Mean daily growth of herring larvae in relation to temperature over a range of 5–20°C, based on weekly repeated cruises in the Greifswalder Bodden

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Reported estimates of mean daily growth of herring larvae generally cover the temperature range 1–12°C and few estimates are available for temperatures >15°C. We use larval surveys on Rügen spring-spawning herring in the Strelasund and the Greifswalder Bodden to estimate larval growth over a wider temperature range because the water temperature in that area normally increases from 5 to 20°C during the larval growth period (i.e. from spring to summer). This large temperature increase has a significant influence on the mean daily growth of herring larvae. Growth estimates were based on the modes of length frequencies observed at individual stations or accumulated over strata from consecutive surveys. Mean daily growth (G; mm d^{-1}) of larvae was primarily determined by the ambient temperature (T) during the growth interval (5–7 d), resulting in the following relationship: $G = 0.011 + 0.037\ T$. A non-linear function is also described. Growth rate was not length-dependent over the size range studied (5–20 mm). The study also showed that herring larvae were growing and surviving in temperatures up to 17.5°C.

Keywords: Baltic Sea, daily growth, herring larvae.

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Introduction

Many different methods have been applied to estimate the mean daily growth of herring larvae, ranging from cohort analysis (Brandhorst, 1956; Hempel, 1960; Waldmann, 1961; Weber, 1971; Das, 1972) and micro-increment analysis of otoliths based on field samples (Moksness and Wespestad, 1989) to the measurement of cohorts (Ehrlich *et al.*, 1976; Checkley, 1984; Gamble *et al.*, 1985) and otolith-increment deposition (Campana and Moksness, 1991; Suneetha *et al.*, 1999; Johannessen *et al.*, 2000) in experimental laboratory or enclosure studies. Houde (1997) suggested that more than 50% of the variability in mean daily growth of herring larvae can be explained by temperature. Folkvord *et al.* (2004) also highlighted the importance of temperature. Therefore, temperature-dependent growth models have been applied in simulating larval development (Heath *et al.*, 1997).

The studies reported in the literature (Table 1) have covered a temperature range of 1–12°C, which is substantially lower than that experienced by many herring larvae in the North Sea and Baltic Sea, where the maximum ambient temperature may reach 20.5°C. Therefore, to avoid extrapolations outside the range of observations, estimates of the mean daily growth above 12°C are needed (e.g. for simulating the effects of climate-change scenarios).

Using weekly larval surveys undertaken annually in the Baltic Sea, we estimated the mean daily growth rates of herring larvae, based on shifts in the modes of the length frequency distributions between sampling dates. This method may not be entirely satisfactory because potential size-selective mortality cannot be taken into account, but it does provide a first indication of larval growth at higher temperatures than those available so far, and the growth estimates obtained can be compared with those in the existing literature. We also evaluated the variability of mean daily growth in relation to the potential effects of average temperature and salinity, and seasonal progression of plankton development.

Material and methods

Larvae from the western Baltic spring-spawning herring stock in ICES Subdivisions 22–24 ("Rügen herring") have been sampled since 1979 in the Strelasund and the Greifswalder Bodden (Figure 1). Detailed descriptions of survey design, the total numbers of samples collected by year and duration of the surveys, and descriptions of the standard sample analyses are given in Oeberst *et al.* (2009). The data used here are from the 1992–2006 surveys.

Mean daily growth of larvae was estimated from the progression of the modes in the length frequencies (number m^{-2}) for either a station or a stratum between consecutive sampling dates. Three criteria were used to select the length frequencies to be included in the analyses (cf. Figure 2): normal (or near-normal)

Table 1. Literature sources (excluding starvation experiments) of daily growth rates (*G*) in relation to ambient temperature (*T*), stock origin, spawner type (A, autumn spawners; S, spring spawners), and method (R, reared; F, field observation; M, mesocosm).

G (mm d^{-1})	T (°C)	Stock origin	Spawner type	Method	Literature source
0.24, 0.35	8	Norwegian Sea	A/S	R	Johannessen *et al.* (2000)
0.13–0.26	4.8–11.2	Western Baltic, spring	S	F	Weber (1971)
0.16–0.28	6–11.5	North Sea–Baltic Sea	–	F	Brandhorst (1956)
0.15, 0.4	4, 12	Norwegian Sea	S	R	Folkvord *et al.* (2004)
0.22	6	Western Atlantic, spring	S	F	Campana and Moksness (1991)
0.17	8	West of Scotland	S	F	Checkley (1984)
0.35–0.40	7–8	Clyde	A/S	M	Gamble *et al.* (1985)
0.33	8–10	Clyde	S	F	Geffen (1986)
0.20–0.23	5–8	Norwegian Sea	S	R	Suneetha *et al.* (1999)
0.21–0.25	8	Baltic	S	R	Klinkhardt (1986b)
0.165	8	North Sea (Downs)	A	F	Hempel (1960)
0.22	9.5	Clyde	S	R	Ehrlich *et al.* (1976)
0.44	9.2	Norwegian Sea	S	M	Øiestad and Moksness (1981)
0.3–0.4	10.1–10.5	North Sea (Buchan)	A	R	Fox *et al.* (2003)
0.14–0.29	1–11.2	Bay of Fundy	–	F	Das (1972)
0.21–0.29	5.3–7.9	Baltic Sea	S	F	Waldmann (1961)

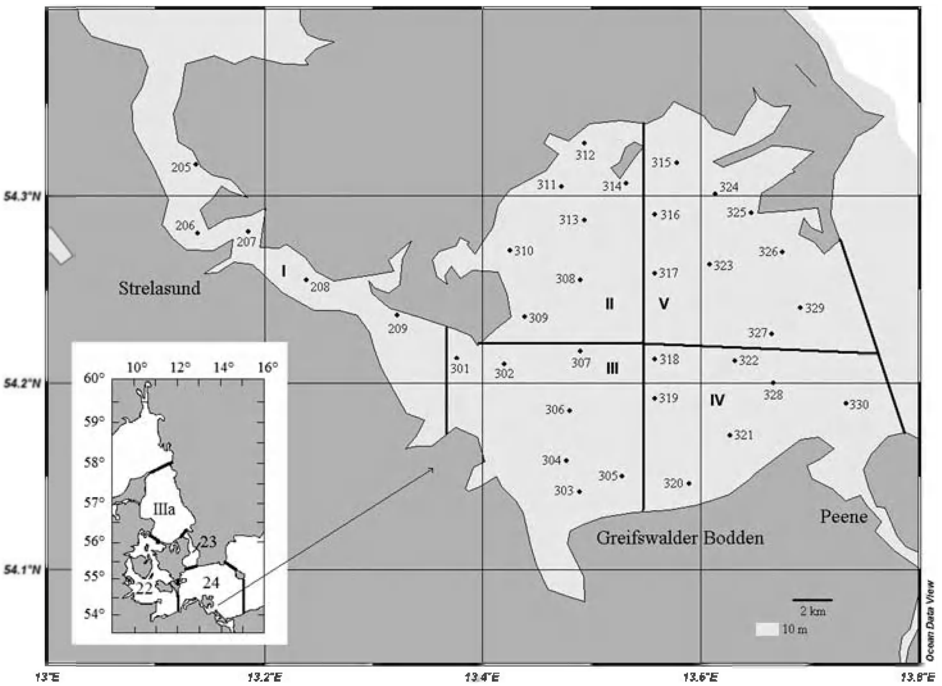

Figure 1. Map of the Strelasund and Greifswalder Bodden with the 35 fixed sampling stations and the strata (I–V) used in the analysis. Inset: southern Baltic Sea, including ICES Subdivisions 22–24.

distribution, clearly defined modes, and similar modal structures during consecutive sampling periods at the same location.

To calculate the mean daily growth (G), the difference between the lengths at the largest modes (L) in two consecutive surveys (see arrows in Figure 2) was divided by the number of days between the two sampling dates (N):

$$G = \frac{L_E - L_B}{N}, \quad (1)$$

where the subscripts B and E refer to the beginning and the end of the period, respectively. Based on the selection criteria, 106 pairs of length frequency distributions from all years (1992–2006) were identified that were suitable for estimating daily growth rates. Suitable pairs of observations covering the period between weeks 14 and 25 were obtained from all years, the number of pairs varying between 2 in 1993 and 15 in 1999. Eighteen pairs were based on single stations, and the remaining pairs on averages by strata. The number of days between consecutive cruises (P) varied between 4 and 9 d (between 6 and 8 d in 101 of 106 cases).

Data processing

Surface and bottom temperatures and salinities at the beginning and the end of a growth period were available for the sampling stations. Although surface and bottom temperatures varied

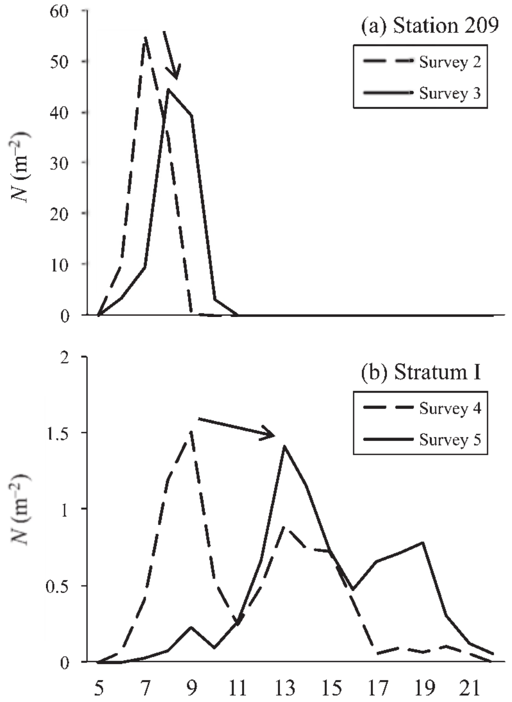

Figure 2. Examples of length frequencies from consecutive surveys used for estimating larval growth, based on shifts in the modes of the length frequencies for: (a) Station 209, from surveys 2 and 3 (in 1994); and (b) Stratum I, from surveys 4 and 5 (in 2000). Arrows identify the largest mode and the difference in modal length.

between 5 and 20°C over the season (cf. Oeberst *et al.*, 2009; Figure 2), the values obtained by station were strongly correlated ($r > 0.96$; Figure 3a and b), and stratification of the water column was not observed. Also, the temperatures at the beginning and the end of each pair of observations were strongly correlated ($r > 0.89$; Figure 3c and d). Surface and bottom salinities (Figure 3e and f) and salinities at the beginning and the end of each pair of observations (Figure 3g and h) were also strongly correlated ($r > 0.83$). Therefore, we calculated the means of these four observations of ambient temperature and ambient salinity as potential explanatory variables (T and S, respectively) of daily growth rate [Equation (2)].

In some cases, relatively large changes in temperature over periods of about 1 week were primarily caused by temporary strong solar radiation, whereas changes in salinity were caused by transport into the area of wind-driven water from the Baltic Sea (higher salinity) or water from the River Peene (lower salinity and high nutrient load). For this reason, the average differences between surface and bottom temperatures (ΔT) and between surface and bottom salinities (ΔS) were included in the analysis as potential explanatory variables (Figure 4; Table 2).

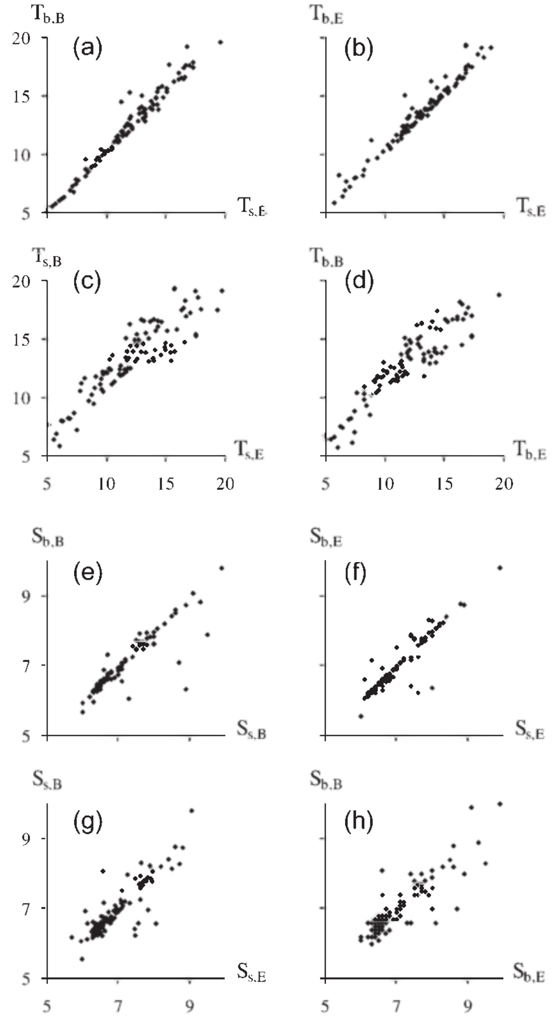

Figure 3. Relationships between surface (s) and bottom (b) temperature (T, °C) and salinity (S, psu) by station or stratum at the beginning (B) and the end (E) of the time intervals for which growth rates were determined (1992–2006): (a) bottom vs. surface temperature at the beginning of the time interval; (b) bottom vs. surface temperature at the end of the time interval; (c) surface temperature at the beginning vs. the end of the time interval; (d) bottom temperature at the beginning vs. the end of the time interval; (e) bottom vs. surface salinity at the beginning of the time interval; (f) bottom vs. surface salinity at the end of the time interval; (g) surface salinity at the beginning vs. the end of the time interval; and (h) bottom salinity at the beginning vs. the end of the time interval.

The mean larval density was <20 larvae m^{-2} in ~80% of all datasets (Figure 5), and although the distribution is highly skewed, we used the mean between the two observations (D) as an explanatory variable. In the absence of direct measurements of phyto- or zooplankton abundance, we assumed the calendar day to be the main determinant of the timing of zooplankton production, because phytoplankton production is primarily determined by solar radiation (Fennel and Neumann, 2003; Moll and Stegert, 2007), and zooplankton production largely follows phytoplankton production. Therefore, the period between the average of the sample dates and 1 April (F) was used as a proxy for seasonal progression in plankton development.

Statistical analyses

Multiple linear regression models were used to describe the variability of mean daily growth (G), based on the potential effects of the mean temperature (T), salinity (S), and density of larvae (D), the initial modal length of larvae (L), the number of days between a paired set of observations (P), the seasonal progression in zooplankton production (F), and the differences in temperature (ΔT) and salinity (ΔS) between the end and the start of the growth

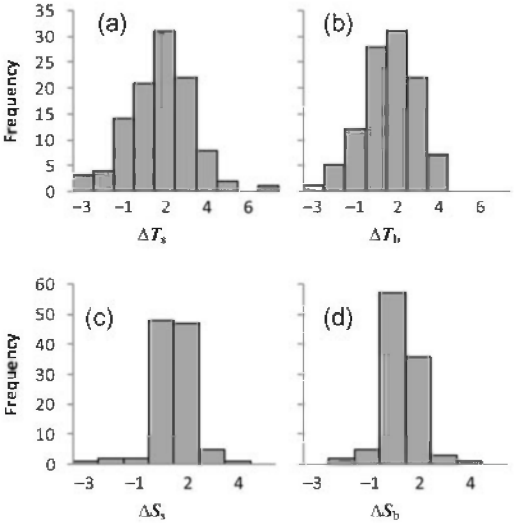

Figure 4. Frequency of weekly differences (1°C classes and 1 psu classes, 1992–2006) in: (a) surface temperature (ΔT_s); (b) bottom temperature (ΔT_b); (c) surface salinity (ΔS_s); and (d) bottom salinity (ΔS_b).

Table 2. Mean differences (with standard deviation and range) in surface temperature (ΔT_s), bottom temperature (ΔT_b), surface salinity (ΔS_s), and bottom salinity (ΔS_b) over the growth period for the 106 paired observations.

	Mean	s.d.	Min.	Max.
ΔT_s (°C)	1.3	1.5	−2.3	6.6
ΔT_b (°C)	1.2	1.3	−2.0	3.9
ΔS_s (psu)	0.0	0.37	−1.5	1.5
ΔS_b (psu)	0.1	0.41	−1.7	1.5

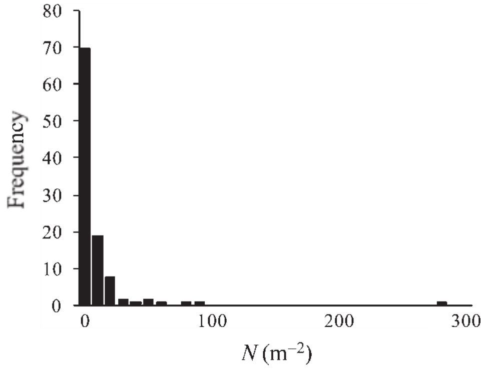

Figure 5. Distribution of larval densities (ind. m^{-2}) at the beginning of the time intervals used to estimate growth (1992–2006).

period:

$$G = b_0 + b_1T + b_2S + b_3D + b_4L + b_5P + b_6F + b_7\Delta T + b_8\Delta S + \varepsilon, \qquad (2)$$

where ε is a random variable. Generalized models were also used for studying possible year (Y) effects, where Y is used as a categorical variable:

$$G = f\,(Y, T). \qquad (3)$$

Separate linear and non-linear regression (e.g. multiplicative and double-reciprocal) models were applied to examine the relationship between G and T. The coefficient of determination and the leverage of the different datapoints were used to decide which model was the most plausible. The leverage is a statistic that measures the influence of each observation on the determination of the model parameters. Ideally, all values should have approximately the same leverage, so that they all contribute equally to the model fit. All statistical analyses were carried out using the software program Statgraphics Centurion Version XV (StatPoint, Inc.).

Results

The results of the stepwise reduction in the explanatory variables for the multiple linear regression models are given in Table 3. For temperature (T), the p-value was always <0.001, whereas for the difference in temperature (ΔT), the p-value was always <0.01. None of the other variables proved significant, even when non-significant stepwise deletion of the variable with the largest p-value was undertaken. In addition, no significant year effect could be shown by applying a model according to Equation (3).

The double-reciprocal model explained most variation in the relationship between the mean daily growth and temperature ($G = 1/(-0.131 + 30.3/T)$; $r^2 = 0.60$). However, within the temperature range observed, the growth rate estimated by the double-reciprocal model differed from the rate estimated by the linear model ($G = 0.011 + 0.037\,T$; $r^2 = 0.51$) by only 0.03 mm d^{-1}, which is probably negligible in relation to the measurement error (measurement of larval length). Moreover, the regression parameters of the double-reciprocal model proved to be strongly influenced by six datapoints with a water temperature <6.5°C (leverage values 3× greater than the average value). In contrast, the leverage of the datapoints in the linear regression model were all within 3× the average (0.057). A linear model based on the surface temperature at the beginning ($G = 0.033 + 0.035\,T_{s,B}$) resulted in a slightly stronger correlation ($r^2 = 0.54$). Oeberst *et al.* (2009) used this relationship to estimate the local production of larvae >20 mm long, which was a reasonable approach for estimating growth with the Greifswalder Bodden dataset. However, for a more general growth–temperature relationship, it is more appropriate to use the average ambient temperature, calculated as the mean of the surface and bottom temperatures at the beginning and the end of the growth interval.

The estimated daily growth increments in relation to average temperature, based on the linear regression model, were compared with the values reported in the literature (Figure 6). Our estimated mean daily growth values are in the same range as the values reported for the temperature range 5–10°C, but they diverge markedly from the regression line describing the published data above 10°C.

Discussion

Our estimates of the mean daily growth of herring larvae, based on the weekly repeated surveys in the Greifswalder Bodden, are similar to estimates from the literature for 5°C, but they appear to increase more rapidly with increasing temperature (Figure 6).

Table 3. Resulting *p*-values from the stepwise-reduced multiple linear regression model $G = f(T, S, D, L, P, F, \Delta T, \Delta S)$, where G is the mean daily growth, T the mean temperature, S the mean salinity, D the mean density of larvae, L the initial length of larvae, P the duration of growth period (days), F the proxy for seasonal progression in zooplankton production, ΔT the difference in temperature over the growth period, and ΔS the difference in salinity over the growth period.

Independent variable	***p*-values**						
T	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
S	0.46	0.46	0.46	0.46	–	–	–
D	0.23	0.21	0.19	0.19	0.21	0.21	–
L	0.74	0.78	–	–	–	–	–
P	0.23	0.22	0.22	0.23	0.30	–	–
F	0.66	0.67	0.69	–	–	–	–
ΔT	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
ΔS	0.76	–	–	–	–	–	–
r^2	0.57	0.57	0.57	0.56	0.56	0.56	0.55

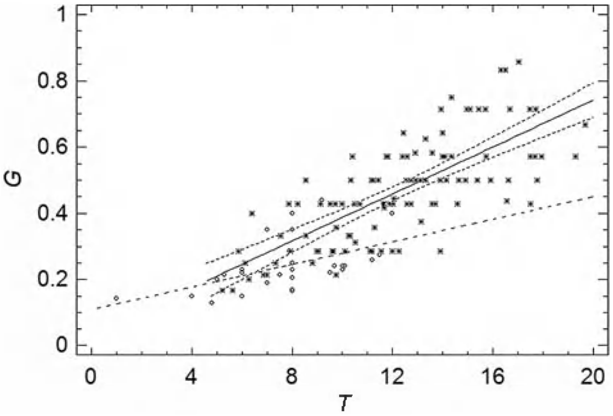

Figure 6. Linear regression model (solid line) with confidence limits (dotted lines) describing the relationship between estimated mean daily growth of herring larvae (G; mm d^{-1}) in the Greifswalder Bodden (asterisks) and average temperature (T; °C) shown compared with data (open diamonds) and fitted linear regression (dashed line; $G = 0.11 + 0.017\ T$, $N = 30$, $r^2 = 0.28$) for literature values (see Table 1 for sources).

An extrapolation of the regression model, based on data from the literature (Fiksen and Folkvord 1999), results in a considerable underestimate of the mean daily growth of these herring larvae under the ambient temperature conditions. In general, the results support the conclusions of Houde (1997) that $>50\%$ of the variability can be explained by temperature alone, because adding other explanatory variables to multiple linear regression models (Table 3) did not increase the explained variance.

Our results also indicate that the variability in mean daily growth for a given temperature can be as high as that seen in rearing experiments (Ehrlich *et al.*, 1976; Øiestad and Moksness, 1981; McGurk, 1984; Klinkhardt, 1986a, b; Suneetha *et al.*, 1999; Johannessen *et al.*, 2000). This variability may be influenced by variability in feeding conditions, which is associated with short-term temperature variations resulting from the inflow of low productivity water from the Baltic Sea or of eutrophic water from the River Peene and the Oder estuary (Fennel and Neumann, 2003). The differences in mean surface temperature between the beginning and the end of the growth intervals investigated varied from -2.3 to 6.6°C. Inflow of water from the Baltic Sea generally causes a decline in temperature, whereas temperature increases of >3°C within a week are typically caused by increased solar radiation in these shallow waters.

Rearing experiments have shown that feeding conditions also significantly influence the mean daily growth of larvae (Ehrlich *et al.*, 1976; Øiestad and Moksness, 1981; McGurk, 1984; Klinkhardt, 1986a; Folkvord *et al.*, 1997; Suneetha *et al.*, 1999; Johannessen *et al.*, 2000). However, Postel *et al.* (1991) found that abundance of nauplii and copepods in the Greifswalder Bodden in May and June 1988 was always >6000 ind. m^{-3}. Fennel and Neumann (2003) estimated abundances of 15 000 ind. m^{-3} for the period April–May in the Arkona Sea, based on a coupled physical–biological model of the Baltic Sea, and stated that higher values may be found in the area of the shallow Oder Bank, which is influenced by the nutrient loads of the Oder River. Similar concentrations may be expected when nutrient-rich water is transported into the Greifswalder Bodden. The inflow of water from the River Peene is clearly detected by a decrease in the salinity of the surface layer and, mostly, of the bottom layer. However, we failed to detect any significant effect of a change in salinity, or of calendar day, which suggests that feeding conditions are not a determining factor.

Baltic Sea herring larvae (<80 days old), caught in coastal areas in late July at temperatures between 17.5 and 17.9°C, grew on average 0.37 mm d^{-1} (Arrhenius and Hansson, 1996), which is close to the maximum growth rate of ca. 0.35 mm d^{-1} estimated at 8°C in the laboratory (Kiørboe and Munk, 1986). A study in the Vistula Lagoon (to the east of ICES Subdivision 26), based on otolith measurements, indicated maximum mean growth rates of 0.58 mm d^{-1} (Fey, 2001), but because those growth rates were averaged over a post-hatch period of 70 d (with the associated variation in thermal regime), the results cannot be readily compared with our estimates. Fey (2001) also suggested that growth rates of larvae might be impaired at temperatures above 17.5°C. However, our observations do not indicate any impairment, and the regression model predicts that growth rate at this temperature would be 0.65 mm d^{-1}.

A possible reason for the observed high mean daily growth is the relatively high zooplankton production in the area, caused by the relatively stable inflow of nutrient-laden water from the River Peene. Our slightly higher growth-rate estimates (compared with those based on otolith analysis) could be caused by size-selective mortality of the larvae: if the smaller larvae had died between sampling events, this could inflate the apparent growth rate. Nevertheless, our results suggest that larvae of Rügen herring are tolerant of relatively high temperatures, which, at least up to ~17.5°C, have no negative effect on their mean daily growth.

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