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Environmental determinants of larval herring (*Clupea harengus*) abundance and distribution in the western Baltic Sea

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Abstract

The analysis of the abundance and distribution of the early life-history stages of the western Baltic spring-spawning herring population, spanning 23 yr, revealed that the abundance of yolk-sac larvae was strongly spatially structured and significantly more abundant during the optimal temperature window for viable hatch of herring larvae (9°C to 13°C). The percentage of time encompassing this optimal temperature window exhibited a major contraction between 1995 and 2000 that may have contributed to reducing the supply of yolk-sac larvae and ultimately contributed to reducing recruitment observed after 2000. Temperature also significantly influenced the abundance of preflexion and flexion larvae, defining dome-shaped responses with maximum abundances observed between 10.27°C and 13.43°C and between 13.68°C and 18.53°C, respectively. The abundances of postflexion stage larvae were greatest at temperatures exceeding 14°C with no apparent decline in abundance at temperatures of up to 20°C. Temperature also played a significant role in influencing the abundance of larvae through its interaction with the abundance of the preceding developmental stage and provided evidence of stage-specific temperature-related mortality. There was also evidence of reduced survival during the preflexion–flexion transition in cohorts produced early in the season relative to those cohorts produced later. Although phenologically plastic species such as herring may be able to alter the dates of spawning, thus partially mitigating the effects of increasing rates of spring warming, constriction of the temperature windows for successful hatching and subsequent ontogenetic development may not be so easily mitigated by changes in phenology.

The western Baltic spring-spawning herring is a complex of different substocks that spawn in various coastal lagoons and estuaries of the western Baltic Sea and the Kattegat between early March and the end of May (Rosenberg and Palmén 1982; Otterlind 1987; Polte et al. 2014). Of these areas, the Greifswald Bay (GWB; Fig.1) is considered to be one of the most important spawning grounds and a significant retention area for larval herring (Biester 1989; Bauer et al. 2013). Oeberst et al. (2009*a*) found a strong correlation between the number of 20 mm larvae within the GWB and the number of recruits in the western Baltic Sea during the hydroacoustic surveys in autumn, thus providing a suitable proxy for the recruitment to the adult stock and an input parameter for the analytical stock assessment. The age group 0 recruitment to the stock has been declining steadily throughout a decade since circa 2000 in an unprecedented way (ICES 2016), and different hypotheses have been developed to explain the decline.

Generally, it is assumed that the year class strength of this stock is determined by changes in egg and early larval mortality (Oeberst et al. 2009*b*; Polte et al. 2014), but the underlying factors and mechanisms are not known. One hypothesis for the decline of the stock was that macrophytes as spawning substrate had declined and caused recruitment decline (Scabell 1988), as documented in the 1930s for the coastal spring-spawning herring population on the Dutch coast (Wolff 2000). However, no explicit decrease in macrophyte cover was recorded in the GWB during the period of reduced herring recruitment (Kanstinger et al. 2016). Therefore, an exclusive effect of spawning bed extent on recruitment dynamics seems unlikely.

Food availability and quality as well as predation on the early life-history stages are also potentially critical factors. Paulsen et al. (2014, 2016) found food limitation for some of the spawning areas of the western Baltic herring population

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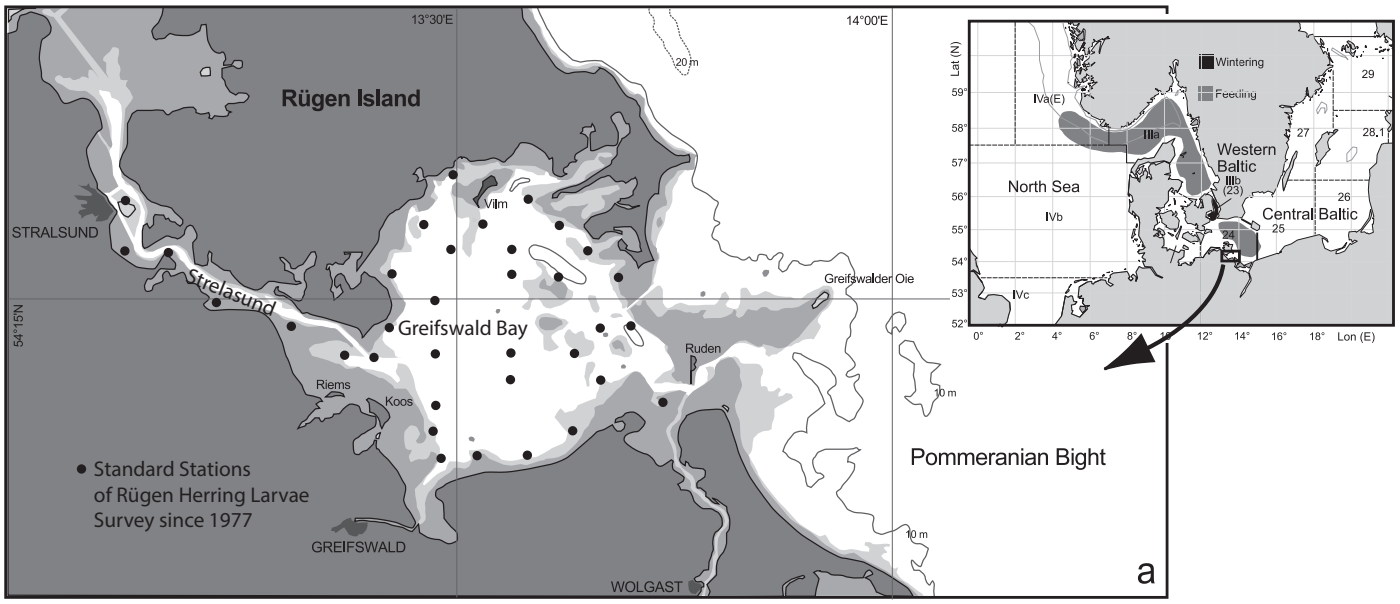

Fig. 1. The GWB and the 35 stations sampled during the Rügen herring larval surveys.

but did not find either food limitation in the GWB or insufficient food quality with regards to the main unsaturated fatty acids. Conversely, predation on herring spawn in GWB by resident predators, particularly the threespine stickleback (*Gasterosteus aculeatus*), may result in the loss of a significant proportion (extrapolated predation of up to 42%) of all eggs between spawning and hatch (Kotterba et al. 2014; Kotterba et al. 2017*a*). These authors concluded that such predation potentially regulates the survival of the early life-history stages although predation on the larval stages in this system was found to be negligible (Kotterba et al. 2017*b*).

Early survival and recruitment of marine fishes are clearly related to climate-driven changes in the entire physical environment (Gröger et al. 2014). Of all such physical factors, temperature is arguably the most important environmental factor influencing development, growth, and survival of fishes during their early life history (Houde 1989; Pepin 1991; Mueller et al. 2015). This is particularly true in GWB where oxygen concentrations are not limiting, and where salinity is quite stable and well within the tolerance range of herring. Temperature acts directly on the metabolic rate and thus on the growth rate provided sufficiently high food densities and sufficient food quality are available. High temperatures, however, result in higher metabolic costs, especially for respiration, and result in incomplete larval development, arrested growth and mortality in spite of food availability (Busch et al. 1996). For larvae, growth rates are decisive. The faster larvae grow, the shorter they remain in the highly vulnerable preflexion stage, which is generally associated with very high mortality rates (Hjort's [1914] critical period hypothesis). Evidence suggests it is essential for good recruitment to grow through the critical stages and small sizes as fast as possible since mortality rates generally decrease with increasing larval size (stage duration hypothesis: Houde [1987] and Anderson [1988]). Furthermore, the early life stages of fishes have relatively narrow thermal tolerance ranges compared to the adult stages (Pörtner and Peck 2010; Peck et al. 2012). Therefore, temperature is likely a dominant factor influencing the key life-history events in the life of fishes, including the timing and location of spawning and hatching (Tsoukali et al. 2016). Intra-annual and interannual differences in meteorological events may thus have significant direct impacts on the survival of the vulnerable early life-history stages as well as in interaction with food availability.

In order to identify the environmental determinants of larval herring abundance and distribution in the western Baltic Sea, we analyzed a 23-yr-long series of larval herring abundances provided by the Rügen Herring Larvae Survey. Our first objective was to quantify the relative importance of key abiotic environmental variables, spawning stock biomass, spatial structure within the nursery area and the timing of spawning in predicting the abundance of yolk-sac larvae in GWB. Second, we aimed to quantify the importance of key environmental variables in predicting the abundance and distribution of the three post-yolk-sac developmental stages (preflexion, flexion, and postflexion). In particular, we hypothesized that although the abundance of a given life-history stage should be related to the abundance of the preceding stage, differences in the slopes of these relationships between different environmental settings may be used to infer differential mortality patterns. Third, we tested if an optimal temperature window for embryonic development and hatching as seen in laboratory experiments (Peck et al. 2012) plays a significant role in predicting the abundance of yolk-sac larvae observed in the field

and, if so, whether annual and interannual variation in the occurrence of such a window has influenced the abundance of yolk-sac larvae. We also quantified the trends in the duration of the optimal window over the 23 yr of the sampling survey.

Material and methods

Study site

The GWB is a semienclosed, inshore basin formed by the Southern Baltic mainland coast and the Island of Rügen, Germany (Fig. 1; see Oeberst et al. 2009*a*, 2009*b*). The GWB is shallow, with a mean depth of 5.6 m, and covers 514 km^2, and is connected to the Baltic Sea in the west by a narrow sound, the Strelasund, and a broad but shallow opening to the east. An exchange of the entire water body of the bay with Baltic Sea water occurs about eight times a year and is predominantly wind driven (Stigge 1989) as tidal amplitudes are minor (< 10 cm, semidiurnal) in the inner Baltic Sea.

The Rügen Herring Larvae Survey

Western Baltic herring larvae have been sampled annually during the spawning period in GWB since the mid-1970s and in a consistent way since 1992. The principal purpose of the Rügen Herring Larvae Survey in GWB and the adjacent Strelasund Sound is to generate annual year-class strength estimates based on the number of larvae which reach the length of 20 mm during the spawning season (Oeberst et al. 2009*a*, 2009*b*). A corrected, validated database of larval herring abundances is now available back to 1992.

Herring larvae are quantitatively sampled weekly at 30 stations within the bay and 5 stations within Strelasund (Fig. 1). From 1992 to 2006, the survey duration was from mid-April to late June. From 2007 to 2014, the survey started in early spring as regular ice cover retreats (circa mid-March) and ends in the last week of June. Herring larvae were sampled weekly using stepwise oblique hauls from the surface to one meter above the seafloor with a Bongo net (diameter: 60 cm; mesh size: 0.335 mm). All samples were taken in daylight and preserved in 4% buffered formaldehyde–seawater solution. Weekly sampling of the 35 stations regularly takes 2 d to complete (see Oeberst et al. [2009*a*] and Polte et al. [2014] for additional details). In the laboratory, herring larvae were identified, counted and measured (total length to 1 mm below; e.g., 8 mm larvae measured from 8 to 8.9 mm). Four developmental stages of larvae were identified based on the developmental sequence defined by Klinkhardt (1986): 5–8.9 mm, yolk-sac larvae; 9–10.9 mm, preflexion larvae; 11–17.9 mm, flexion larvae; and 18–25.9 mm, postflexion larvae. The number of larvae per meter square by developmental stage was estimated based on the volume of filtered water and the water depth (see Oeberst et al. 2009*b*).

The analysis

To explore the relation between a response variable (in this case, the abundances of different developmental stages of herring larvae expressed per square meter) and a number of predictor variables (see below), we used a generalized additive mixed model (GAMM). The GAMM was preferred over the traditional linear mixed model since the relationships between the abundances of larvae and explanatory variables are nonlinear. The model contains a fixed and random part. The fixed part is composed of two components; the first formed with predictor variables through smoothed relationships with the response variable and the second formed with binary variables with no smoothing (the parametric model component; described in detail below). The random part of the model was constructed in order to include exponential spatial correlation structure among stations (described in detail below). The abundance of each developmental stage (size class) was log transformed to approach normality for the model's error terms after adding 0.01 to each value to correct for zeros in the dataset.

Environmental monitoring

During each sampling survey and at each station, a number of environmental variables were measured coincident with the sampling of larvae. These included point measures of water temperature, salinity, oxygen, chlorophyll and turbidity in both surface and bottom waters. There were too many missing values for chlorophyll and turbidity measurements and these variables were excluded from the analysis. Surface and bottom measurements of salinity and temperature were highly correlated ($r > 0.90$) and only bottom values were retained for the analysis to avoid a multicollinearity problem. This was not the case for oxygen measurements since the correlation was relatively weak ($r = 0.47$). Both surface and bottom oxygen values were thus retained for the analysis.

Meteorological variables

Wind speed (m s^{-1}) and wind direction (° compass) were obtained from the German Meteorological Service (Deutscher Wetterdienst) for three weather stations situated around GWB (Fig. 1): (1) HGW: City of Greifswald (N 54.0967, E 013.4056: data available from 1992 to 2014), (2) PB: Putbus, Rügen (N 54.3643, E 013.4771: data available from 1978 to 2014), and (3) Oie: Greifswald Oie (N 54.2437, E 013.9102: data available from 2007 to 2014). Given the hourly frequency of meteorological observations, for each sampling station and for each sampling date, we calculated the average wind speed and direction as the mean of wind speed and direction over the 24 h immediately prior to each sampling of larvae. Wind strength was decomposed into east–west (u) and north–south (v) vectors, by the sine and cosine of wind direction, respectively, for the final analysis. Measurements at stations were derived from interpolating values from the 2 or 3 meteorological stations as a function of the distance between the sampling stations and the meteorological stations (a form of kriging). The calculated mean values are expressed as the u vector (windspeed_sin24) and the v vector (windspeed_cos24) for inclusion in the statistical model.

We also explored the effect of storm events on the abundances of the four developmental stages. The frequency distribution of wind speeds generated from the datasets of the three meteorological stations revealed a clear discontinuity in the occurrence of wind events greater than 6 m s^{-1}, representing winds greater than 93% of all wind measurements taken over the 23-yr period. We thus considered wind speeds exceeding 6 m s^{-1} in the 24 h prior to larvae sampling as indicative of a storm event. This factor was included as a binary variable in the parametric part of the GAMM models.

Additional explanatory variables

We added two binary variables in the parametric component of the fixed part of the model. Preliminary analyses revealed high abundances of yolk-sac larvae in Strelasund relative to the Bay, consistent with earlier observations of high larvae abundance and distinctive environmental characteristics associated with this narrow sound (Polte, unpublished). We thus designated stations as being in GWB (1) or in Strelasund (0) (variable GWB). Secondly, another binary variable was added to test specifically the hypothesis that spawning activity early in the season (prior to week 17 [late April]) contributes less to the abundance of subsequent size-classes than does spawning activity after week 17 (Polte et al. 2014). We thus distinguished samples collected between the beginning of the survey up to week 17 (1) and those samples collected during and after week 17(0) (variable week < 17). If early hatched larvae contribute relatively little to future developmental stages, we hypothesized that the power of a younger developmental stage to predict the abundance of an older developmental stage should interact significantly with week of sampling, such that the slope of the relationship would be lower before week 17 and greater after week 17.

Finally, we included annual estimates of spawning stock biomass of the western Baltic spring-spawning herring (ICES 2015) as a predictor of the abundance of yolk-sac larvae.

Statistical models

The GAMM. The final GAMM is based on a total of 8655 observations covering 23 yr (1992–2014). The GAMM model used penalized regression splines to describe the relationships between predictor and response variables (Wood 2006). In order not to overfit the data, the appropriate smoothness for each continuous model term was chosen using the generalized cross-validation (GCV) technique (Craven and Wahba 1979).

Four GAMMs were fitted to quantify the influence of explanatory variables (fixed part of the model) on the abundance of (1) yolk-sac larvae (5–8.9 mm), (2) preflexion larvae (9–10.9 mm), (3) flexion larvae (11–17.9 mm), and (4) postflexion larvae (18–25.9 mm). In all models, the explanatory variables tested were the abundance of the preceding developmental stage (except for model 1), temperature_bottom; salinity_bottom; O_2_surf; O_2_bottom; windspeed_sin_24 (E-W); wind_speed_cos_24 (N-S); wind_speed24 > 6; GWB; week < 17. The spawning stock biomass (SSB) was included as a predictor variable in model 1.

We illustrate the findings of the GAMMs using scatter plots of the observed log-abundance values at each specific developmental stage as a function of the explanatory variable under study. We then superimpose curves and their 95% confidence intervals upon the scatter plots that represent the log-abundance values predicted by the GAMM for the target explanatory variable when all other explanatory variables are fixed to their mean values. Curves representing the log-abundance values predicted by the GAMM do not appear to traverse the bulk of points composing the scatter plots. This is simply a result of the high proportion of samples that did not contain larvae (26.3% for the 5–8.9 mm stage, 22.8% for the 9–10.9 stage, 22.3% for the 11–17.9 stage, and 48.7% for the 18–25.9 mm stage). Null values of abundance are presented along the x-axis of each graph at a log abundance = −4.6, corresponding to the log of (abundance = 0 + 0.01).

The spatial dependency between observations from the 35 stations, or the temporal dependency between observations taken at each station across time may be taken into account in the random part of the GAMM, but not simultaneously. Based on the Akaike Information criterion, the spatial dependency's structure best fit the data. It was modeled by an exponential spatial correlation structure that provided estimates of the nugget and the range, the latter being defined as the distance beyond which the data are no longer correlated (Fischer and Getis 2010). The metric used for calculating the between-pairs distances is the Euclidean distance.

Each model was built in three steps. The initial model was adjusted to data with all explanatory variables (step 1). We then kept only the significant variables and all interactions between those variables were added to the model (step 2). Finally, nonsignificant interactions were removed to give the final model (step 3). Only the final models retaining significant variables and interactions are presented in the results section. The $p < 0.01$ level was chosen to infer significance in all analyses.

Regression models. We conducted regression analyses to examine the dynamics of an optimal temperature window that we found was a major contributory factor in explaining the abundance of yolk-sac larvae. A mixed regression model was used to study the relationship between the average abundance of yolk-sac larvae and the absolute number of weeks per sampling season when the water temperature was in the optimal window. We also included the total number of transitions from suboptimal to optimal temperature windows. Finally, we included the longitude and latitude coordinates as variables in the analysis.

The observation units are all the combination of station × year (35 stations × 22 yr = 770 data points). The year 1993 was excluded from this particular analysis, as weeks 17–19 were not sampled in that year. These weeks are critical for spawning and in their absence, few optimal temperature

Table 1. The predictive power of the four GAMMs as estimated by the pseudo r^2 statistic between the observed values and (a) the predicted values derived from the fixed part of the GAMM and (b) the predicted values derived from the fixed and the random part of the model. The initial model was adjusted to data with all explanatory variables and only the significant variables at the $p < 0.01$ level were subsequently retained (step 1). All interactions between those variables were then added to the model (step 2). Finally, nonsignificant interactions were removed to give the final models (step 3).

Models	5–8.9 mm (a)/(b)	9–10.9 mm (a)/(b)	11–17.9 mm (a)/(b)	18–25.9 mm (a)/(b)
Step 1	0.248/0.713	0.695/0.765	0.678/0.678	0.569/0.575
Step 2	0.320/0.719	0.695/0.771	0.696/0.786	0.636/0.636
Step 3	0.254/0.714	0.694/0.770	0.689/0.742	0.637/0.637

Table 2. Results of GAMM to predict the abundance of yolk-sac herring larvae (5–8.9 mm size class) retaining only the significant variables and interactions (at the $p < 0.01$ level). Parametric coefficients are binary variables: GWB, stations located in GWB (1) or in Strelasund (0); week < 17, stations sampled prior to week 17 (1) or after (0). See text for definition of the smoothed terms. *p* values (0) "***," 0.001 "**," and 0.01 "*."

Model components		
Parametric coefficients	*t* value	*p* value
GWB	−8.883	$< 2 \times 10^{-16}$***
Week < 17	−3.051	0.00229**
Smooth terms	*F*	*p* value
Temperature	10.417	3.86×10^{-09}***
Spawning stock biomass	9.173	4.13×10^{-06}***
Temperature × GWB	3.371	0.00803**

windows were recorded in 1993. The spatial dependence between stations was taken into account using the spatial exponential structure of correlation.

Finally, a logistic regression model was used to determine if the percentage occurrence of the optimal temperature window during the spawning season has changed across years. Latitude and longitude were integrated in the model as well as their interaction with year to determine if the evolution across years of the probability of observing an optimal water temperature for hatching was different between stations in the east and the west, or between those in the north and the south of the study area.

Results

Predicting the distribution and abundance of yolk-sac larvae (5–8.9 mm in total length)

The fixed part of the GAMM fitted to quantify the influence of explanatory variables on the abundance of yolk-sac larvae (5–8.9 mm) explained 25.4% of the variance. However, this increased to 71.4% when including spatial dependency in the random part of the model (Table 1). The estimate of the range parameter in the spatial dependency structure for the case of yolk-sac larvae was 8.09 km. Thus, the correlation of abundances of yolk-sac larvae between stations did not exceed 8 km. The most significant explanatory variable in the fixed part of the model was water temperature (Table 2). The abundance of yolk-sac larvae was significantly greater when water temperatures were within a well-defined temperature window situated between 9.06°C and 12.95°C (Fig. 2A). Water temperature also interacted significantly with location within the spawning area to influence the abundance of larvae, although the effect was relatively minor (Table 2). The abundance of the yolk-sac stage peaked at intermediate levels of spawning stock biomass (163.47×10^3 and 230.31×10^3 tons), declining thereafter, apparently driven by an exceptionally high spawning stock biomass (310×10^3 tons) recorded in 1992 (data not shown). The abundance of yolk-sac larvae was significantly greater in Strelasund relative to GWB and significantly less abundant early in the season relative to later in the season (Tables 2 and 3). Finally, storm events, wind direction, surface O_2 and bottom O_2 levels did not significantly influence the abundance of yolk-sac larvae (results not shown).

Predicting the distribution and abundance of post-yolk-sac developmental stages

The explanatory power of the fixed part of the GAMMs fitted to quantify the influence of explanatory variables on the abundance of the preflexion, flexion, and postflexion stages varied from 63.7% to 69.4% (Table 1). Inclusion of spatial dependency in the random part of the models increased their predictive power, but by much less relative to that of the yolk-sac stage (Table 1). The range of the preflexion stage reached 13.36 km, 24.72 km for the flexion stage and approached thousands of kilometers for the postflexion stage. In the latter case, the abundance of postflexion larvae was correlated between all sampling stations.

The abundance of post-yolk-sac life-history stages was largely determined by the abundance of the preceding developmental stages (Fig. 3; Tables 4–6). All developmental stages were significantly more abundant later in the sampling season and almost all developmental stages were more abundant in Strelasund than in the Bay (Tables 3–6) with the exception of postflexion larvae that were equally abundant (Table 3). The slope of the positive association between the abundances of yolk-sac and preflexion larvae was greater in Strelasund than in GWB (Table 4; Fig. 4A), suggesting greater mortality during

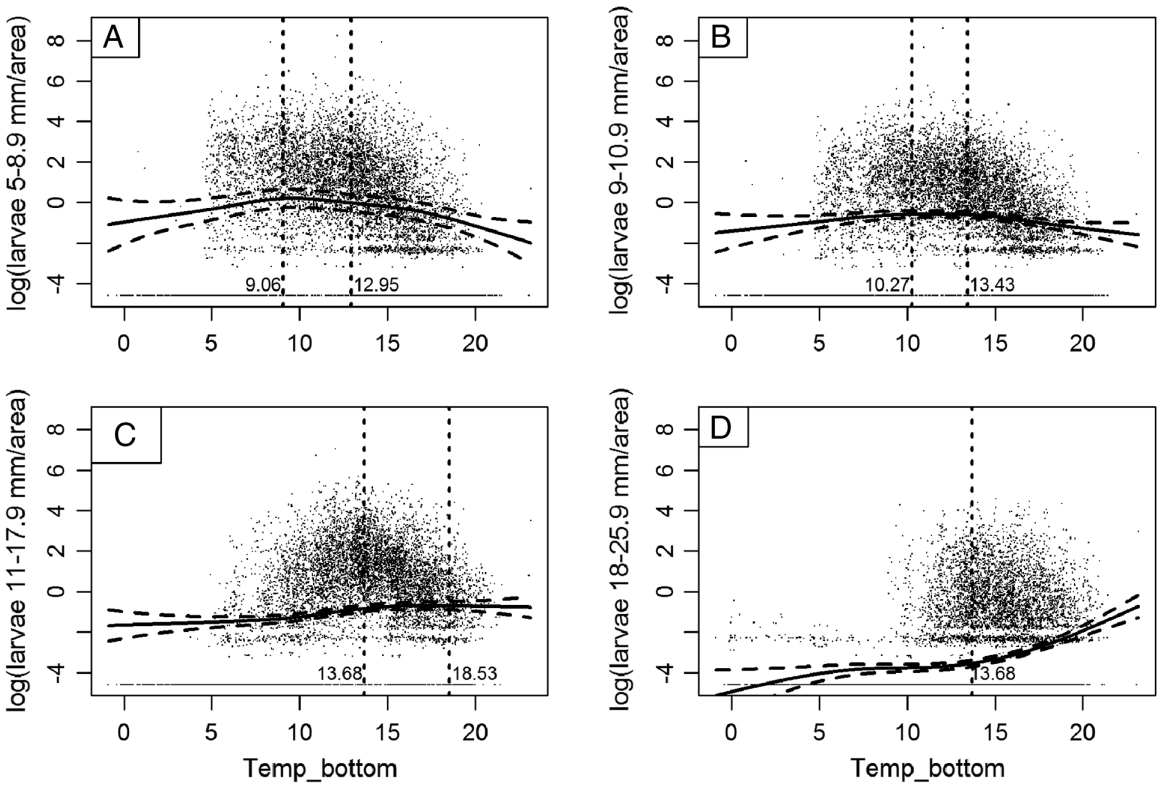

Fig. 2. Scatter plots of the observed log-abundance values at each developmental stage **(a)** yolk-sac (5–8.9 mm), **(B)** preflexion (9–10.9 mm), **(C)** flexion (11–17.9 mm), and **(D)** postflexion (18–25.9 mm) as a function of bottom temperature. The solid curves are the GAMM predicted log-abundance values at various bottom temperature values, when all other explanatory variables are fixed to their mean. The dashed curves are the 95% confidence intervals for the predicted log-abundance values. We used the intersections of the lower confidence interval with the zero response line to define values of the bottom temperature (vertical lines) that most influence the response variable.

Table 3. Mean abundances (n m^{-2}) of the four developmental stages and their standard errors, as predicted by the four GAMMs, as a function of stations sampled in GWB (1) or in Strelasund (0) (variable GWB) and as a function of samples collected between the beginning of the survey up to week 17 (1) and those samples collected during and after week 17(0) (variable week < 17).

Variable	Variable	5–8.9 mm	9–10.9 mm	11–17.9 mm	18–25.9 mm
GWB	Week < 17	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)
0		32.01 (3.73)	15.55 (4.73)	6.74 (1.04)	0.53 (0.21)
1		9.15 (2.82)	2.10 (2.67)	3.74 (0.94)	0.53 (0.21)
	0	14.93 (2.51)	5.05 (2.51)	4.78 (0.89)	0.51 (0.21)
	1	3.62 (6.00)	3.62 (5.37)	1.96 (2.14)	0.61 (0.38)

this critical transition to exogeneous feeding in the open Bay than in the sheltered sound. The slope of the relationship between the densities of preflexion and flexion larvae was greatest when spawning occurred during or after week 17 (Table 5; Fig.4B). There was thus evidence of reduced survival during the preflexion–flexion transition in cohorts produced earlier in the season (prior to week 17) relative to those cohorts produced later (during or after week 17).

As in the case of yolk-sac larvae, temperature played a significant role in influencing the abundance of all post-yolk-sac developmental stages (Fig. 2, Tables 4–6). The simple effect of temperature on the abundance of preflexion (Fig. 2B) and flexion (Fig. 2C) larvae, although significant, was relatively weak, defining shallow, dome-shaped responses with maximum abundances observed between 10.27°C and 13.43°C and between 13.68°C and 18.53°C, respectively. In the case of postflexion larvae, the simple effect of temperature was strong with greater abundances of larvae occurring when temperatures were greater than 13.7°C (Fig. 2D).

Temperature also played a significant role in influencing the abundance of larvae through its interaction with the abundance of the preceding developmental stage (Tables 4–6), and provided evidence of temperature-related mortality that changed during transitions between developmental stages.

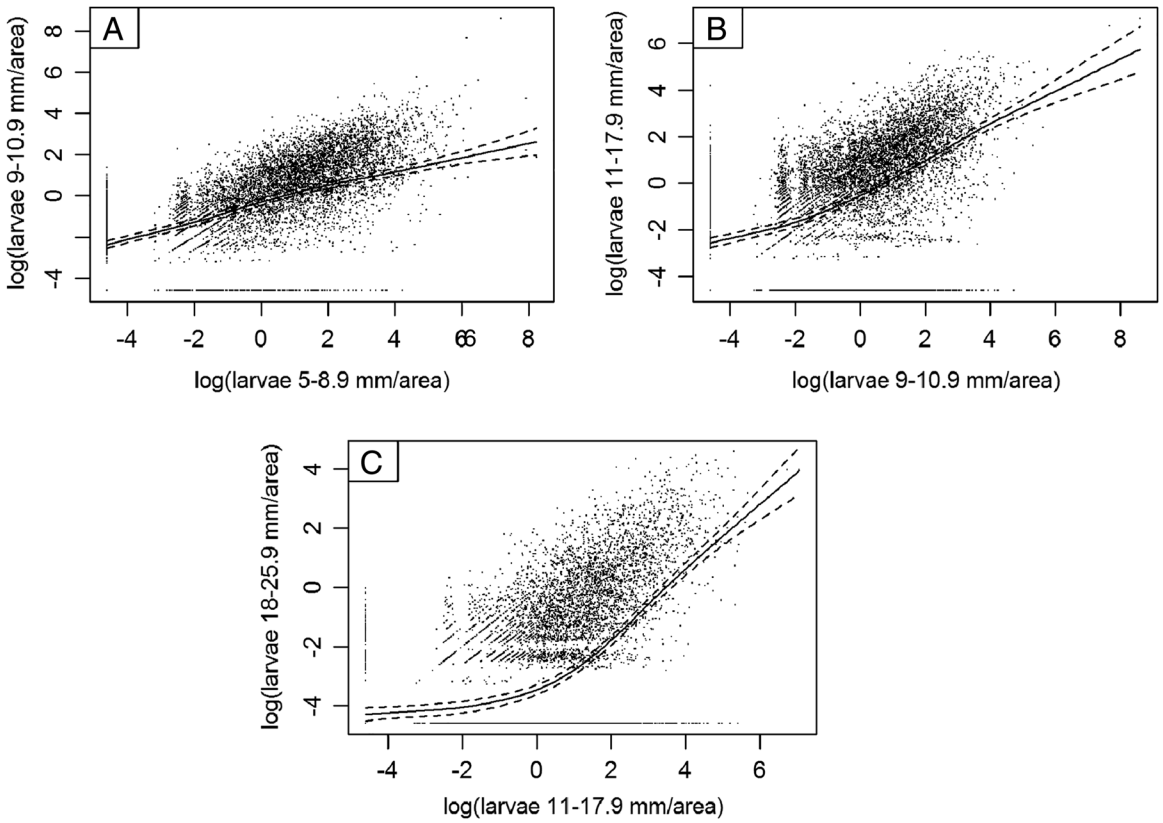

Fig. 3. Scatter plots of the observed log-abundance values at each developmental stage as a function of the log abundance of the preceding developmental stage: **(A)** abundance of the preflexion stage as a function of the abundance of the yolk-sac stage, **(B)** abundance of the flexion stage as a function of the abundance of the preflexion stage, and **(C)** abundance of the postflexion stage as a function of the abundance of the flexion stage. The solid curves are the log-abundance values predicted by the GAMM from log-abundance values observed at the preceding stage, when all other explanatory variables are fixed to their mean. The dashed curves are the 95% confidence intervals for the predicted log-abundance values.

Table 4. Results of the GAMM to predict the abundance of preflexion herring larvae (9–10.9 mm size class) retaining only the significant variables and interactions (at the $p < 0.01$ level). Parametric coefficients are binary variables: GWB, stations located in GWB (1) or not (0); week < 17, stations sampled prior to week 17 (1) or after (0). See text for definition of the smoothed terms. *p* values (0) "***," 0.001 "**," and 0.01 "*."

Model components		
Parametric coefficients	*t* value	*p* value
GWB	−6.274	3.70×10^{-10}***
Week < 17	−6.753	1.54×10^{-11}***
Smooth terms	*F* value	*p* value
Larvae 5–8.9	251.283	$< 2 \times 10^{-16}$***
Temperature	7.648	1.85×10^{-05}***
Larvae 5–8.9 × temperature	18.039	$< 2 \times 10^{-16}$***
Larvae 5–8.9 × GWB	46.797	7.59×10^{-12}***

Table 5. Results of the GAMM to predict the abundance of flexion larvae (11–17.9 mm size class) retaining only the significant variables and interactions (at the $p < 0.01$ level). Parametric coefficients are binary variables: GWB, stations located in GWB (1) or not (0); week < 17, stations sampled prior to week 17 (1) or after (0). See text for definition of the smoothed terms. *p* values (0) "***," 0.001 "**," and 0.01 "*."

Model components		
Parametric coefficients	*t* value	*p* value
GWB	−3.738	0.000186***
Week < 17	−16.636	$< 2 \times 10^{-16}$***
Smooth terms	*F* value	*p* value
Larvae 9–10.9 mm	379.37	$< 2 \times 10^{-16}$***
Temperature	11.03	1.14×10^{-08}***
Larvae 9–10.9 × temperature	28.98	$< 2 \times 10^{-16}$***
Larvae 9–10.9 × week < 17	20.64	5.60×10^{-06}***

The slope of the interaction between the abundances of yolk-sac and preflexion larvae was significantly greater at colder temperatures, suggesting greater mortality during transition from yolk-sac to preflexion stages at high temperatures (Table 4; Fig. 5A). The slope of the relationship between the abundance of preflexion and flexion larvae was significantly greater at intermediate temperatures. (Table 5; Fig. 5B). Finally, the slope relating the abundance of flexion and postflexion

larvae was significantly greater at warm temperatures (Table 6; Fig. 5C). This suggests greater mortality at colder temperatures during the transition to the postflexion stage (Fig. 5C).

Of all the developmental stages examined, only the abundance of postflexion larvae was affected by wind velocity, and this was most evident in the interaction between the abundance of flexion larvae and wind velocity (Table 6). As the abundance of flexion larvae increased, the abundance of postflexion larvae also increased, but the response was suppressed at high values of easterly winds (not shown). Finally, storm events as well as salinity and oxygen concentrations had no discernable effect alone or in interaction on the abundance of any of the post-yolk-sac developmental stages (results not shown).

Table 6. Results of the GAMM to predict the abundance of postflexion larvae (18–25.9 mm size class) retaining only the significant variables and interactions (at the $p < 0.01$ level). Week < 17, stations sampled prior to week 17 (1) or after (0). See text for definition of the smoothed terms.

Model components		
Parametric coefficients	*t* value	*p* value
Week < 17	−4.54	5.69×10^{-06}***
Smooth terms	*F* value	*p* value
Larvae 11–17.9 mm	193.539	$< 2 \times 10^{-16}$***
Temperature	155.874	$< 2 \times 10^{-16}$***
Ws_sin24	11.298	2.28×10^{-10}***
Larvae 11–17.9 × temperature	77.493	$< 2 \times 10^{-16}$***
Larvae 11–17.9 × ws_sin24	11.852	9.80×10^{-08}***
Temperature × ws-sin24	4.387	0.000777**

The optimal temperature window and the abundance of yolk-sac larvae

The mixed regression model revealed a significant relationship between the abundance of yolk-sac larvae and the absolute number of weeks water temperature occupied the optimal temperature window (Table 7). This relationship diminished in magnitude with an increase in longitude, i.e., moving from the west (Strelasund) to the east (the eastern entrance of the Bay; Table 7). Neither latitude or longitude alone nor the number of transitions into the optimal window had a discernible effect on yolk-sac larvae abundance.

Finally, the logistic regression model used to determine if the percentage occurrence of the optimal temperature window during the spawning season has changed across years revealed that it had significantly decreased over the study period ($t = -2.18$, df = 764, $p = 0.0299$, Fig. 6). A particularly steep decline, from 40% to 20% of the sampling season, was observed between 1995 and 2000. There was no effect of longitude and latitude, and no interaction of latitude and longitude with year (data not shown).

Discussion

Our analysis of 23 yr of larval herring abundance and distribution, comprising 8655 samples and 10 explanatory

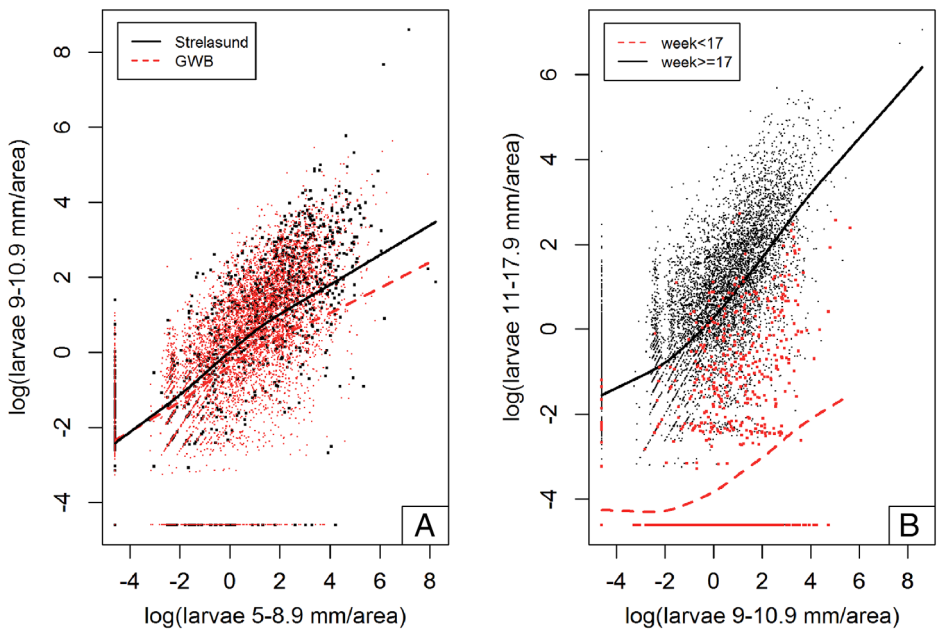

Fig. 4. (left panel) scatter plots of the observed log-abundance of preflexion larvae (9–10.9 mm) as a function of the log-abundance of yolk-sac larvae (5–8.9 mm) at stations sampled in Strelasund and in Greifswalder Bay. (right panel) scatter plot of the observed log-abundance of flexion larvae (11–17.9 mm) as a function of the log-abundance of preflexion larvae (9–10.9 mm) at stations sampled before or after week 17. The curves are the log-abundance values predicted by the GAMM from log-abundance values of the preceding developmental stage when all other explanatory variables are fixed to their mean.

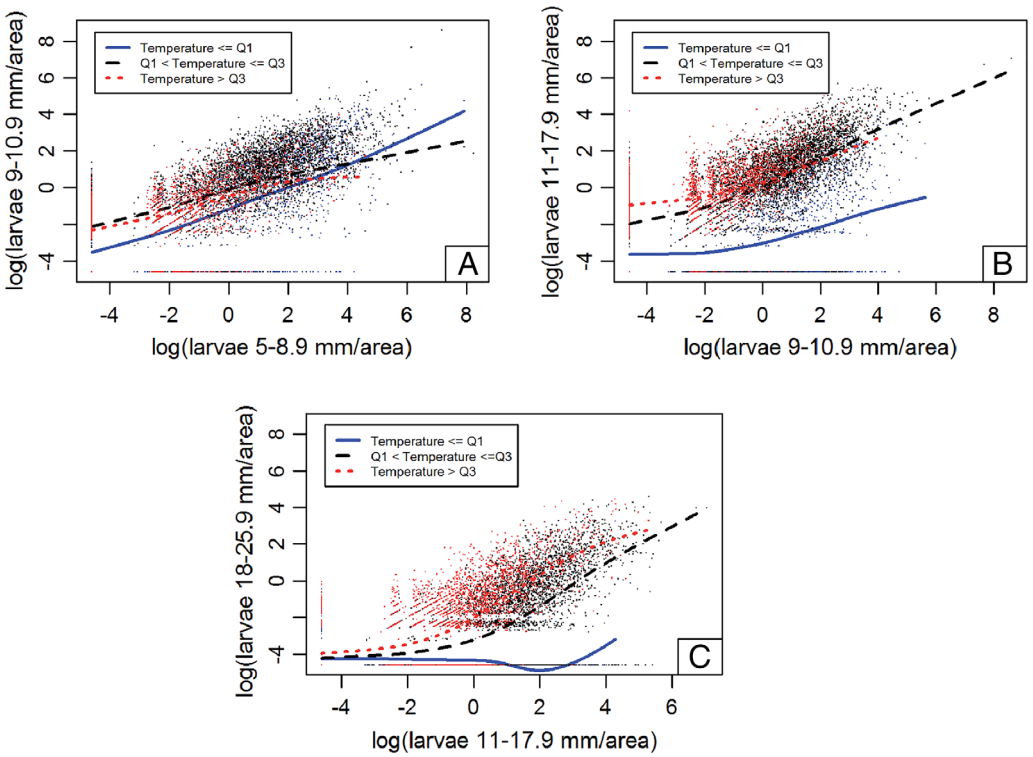

Fig. 5. Scatter plots of the observed log abundance of **(A)** preflexion, **(B)** flexion, and **(C)** postflexion larvae as a function of the log abundances of the preceding developmental stage observed at low temperatures (less than the first quartile), intermediate temperatures (between the first and the third quartiles), and high temperatures (greater than the third quartile). The curves are the log-abundance values predicted by the GAMMs from log-abundances of the preceding stages, when all other explanatory values are fixed to their mean.

Table 7. The mixed regression model illustrating the relationship between the average abundance of 5–8.9 mm larvae and the optimal temperature window. Nb_sequence_01: The absolute number of times water temperatures transitioned into the optimal window Sum_op: The absolute number of weeks when the water temperature was in the optimal window: Longitude (long) and latitude (lat) coordinates. Bold indicates significant variables at $p < 0.05$.

Effect	Estimate	DF	*t* value	*p*
Intercept	7.2714	21	0.91	0.3714
Nb_sequence_01	−0.8136	760	−0.16	0.8724
Sum_op	**5.1278**	**760**	**2.17**	**0.0302**
Longitude	−0.00590	760	−0.20	0.8420
Latitude	0.03238	760	0.40	0.6869
Nb-sequence_01 x Sum_op	0.4394	760	0.40	0.6877
Nb-sequence_01 x long	−0.00430	760	−0.31	0.7564
Nb_sequence_01 x lat	0.05408	760	1.26	0.2069
Sum_op x long	**−0.01708**	**760**	**−2.01**	**0.0444**
Sum_op x lat	−0.01102	760	−0.48	0.6330

variables, provides quantitative evidence of the dominant and pervasive influence of temperature on the distribution and abundance of successive developmental stages of herring larvae. First and foremost, we demonstrate the existence of a critical temperature window occurring between 9°C and 13°C when yolk-sac larvae are most abundant. This range coincides closely with the optimal thermal window for viable hatching of herring larvae (7–13°C) determined in the laboratory under controlled conditions (Peck et al. 2012). In addition to temperature, spawning stock biomass is also a significant determinant of the abundance of yolk-sac larvae. The spatial distribution of yolk-sac larvae is highly heterogeneous and their abundance is greatest later in the spawning season. The abundances of preflexion and flexion larvae also reveal dome-shaped responses to temperature, forming warmer temperature windows coincident with ontogenetic development. In contrast, the abundances of postflexion stage larvae are greatest at temperatures exceeding 14°C with no apparent decline in abundance at temperatures of up to 20°C.

A common feature of the survival of fish eggs as a function of temperature is the presence of high survival at some intermediate range of temperatures and developmental rates. Egg survival is reduced at temperatures that promote very fast or very slow development (reviewed by Tsoukali et al. 2016). These authors analyzed the survival of fish eggs of 32 populations of 17 species from the North Atlantic derived from laboratory egg incubation experiments. In 21 species or stocks,

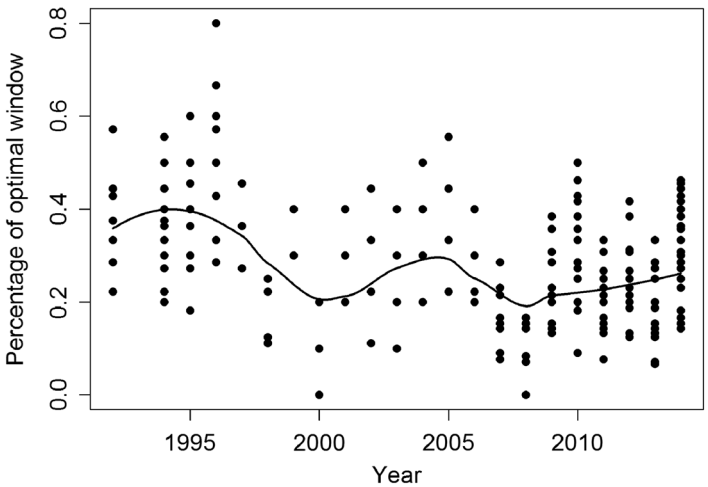

Fig. 6. The evolution of the percentage of time encompassing the optimal temperature window (9.06°C to 12.95°C) from 1992 to 2014 (omitting 1993), illustrated by a locally weighted scatterplot smoothing curve (Loess curve).

significant estimates of the optimal temperature could be identified and in 12 cases, the spread of the optimal thermal range was calculated giving a mean range of 4°C, as we observed in the present field study. In aquatic animals, a decrease in aerobic scope characterizes the onset of thermal limitation at both extremes of the thermal window. The reduction in aerobic scope is caused by reduced capacity of circulatory and ventilatory systems to meet oxygen demand. The reduced aerobic performance may enhance sensitivity to other stressors, including the availability of prey and predators, and result in reduced survival (Pörtner and Knust 2007; Neuheimer et al. 2011; Arula et al. 2015, 2016).

Numerous studies conducted in controlled and semicontrolled conditions have demonstrated that larval and juvenile growth is also temperature dependent with growth in length increasing to an optimal temperature, followed by a declining trend (e.g., Otterlei et al. 1999; Folkvard 2005; Imsland et al. 2005). Given these findings, one would expect that the distribution and abundance of the developmental stages of larval fishes should reflect the occurrence and distribution of optimal temperatures needed for successful development and survival. Few studies, however, have been successful in demonstrating such a match. In the Gulf of Riga (Baltic Sea), the abundance of herring larvae measuring between 17.1 and 20 mm (overlapping our flexion and postflexion life-history stages) were most abundant at average sea surface temperatures varying between 15°C and 19°C. Peak abundances occurred at about 16.5°C and declined thereafter (Arula et al. 2015, 2016). A similar relationship was observed in the present study for flexion larvae. In laboratory experiments, the impairment of cardiac function in the Baltic herring larvae started at 16°C (M. Moyano pers. comm.) and increased mortality was observed at 21–23°C. (M. Moyano unpubl. data, cited in Arula et al. 2016). These authors concluded that the dome-shaped relationship probably lies in decreased respiration activity. In the North Sea, a study by Röckman et al. (2010) of the realized habitats of larval and juvenile herring, estimated over the past 30 yr, revealed that newly hatched larvae were mainly associated with water masses of 9–11°C, well within the optimal temperature window observed in the present study.

The influence of temperature we observed at the preflexion, flexion, and postflexion stages was principally manifest in its interaction with the abundance of the preceding developmental stage. In the absence of stage-specific mortality rates documented for this population, these interactions provide us with a means to infer trends in differential mortality that can be related to temperature. For example, the positive relationship between the abundances of yolk-sac and preflexion stage larvae is greatest at low temperatures relative to intermediate and high temperatures as evidenced by the difference in their slopes (Fig. 5A). This observation suggests that the transition from yolk-sac stage to the preflexion stage is temperature dependent, with greater mortality occurring at higher temperatures during transition. The positive relationship between the abundances of preflexion and flexion stage larvae is greatest at intermediate temperatures and the positive relationship between the abundances of flexion and postflexion is greatest at the warmest temperatures (Fig. 5B,C).

We may only speculate as to the mechanisms responsible for these apparent mortality patterns. On one hand, physiological limitations (sensu Busch et al. 1996; Pörtner and Knust 2007) imposed by higher temperatures may contribute to significant mortality during the yolk-sac-preflexion stage transition. The cost of development increases at higher temperatures and this is particularly critical at yolk-sac absorption and the beginning of exogenous feeding (Mueller et al. 2015). On the other hand, higher temperatures could contribute to a greater availability of prey and faster growth that may favor later developmental stages. Oeberst et al. (2009*a*) demonstrated that above 10°C the growth of herring larvae increases and that postflexion larvae are tolerant towards higher temperatures with no negative effects apparent up to 17.5°C. Our findings did not detect any negative impact of temperatures on the abundance of postflexion larvae in the range of 14–20°C.

We also obtained evidence of spatial trends in mortality during the transition from yolk sac to preflexion larvae (Fig. 4A). It appears that greater mortality is associated with the transition from endogenous to exogenous feeding in the open bay than in the sheltered western sound. The Strelasund is known to be a principal migratory corridor and spawning site for herring (Bauer et al. 2014). The high concentrations of yolk-sac larvae observed in Strelasund and the apparently greater survival of larvae during the yolk-sac-preflexion transition suggests that Strelasund is an important, albeit geographically constrained, nursery area for the western Baltic herring stock.

An additional case of differential mortality was observed in the transition between preflexion and flexion larvae and the date of production of cohorts (before and after week 17). An independent analysis of a subset of the Rügen Herring Larvae Survey led Polte et al. (2014) to conclude that cohorts produced later in the spawning season contributed most to the surviving year class. These authors suggested that a major mortality event associated with the spring plankton bloom occurs during the transition from yolk sac to preflexion stages. The present analysis suggested a later event (preflexion to flexion stages), but as the length classes analyzed in the two studies were different but overlapping, a direct comparison of the results of the two studies is not possible. Nevertheless, both studies identify a major mortality event at some point before the flexion stage for cohorts produced early in the spawning season. Furthermore, the lower abundances of all developmental stages associated with early hatching cohorts (relative to cohorts produced after week 17) also indicate that these early cohorts contribute to a lesser degree to the surviving year class.

The duration of temperatures suitable for hatching (9–13°C) measured during the sampling season significantly influenced the abundance of yolk-sac larvae and this was most evident in Strelasund. Furthermore, the percentage of time encompassing the optimal temperature window for hatching exhibited a significant decline over the 23-yr time series of larval herring abundance. In particular, this decline was most notable between 1995 and 2000, declining from 40% to approximately 20% of the sampling season and subsequently fluctuated between 20% and 30% thereafter (Fig. 6). We speculate that given the key role played by the optimal hatching window in favoring the abundance of yolk-sac larvae and, as a consequence, all subsequent developmental stages, constriction of this temperature window may have contributed to reducing the supply of yolk-sac larvae and recruitment after 2000.

Given the pervasive influence of temperature throughout larval development, ongoing climate change is of critical importance in considering the fate of the western Baltic spring spawning herring population. Both global and regional climate models generally agree that the Baltic region is likely to warm up by about 2–4°C by the end of the 21st century (Elmgren et al. 2015). More importantly, changes in the phenology of a variety of physical and ecological variables measured by satellite sensors for the past 17–36 yr have been quantified (Kahru et al. 2016). Of particular importance in the present context, the cumulative sum of a phenological indicator of incoming shortwave irradiance, a key variable affecting sea surface temperature, was reached 23 d earlier in 2014 compared to the beginning of the time series in 1983. This is reflected in springtime warming that has become significantly earlier. In combination with later cooling during the autumn, the period with sea surface temperature above 16°C has increased at a mean rate of 0.98 d yr^{-1} (Kahru et al. 2016).

We speculate that the combination of a constriction of the optimal hatching temperature window due to accelerated spring warming and potentially increased mortality during the transition between the earliest life-history stages because of higher temperatures could have a significant impact on the recruitment of the population. In addition, summer temperatures in excess of 16°C persisting for longer periods of time may impede the growth and survival of postflexion larvae. Although phenologically plastic species such as herring may be able to alter the dates of spawning thus partially mitigating the effects of the warming trend, the negative impacts of the contraction of the temperature window for successful hatching due to accelerated spring warming and prolonged summer temperatures in excess of 16°C may not be so easily mitigated by changes in phenology.'

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Conflict of Interest

None declared.

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