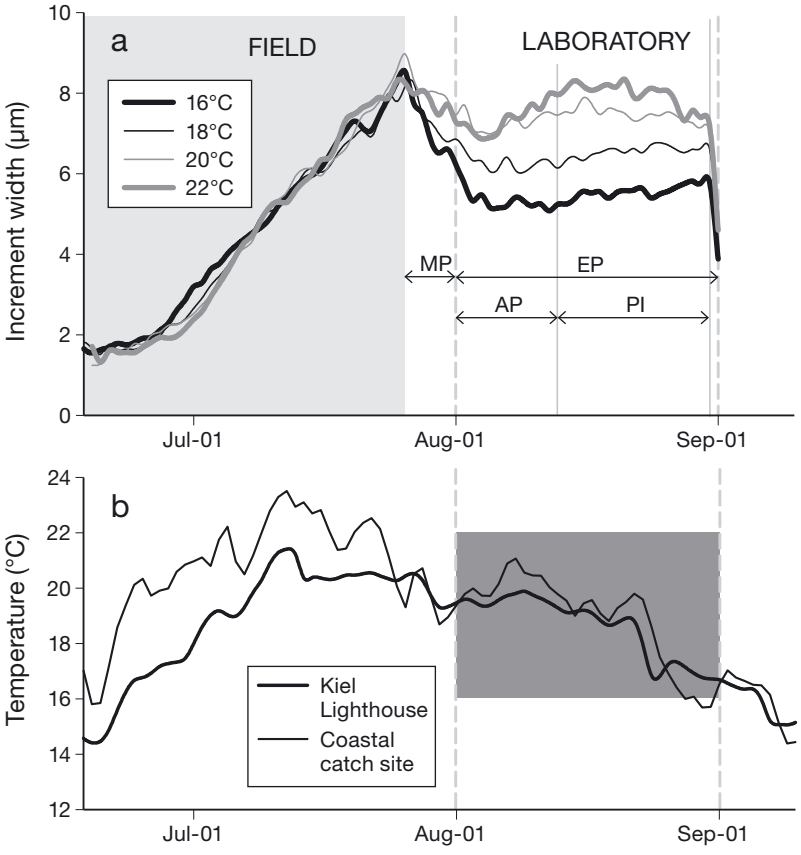

Fig. 3. Mean increment width pattern of individuals from the experiment in 2010, averaged by (a) temperature treatments starting with the last day in life and (b) mean water surface temperatures in the field. Grey background in (a) indicates the period in the field, while the white background indicates the time in the laboratory. Life-time in the laboratory is divided (grey dashed lines) into the maintenance period (MP) and the experimental period (EP). EP is split (thin grey lines) into the acclimation period (AP) and the period of interest (PI). Dark grey background in (b) shows the temperature range investigated during the laboratory experiment

produced the same result as on non-inverted wet mass data with a slight effect of temperature and no tank effect. A post hoc Scheffè significance test revealed that the 18 and 22°C treatments were significantly different from each other (Fig. 1h).

As we found no replicate tank effect in Dataset 1, we pooled individuals from all replicate tanks by temperature treatment in the following analyses.

For the analysis of otolith growth and relative dry mass (dry mass as a percentage of wet mass), we excluded poorly growing individuals (Fig. 2). In general, the faster growing individuals comprise the bulk of all individuals (88%). After the exclusion of poor growers (n = 74), standard length data followed a normal distribution (Shapiro-Wilk test: $p > 0.05$). For Dataset 2 (Fig. 1d–f), we found no temperature effect for standard length ($p > 0.1$) or wet mass ($p > 0.1$). However, mean increment width over the period of interest (last 20 d of the experiment) differed significantly between temperature treatments (Fig. 3, Table 2). Mean increment width increased with temperature within the observed temperature range (Table 3). A post hoc Scheffè significance test revealed that the 16, 18 and 20°C treatments were significantly different from each other, whereas there was no significant difference between

Table 3. Mean sizes at the beginning and end of the experiment, daily growth rates (means and 10th and 90th percentiles) and temperature-dependent daily growth rates of body morphometrics and otoliths during the laboratory experiment. Dataset 1 comprises all individuals at the end of the experiment. In Dataset 1*, poorly growing fish were excluded. Dataset 2 contains sprat used for otolith analysis, and Dataset 3 includes individuals used for dry mass estimation

	Dataset	Unit	Mean size		Daily growth rate			Temperature-dependent daily growth rate			
			Start	End	Mean	Percentile					
						10th	90th	16°C	18°C	20°C	22°C
Standard length	1	mm	29.09	49.98	0.67	0.50	0.81	0.67	0.66	0.68	0.70
	1*	mm	29.09	51.21	0.71	0.61	0.82	0.69	0.71	0.73	0.73
Wet mass	1	mg	147.18	1298.26	37.13	23.38	48.38	36.71	35.32	37.74	39.01
	1*	mg	147.18	1385.13	39.93	30.99	49.99	38.40	39.10	41.29	41.32
Body height	1	mm	4.20	10.52	0.20	0.14	0.24	0.21	0.20	0.20	0.21
	1*	mm	4.20	10.89	0.22	0.18	0.25	0.22	0.21	0.21	0.22
Otolith radius	2	µm	219.68	418.44	6.80	5.31	8.20	5.53	6.53	7.46	7.94
Dry mass	3	mg	27.63	327.12	9.66	7.22	11.35	8.66	9.43	10.02	10.54

the 20 and 22°C treatments, denoting an approaching maximum in otolith growth beyond 22°C. For Dataset 3 (Fig. 1g–i), we found no differences in wet mass between temperatures ($p > 0.05$). There was a slight effect on standard length ($p = 0.03$) indicated by the ANOVA. However, the post hoc statistic was not capable of detecting a difference between temperature treatments. In contrast, dry mass and relative dry mass depend on temperature (Fig. 1h,i). A post hoc Scheffè significance test revealed that relative dry mass of the 16, 18 and 22°C treatments were significantly different from each other, whereas there was no significant difference between 18 and 20°C.

In summary, we found no temperature effect on standard length, but a distinctive temperature effect on increment width. Temperature had a slight effect on body height. We observed only a weak or negligible increase of wet mass with temperature (Table 3); this finding stood in contrast to a clear and pronounced increase in dry mass and relative dry mass (dry mass as a percentage of wet mass).

Deducing feeding conditions of wild sprat

Mean increment width during the period of interest (last 20 d of the experiment) was described as a non-linear function of temperature (T). The resulting quadratic equation ($IW = -0.0326T^2 + 1.6472T - 12.506$; $r^2 = 0.99$) was used to compare increment widths from the laboratory with the increment widths of wild sprat. The daily increment widths of wild sprat were averaged according to the water temperature measured at Kiel Lighthouse. This resulted in 7 one-degree temperature classes in 2003 and 5 in 2007 (Fig. 4). One individual in 2007 experienced 15°C during its early juvenile stage (outside the investigated temperature range) and was not considered in the analysis. In each temperature class, a different number of increments contributed to the mean, whereby most increments were deposited at 17 and 18°C, irrespective of the year. No increments were observed at 20, 21, or 22°C in 2007. Only 5 increments constitute the mean at 16°C in 2003.

Increment widths of wild individuals were, on average, equal to or smaller than the mean increment widths of laboratory-reared sprat, except for the 16°C temperature class in 2003. In 2003, the comparison of laboratory and field increment widths indicated similar food availability at 17, 18 and 19°C, suggesting optimal feeding conditions for wild juveniles. However, at 20, 21 and 22°C, mean increment widths of wild sprat were considerably smaller than increment widths of laboratory-reared sprat. This difference indicates sub-optimal food availability at higher temperatures in 2003. In contrast to 2003, when optimal food availability was suggested until 19°C, most individuals in 2007 suffered under unfavourable conditions. On average, temperatures in 2007 were lower than in 2003 (Fig. 4). However, only the mean increment width at 16°C exhibited a similar width to the laboratory ref-

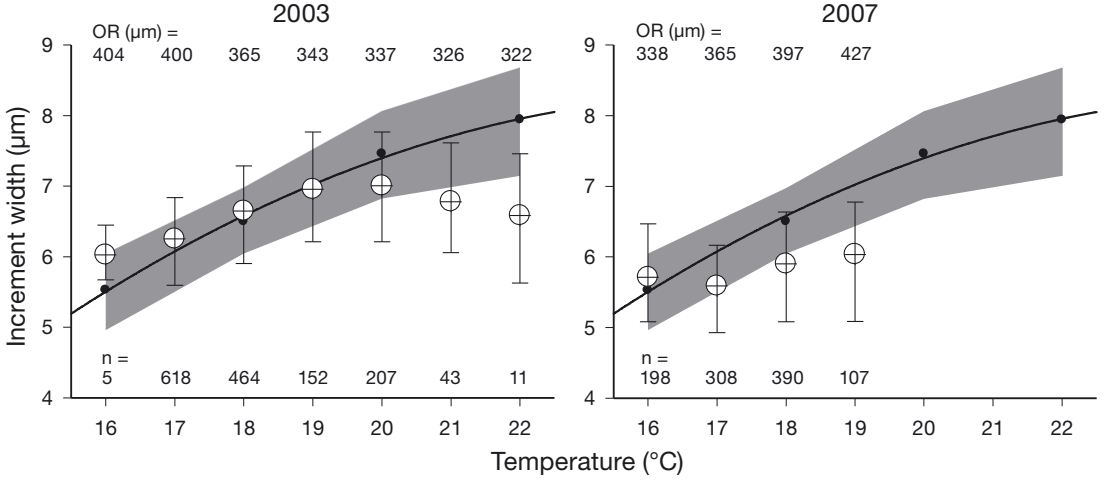

Fig. 4. Comparison of mean increment growth of laboratory and field fishes from 2003 (left panel) and 2007 (right panel) corresponding to water temperature during a 20 d period in the juvenile life-stage. Increment widths were pooled in temperature classes of 1 degree. Black dots and lines represent mean increment widths of laboratory temperature treatments and a fitted quadratic model, respectively. Grey area indicates the range between the 25th and 75th percentiles of single increment widths observed during the 20 d period in the laboratory. White crossed dots indicate mean increment width at ambient field temperature, and corresponding error bars represent 25th and 75th percentiles of data. OR: numbers of mean otolith radii when increments occurred; n: numbers of increments corresponding to a mean increment width of a temperature class

erence. Thus, only individuals which experienced their early juvenile stage at 16°C in 2007 had increment widths suggesting suitable feeding conditions for optimal growth.

Individuals from 2003, which experienced 20, 21 and 22°C and probably suffered sub-optimal feeding conditions, were born early in the season (June; Fig. 5). These individuals underwent their early juvenile stage during peak temperatures of the season. In contrast, water temperatures during post-metamorphic life-stages were lower for fellows born later which seemed to experience optimal feeding conditions. Individuals from 2007 were born almost 2 mo earlier (May) than those from 2003. Sprat with a DFIF early in the season in 2007 experienced lower temperatures during the early juvenile stage than those with later DFIFs.

We established a relationship between the experimentally observed increment widths and length growth rates (Fig. 6) to convert field increment data into the respective field length growth rates using a linear random intercept model:

$$IW_T = 4.143 + 3.764 \cdot LGR_T + \varepsilon_T$$
$$\varepsilon_T \sim N(0, \sigma^2) \quad (9)$$

where ε_T is the error term, which is normally distributed with mean 0 and variance σ^2. The residual variance of the model was 0.43, and the variance for the random intercept was 1.03 µm. This model implies that slight differences in increment width correspond to pronounced changes in length growth rate.

Mean increment widths of field sprat in 2007 were 5.59, 5.90 and 6.03 µm at 17, 18 and 19°C, respectively. Compared with the laboratory reference, these field increments were on average 0.35, 0.78 and 0.79 µm lower. The application of Eq. (9) for these 3 temperature classes revealed that the length growth rates in 2007 were 0.09, 0.21 and 0.21 mm d^{-1}, respectively, lower than those in the laboratory. Mean increment widths in 2003 were 7.00, 6.78 and 6.58 µm at 20, 21 and 22°C, respectively. Increments of field sprat were thus 0.39, 0.93 and 1.38 µm smaller than those of the laboratory reference. This corresponds to differences in length growth rates of 0.10, 0.25 and 0.37 mm d^{-1} between field and laboratory sprat.

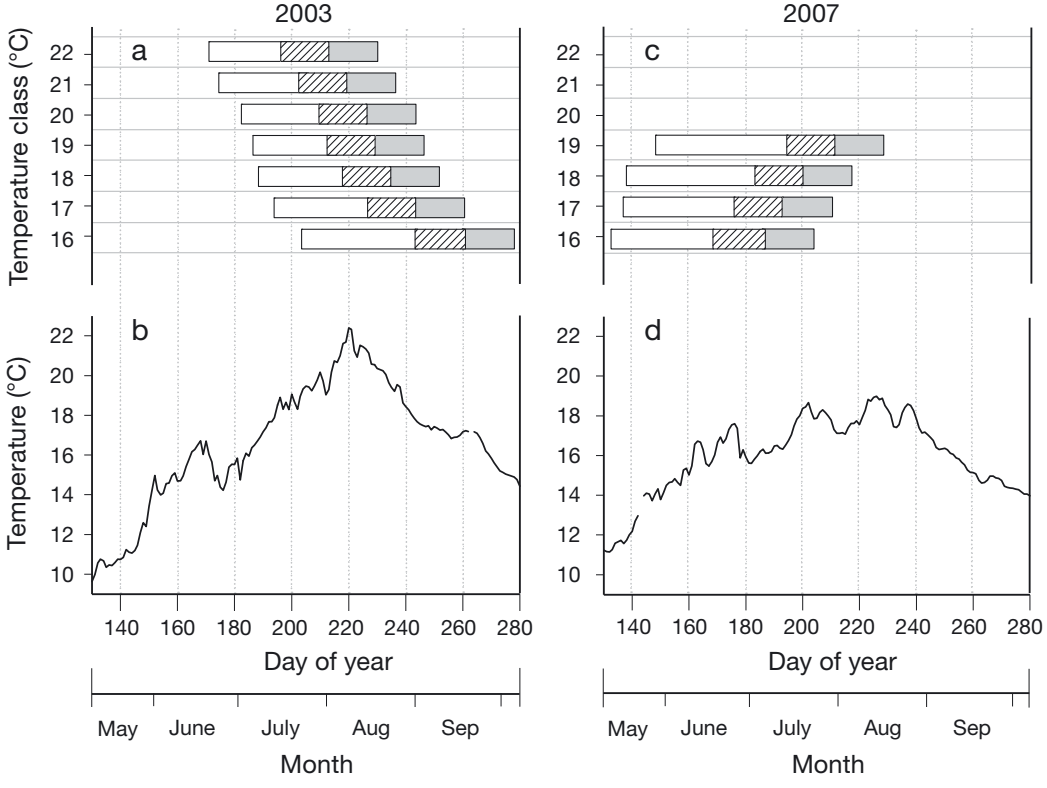

Fig. 5. Temporal occurrence of (a,c) life-stages grouped in different temperature classes of survivors and (b,d) surface water temperatures at Kiel Lighthouse in 2003 (left side) and 2007 (right side). Each temperature class in (a) & (c) comprised individuals that contributed to the mean increment width illustrated in Fig. 4. Total length of bar in a temperature class illustrates the period from the day of first increment formation (DFIF) to Day 37 after metamorphosis; open section illustrates the larval stage; striped section, the beginning of the juvenile stage after metamorphosis; and grey section, the life-stage that was compared with the laboratory reference (Fig. 4)

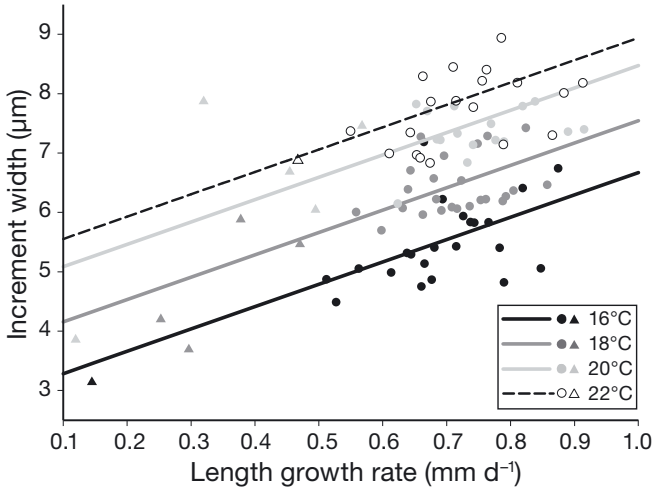

Fig. 6. Relationship between increment width and observed length growth rate during the experimental period for investigated temperature treatments. Circles represent individuals used for deducing feeding conditions from otoliths; triangles indicate poorly growing fish. Lines represent the fitted random intercept models for 16, 18, 20 and 22°C

Estimated ad libitum prey concentrations

Using the bioenergetic budget approach we estimated the consumed prey items per day under ad libitum feeding conditions. We assumed feeding on *Acartia* spp. and calculated mean biting rates of 0.01 and 0.18 prey items s^{-1} at the beginning and at the end of the experiment, respectively (Table 4). This increase in biting rate corresponds to an average increase in consumed prey items from ~650 d^{-1} for a sprat of 30 mm standard length to ~7500 d^{-1} for a sprat of 50 mm standard length. An increase in temperature from 16 to 22°C resulted in an increase of about 100 (~15%) and 2500 (~33%) prey items d^{-1} for sprat of 30 and 50 mm standard lengths, respectively. Following the equation of Brachvogel et al. (2013), the prey concentrations needed to maintain these biting rates for optimal growth are 0.23 and 0.25 prey items l^{-1} at the beginning of the experiment and 3.47 and 5.10 prey items l^{-1} at the end of the experiment at 16 and 22°C, respectively.

Table 4. Results of the bioenergetic budget approach: estimated temperature-dependent number of prey items (*Acartia* spp.) ingested per day (assuming 14 h feeding d^{-1}) and per second (biting rate) as well as corresponding mean prey concentrations required for the observed growth on the first (Day 1) and last (Day 31) day of the experiment

Temperature (°C)	Daily prey number ingested (prey items d^{-1})	Biting rate (prey items s^{-1})	Prey concentration (prey items l^{-1})
Day 1			
16	610	0.01	0.23
18	648	0.01	0.24
20	683	0.01	0.24
22	723	0.01	0.25
Day 31			
16	6410	0.13	3.47
18	7320	0.15	4.04
20	8073	0.16	4.53
22	8929	0.18	5.10

DISCUSSION

Growth during the laboratory experiment

Contrary to our expectations, we detected no temperature-related increase in length growth rate and only a slight and negligible temperature effect on wet mass growth under ad libitum feeding conditions. However, temperature had a considerable effect on otolith and dry mass growth. Initially, we discuss whether these findings are potentially an artifact of the experimental setup. In the next subsection, we focus on the meaning of different responses in somatic, dry mass and otolith growth in relation to temperature.

There are 2 different ways in which growth performance in laboratory experiments can be explained. On the one hand (Explanation A), somatic growth might have been maximal and laboratory conditions might have been comparable to optimal conditions in the field. As food in the laboratory was available in excess, sprat increased in dry mass, probably building up fat reserves. This implies that young sprat can consume food in excess of their needs for maximal somatic growth. On the other hand (Explanation B), somatic growth might have been limited, even under ad libitum feeding, because the food given in the laboratory might have lacked certain essential components. Hence, laboratory conditions were not necessarily identical to optimal conditions in the field. In this case, sprat would have stored energy and increased in dry mass instead of growing in body size. In 2002 and 2003, when high length growth rates of autumn-caught juvenile survivors were reported (up to ~1.0 mm d^{-1}; Baumann et al. 2008), length growth rates during the early juvenile stage were similar to growth rates in the laboratory (up to ~0.8 mm d^{-1}). Thus, we assume that con-

ditions in the laboratory and in the field in 2002 and 2003 were similar and supported maximal length growth during the juvenile stage. This conclusion also implies that maximal length growth was realized in the field, at least in 2003. Growth rates of survivors in 2003 are among the highest growth rates of sprat observed in the field (Huwer 2004, Lee et al. 2006, Voss et al. 2012). Thus, the comparison between laboratory and field growth in 2003 supports our observation that maximal growth rates were reached in the experiment, which substantiates Explanation A. During the experiment, in addition to *Artemia salina* nauplii, we fed sprat pellets that were primarily composed of fish meal and were assumed to have all essential nutrients for the growth of young fish. In a previous study on growth of juvenile Baltic sprat, Baumann et al. (2005) exclusively provided living *A. salina* nauplii. Mean increment width of post-metamorphic sprat in the ad libitum food treatment at 18°C in the study by Baumann et al. (2005) was about 30% lower than the mean increment at 18°C in the present study. Thus, we assume that *A. salina* nauplii as an exclusive food lack essential nutrients needed for growth of juvenile sprat. As increment widths during our experiments were similar to those of wild individuals, we conclude that the mixture of pellets and *A. salina* nauplii offered a comparable quality as food in the field. Finally, we exclude Explanation B and assume that maximal growth rates occurred in the laboratory and that the lack of a temperature effect in length and wet mass growth is no artifact of the experimental setup.

Temperature influence on somatic, dry mass and otolith growth

Our results indicate different responses in length and otolith growth to increasing temperature. This shows that the relation between fish length and otolith length is less rigid than normally assumed in length back-calculation models (Campana & Neilson 1985). However, in our data, dry mass growth responded in a similar way as otolith growth to temperature, indicating that fish growth and otolith growth were not completely uncoupled as described by e.g. Mosegaard et al. (1988) and Secor & Dean (1989).

It remains to be explained why dry mass increased with temperature in our experiments, but not wet mass or length. Somatic growth, as measured in length or wet mass increase, implies an increase in the number of cells. Increasing cell numbers, however, are also reflected in increasing wet mass due to the amount of water that is associated with newly generated cells. Since we only observed an increase in dry mass, we speculate that, in our case, only the mass of existing cells has increased due to the incorporation of lipids. Lipid reserves are stored in the cells and substitute their water content (Pedersen & Hislop 2001). Hence, the supposed increase in lipid reserves with temperature is probably the underlying metabolic process which is reflected in an increased otolith accretion rate with temperature.

The onset of lipid storage and thus its potential influence on the relationship between somatic and otolith growth starts in the post-metamorphic early juvenile stage, during the development of young clupeids (e.g. Blaxter & Hunter 1982, Deegan 1986, Peck et al. 2012). A reversed conclusion is that different responses in somatic and otolith growth in relation to temperature should be absent in the larval stage. Confirming this, studies on the larval life-stage in sprat and other clupeids have reported a tight relationship between somatic and otolith growth below the temperature optimum of growth (e.g. Folkvord et al. 2004, Aldanondo et al. 2008). Thus, we conclude that somatic growth is fixed more closely to otolith growth in early life-stages, when storing energy is of minor importance. In contrast, the response in otolith and somatic growth can differ in juvenile life-stages, when the storage of energy reserves becomes more important (Sogard 1997).

Methodological problems of deducing feeding conditions from otoliths

When reconstructing feeding histories of field-caught fish using otoliths from laboratory-raised fish as a reference, 3 main potential sources of error have to be considered which can influence the reliability of the results: (1) the uncoupling of somatic and otolith growth, (2) a time-lag in otolith response to changes in somatic growth and (3) the quality of the laboratory reference which is used as a proxy for optimal growth.

(1) Contrary to our expectations we observed different responses in otolith and length growth due to temperature as discussed in previous sections. We concluded that the otolith recorded not only the somatic growth but also the storage of energy. While these findings generate a certain bias for the reconstruction of length growth from daily increments, the reconstructed feeding history is actually less biased because the ingested food that is allocated to energy reserves is likewise recorded in the increment width.

(2) Previous studies observed a delay in the response of otolith growth to changes in somatic growth varying from a response of a few days (Tonkin et al. 2008, Aguilera et al. 2009) to 15 d (Molony & Choat 1990) or even 3 wk (Neilson & Geen 1985), depending on species and/or life-stage. Such a temporal uncoupling can bias the interpretation of increment width in relation to environmental factors on smaller temporal scales. Baumann et al. (2005) observed temporal uncoupling in juvenile Baltic sprat by abruptly changing the feeding conditions in laboratory growth trials. They found that the otolith required about 9 d after a drastic change in the feeding regime to fully display the new feeding level. Our reference otoliths are therefore most likely unaffected by any temporal uncoupling effect, since we established the ad libitum feeding regime 10 d before the actual reference period. In the interpretation of the field data, the temporal uncoupling of 9 d can mean at worst that, e.g., observed narrow increments in Week 31 actually reflect poor feeding conditions in Week 30 instead. However, our focus is less on isolated short-term events than on overall feeding conditions in different seasons at a more extended time scale. We also believe that the changes in the natural feeding regime will be less abrupt than those generated in the experiments of Baumann et al. (2005).

(3) For the estimation of ambient food availability from otolith growth patterns we assumed that the laboratory growth rates under ad libitum conditions represent maximal growth in the field. Laboratory growth rates varied between 0.6 and 1.0 mm d^{-1}, indicating variable feeding success for individuals in the tank. This may reflect reduced fitness of some of the experimental individuals, and the individuals with low food intake rates might, under field conditions, not have survived until the end of the year. There is some supporting evidence for this interpretation from a group of very poorly performing fish (Fig. 2), which had been excluded entirely from the reference analysis. In contrast, mean back-calculated post-metamorphic length growth rates of field sprat in 2003, a year with high growth rates of survivors, were about 1.0 mm d^{-1} (see Fig. 7 in Baumann et al. 2008). Assuming selective survival of faster growing sprat in the field (Baumann et al. 2007), only the upper range of laboratory length growth rates is comparable with field growth rates of the surviving group. Thus, the fastest growing fish from the laboratory reference actually represent maximum field growth. Hence, increments that are smaller than the laboratory reference at a given temperature clearly indicate sub-optimal feeding conditions. And likewise, increments of wild fish that are equal to or even larger than increments from the laboratory fish indicate excellent feeding conditions.

In the context of recording ambient environmental conditions in otolith increments, we observed another interesting phenomenon in the laboratory reference fish: the mean increment width of fish groups from different temperature treatments already showed differences before the start of the experiment, i.e. before the fish experience the conditions that are causing the differences in otolith growth. There are 2 possible reasons for that observation: (1) our otolith readings were inaccurate; thus we failed to estimate the exact starting day of the experiment; or (2) the width of an increment is not only defined by conditions on the day of its formation, but also by conditions during the following days. Our findings indicate that conditions on a specific day may influence the width of an increment accreted ca. 3 to 4 d before. We exclude possibility (1), because increments were very clear during the experimental period. Reason (2) was confirmed by Baumann et al. (2005) performing a comparable experiment, which was validated by alizarin marking: before they started the experiment and changed the feeding regimes, the increment widths of different fish groups already indicated a treatment effect. These findings and the associated hypothesis require further experimental investigations to improve our understanding of material accretion and increment formation in otoliths. However, we conclude that these observations do not contribute a substantial bias to our approach to deduce *in situ* food availability, as the resulting temporal bias is rather short (3 to 4 d).

Influence of food availability on juvenile growth and recruitment

The otolith approach to investigate *in situ* food availability was used to analyse the feeding histories of surviving juvenile sprat in 2 years, characterised by contrasting environmental conditions and contrasting recruitment success. We found narrow increments indicating sub-optimal feeding conditions occurring in the juvenile stage for most survivors in 2007, while the bulk of surviving individuals in 2003 exhibited large increments, suggesting optimal feeding conditions after metamorphosis.

The possible influence of food availability in the post-larval stage as a factor regulating growth, survival and recruitment was suggested in previous

studies (Baumann et al. 2007, Voss et al. 2012). Assuming that faster growing individuals have a higher survival probability (Baumann et al. 2007), sprat recruitment in the western Baltic Sea should have been higher in 2003 than in 2007. Hence, the fact that recruitment was quite different in both years with a >3-fold higher recruitment in 2003 than in 2007 (ICES 2012) can be taken as supporting evidence for this hypothesis. Furthermore, the role of low food availability in 2007 as a reason for weak recruitment is supported by measurements of plankton concentrations in the central Kiel fjord (Javidpour et al. 2009, Diekmann et al. 2012). Although the absolute plankton concentrations may differ between shallow areas and the central fjord, plankton concentrations in 2007 were much lower than in other investigated years (2006, 2009 and 2010). Hence, this supports our idea of a bottom-up regulation of recruitment during the juvenile stage.

Apart from a pronounced inter-annual difference, we found that the timing of metamorphosis in the season can regulate post-metamorphic growth performance due to the interaction of food and temperature effects. In 2003, while most survivors exhibited optimal feeding conditions, a small portion of individuals had smaller increments than the laboratory reference (Fig. 4). These individuals were born early in 2003 (end of June) and experienced temperatures >20°C at a relatively large body size. In contrast, the majority of survivors in 2003 were born later in the year (July) and experienced maximum temperatures at a smaller body size. A similar advantage of summer- over spring-born sprat due to better feeding conditions and more suitable temperature fields has been reported by Baumann et al. (2008) for the central Baltic Sea. However, those authors stated that surviving recruits mainly originated from the summer months and concluded that these individuals benefited from high temperatures and good feeding conditions during the larval stage. In the present study, we found an additional explanation as to why early born individuals (here individuals from June) may suffer: these cohorts pass through their late juvenile stage during the highest water temperatures of the year. Food requirements for the optimal growth of these large juveniles at maximum temperatures may actually be rarely encountered in the field. Cohorts born later experience their larval stage during peak temperatures, and the post-metamorphic life-stage is passed through when temperatures have already begun to decrease. Thus, they have lower metabolic rates and can hence achieve high growth rates at comparatively lower prey densities. We estimated that juvenile sprat of ~50 mm standard length require >10 times higher food densities than metamorphosing sprat of ~30 mm standard length to grow at maximum rates at temperatures between 16 and 22°C. The rapidly increasing food demand of growing post-larvae highlights the crucial importance of an overall productive juvenile nursery area and is probably the reason why sprat juveniles are migrating to inshore habitats.

CONCLUSIONS

We conclude that 2003 was a year with good recruitment due to a combination of 4 factors: (1) a colder spring causing a delay in spawning and egg development shifting metamorphosis of the larvae later into the summer. This pattern leads, in combination with a (2) warm summer and (3) sufficient prey conditions, to small larvae being able to grow at the highest temperatures and with maximal rates. Subsequently, larger juveniles, with their very high food demand, benefit from (4) lower temperatures later in the season, which reduce metabolic costs and, hence, increase growth rates at a given prey density. The same factors impacted recruitment in 2007 in a different way: (1) a warm spring induced early spawning and egg development. As a consequence, (2) the offspring experienced, overall, colder temperatures during the larval stage, leading to lower growth rates than in 2003. Finally, (3) insufficient prey concentrations in juvenile nursery areas led to sub-optimal growth, despite (4) low ambient temperatures actually reducing metabolic costs. Thus, a match or mismatch situation modulated by the interaction of temperature and food availability acts in the larval, as well as post-larval, stages and determines the survival of seasonal cohorts and the strength of the Baltic sprat year-class. Hence, it can be concluded that both a match of the larval phase with maximum temperatures and moderate prey concentrations and a match of the juvenile stage with sub-maximal temperatures but maximal prey concentrations are crucial for optimal growth and the survival of sprat recruits.

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