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Maternal, temperature, and seasonal effects on yolk-sac larvae of Atlantic herring *Clupea harengus* in the western Baltic Sea

Amy T. Huang [a,*], Katharina Alter [b,1], Patrick Polte [c], Myron A. Peck [b,d]

[a] Institute for Marine Ecosystem and Fisheries Science (IMF), University of Hamburg, Große Elbstraße 133, 22767 Hamburg, Germany
[b] Department of Coastal Systems, Royal Netherlands Institute for Sea Research (NIOZ), PO Box 59, 1790, AB, Den Burg, the Netherlands
[c] Thünen Institute of Baltic Sea Fisheries, Alter Hafen Sued 2, 18069 Rostock, Germany
[d] Marine Animal Ecology Group, Department of Animal Sciences, Wageningen University, Wageningen, the Netherlands

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ABSTRACT

In marine fishes that spawn at specific times of the year, maternal effects interact with seasonal abiotic factors to influence offspring phenotypes that can affect growth, development, and survival of the early life stages. The relative importance of maternal versus abiotic processes throughout ontogeny is unclear. We incubated the progeny of 22 Atlantic herring *Clupea harengus* females from either early-, mid-, or late-spring spawning periods at both early- (7 °C) and late-season (13 °C) in situ temperatures. After yolk-sac larvae had hatched, changes in yolk sac area, notochord length, body depth, somatic body area, and cases of deformities were tracked until the point-of-no-return (beyond which starvation is irreversible), also allowing somatic growth rate and yolk utilization efficiency to be estimated. We then quantified the contributions of maternal effects, incubation temperature, and seasonal effects on offspring traits. Among newly-hatched larvae, the variance in body area was explained by temperature (18 %) and seasonal (12 %) but not maternal effects. As yolk-sac larvae reached maximum size, egg size and individual females together accounted for more than two-thirds (77 %) of the variance in body area, while seasonal and temperature effects did not explain additional variance. The maternal effects were, however, unrelated to female size (total length of 26.0–31.3 cm). As a result, size classes of females matched poorly (14–36 %) with those of egg and yolk-sac larval stages, while size classes of eggs matched well with those of maximum-sized larvae (59 %) and less with those of newly-hatched larvae (36 %). Furthermore, yolk-sac larvae from later in the season or from the 13 °C treatment had a relatively longer post-hatch, free-swimming yolk-sac larval stage with respect to the whole yolk period. Yolk utilization efficiency was similar and deformity percentage was low (<5.3 %) across seasonal timing and temperature treatments. In conclusion, our study revealed that the seasonal effects on offspring size at the transition period from endo- to exogenous feeding were attributed to differences in egg size, with herring females spawning earlier in the season producing larger eggs.

1. Introduction

In marine fish populations, high and unpredictable mortality of the early life stages can lead to large fluctuations in recruitment (Houde, 1987). Mass mortality exceeding 50 % has been observed even under controlled, laboratory settings (e.g. Pedersen et al., 1990; van der Meeren and Næss, 1993), especially during the transitional period from relying on yolk (endogenous) to feeding on external food (exogenous). It has been demonstrated that individuals with larger body size tend to exhibit lower mortality rates during this phase in both low and optimal prey conditions compared to those with smaller body size (Garrido et al., 2015; Rosenberg and Haugen, 1982). Reasons for this could be that a larger body size leads to better abilities to catch prey and more resistance against starvation (Ellertsen et al., 1980; Knutsen and Tilseth, 1985). Understanding the factors that drive variation in body size at this stage will, therefore, help identify the underlying causes of differences in survival.

As most marine fishes do not perform parental care, body size at the transitional period from endo- to exogenous feeding is determined by the total energy available in the egg as well as the environment the egg

* Corresponding author.
E-mail address: tzu-yu.huang@studium.uni-hamburg.de (A.T. Huang).
[1] Present address: University of Rostock, Institute of Biological Sciences, Department of Marine Biology, Albert Einstein Str. 3, 18057 Rostock, Germany

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experiences. The energy source of eggs is supplied by adult females, representing a form of maternal effects with egg size commonly used as a proxy (Bernardo, 1996). The predetermined, fixed amount of energy reserves (yolk) supports embryos until first feeding, which happens when most of the yolk has been utilized to allow opening of the oesophagus (Kamler, 2008; Yúfera and Darias, 2007). After the eggs are spawned, environmental factors such as temperature interact with body size to influence developmental, growth, and metabolic rates, and thus the allocation of energy to somatic growth (Kamler, 2008). Many studies have examined the effects of egg size or temperature on body size of yolk-sac larvae. First, for some fish, egg diameter was found to be positively correlated with length-at-hatch, but the explained variation ranged widely among studies of the same species (Atlantic cod *Gadus morhua*, 6 to 71 %; Marteinsdottir and Steinarsson, 1998; Miller et al., 1995; Nissling et al., 1998; Pepin et al., 1997), or was even absent in a different species (European sardine *Sardina pilchardus;* Garrido et al., 2015). Second, increasing length-at-hatch has been associated with decreasing (Nissling, 2004; Peck et al., 2012b) or increasing (Pepin et al., 1997) incubation temperatures. Patterns of changes in length-at-hatch with temperature are species-specific and differ among relatively cold (temperate) and warm (tropical) marine fishes (Peck et al., 2012a). In summary, both maternal effects and temperature may explain a large amount of variance in offspring body size but the results are not uniform across studies. Quantifying the relative contributions of maternal effects and environmental effects on offspring body size helps provide a clearer picture of the drivers of early-life developmental variation.

Maternal and temperature effects in temperate seas are linked with seasonal changes. Most temperate marine fish populations spawn in spring or autumn, with a protracted spawning season lasting from a few weeks up to three months (Wright and Trippel, 2009). Offspring produced earlier in the spawning season tend to come from larger females (e.g. in Atlantic cod (Kjesbu et al., 2010) and Atlantic herring *Clupea harengus* (Lambert, 1987; Óskarsson et al., 2002)). Also, water temperature rises (spring) or decreases (autumn) as the spawning season progresses. However, far fewer studies have considered how seasonal changes affect both females and their progeny. Miller et al. (1995) incubated cod eggs throughout the spawning season from October to May at ambient temperatures and found that most (70 %) of the variation in length-at-hatch was explained by temperature rather than egg size, with a consistent correlation among years. Another study on Atlantic silverside *Menidia menidia* showed that, when comparing eggs of similar diameter, newly-hatched larvae from early season at colder temperature were longer than those from late season at warmer temperature (Bengtson et al., 1987). Both cod and silverside, as well as most other temperate marine fishes, are batch spawners that release eggs multiple times within a season (Murua and Saborido-Rey, 2003). In batch-spawning fish, offspring released at different time periods of the season may be spawned by the same individuals. In contrast, Atlantic herring are total (single-batch) spawners; i.e. individuals release all of their eggs at once within a season (Murua and Saborido-Rey, 2003). In herring, offspring from different time periods of the season are from different females. Hence, maternal effects in herring have a tighter link with seasonal abiotic factors compared to batch-spawning fish.

In the present study, maternal, temperature, and seasonal effects on herring offspring were tracked from hatch until the end of the yolk-sac larval stage. We performed laboratory trials at early- (7 °C) and late-season (13 °C) temperatures with the offspring of western Baltic spring-spawning (WBSS) herring that were spawned by early-, mid-, and late-season females, which differed in size. Larval morphometric traits (yolk sac area, notochord length, body depth, and somatic body area), duration from hatch to growth thresholds (zero yolk reserves and maximum size), and morphological deformities were measured throughout ontogeny. The contributions of maternal, temperature, and seasonal effects to the variances in larval traits were then quantified. The correlations between seasonal timing and size classes of different life stages (females, eggs, newly-hatched larvae, and yolk-sac larvae reaching maximum size) were compared with one another. We expected that the variation in larval traits to be larger among seasonal cohorts than within seasonal cohorts. Our hypothesis was that the initial size class would be transferred to later life stages, such that size classes would remain consistent among eggs and yolk-sac larvae.

2. Materials and methods

All experimental and sampling procedure complied with the German Animal Welfare Act and the Animal Welfare Regulation Governing Experimental Animals.

2.1. Adult spawning and pre-hatch incubation

The spawning season of western Baltic spring-spawning (WBSS) herring *Clupea harengus* L. was separated into three periods: early season (day of the year; doy 53–78), mid season (doy 79–104), and late season (doy 105–130; Huang et al., 2022). Adult herring were caught using gill nets in Greifswald Bay (54.25°N, 13.23°E) within the western Baltic Sea during mid and late seasons in 2019 and early season in 2020, corresponding to doy 81, 107, and 65, respectively. Selected females from early ($n = 8$), mid ($n = 8$) and late ($n = 6$) seasons ranged from 28.7 to 31.3, 27.7 to 29.9, and 26.0 to 28.5 cm in total length, respectively. The eggs of each female were stripped onto eight glass plates (63–379 eggs per plate). Upon contact with water, herring eggs became adhesive to the glass plates and then were fertilized with pooled milt from 5 to 26 males. The egg plates were placed into individual 250-ml cylindrical chambers. Per female, the eight egg chambers were randomly distributed to a 7 ($n = 4$) or 13 °C ($n = 4$) 30-l water bath under a 14:10 h light: dark regime (Fig. 1). The water baths were connected to a 500-l recirculating aquaculture system with a mechanical filter, a biofilter, UV lights, a protein skimmer, and a cooling unit (Titan 1500, 790 W, Aqua Medic, Bissendorf, Germany). After filtration, water flowed into six 45-l header tanks and then into each egg chamber at 40 ml min^{-1}. The system was maintained at 7 °C and salinity 7, with heating applied only to the header tanks and water baths for the 13 °C treatments (600 W titanium heaters with TRD thermostatic controllers, Schego, Offenbach am Main, Germany). It is important to note that a single large recirculation system was used and, due to the water treatment, we do not consider our treatments and replicates to be pseudoreplicates. For a detailed description, see Huang et al. (2022).

2.2. Post-hatch incubation and sampling

Embryos from the same seasonal timing and incubation temperature group reached the embryonic stage of eye pigmentation on the same day. Starting from one day following eye pigmentation, egg plates were transferred into individual 1000-ml cylindrical chambers within the same water baths previously described. The chambers were supplied with gentle aeration but no water inflow to retain potentially hatched larvae. The chambers were checked for hatching at 2, 6, and 10 h after the onset of darkness. If more than five yolk-sac larvae were present in any one chamber, all egg plates of that corresponding treatment group were transferred into new chambers. This was done to ensure the yolk-sac larvae that were subsequently sampled were of similar ages (difference $\leq$ 4 h). In case fewer than five larvae had hatched, all egg plates of the corresponding treatment were transferred to new chambers at the start of the next light period to maintain water quality. During the night of mass hatching, the most abundant larval batch across females (visual inspection) from the same hatching interval (0–2, 2–6, or 6–10 h) was chosen for both morphometric determinations and further incubation of yolk-sac larvae. For morphometric measurements at hatch, approximately 40 larvae (10 larvae × 4 chambers per temperature; Table A1) per female were carefully siphoned via a 4-mm diameter tube into a 63 μm-mesh sieve cup on a petri dish. The petri dish contained seawater (salinity 7) with anaesthetic aquacalm (metomidate hydrochloride,

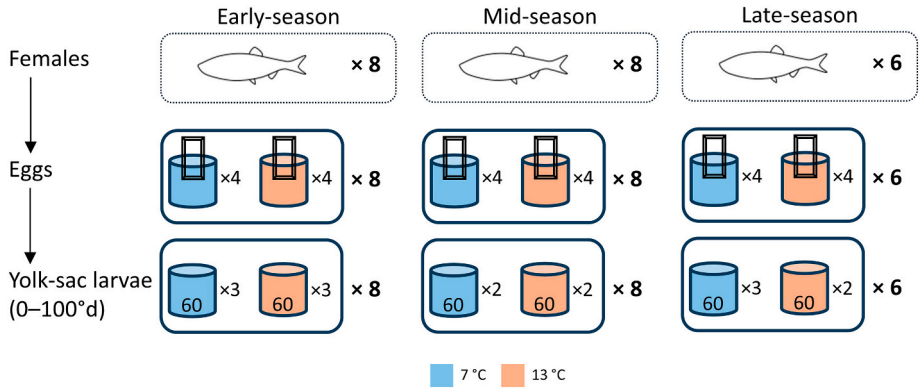

Fig. 1. Scheme of the experimental design. For each seasonal timing and temperature treatment (7 and 13 °C), yolk-sac larvae hatched from four egg chambers per female (n = 6–8 per seasonal timing) were mixed to form two to three replicate chambers, each containing approximately 60 larvae (Table A1).

Western Chemical Inc., Washington, USA, 20 mg l^{-1}). Yolk-sac larvae were photographed on their left or right lateral side under a stereomicroscope (Leica M165 C, Leica Microsystems, Wetzlar, Germany) connected to a digital camera (Leica MC170 HD, Leica Microsystems, Wetzlar, Germany) for later measurements. After being photographed, yolk-sac larvae were placed into a −80 °C freezer.

For incubation, approximately 15 larvae from each of the four replicate chambers per female (total of 42–65 larvae realized) were mixed to form new 1000-ml replicate cylindrical chambers (n = 2 or 3; Fig. 1, Table A1) with the same set up as the chambers for hatching. This was done to neutralize any chamber effects during egg incubation. The difference in the number of replicate chambers was due to an overlap of trial periods between mid- and late-season cohorts and limited laboratory space. The midpoint of the selected hatching interval for each seasonal cohort at each incubation temperature was defined as the hatch time for the respective cohorts. The duration from the hatch time to the time each individual was photographed was calculated as the age in degree-days (°d; temperature in °C multiplied by time in days) post-hatch. For each larval chamber, approximately 10 larvae were sampled, using the same method (careful siphoning) previously described. The sampling was repeated at a mean(± SD) interval of 18(5) °d until 100 °d, which is the point-of-no-return (beyond which starvation is irreversible even if prey are added and feeding begins) in WBSS herring yolk-sac larvae (Blaxter and Hempel, 1963). After hatch, larvae were sampled five times, except for the mid-season cohort in the 13 °C treatment group, which was sampled only four times due to unintended loss of larvae during water exchange (Table A1).

Each replicate chamber had a 50 to 65 % water exchange with seawater from the recirculating aquaculture system daily (13 °C) or every other day (7 °C). This ensured that total ammonium/ammonia, nitrite, and nitrate concentrations remained below 0.02, 0.001, and 0.05 mg l^{-1}, respectively (Tropic Marin NH_4^+/NH_3 Test and NO_2/NO_3 Test Professional, Dr. Biener GmbH, Wartenberg, Germany). During yolk-sac larval incubation, the mean(± SD) water temperature in the chambers was 7.2(± 0.3) °C and 12.6(± 0.3) °C in the cold and warm treatment, respectively (TLog64-USB, ± 0.5 °C, Hygrosens Instruments GmbH, Löffingen, Germany). Salinity was maintained at a range from 6.6 to 7.4 (Cond 3110, WTW GmbH, Weilheim in Oberbayern, Germany). Dissolved oxygen was >90 % air saturation (Oxi 3210, WTW GmbH, Weilheim in Oberbayern, Germany).

2.3. Morphometric traits and deformities

Yolk sac area, notochord length, body depth, and body area were measured to the nearest 0.001 mm or 0.001 mm^2 on digital photographs of individual larvae (10× magnification) using ImageJ (version 1.52, Wayne Rasband, National Institute of Mental Health, Bethesda, Maryland, USA). Notochord length was measured from the end of the notochord to the tip of the snout. Body depth was measured at the midpoint of the body. For body area, finfold area was excluded. Somatic body area was calculated as body area minus yolk sac area. Any morphological deformities such as curved bodies or yolk sac edema (Ojaveer, 1981) were noted and deformed larvae were excluded from further analyses.

2.4. Data analyses

To determine growth curves for each morphometric trait, Gompertz models were fitted to chamber averages at all sampling points (2–4 replicate chambers × 5–7 sampling points per female per temperature; Table A1). From the fitted values, we obtained the predicted size-at-hatch as well as the predicted age and size at which each trait reached its maximum value (length, depth, body area) or when the yolk sac was fully depleted. Size-at-hatch was calculated to minimize the effects of the time differences (up to 7 °d) between first- and last-sampled larvae within seasonal cohorts. A total of 44 Gompertz models (22 females × 2 temperatures) were fitted per trait (Table A2). Yolk utilization efficiency was calculated by dividing the predicted growth in somatic body area by the initial predicted yolk sac area (Hardy and Litvak, 2004).

Variance in each morphometric trait was compared among replicate chambers, females, incubation temperatures, and seasonal timing using random effects models. The proportion of variance at each level was estimated with intraclass correlation coefficients (ICC; Nakagawa and Schielzeth, 2010).

Linear-mixed effects models (LMM) were used to compare the predicted durations from hatch to yolk depletion, maximum body depth, and maximum somatic body area. In addition, LMMs were used to quantify the contribution of maternal, temperature, and seasonal effects on offspring traits. For this, we included female total length (cm), egg area (mm^2), incubation temperature (7 or 13 °C), and seasonal timing (interval variable of 1–3 representing early, mid, and late season) as fixed effects. Seasonal effect was assumed to be linear because linear relationships were observed between seasonal timing and both in situ temperature and egg area (Huang et al., 2022). Individual female (female ID) was included as a random intercept effect to account for maternal effects that were not explained by female length or egg area. The contribution of each fixed effect was represented by semi-partial R^2 (Jaeger, 2017), while the contribution of the random effect was calculated as the difference between marginal and conditional R^2 (Nakagawa and Schielzeth, 2013).

To correlate size classes across life stages, we scaled the size ranges of 1) females (total length), 2) eggs (diameter, calculated from area), 3) newly-hatched larvae (notochord length), and 4) yolk-sac larvae reaching maximum length (notochord length) to a range between 0 and 1. For yolk-sac larvae, average lengths across temperature treatments were used for scaling. The scaled sizes were then classified into quintiles

from Q1 (largest 20 percentile) to Q5 (smallest 20 percentile). The correlations among seasonal timing and size classes at each stage were compared using Spearman's rank correlation.

All analyses were conducted in R version 4.0.3 (R Core Team, 2020). Gompertz models and LMMs (including random effects models) were fitted using the functions "minpack.lm::nlsLM" (Elzhov et al., 2016) and "lme4::lmer" (Bates et al., 2015), respectively. Model assumption was checked with QQ plots and residuals versus fits plots. P values and R^2 of models and effects were obtained using the packages "lmerTest" (Kuznetsova et al., 2017), "MuMIn" (Bartoń, 2020), and "r2glmm" (Jaeger, 2017). The significance level was set at $P \leq 0.05$.

3. Results

Among replicate chambers of females, the within-female variance in notochord length, body depth, and somatic body area of yolk-sac larvae at both hatch and maximum size was small (ICC = 0.027–0.059). The variance in yolk sac area at hatch was slightly higher (ICC = 0.098) but was half of the variance among offspring of different females (ICC = 0.198).

3.1. Growth during the yolk-sac larval stage

After hatching, yolk sac area decreased gradually as notochord length, body depth, and somatic body area of yolk-sac larvae grew (Fig. 2). Averaged across seasonal timing, the mean(±SE) duration from hatch to yolk depletion was 44.2(2.2) and 53.7(3.8) °d, which corresponded to 6.3 and 4.1 days at 7 and 13 °C, respectively. Notochord length started to plateau on average 11.0 °d before yolk depletion, when its growth rate fell below 0.01 mm $°d^{-1}$. Body depth reached its maximum 17.4 °d before yolk depletion ($P < 0.0001$), whereas somatic body area of yolk-sac larvae reached its maximum 6.3 °d after yolk depletion ($P < 0.0001$; Table 1). After which, both body depth and somatic body area declined (Fig. 2).

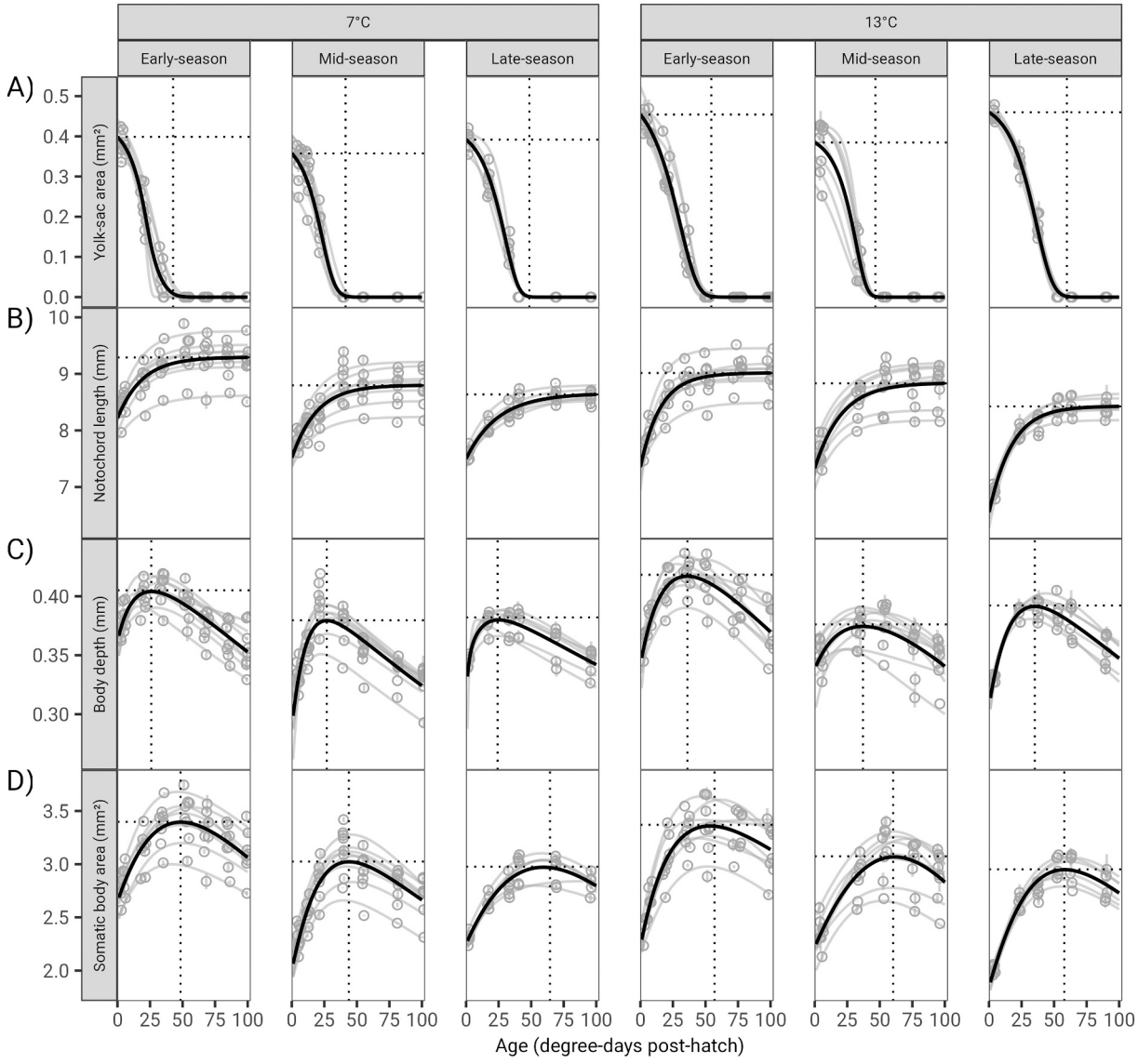

Fig. 2. Change in A) yolk sac area, B) notochord length, C) body depth, and D) somatic body area versus age from 0 (hatch) to 100 (point of no return) degree-days post-hatch in *Clupea harengus* yolk-sac larvae from eggs of early-, mid-, and late-season females and incubated at 7 or 13 °C. Total *n* observations per female ranged from 10 to 22 at each temperature treatment (Table A1). Circles are mean (± SE) observed values for offspring of individual females at each sampling point. Grey curves display Gompertz models fitted for yolk-sac larvae of individual females, while thick black curves represent the averaged curves within corresponding seasonal timing and incubation temperature groups. Vertical dotted lines denote the average age at zero yolk reserves or maximum size. Horizontal dotted lines indicate the average maximum values for the given age range.

Table 1
Size-at-hatch, maximum size during the yolk period, and duration to yolk depletion and maximum size in *Clupea harengus* yolk-sac larvae from early- ($n = 8$), mid- ($n = 8$), and late-season ($n = 6$) females and incubated at 7 or 13 °C. All values are mean (±SE). Tukey post-hoc tests were performed across seasonal timings and temperature treatments. Different lowercase letters indicate significant differences ($P < 0.05$). Abbreviations: Body = somatic body area; depth = body depth; length = notochord length; max = maximum; temp = temperature; yolk = yolk sac area.

	Grand mean	7 °C			13 °C		
		Early-season	Mid-season	Late-season	Early-season	Mid-season	Late-season
Size-at-hatch							
Yolk (mm^2)	0.408 (0.018)	0.399 (0.012)^{ab}	0.357 (0.018)^{b}	0.392 (0.008)^{ab}	0.454 (0.013)^{a}	0.385 (0.021)^{b}	0.460 (0.007)^{a}
Length (mm)	7.41 (0.22)	8.22 (0.08)^{a}	7.52 (0.04)^{b}	7.50 (0.05)^{b}	7.35 (0.07)^{b}	7.33 (0.09)^{b}	6.55 (0.07)^{c}
Depth (mm)	0.326 (0.013)	0.362 (0.006)^{a}	0.289 (0.018)^{c}	0.318 (0.018)^{bc}	0.342 (0.006)^{ab}	0.338 (0.006)^{ab}	0.307 (0.004)^{bc}
Body (mm^2)	2.20 (0.12)	2.65 (0.05)^{a}	2.01 (0.04)^{c}	2.25 (0.02)^{b}	2.23 (0.04)^{b}	2.22 (0.05)^{b}	1.85 (0.03)^{c}
Maximum size during the yolk period							
Length (mm)	8.83 (0.18)	9.29 (0.12)^{a}	8.80 (0.11)^{bc}	8.64 (0.04)^{bc}	9.02 (0.10)^{ab}	8.83 (0.13)^{bc}	8.42 (0.07)^{c}
Depth (mm)	0.392 (0.010)	0.405 (0.004)^{ab}	0.380 (0.005)^{c}	0.382 (0.003)^{c}	0.418 (0.005)^{a}	0.376 (0.005)^{c}	0.392 (0.003)^{bc}
Body (mm^2)	3.13 (0.13)	3.40 (0.08)^{a}	3.02 (0.07)^{b}	2.98 (0.05)^{b}	3.37 (0.07)^{a}	3.07 (0.08)^{b}	2.95 (0.05)^{b}
Duration from hatch to growth thresholds							
Zero yolk (°d)	48.9 (3.0)	42.7 (3.3)^{c}	41.3 (1.4)^{c}	48.6 (0.7)^{bc}	54.5 (1.5)^{ab}	46.6 (0.6)^{c}	59.8 (1.4)^{a}
Max depth (°d)	30.9 (0.7)	25.9 (2.1)^{bc}	26.9 (0.9)^{abc}	24.2 (3.5)^{c}	36.1 (2.5)^{ab}	37.1 (3.8)^{a}	35.2 (2.2)^{abc}
Max body (°d)	55.3 (2.9)	48.5 (1.5)^{ab}	43.9 (1.1)^{b}	64.5 (7.0)^{a}	57.0 (6.5)^{ab}	60.3 (2.0)^{a}	57.9 (1.9)^{ab}

On newly-hatched larvae, maternal effects (female ID and egg area) only influenced yolk sac area but not notochord length, body depth, or somatic body area (Table 2). Yolk sac area differed up to 56.3 % among offspring of different females (female ID, $R^2 = 0.329$) within the same seasonal cohorts. The differences were not influenced by female total length ($P = 0.155$) but by egg area, with larger eggs giving rise to larger yolk sacs at hatch ($P = 0.005$, $R^2 = 0.278$). In contrast, seasonal effects influenced all metrics of somatic body size but had less impact on yolk sac area (Table 2). Mean notochord length, body depth, and somatic body area of early-season larvae were significantly larger than those of late-season larvae (Table 1, Fig. 3). The differences between early- and late-season larvae across both temperature treatments were 0.76 mm for notochord length (11.5 %, $P < 0.001$, $R^2 = 0.285$), 0.04 mm for body depth (12.6 %, $P = 0.034$, $R^2 = 0.101$), and 0.39 mm^2 for somatic body area (19.2 %, $P = 0.019$, $R^2 = 0.122$). Moreover, larvae at 13 °C hatched at shorter lengths ($P < 0.0001$, $R^2 = 0.613$) and smaller somatic body areas ($P = 0.004$, $R^2 = 0.182$) but larger yolk sacs ($P < 0.0001$, $R^2 = 0.259$) compared to larvae at 7 °C.

On yolk-sac larvae reaching maximum size, maternal effects influenced all metrics of somatic body size (Table 2). Mean maximum notochord length, body depth, and somatic body area differed among offspring of different females (female ID, $R^2 = 0.169$–0.315) and increased with egg size. Within seasonal cohorts, differences between larvae hatching from the largest and smallest eggs were up to 0.96 mm (11.7 %, $P < 0.0001$, $R^2 = 0.505$), 0.04 mm (12.0 %, $P = 0.002$, $R^2 = 0.352$), and 0.61 mm^2 (22.8 %, $P < 0.0001$, $R^2 = 0.560$), respectively. Apart from the effect of egg area, seasonal timing explained no additional variance in maximum size (all $P > 0.05$; Fig. 4). Averaged across seasonal timing, larvae incubated at 13 °C compared to 7 °C had 0.006 mm deeper maximum body depths (1.6 %, $P = 0.009$, $R^2 = 0.114$) and 0.14 mm shorter maximum notochord lengths (1.6 %, $P = 0.001$, $R^2 = 0.053$) but similar maximum somatic body areas ($P = 0.960$) (Table 2, Fig. 3).

Mean duration from hatch to yolk depletion was influenced, with decreasing importance, by incubation temperature ($P < 0.0001$, $R^2 = 0.429$), egg area ($P = 0.003$, $R^2 = 0.254$), and seasonal timing ($P = 0.033$, $R^2 = 0.137$) (Table 2, Fig. 4). Considering all effects, early- and mid-season larvae hatching from larger eggs reached yolk depletion one to two days later than those hatching from smaller eggs. Late-season larvae, on the other hand, depleted their yolk on the same day at both temperature treatments. The mean(± SE) yolk utilization efficiency was 2.28(0.09) and was not significantly related to differences in egg area, incubation temperature, or seasonal timing (all $P > 0.05$). Within offspring of the same individuals, the somatic body area to yolk sac area ratio was similar between larvae reared at 7 and 13 °C. In addition, the growth trajectories of larvae at both temperatures overlapped (Fig. 5). The mean(± SE) yolk-sac larval duration accounted for 26.0(1.7) and 33.6(2.0) % of the total yolk period (from egg fertilization to yolk depletion) at 7 and 13 °C, respectively.

Table 2
Summary of the linear mixed-effects models describing the effects of female total length (cm), egg area (mm^2), incubation temperature (7 and 13 °C), and seasonal timing (early-, mid-, and late-season) on size-at-hatch, maximum size during yolk period, and duration to yolk depletion and maximum size in *Clupea harengus* yolk-sac larvae. Values for fixed effects are coefficient estimates (±SE), while random effects are reported as ±SD. The coefficient in the 13 °C column indicates the effect of 13 °C relative to the 7 °C treatment. Total n of observations per trait = 22 females × 2 temperatures = 44. Significant codes: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$. Abbreviations: Body = somatic body area; depth = body depth; ID = female ID; length = notochord length; max = maximum; yolk = yolk sac area.

	Range	Fixed effects					Random effects		Marginal/ conditional R^2
		Intercept	Female length	Egg area	13 °C	Seasonal timing	(1|ID)	Residual	
Size-at-hatch									
Yolk (mm^2)	0.263–0.523	0.233 (0.309)	−0.014 (0.009)	0.360 (0.111)**	0.049 (0.008)***	0.017 (0.016)	0.032	0.027	0.434/0.763
Length (mm)	6.27–8.46	8.08 (1.52)***	−0.03 (0.05)	0.77 (0.55)	−0.64 (0.08)***	−0.33 (0.08)***	0.00	0.26	0.751/0.751
Depth (mm)	0.227–0.389	0.453 (0.165)**	−0.009 (0.005)	0.107 (0.059)	0.008 (0.008)	−0.019 (0.009)*	0.000	0.028	0.329/0.329
Body (mm^2)	1.76–2.81	2.21 (1.17)	−0.03 (0.04)	0.85 (0.42)	−0.19 (0.06)**	−0.15 (0.06)*	0.00	0.20	0.498/0.498
Maximum size during the yolk period									
Length (mm)	8.18–9.75	5.78 (1.53)**	−0.03 (0.05)	2.87 (0.55)***	−0.14 (0.04)**	−0.07 (0.08)	0.16	0.13	0.727/0.895
Depth (mm)	0.351–0.434	0.281 (0.103)*	−0.003 (0.003)	0.137 (0.037)**	0.006 (0.002)**	−0.003 (0.005)	0.011	0.007	0.554/0.869
Body (mm^2)	2.65–3.68	1.19 (1.06)	−0.03 (0.03)	2.09 (0.38)***	0.00 (0.02)	−0.05 (0.06)	0.12	0.06	0.748/0.955
Duration from hatch to growth thresholds									
Max depth (°d)	8.7–51.9	10.7 (42.8)	−0.8 (1.3)	25.9 (15.4)	10.4 (1.9)***	1.1 (2.3)	2.4	6.5	0.401/0.471
Max body (°d)	39.6–100	70.4 (64.2)	−3.7 (2.0)	53.4 (23.1)*	7.3 (3.3)*	5.4 (3.4)	0.0	10.9	0.271/0.271
Zero yolk (°d)	28.3–63.7	36.0 (36.0)	−2.2 (1.1)	43.9 (13.0)**	9.3 (1.4)***	4.4 (1.9)*	2.8	4.6	0.561/0.681

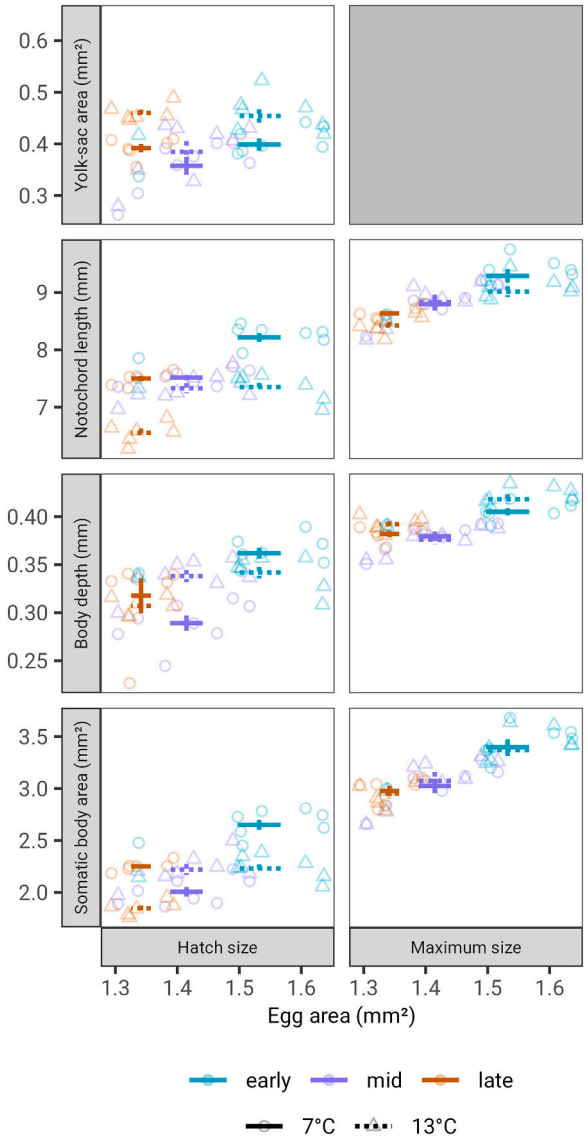

Fig. 3. Size (mm or mm^2) at hatch and at maximum versus egg area (mm^2) for early-, mid- and late-season *Clupea harengus* yolk-sac larvae incubated at 7 or 13 °C. Circles (7 °C) and triangles (13 °C) are predicted values from growth curves (Fig. 2). Solid (7 °C) and dotted (13 °C) lines represent the grand mean (± SE) for larval size and egg area (n = 6–8) at each seasonal timing.

3.2. Matching of size classes across stages

Among the 22 females in the present study, early-, mid-, and late-season individuals were in Q1 to 3, Q2 to 4, and Q3 to 5, respectively (Fig. 6). Compared to the size classes of females, size classes of their eggs and yolk-sac larvae were more aligned with the timing of season (Table 3). At least 75 % of the early-season eggs or larvae were in Q1 to 2, while 100 % of the late-season larvae were in Q4 to 5. Mid-season eggs and yolk-sac larvae reaching maximum size were distributed in Q2 to 5, but most (88 %) of mid-season newly-hatched larvae were within Q3 to 4.

Comparing across life stages, 14 to 36 % of females produced eggs and yolk-sac larvae (at hatch and at maximum size) that fell within the same size classes. In contrast, 36 to 59 % of eggs from individual females gave rise to yolk-sac larvae that remained within the same size classes. Compared to females, size classes of eggs explained 1.7-fold and 3.3-fold more variance in size classes of newly-hatched larvae and yolk-sac larvae reaching maximum size (all $P < 0.018$; Table 3), respectively. Shifts in size classes across stages, when they occurred, were within one to two quintiles, except for one shift where a Q5 early-season egg produced Q2 newly-hatched larvae (Fig. 6). The strongest correlation was between size classes of eggs and that of yolk-sac larvae reaching maximum size, with 59 % in the same quintile and the other 41 % differing by only one quintile.

3.3. Deformities

The mean(± SE) percent deformity in early-, mid-, and late-season yolk-sac larvae was 1.9(1.0), 0.4(0.1), and 1.0(0.2) % at 7 °C, respectively, and 1.3(0.7), 1.0(0.3), and 5.3(1.5) % at 13 °C, respectively. The highest percent deformity in progeny from any female was 8.4, 1.9, and 11.3 % for early-, mid-, and late-season larvae, respectively, whereas the majority (86 %) showed <3 % incidence of deformity. In mid- and late-season larvae, deformities appeared as black or curved bodies and were observed in larvae that had either hatched successfully or were unable to free themselves from the chorion. Deformed yolk sacs (edema) were only present in early-season larvae and were most prevalent in the 7 °C treatment, accounting for 92.6 % of all deformed larvae.

4. Discussion

Understanding the interaction between environmental and maternal effects is essential for identifying influences on the early survival, growth, and development of marine fish (Chambers, 1997; Marshall et al., 2008). The present study examined the contribution of maternal, temperature, and seasonal effects to body size variation in yolk-sac larvae of a herring population. At hatch, somatic body size was largely controlled by incubation temperature and only yolk sac area was influenced by maternal effects. As larvae depleted their yolk and reached maximum size, variation in somatic body size was attributed to egg size and individual females. We revealed that the seasonal decrease in body size of newly-hatched and maximum-sized larvae during the yolk period stemmed from seasonal differences in water temperature and egg size, respectively.

The lengths-at-hatch we observed agree well with those reported in a three-year study using herring eggs collected from the same spawning ground as the present study (Busch et al., 1996). The total hatching period at the spawning ground lasted for around one to two months between April and June (Busch et al., 1996; Polte et al., 2014). Mean length-at-hatch was largest in early-season cohorts and decreased with subsequent seasonal timing, with a difference of 11–28 % between early- and late-season cohorts (Busch et al., 1996). In other studies on WBSS herring, eggs were collected from later spawners in the season, and their reported lengths-at-hatch matched with those of the late-season offspring in the present study (Franke and Clemmesen, 2011; Illing et al., 2015; Moyano et al., 2016; Peck et al., 2012b). Compared to which, lengths-at-hatch of the early- and mid-season offspring in the present study were 14 and 9 % longer, respectively. The seasonal decrease in size-at-hatch during spring has also been observed in other temperate marine fish populations such as Atlantic cod and Atlantic silverside, with reported seasonal differences of 9 to 12 % in length (Bengtson et al., 1987; Miller et al., 1995).

Although both egg area and somatic body size (length, depth, and area) of newly-hatched larvae decreased as the season progressed (Huang et al., 2022; this study), egg area did not contribute to the variation in size-at-hatch in the present study. A similar pattern was reported by Miller et al. (1995), who found that the correlation between egg diameter and length-at-hatch was not significant in half of their sampling cruises. By pooling data from the whole season across three years, they estimated that egg diameter was only weakly correlated with length-at-hatch. Further, in the present study, individual females also did not contribute to the differences in somatic body size at hatch. In studies of other marine fish populations that have followed the offspring of individual females until hatch, the reported contribution of individual

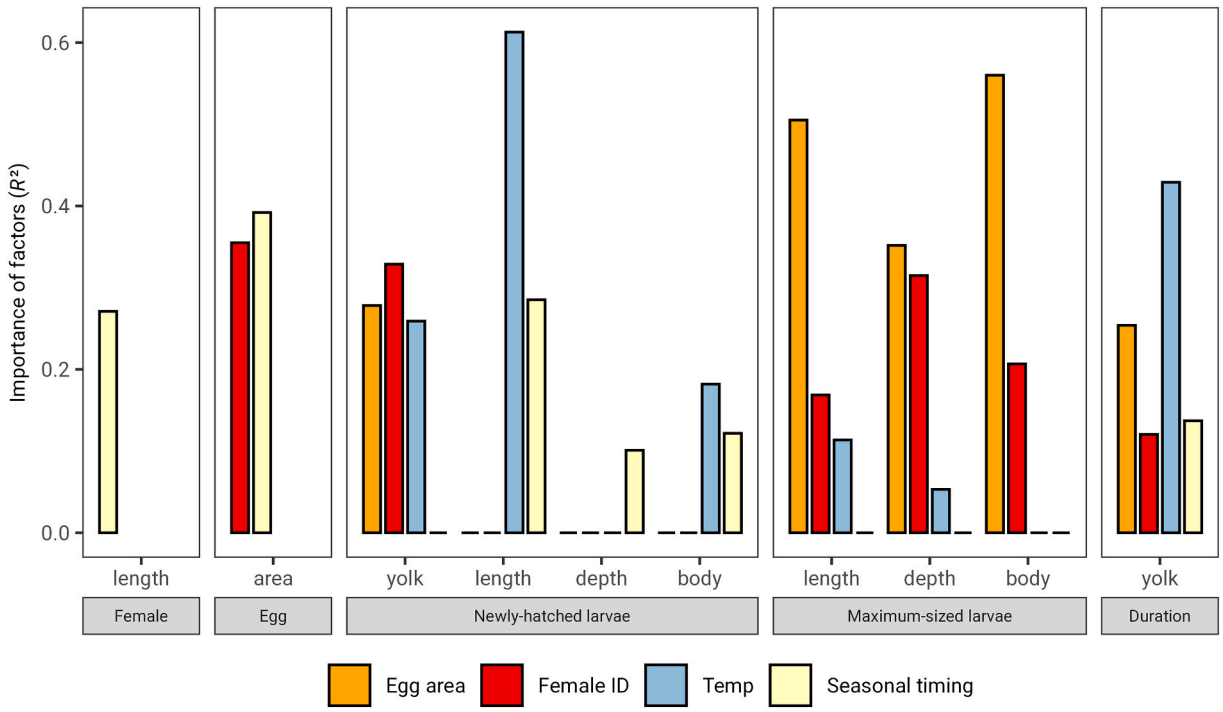

Fig. 4. Contribution of egg area, individual females, incubation temperature, and seasonal timing to total variance in morphometric traits of *Clupea harengus* (females, eggs, and yolk-sac larvae) and in durations from hatch to yolk depletion. Data on the female and egg stages are from Huang et al. (2022).

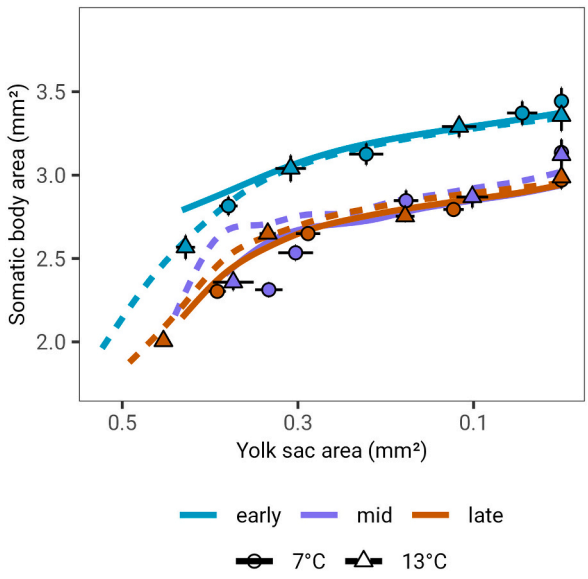

Fig. 5. Growth trajectories of somatic body area (mm^2) versus yolk sac area (mm^2) in early-, mid-, and late-season *Clupea harengus* yolk-sac larvae. Circles (7 °C) and triangles (13 °C) are mean (± SE) observed values for offspring across females ($n = 6–8$) within seasonal timing. Solid (7 °C) and dotted (13 °C) lines represent the average predicted values from Gompertz models (Fig. 1). Note that the x-axis is reversed in direction (decreasing going to the right) to represent the assumption of yolk sac.

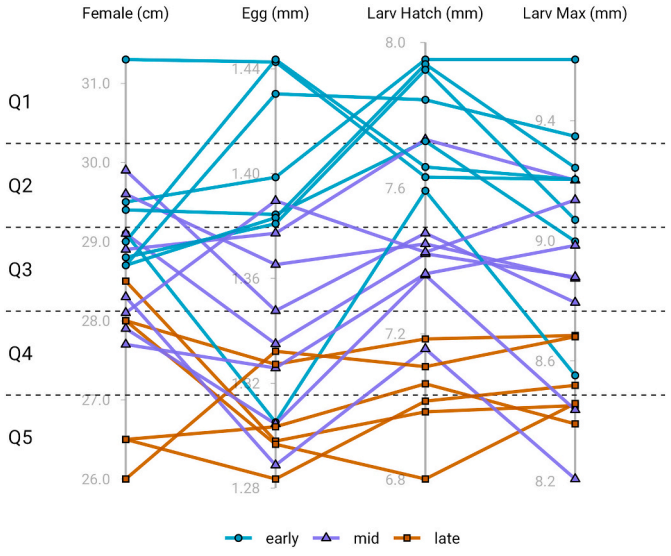

Fig. 6. Size classes (from large (Q1) to small (Q5)) of early-, mid-, and late-season *Clupea harengus* across four life stages, 1) females (total length), 2) eggs (diameter, calculated from area), 3) newly-hatched larvae (notochord length; Larv Hatch), and 4) yolk-sac larvae reaching maximum length (notochord length; Larv Max). To standardize differences across stages, the size ranges of each life stage were rescaled between 0 and 1 and categorized into quintiles. Actual size scales are labelled in grey along the vertical lines. Lines connect females with their progeny.

females to variation in length-at-hatch was less than one-third of their contribution to variation in egg diameter (Benoît and Pepin, 1999; Chambers et al., 1989; Green and Chambers, 2007). These results were in line with our findings that female effects were stronger on egg size than on size-at-hatch.

Despite the absence of maternal effects on somatic body size at hatch in the present study, maternal effects did explain a large portion of variance in yolk sac area at hatch as well as the maximum size (length, depth, and area) achieved after yolk sac depletion. A number of studies on marine fish populations have quantified the influence of individual females on larval length and yolk sac size on day 0 and 5 after hatch. A pattern appeared that, with increasing larval age, the contribution of individual females to variance in yolk sac size became smaller whereas their contribution to variance in larval length became larger (Probst

Table 3
Pairwise comparisons of seasonal timing (early-, mid-, and late-season) and size classes of *Clupea harengus* across four life stages: 1) females, 2) eggs, 3) newly-hatched larvae (Larv Hatch), and 4) yolk-sac larvae reaching maximum size (Larv Max). Values are Spearman's rank correlation coefficients. Significant codes: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

	Season	Female	Egg	Larv Hatch
Female	−0.68 ***			
Egg	−0.72 ***	0.56 **		
Larv Hatch	−0.90 ***	0.59 **	0.76 ***	
Larv Max	−0.72 ***	0.50 *	0.91 ***	0.81 ***

et al., 2006; Rideout et al., 2005), or vice versa (Trippel et al., 2005). In the present study, we followed yolk-sac larvae beyond yolk depletion and detected significant effects of egg size (50 %) and individual females (30 %) on differences in maximum body size. This agrees with previous studies which reported that egg size explained 61 to 78 % of the variance in length of older yolk-sac larvae (Nissling et al., 1998; Probst et al., 2006; Rideout et al., 2005). The absence and subsequent reappearance of maternal effects on yolk-sac larval size from hatch to older ages were also supported by the observation of Blaxter and Hempel (1963) on various herring populations, in which the positive linear relationship between egg dry weight and yolk-sac larval length became stronger some time after hatching. In marine fishes that lack a free-swimming yolk-sac stage (i.e. hatching without a yolk sac), the correlation between egg size and size-at-hatch was strong and consistent (e.g. mouthbrooders (Segers and Taborsky, 2011) and wolffish *Anarhichas* spp. (Hansen and Falk-Petersen, 2001)). Thus, maternal effects on somatic body size appeared to be confounded with those on yolk sac size, which likely explains the low contribution of maternal effects to variance in size-at-hatch observed in the present and some previous studies.

Temperature, in contrast to maternal effects, showed the opposite trend in its contribution to differences in somatic body size, with a stronger influence on size-at-hatch than on maximum size during the yolk period. Indeed, temperature was the dominant effect (18–61 %) influencing body size of newly-hatched larvae, but its contribution dropped to 0–11 % as maximum body size was reached. Other studies that followed yolk-sac larvae until yolk depletion showed that yolk-sac larvae reached similar maximum lengths at different incubation temperatures (in herring (Overnell, 1997), haddock *Melanogrammus aeglefinus* (Martell et al., 2005), and summer flounder *Paralichthys dentatus* (Johns et al., 1981)). This is supported by the review in Kamler (2008) on freshwater and marine fishes, which reported that a temperature effect was detected in over 90 % of studies on length-at-hatch but reduced to 65 % of studies on length at yolk depletion. In other words, the influence of temperature on variance in somatic body size decreased as yolk-sac larvae grew.

We found that yolk-sac larvae at 7 and 13 °C followed the same growth trajectory in terms of somatic body to yolk sac area ratio, only with those at 13 °C hatching earlier at a smaller body size. Larvae at 13 °C grew to obtain the same body to yolk sac area ratio and eventually the same maximum body area as larvae at 7 °C. Comparing embryos incubated at different temperatures, those that hatched at a smaller size possessed larger yolk sacs than those that hatched at a larger size (Galloway et al., 1998; Johns et al., 1981; Mäkinen et al., 2023). In Atlantic silverside, embryos which had been incubated at temperatures colder than 30 °C even hatched without a yolk sac (Austin et al., 1975). The phenomenon of temperature-related differences in body size and yolk sac size at hatch resembled the asynchronous hatching within the same egg batch across several days (Geffen, 2002; Laurel et al., 2008; Politis et al., 2014). Geffen (2002) compared the growth of herring yolk-sac larvae that had hatched naturally and those that were released from the egg shells. The released larvae were smaller but grew faster and reached the same length as those that had hatched naturally. Taken together, these results suggest that temperature influences the specific time point along the growth trajectory (i.e. specific body to yolk sac area ratio) at which hatching occurs.

Offspring incubated at 13 °C hatched with smaller bodies and spent a relatively longer portion (7.6 %) of the yolk period as post-hatch, free-swimming yolk-sac larvae compared to those at 7 °C, which spend more portion of time as unhatched embryos. We used the data in Busch (1996) to calculate the relative durations of egg and yolk-sac larval stages and found that later in the season, when water temperature was warmer, the proportion of yolk period as eggs tended to be shorter (i.e. hatching earlier at a smaller body). This may benefit offspring at the spawning ground since predators are more active at higher water temperatures later in the season (Kotterba et al., 2014). A longer relative duration as free-swimming yolk-sac larvae rather than benthic static eggs may allow offspring to escape predators.

In WBSS herring, the sizes of females, eggs, newly-hatched larvae, and yolk-sac larvae reaching maximum size all decreased from early to mid to late season. The size at each stage, however, did not show a consistent correlation with one another (e.g. the size of eggs compared to that of newly-hatched larvae). Our findings indicate that the inconsistency arose from the influences of different factors on size-at-hatch versus the maximum size reached during the yolk period. At hatch, temperature was the primary factor affecting variance in body size, with additional influence from seasonal effects. Early-season cohorts hatched at a larger size compared to subsequent cohorts. This pattern is likely linked to the colder temperatures experienced by early-season females during oogenesis. Thus, the observed seasonal variation in size-at-hatch may also be a temperature effect (Miller et al., 1995). At maximum size during the yolk period, all seasonal effects were attributed to the differences in egg size. Early-season eggs produced at colder temperatures were larger than mid- or late-seasons eggs and gave rise to larger larvae at yolk depletion, a pattern also observed in haddock yolk-sac larvae (Rideout et al., 2005). To understand the mechanisms underlying seasonal and temperature-related patterns in offspring size, future studies could incorporate genetic tools such as gene expression analysis. For instance, Skjærven et al. (2024) and V. Fischbach (personal communication) examined gene expression in immature cod eggs and early herring life stages under different temperature regimes. Their findings suggest the presence of an adaptive mechanism that continues throughout ovary maturation and ontogeny, highlighting the importance of maternal, temperature, and seasonal effects on later life stages.

CRediT authorship contribution statement

Amy T. Huang: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Katharina Alter:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization. **Patrick Polte:** Writing – review & editing, Supervision, Resources. **Myron A. Peck:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Table A1
Sampling size of *Clupea harengus* yolk-sac larvae for morphometric measurements. Values are the mean(±SE) number of larvae sampled across chambers (n = 2–4) for each female at each sampling point. Deformed larvae were excluded. If the sampling size was fewer than three within any chamber, these values at the respective sampling point were excluded. In two cases, values are from one single chamber and indicated by a missing standard error (ND). Abbreviation: ND = not determined.

	7 °C				13 °C			
	At hatch		Post-hatch		At hatch		Post-hatch	
Female no. (rank)	*n*	larvae/ chamber	*n*	larvae/ chamber	*n*	larvae/ chamber	*n*	larvae/ chamber
Early-season								
				12(1) + 12(2) + 12(1) + 8 (1) + 10				10(0) + 11(1) + 9 (1) + 11 (1) + 6
1 (1)	4	9(0)	3	(1) + 6(3)	4	12(0)	3	(3)
				10(1) + 11(0) + 11(1) + 7 (1) + 10				10(4) + 11(0) + 9 (1) + 13 (2) + 10
2 (4)	4	11(1)	3	(1) + 5(1)	4	13(1)	3	(0)
				11(1) + 10(1) + 12(1) + 8 (1) + 12				10(0) + 11(1) + 9 (1) + 11 (1) + 9
3 (5)	4	11(1)	3	(1) + 7(0)	4	12(1)	3	(2)
				11(1) + 10(1) + 11(2) + 7 (2) + 11				11(1) + 10(1) + 11(4) + 11(1) + 7
4 (6)	4	12(1)	3	(1) + 7(1)	4	10(1)	3	(2)
				12(2) + 8 (1) + 9(1) + 9(1) + 11(1) + 4				11(1) + 10(1) + 9 (1) + 10 (1) + 8
5 (8)	4	11(1)	3	(1)	4	11(1)	3	(2)
				11(1) + 10(0) + 10(0) + 7 (1) + 11				10(1) + 10(0) + 7 (2) + 9 (0) + 9
6 (10)	4	13(1)	3	(0) + 9(1)	4	12(1)	3	(1)
				9(0) + 10 (0) + 11 (0) + 8(2) + 11(0) +				10(1) + 8 (2) + 8 (1) + 11 (1) + 10
7 (11)	4	11(0)	3	6(2)	4	16(3)	3	(0)
				10(1) + 11(1) + 11(1) + 8 (1) + 11				11(0) + 11(1) + 9 (1) + 13 (3) + 7
8 (12)	4	11(1)	3	(1) + 7(2)	4	10(2)	3	(2)
Mid-season								
				10(0) + 14(2) + 10(0) + 10(0) + 12(2) +				9(1) + 8 (2) + 9 (1) + 10
9 (2)	4	9(1)	2	10(0)	4	5(0)	2	(0)
				10(1) + 10(1) + 10(0) +				9(0) + 8 (2) + 5 (2) + 3
10 (3)	4	11(3)	2	11(0) +	4	4(1)	2	(0)

(*continued on next column*)

Table A1 (*continued*)

	7 °C				13 °C			
	At hatch		Post-hatch		At hatch		Post-hatch	
Female no. (rank)	*n*	larvae/ chamber	*n*	larvae/ chamber	*n*	larvae/ chamber	*n*	larvae/ chamber
				11(0) + 10(0)				
				10(1) + 13(1) + 10(1) + 11(1) + 12(0) +				11(1) + 9 (1) + 8 (3) + 8
11 (7)	4	12(2)	2	10(1)	3	4(0)	2	(4)
				9(0) + 13 (1) + 10 (0) + 10 (1) + 11 (1) + 10				9(1) + 11 (2) + 10 (0) + 7
12 (9)	4	12(1)	2	(1)	4	3(1)	2	(1)
				13(3) + 12(1) + 10(0) + 11(1) + 10(1) +				7(3) + 12 (ND)[a] + 8 (4) + 6
13 (14)	4	10(1)	2	10(0)	4	5(2)	2	(ND)
				10(0) + 11(1) + 11(1) + 11(2) +12(1) +				9(1) + 9 (1) + 10 (0) + 11
14 (15)	4	10(2)	2	7(1)	3	6(1)	2	(1)
				10(0) + 12(1) + 10(0) + 13(2) + 8				11(0) + 8 (1) + 8 (3) + 4
15 (18)	4	10(2)	2	(3) + 6(3)	3	5(0)	2	(1)
				7(2) + 9 (1) + 10 (0) + 11 (1) + 12				10(1) + 9 (2) + 9 (2) + 10
16 (19)	4	11(1)	2	(3) + 5(1)	4	5(0)	2	(ND)
Late-season								
				7(1) + 7 (1) + 8(0) + 8(0) +				11(1) + 9 (0) + 10 (0) + 11 (1) +12
17 (13)	4	11(0)	3	7(1)	4	15(2)	2	(1)
				8(1) + 7 (1) + 7(1) + 7(1) +				12(1) + 10(1) + 11(1) + 10(0) +
18 (16)	4	12(1)	3	5(1)	4	14(1)	2	11(1)
				6(0) + 8 (0) + 7(0) + 7(1) +				11(1) + 11(1) + 12(2) + 10(1) + 7
19 (17)	4	11(1)	3	5(1)	4	12(1)	2	(2)
				7(1) + 8 (0) + 6(0) + 6(1) +				8(1) + 10 (1) + 10 (1) + 10
20 (20)	4	10(1)	3	4(0)	4	10(0)	2	(0)
				7(0) + 6 (0) + 6(1) + 8(1) +				10(1) + 11(1) + 10(0) + 10(0) +
21 (21)	3	11(1)	3	7(1)	4	12(1)	2	10(1)
				8(1) + 6 (1) + 6(0) + 7(1) +				11(1) + 12(0) + 11(1) + 10(0) +
22 (22)	4	12(1)	3	8(2)	4	12(1)	2	10(0)

Table A2
Parameter estimates of the models describing changes in yolk sac area, notochord length, body depth, and somatic body area with age in *Clupea*

harengus yolk-sac larvae.

	Range	Mean (SD)
Yolk sac area	$Y_t = Ae^{-e^{-\beta(T_I - t)}}$	
A	0.307–0.649	0.447 (0.072)
β	0.054–0.280	0.100 (0.040)
T_I	20.9–38.6	28.2 (5.3)
Notochord length	$L_t = \alpha e^{\gamma\left(1-e^{(-\beta t)}\right)}$	
α	6.27–8.46	7.45 (0.51)
β	0.093–0.288	0.176 (0.050)
γ	0.026–0.113	0.057 (0.013)
Body depth	$M_t = \alpha e^{\gamma\left(1-e^{(-\beta t)}-\delta t\right)}$	
α	0.227–0.389	0.327 (0.033)
β	0.066–3.438	0.460 (0.592)
γ	0.006–0.594	0.083 (0.086)
δ	0.001–0.017	0.003 (0.003)
Somatic body area	$M_t = \alpha e^{\gamma\left(1-e^{(-\beta t)}-\delta t\right)}$	
α	1.76–2.81	2.21 (0.27)
β	0.25–6.62	1.19 (1.41)
γ	0.006–0.108	0.035 (0.020)
δ	0–0.025	0.006 (0.006)

Data availability

Data are available on Mendeley Data: https://data.mendeley.com/preview/37388z3sp7?a=2c40e97f-0c8b-47cd-a15d-85d0ec969cf7.

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