Received: 15 July 2022 | Accepted: 4 September 2022
DOI: 10.1111/jfb.15210

REGULAR PAPER

JOURNAL OF FISH BIOLOGY fsbi

Disentangling seasonal from maternal effects on egg characteristics in western Baltic spring-spawning herring *Clupea harengus*

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Funding information
Konrad-Adenauer-Stiftung; Ministry of Education

Abstract

In marine fishes, the timing of spawning determines the environment offspring will face and, therefore, the chances of early life stage survival. Different waves of Atlantic herring *Clupea harengus* spawn throughout spring in the western Baltic Sea, and the survival of offspring from early in the season has been low in the most recent decade. The authors assessed changes in egg traits from early, middle and late phases of the spawning season to examine whether seasonal and/or maternal effects influenced embryo survival. At each phase, fertilized eggs of six to eight females were incubated at two temperatures (7 and 13°C), and egg size, fertilization success, mortality and time to hatch were recorded. A compilation of data from 2017 to 2020 spawning seasons indicated that mean total length of females decreased with progression of the season and increasing *in situ* water temperature. For the sub-set of females used in the laboratory study, early spawners were 7.6% larger and produced 14.2% larger eggs than late-spring spawners. Fertilization success was consistently high (>90%), and mortality to hatch was low (<3%). Neither the former nor latter were influenced by season, but both were influenced by maternity. This significant female effect was, however, not related to any maternal trait measured here (total length, Fulton's condition factor or age). There was no maternal effect on development rate at 7 or 13°C. The results suggest that intrinsic differences among females or among spawning waves are unlikely to markedly contribute to the poor survival observed for progeny from early in the season in this population and point towards other extrinsic factors or processes acting on eggs or early larval stages (*e.g.*, seasonal match–mismatch dynamics with prey) as more likely causes of mortality.

KEYWORDS
cohort mortality, life history, phenotypic plasticity, Rügen herring, spawning waves

1 | INTRODUCTION

Marine fishes are characterized by high rates of mortality during the earliest life stages which decline at some point before or soon after larval–juvenile metamorphosis (Bailey & Houde, 1989). In marine fishes providing no parental care, the timing of spawning determines the environment the offspring will face and, therefore, the chances of early life stage survival. In the temperate zone, fish populations reproduce during specific seasons, and spawning typically lasts for several weeks to 3 or 4 months (reviewed in Chambers, 1997). Atlantic

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herring *Clupea harengus* L. 1758 (Clupeiformes, Clupeidae) is a central species linking lower (planktonic) and upper (*e.g.*, piscivorous) trophic levels in the northern Atlantic (Link & Garrison, 2002; Sveegaard *et al.*, 2012). Populations of *C. harengus* are distinguished by their spawning seasons, *e.g.*, winter–spring or summer–autumn, and spawning areas (Haegele & Schweigert, 1985). *C. harengus* are iteroparous, total spawners with demersal eggs (Blaxter & Hunter, 1982). It has been demonstrated for some populations of spring-spawning *C. harengus* (*e.g.*, Gulf of St. Lawrence, southern Iceland, southwestern Norwegian coast) that larger, repeated spawners tend to spawn earlier compared to smaller, first-time spawners which often spawn last, resulting in a series of egg depositions at the spawning ground across one season (Lambert & Messieh, 1989; Óskarsson & Taggart, 2009; Slotte *et al.*, 2000).

Larger *C. harengus* migrate longer distances than smaller individuals (Payne *et al.*, 2009; Slotte, 1999) and encounter different environmental conditions during oogenesis as well as at the point of spawning. Depending on the location, eggs produced at the beginning or end of the spring spawning season can experience large temperature differences (reviewed in Haegele & Schweigert, 1985) such as 3 to 10°C in southern Norway and 5 to 13°C in northeastern Baltic Sea (Berg *et al.*, 2017; Ojaveer, 1981). In the transition waters between the North Sea and Baltic Sea, salinities at spawning, feeding and overwintering grounds range from 7 to 35 (Leder *et al.*, 2021). Both abiotic factors, temperature and salinity, have inverse relationships with egg size within a population (Chambers, 1997). On the contrary, intraspecific differences in egg size have been commonly reported among females, and in some cases, these inter-individual differences have been related to maternal status, such that females that are larger, with more spawning experience, and/or in better condition produce larger eggs (reviewed in Chambers & Leggett, 1996; Green, 2008; Kamler, 2005). Egg size not only reflects seasonal and female characteristics in fish but can also be an indicator of offspring performance with impacts on the probability of survival at later stages (Chambers, 1997; Chambers & Leggett, 1996; Kamler, 2005). For example, larger eggs hatch into larger larvae which could survive longer without food and are less susceptible to predation (Bailey & Houde, 1989). Many laboratory studies have examined differences in the traits of *C. harengus* eggs between different seasons, *i.e.*, winter–spring and summer–autumn, among different *C. harengus* populations (Blaxter & Hempel, 1963; Bradford & Stephenson, 1992; Hempel & Blaxter, 1967) and among females (size, age or condition) within populations (Bradford & Stephenson, 1992; Hempel & Blaxter, 1967; Óskarsson *et al.*, 2019; Zijlstra, 1973). Few studies, however, have considered both seasonal (early, middle and late phases) and maternal effects on eggs within a spawning season (*e.g.*, Laine & Rajasilta, 1998; Temple *et al.*, 2000).

The western Baltic spring-spawning (WBSS) *C. harengus* is a well-studied stock with long time series data available (Oeberst *et al.*, 2009). In contrast to other stocks in the central and eastern Baltic Sea that remained in waters of reduced salinity, WBSS *C. harengus* migrate to the North Sea and Skagerrak for feeding (Hay *et al.*, 2001). Their dominant spawning and nursery ground, Greifswald Bay, is a shallow, well-oxygenated, brackish lagoon (Figure 1; Munkes, 2005) where *in situ* water temperature during spring increases from approximately 4 to 9°C (Table 1), whereas salinity remains stable at 7 (Munkes, 2005). The recruitment strength and the size of the WBSS *C. harengus* stock have continuously declined since the early 2000s with the lowest recorded value occurring in 2019 (ICES, 2021). Polte *et al.* (2014) observed that during this period, the survival of offspring produced by early-season spawners has been low. Anecdotal reports exist that larger or older females tend to form the earliest-spawning waves in this stock, but the effect of female traits on spawning time or egg characteristics has not been quantified. Moreover, although the low survival of the earliest life stages has been linked to warming water temperatures (Moyano *et al.*, 2020; Polte *et al.*, 2021), the processes causing losses in the productivity of this stock are unclear, and both bottom-up and top-down processes are being examined (Moyano *et al.*, 2022).

The present study examined the importance and relative contribution of seasonal and maternal effects on the size and performance (survival) of eggs of WBSS *C. harengus*. The authors sampled adult *C. harengus* in Greifswald Bay throughout the spawning season and reared the embryos of six to eight females from early, middle and late phases in the spawning season at 7°C (a historical average temperature experienced during the mid-spawning season) and 13°C [above which egg survival declines during laboratory incubation (Peck, Kanstinger, *et al.*, 2012)] to understand the causes of low survival in wild offspring from early in the season. The authors examined if female traits (total length, total wet mass, Fulton's condition factor and/or age) were related to spawning time or *in situ* water temperature and if seasonal, maternal effects, egg size and/or incubation temperature affected the success of embryonic development. Thus, this study tested whether "bigger is better" and whether warm temperatures experienced by eggs could be a reason for the decline in the productivity of the WBSS herring stock observed in the wild.

2 | MATERIALS AND METHODS

2.1 | Ethical statement

The handling and care of experimental animals in the present study complied with the German Animal Welfare Act and the Animal Welfare Regulation Governing Experimental Animals.

2.2 | Field sampling and strip-spawning

The authors sampled adult *C. harengus* throughout the spawning season at Greifswald Bay (54.25° N, 13.23° E; Figure 1) in 2017, 2019 and 2020 during the Rügen Herring Larvae Survey (Oeberst *et al.*, 2009). Sampling did not take place in 2018 due to a sudden decrease in temperature in mid-spring and the formation of solid ice cover in Greifswald Bay. Adult *C. harengus* were caught using set gillnets with mesh-sizes 25, 27 and 29 mm. Sampling started between late February and late March and lasted until the end of the spawning

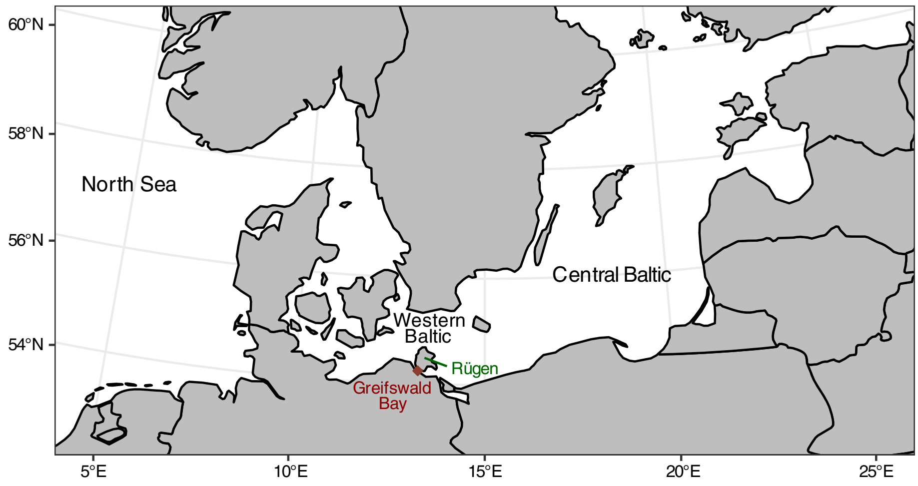

FIGURE 1 Map of the Baltic and eastern North Sea showing the study area. The red dot represents the sampling site (54.25° N, 13.23° E) in Greifswald Bay in the western Baltic Sea where adult herring were captured

TABLE 1 *In situ* water parameters in Greifswald Bay in the western Baltic Sea and traits of spawning females at early, middle and late phases of the season

Spawning time	Period (DOY)	*In situ* water		Female					
		T (°C)	Sal	N	n	L_T (cm)	M_W (g)	K	Age (years)
Early	53–78	4.3 (±0.1)	8.0 (±0.2)	2	79	29.0 (±0.5)	187 (±2)	0.76 (±0.03)	6.8 (±0.2)[a]
Middle	79–104	6.5 (±0.8)	8.2 (±0.2)	4	209	27.7 (±0.4)	168 (±7)	0.79 (±0.01)	5.5[b]
Late	105–130	8.7 (±0.6)	7.8 (±0.3)	3	100	26.6 (±0.4)	146 (±4)	0.78 (±0.01)	ND

Note: The difference between the earliest and latest sampling dates (in day of the year, DOY) across all years is defined as the potential duration of the spawning season and is then evenly separated into three periods. *In situ* water temperatures (T) and salinities (Sal) were calculated with pooled mean values of the years from 2015 to 2019 from ICES Ocean hydrochemistry data set (2022). Female data from 2017, 2019 and 2020 were averaged per sampling date (N) before calculation, and the number of total females sampled (n) per spawning time is provided. Values with brackets are grand mean (±S.E.).

Abbreviations: K, Fulton's condition factor; L_T, total length; M_W, total wet mass; ND, not determined.

[a] $n = 16$.

[b] $N = 1$; $n = 8$; S.E. not determined because of single sampling date.

season which was 10 May in 2017 and 17 April in 2019. In 2020, sampling after the early season was not conducted due to COVID-19 pandemic restrictions, and therefore the end point of the spawning season in that year was not determined. The sampling dates were during days of the year (DOY) 81 and 130 ($n = 5$) in 2017, 53 and 107 ($n = 3$) in 2019 and DOY 65 ($n = 1$) in 2020. Across the 3 years, 388 females were sampled. At the sampling site, a conductivity-temperature-depth (CTD) instrument was deployed. *In situ* water temperature and salinity were calculated as the average of those measured just below the water surface and at the bottom (range of 6.1–7.1 m) of the sampling site. The difference between surface and bottom temperatures and salinities was <0.1°C and <0.05, respectively. The total length (L_T ± 0.1 cm) and total wet mass (M_W ± 1 g) of each specimen were measured. Fulton's condition factor (K) was calculated with the formula: $M_W \times L_T^{-3}$.

The early, middle and late phases of the spawning season were defined by taking the difference between the earliest and latest sampling dates (in DOY) across all years and then evenly separating the duration into three periods (Table 1). Within the total catch during the middle (n of females $= 39$) and late ($n = 6$) seasons in 2019 and early ($n = 70$) season in 2020, the authors selected 6 to 8 females representing the range in sizes captured and 5 to 26 males, all at spawning stage (maturity scale 6; Bowers, 1961), for the laboratory trials (Table 2). For the trial conducted early in the season, the strip-spawned fish were selected from the first half of the fish freed from the net. The sizes of randomly selected females were towards the upper part of the range of fish in the total catch which was unintended. The females used were still representative of the size of early spawners captured at that time (Table 1). The age (years) of each of these randomly selected females was estimated from sagittal otoliths readings following the methods of McCurdy *et al.* (2005), by which the sagittae were dissected from fresh specimens, soaked in distilled water and then stored dried, and the whole otoliths without polishing were examined under a binocular microscope for ring counting.

For the on-site fertilization and the later egg incubation in the laboratory, the authors used offshore North Sea sea water (salinity 33) that was sand-filtered, UV-sterilized and diluted with tap water to salinity 7. A salinity of 7 represents the average salinity of the local waters (Munkes, 2005). The years from 2015 to 2019 showed a higher salinity of 8 probably due to less formation of ice at the spawning ground in the early months of the years. Eggs from each female were strip-spawned onto eight glass plates submerged in sea water at

TABLE 2 Details of the three trials examining seasonal and maternal effects on embryos of spring-spawning *Clupea harengus* from Greifswald Bay in the western Baltic Sea

Spawning time	DOY	*In situ* water		Female						Male			Date of sampling
		T (°C)	Sal	*n*	L_T (cm)	L_T (cm)	M_W (g)	*K*	Age (years)	*n*	L_T (cm)	M_W (g)	
					Mean (±S.E.)	Range	Range	Range	Range		Mean (±S.E.)	Range	
Early	65	4.6	7.9	8	29.3 (±0.3)	28.7–31.3	178–248	0.75–0.85	6–9	26	28.5 (±0.2)	26.0–30.0	05 Mar 2020
Middle	81	6.4	9.3	8	28.7 (±0.3)	27.7–29.9	171–202	0.75–0.83	4–7	10	28.0 (±0.3)	26.0–29.5	22 Mar 2019
Late	107	7.6	8.1	6	27.2 (±0.4)	26.0–28.5	132–181	0.67–0.80	ND	5	27.5 (±0.4)	26.5–29.0	17 Apr 2019

Abbreviations: *K*, Fulton's condition factor; L_T, total length; M_W, total wet mass; *n*, number of individuals; ND, not determined; Sal, salinity; T, temperature.

10°C, with 63–379 and a mean (±standard deviation, S.D.) of 224 (±60) eggs per plate. Eggs were spread gently with the caudal fins of the females to ensure that only a single layer of eggs adhered to each plate. The milt from a group of males was mixed and then activated in water at the same temperature and salinity to fertilize the eggs. After 30 min of incubation, the egg plates were rinsed with equivalent sea water and placed into insulated and aerated transport containers to ensure stable temperature (9.6–10.4°C) and oxygen conditions, respectively, during the 3 h transport to the Elbe Aquarium research facility at the University of Hamburg. It was logistically impractical to fertilize and transport the eggs from the ship to the laboratory at the two incubation temperatures (7 and 13°C). The 10°C temperature was chosen because this was the mean temperature of the two incubation temperatures, yet a 3°C increase may affect herring eggs differently than a 3°C decrease. The small amount of time needed for the adult measurements and to strip-spawn and fertilize the eggs (<1 h) has been demonstrated to not influence fertilization success (Alderdice & Velsen, 1978).

2.3 | Egg incubation

Upon arrival at the laboratory, the eight egg plates from each female were randomly and evenly distributed to either cold (7°C, $n = 4$) or warm (13°C, $n = 4$) 250 ml glass incubation chambers which were placed in water-baths (Figure 2). Each chamber was gently aerated and constantly supplied with sea water (*c*. 40 ml min^{-1}) from head tanks connected to a 500-l recirculating aquaculture system (RAS) in a controlled environment room. The 7°C treatment was ambient room temperature, whereas the 13°C treatment was created using heaters (600 W titanium heaters with TRD thermostatic controllers, Schego, Offenbach am Main, Germany) in the head tanks and water-baths. All water was within a RAS. Water was filtered through a filter floss pad, a biofilter and activated carbon, sterilized by UV lights and cooled to 7°C (Titan 1500, 790 W, Aqua Medic, Bissendorf, Germany). The water salinity was maintained at 6.6–7.4 (Cond 3110, WTW GmbH, Weilheim in Oberbayern, Germany) by adding fresh water to the RAS. A light regime of 14:10 h light:dark, the average condition during spring, was used in all trials.

One day after the eye-darkening stage, each egg plate was transferred from its 250- to a 1000-ml chamber, and water inflow was switched off at night. This was done to prevent the outflow of hatched larvae as clupeid larvae primarily hatch at night (Alderdice & Velsen, 1971). Water temperatures were continuously recorded using temperature probes (TLog64-USB, ±0.5°C, Hygrosens Instruments GmbH, Löffingen, Germany) in one random chamber per water-bath. The temperature and salinity in each chamber were measured daily using a hand-held probe (Cond 3110, WTW GmbH, Weilheim in Oberbayern, Germany) to verify similar conditions among chambers and water-baths. Through all trials, the mean (±S.D.) temperatures for the warm and cold treatments were 12.6 (±0.3)°C and 7.2 (±0.2)°C, respectively. The dissolved oxygen was measured each day (Oxi 3210, WTW GmbH, Weilheim in Oberbayern, Germany) and was >90% air saturation. Total ammonium/ammonia, nitrite and nitrate concentrations in the RAS were measured once a week and 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).

2.4 | Egg characteristics

Egg plates were examined daily under a stereomicroscope (Leica M165 C, Leica Microsystems, Wetzlar, Germany; at 5.84× magnification). Eggs without cell division were considered unfertilized. Fertilized eggs that stopped developing and turned dark at a later embryonic stage were considered dead. Images of the whole egg plate were taken using a digital camera (Leica MC170 HD, Leica Microsystems, Wetzlar, Germany) connected to the stereomicroscope 1 day post-fertilization (dpf) to measure egg size and to assess fertilization success (%). Because almost all dead eggs appeared during the mid-blastula stage, digital images of all eggs were taken again at this stage (2–3 dpf) and at the eye-darkening stage (16 and 6 dpf at 7 and 13°C, respectively) to confirm the mortality estimates. Areas of fertilized eggs at 1 dpf, as a proxy for egg size, were measured using ImageJ software (version 1.52, Wayne Rasband, National Institute of Mental Health, Bethesda, Maryland, USA). The contrast of digital images was increased, and eggs that touched one another were separated semi-automatically using the ImageJ "watershed" tool. All measurements were made using the ImageJ "particle analysis" tool with 49–164 eggs per plate measured (representing *c*. 50% of the eggs per plate; frequency histograms of egg area measured per plate are shown in

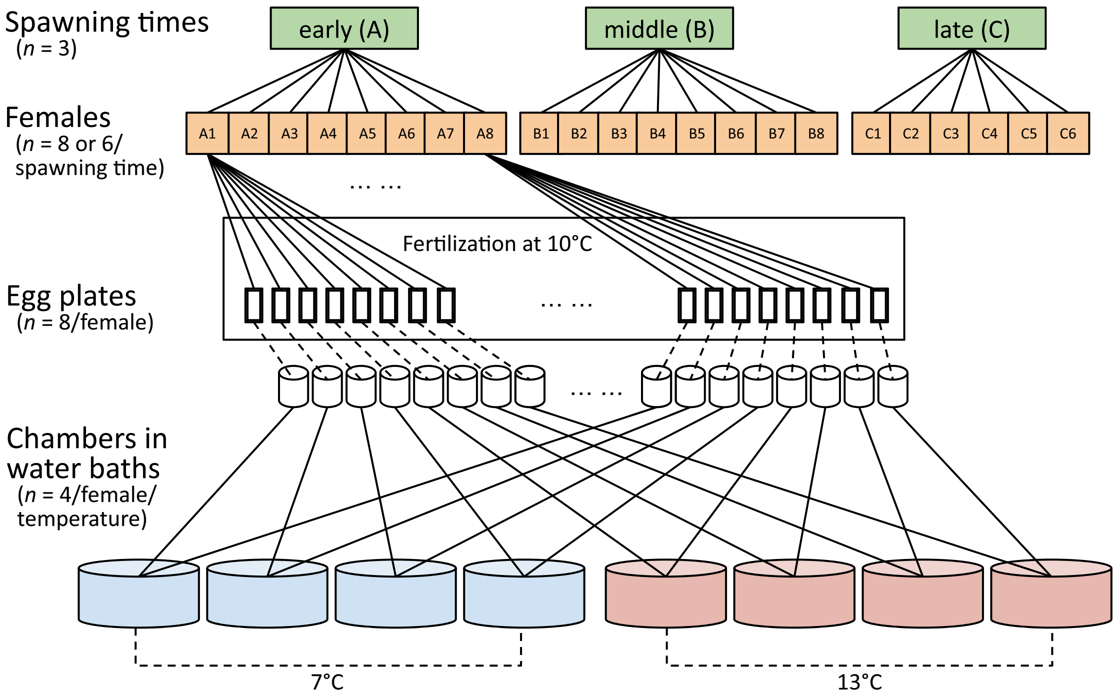

FIGURE 2 Scheme of the experimental design. Replicates of two females from the early season were drawn as examples (*e.g.*, Females A1 and A8). All females from all spawning times followed the same scheme

Supporting Information Figures S1–S3). Eggs on all digital images were counted and specified as fertilized, unfertilized or dead using the ImageJ "multi-point" tool. Fertilization success was calculated as the percentage of fertilized eggs in total eggs, and mortality was calculated the percentage of dead eggs in fertilized eggs. After completion of the eye-darkening stage, eggs were checked for hatching at 2, 6, and 10 h (three intervals of 2–4–4 h) after darkness each night until peak hatch (50% viable hatch) occurred. Hatching during daylight hours (assessed in 2019) was minimal (<2.5% of eggs per chamber in total). Time to peak hatch was expressed in degree-days (°d; temperature in °C × time in days) post-fertilization.

2.5 | Data analyses

All analyses were performed in R version 4.0.3 (R Core Team, 2020). Linear mixed-effect models (LMMs) were used to account for the variance within replicates. For the female data from the field work in the years 2017, 2019 and 2020, the authors tested whether female L_T and K changed throughout the season with spawning time (in DOY) or *in situ* water temperature, which were included separately as the fixed effect because of collinearity (variation inflation factor >3). Sampling year and date within year were included as random intercepts. For data from the three laboratory trials, they assessed whether egg area, fertilization success and mortality were influenced by spawning time, female traits, egg size (on fertilization success and mortality) and/or incubation temperature (on mortality). Fertilization success and mortality percentages were arcsine square root-transformed to meet the normality assumption assessed *via* QQ plots. In all analyses, we included spawning time, an ordinal variable with three levels (early < middle < late), as a fixed (seasonal) effect. Because the magnitudes of seasonal effects might differ early, middle and late in the season, the authors estimated both linear and quadratic trends of spawning time effect. For fixed (maternal) effects, they included female L_T, K and age as continuous variables in all models, whereas female M_W was not added because it was collinear with L_T (variation inflation factor >3). Age data for females from late in the season were missing, and two sets of analyses (including and excluding age) were performed. The variance among individual females and among egg plates within females (in egg area model) was addressed as random intercepts. In addition, egg area was included as another fixed effect in models on fertilization success data, whereas egg area and incubation temperatures (categorical variable: cold and warm) were added as fixed effects in models on mortality data. The best model structures based on conditional AICc were determined using the "MuMIn::dredge" function, which fitted models in all possible combinations of all fixed effects (Barton, 2020). Selected models were then fitted with the restricted maximum likelihood (REML) approach using the "lme4::lmer" function (Bates *et al.*, 2015). Data of egg development time were averaged at each spawning time and incubation temperature and analysed with incubation temperature as the only (fixed) effect using the "lm" function. All models were validated by plotting residuals *vs.* fitted values.

The significance level was set at $\alpha = 0.05$. P-values of each fixed variable were obtained from t-statistics with approximate degrees of freedom calculated by Satterthwaite's method with "LmerTest" (Kuznetsova *et al.*, 2017). The variance explained by random effects was represented by intraclass correlation coefficients (ICC; Nakagawa & Schielzeth, 2010). Three types of R^2 were calculated using "MuMIn" and "r2glmm" to assess the amounts of variation explained by the model (Barton, 2020; Jaeger, 2017): partial R^2 for each significant fixed effect, marginal R^2 for all fixed effects and conditional R^2 for the whole model including random effects (Nakagawa & Schielzeth, 2013).

3 | RESULTS

The mean (±standard error, S.E.) L_T of females captured across sampling dates in 2017, 2019 and early in 2020 were 27.0 (±0.4), 28.4 (±0.6) and 28.6 (S.E. not determined because of single sampling date), whereas K was 0.80 (±0.00), 0.75 (±0.02) and 0.79, respectively. Pooling all data from all years, L_T of females decreased linearly (Table 1) with the progression of spawning time ($t = -8.899$, $P < 0.001$, partial $R^2 = 0.311$, Table 3; Figure 3a) and with increasing *in situ* water temperature ($t = -7.495$, $P < 0.001$, partial $R^2 = 0.190$, Table 3; Figure 3b). In the spawning time model, little variance was explained by the random effects (ICC of year = 0.019, ICC of date: year = 0.009), whereas in the *in situ* water temperature model, additional variance was explained by the random effect of year (ICC of year = 0.132, ICC of date: year = 0.006). Comparing the years 2017 and 2019, females in the former were estimated to be 0.2 cm smaller in L_T on the same DOY (Figure 3a) and 1.0 cm smaller at the same *in situ* water temperature (Figure 3b). No relationship was found between K and spawning time ($P = 0.823$, Table 3) or *in situ* water temperature ($P = 0.498$, Table 3). Whereas all females sampled from 2017 to 2020 were caught on DOY between 53 and 130, at water temperatures between 3.2 and 9.2°C and ranged from 23.0 to 31.5 cm in L_T, the females selected for the laboratory study were caught on DOY between 65 and 107, at water temperatures between 4.6 and 7.6°C and ranged from 26.0 to 31.3 cm in L_T (Table 2; Figure 3).

3.1 | Egg size

In the laboratory trials, the mean (±S.E.) egg area across spawning times ($n = 3$) was 1.43 (±0.06) mm^2, equivalent to an egg diameter of 1.35 (±0.03) mm. Egg area decreased linearly throughout the season (linear trend of spawning time effect in the best model: $t = -4.570$, $P < 0.001$, partial $R^2 = 0.392$; Table 4) and eggs from late in the spawning season were estimated to be 12.5% smaller than those from early in the season (Figure 4). In addition, similar variance in egg area was explained by the random effects, by which variance among individual females (ICC = 0.592) was 18.5 times the variance among replicated plates within females (ICC = 0.032). Nonetheless, neither L_T nor K was related to the female effect on egg area ($P > 0.05$ or not selected in models; Table 4). Similarly, age had no effect on egg area (not selected in models; Supporting Information Table S2). Although the mean L_T of females was progressively larger earlier compared to later in the season, ranges of L_T overlapped among different spawning times (Figure 3a) and females

TABLE 3 Summary of the linear mixed-effect models (LMM) to assess the influence of time (in day of the year, DOY) or *in situ* water temperature (°C) on total length (L_T) and Fulton's condition factor (K) of spawning females in Greifswald Bay in the western Baltic Sea

	Fixed effects			Random effects				Model selection		
	Intercept	Time	Temperature	(1|year)	(1|year:date)	Residual	Marginal/conditional R^2	*df*	AICc	Weight
Female L_T	31.6 (±0.4) ***	−0.0437 (±0.0049) ***	-	(±0.2)	(±0.1)	(±1.3)	0.311/0.330	5	1318.69	1.00
	27.8 (±0.6) ***	0	-	(±0.8)	(±0.9)	(±1.3)	0/0.441	4	1342.44	0.00
	31.0 (±0.5) ***	-	−0.53 (±0.07) ***	(±0.5)	(±0.1)	(±1.3)	0.190/0.302	5	1325.06	1.00
	27.8 (±0.6) ***	-	0	(±0.8)	(±0.9)	(±1.3)	0/0.441	4	1342.44	0.00
Female K	0.78 (±0.02) ***	<0.01 (±0.00)	-	(±0.01)	(±0.01)	(±0.05)	<0.001/0.069	5	−1134.11	0.27
	0.78 (±0.01) ***	0	-	(±0.01)	(±0.00)	(±0.05)	0/0.055	4	−1136.11	0.73
	0.77 (±0.02) ***	-	<0.01 (±0.00)	(±0.01)	(±0.01)	(±0.05)	0.002/0.068	5	−1134.49	0.31
	0.78 (±0.01) ***	-	0	(±0.01)	(±0.00)	(±0.05)	0/0.055	4	−1136.11	0.69

Note: Time and *in situ* water temperature were included in separate models because of collinearity (variation inflation factor >3). Comparisons of each model to the intercept-only (no fixed effect) model are provided with conditional AICc. Models for comparisons were fitted by maximum likelihood, whereas models for estimates were refitted by restricted maximum likelihood (REML). Year: date denotes nested random effect of dates within years. Values are estimated coefficients (±S.E.) for fixed effects and variance (in ±S.D.) for random intercepts. A dash indicates the effect was not included in the full model, whereas an estimate of zero denotes the effect was assumed to be zero.

Significant codes: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

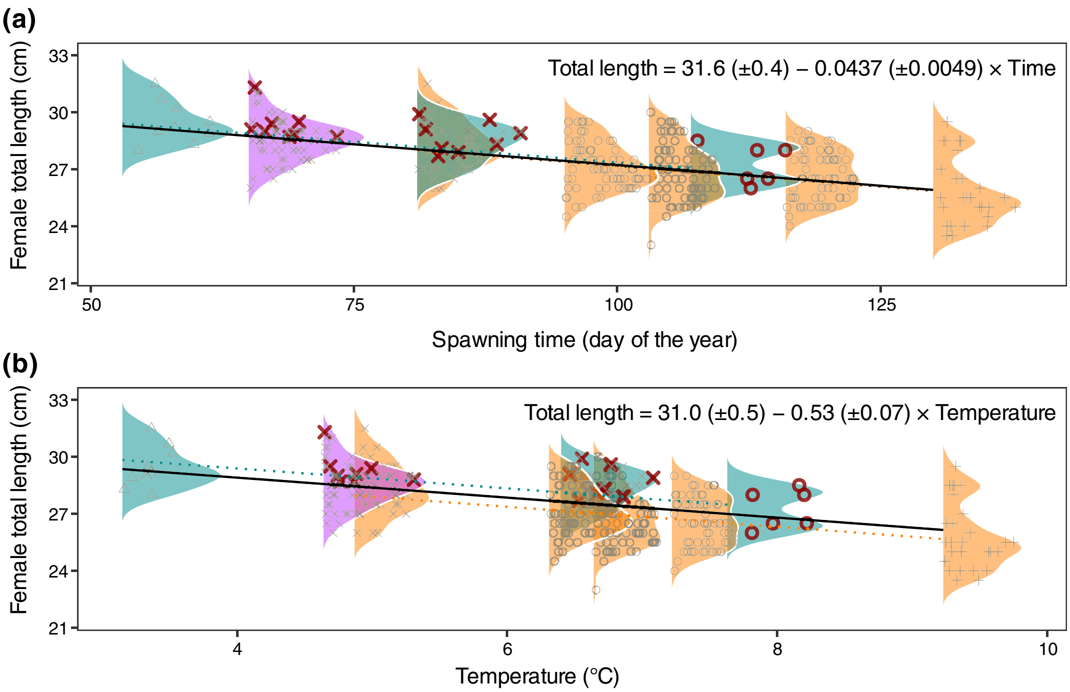

FIGURE 3 Total length (cm) of *Clupea harengus* females *vs*. spawning time (day of the year, panel a) and *in situ* water temperature (°C, panel b) in Greifswald Bay, Germany, in 2017 🟧, 2018 🟦 and 2020 🟪. Symbols represent individual females sampled in February ▨, March ▨, April ▨ or May ▨ whereas red symbols are females that were strip-spawned for the laboratory experiments. Black lines show the regression across all data, and dotted lines show the different estimated intercepts for 2017 and 2019 (not applicable for 2020 because of single sampling date). For both regressions, *n* of years = 3, *n* of sampling dates = 9 and *n* of females = 388

from earlier in the season produced larger eggs regardless of L_T compared to those from subsequent spawning times (with a few exceptions; Figure 5).

3.2 | Fertilization success and mortality

The mean (±S.E.) percent (%) egg fertilization of all females (n = 22) across spawning times was 92.8(±0.8)%. Out of all the females, the eggs of one female from early in the season had 13.9% lower fertilization success than the mean (Figure 6). Egg mortality occurred predominantly during the mid-blastula stage and was negligible at later egg stages. The mean percent egg mortality during the blastula stage of all females (n = 22) across spawning times and rearing temperatures (7 and 13°C) was 2.4(±0.8)%. Eggs of one female from late in the season had a 15.0% higher total mortality than the mean (Figure 7). The overall percent egg viability, the amount of fertilized eggs that survived until hatch, across spawning times was >85% at both temperatures. The overall percent viability for eggs from the aforementioned early- and late-spawning females was 75.1% and 77.0%, respectively. The differences in egg fertilization success and mortality were explained only by random effects of females (the best models: ICC = 0.691 and 0.718, respectively) and were not related to female L_T, K or egg area (P > 0.05 or not selected in models; Table 4) nor to age (not selected in models; Supporting Information Table S2).

3.3 | Development time

The mean (±S.E.) time to peak hatch from early, middle and late in the season at 7°C was 132(±1), 127(±1), 117(±0)°d, respectively, and at 13°C, values were 114(±1), 104(±0), 99(±0)°d at 13°C, respectively. Eggs at 13°C were estimated to hatch 18.7°d earlier than those at 7°C (df = 4, t = −3.170, P = 0.034, marginal R^2 = 0.668).

4 | DISCUSSION

In marine fish with protracted spawning seasons, it is important to identify and attempt to disentangle the processes that impact embryo quality, particularly because of the high rates of mortality experienced by early life stages (Houde, 1987). The size of the WBSS *C. harengus* population has continuously declined since the early 2000s, and the causes have been linked to low survival of the earliest life stages (Polte *et al*., 2014). The present study helps to disentangle the effects of spawning time and among-female differences on egg characteristics in *C. harengus* in the western Baltic Sea. Although it appeared that larger females produced larger eggs, the results indicate that similar-sized females had larger eggs earlier in the season at colder *in situ* water temperatures than females that spawned later. In the following, the authors discuss the roles of female traits, *in situ* water temperature and salinity in the seasonal dynamics of egg quality and whether

TABLE 4 Summary of the three best linear mixed-effect models (LMM) to examine whether *Clupea harengus* egg area, fertilization success and mortality at the blastula stage were influenced by spawning time and/or female traits (and/or egg area and/or incubation temperature if included)

	Fixed effects							Random effects			Marginal/	Model comparison		
	Intercept	TIME.L	TIME.Q	L_T	*K*	AREA	T_I	(1|ID)	(1|ID: plate)	Residual	conditional R^2	*df*	AICc	Weight
Egg area	1.429 (±0.017) ***	−0.135 (±0.030) ***	0.018 (±0.028)	0	0	-	-	(±0.077)	(±0.018)	(±0.061)	0.399/0.773	6	−43,519.01	0.324
	0.835 (±0.563)	−0.104 (±0.041) *	0.025 (±0.029)	0.021 (±0.020)	0	-	-	(±0.077)	(±0.018)	(±0.061)	0.409/0.777	7	−43,518.33	0.230
	1.086 (±0.383) **	−0.122 (±0.033) ***	0.025 (±0.029)	0	0.442 (±0.492)	-	-	(±0.077)	(±0.018)	(±0.061)	0.408/0.778	7	−43,517.98	0.193
Fertilization success	1.307 (±0.013) ***	0	0	0	0	0	-	(±0.059)	-	(±0.039)	0/0.691	3	−569.24	0.162
	1.307 (±0.013) ***	0.018 (±0.022)	−0.034 (±0.021)	0	0	0	-	(±0.057)	-	(±0.039)	0.099/0.709	5	−568.62	0.119
	1.482 (±0.148) ***	0	0	0	0	−0.122 (±0.102)	-	(±0.064)	-	(±0.039)	0.030/0.735	4	−568.24	0.098
Mortality at blastula	0.128 (±0.017) ***	0	0	0	0	0	0	(±0.078)	-	(±0.049)	0/0.718	3	−489.43	0.132
	0.701 (±0.407)	0	0	−0.020 (±0.014)	0	0	0	(±0.076)	-	(±0.049)	0.063/0.726	4	−489.41	0.131
	0.716 (±0.415)	0	0	−0.028 (±0.016)	0	0.147 (±0.144)	0	(±0.078)	-	(±0.049)	0.078/0.739	5	−488.31	0.076

Note: Models were fitted by maximum likelihood to compare conditional AICc, and then the best models were refitted by restricted maximum likelihood (REML) for estimates. Values are estimated coefficients (±S.E.) for fixed effects and variance (in ±S.D.) for random intercepts. A dash indicates the effect was not included in the full model, whereas an estimate of zero denotes the effect was not selected (assumed to be zero).

Abbreviations: AREA, mean egg area; ID, individual female, ID: plate, denotes nested random effect of plates within individual females; *K*, Fulton's condition factor; L_T, total length; T_I, incubation temperature; TIME.L, linear trend of spawning time; TIME.Q, quadratic trend of spawning time.

Significant codes: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

these factors may be responsible for the relatively low survival of early cohorts observed in this population (Polte *et al.*, 2014).

During sampling early, middle and late in the spawning season, female L_T and age decreased and *K* remained similar with the progression of the spawning season. Comparison with earlier observations from the same spawning ground suggests decadal changes in the average L_T of spawning females. The seasonal decrease in mean size ranged from 1.5 cm (29.4 to 27.9), 4.5 cm (27.4 to 22.9), 6.6 cm (28.8 to 22.2) and 2.9 cm (24.8 to 21.9 cm) in the 2000s, 1990s, 1970s and 1960s, respectively (Anwand, 1962; Biester *et al.*, 1978; Jørgensen *et al.*, 2005; Rajasilta *et al.*, 2006). These decadal differences in size are not simply due to the presence of larger females in recent years but could be due, in part, to differences in the sampling methods used across the decades. Trap nets and gillnets were used in the studies before 2000, and spawning and non-spawning fish were not separated (*i.e.*, the total lengths of *C. harengus* at all maturity scales were included). Therefore, it is difficult to determine if the size (and/or age) of females has shifted in the most recent decade (when recruitment failure has been reported) compared to earlier decades when the stock was more productive.

When comparing females among sampling years, females in 2019 were caught earlier (DOY), larger in size (L_T) and appeared to be in lower conditions (*K*) than those in 2017. Indeed, recruitment was estimated to be lower in 2019 than in previous years, part of a negative trend with time that has been observed for about two decades (ICES, 2021). In the three sampling years, *in situ* water temperatures recorded early in the seasons were similar (differences <0.4°C) to the documented range of the onset spawning temperature (3.5–4.5°C) in WBSS *C. harengus* from Greifswald Bay (Polte *et al.*, 2021). As *C. harengus* rely on temperature cues for migration to the spawning ground (Lambert, 1987), milder and shorter winters in the recent decade have led to a reduced overwintering period and earlier spawning in the Baltic Sea (Arula *et al.*, 2019; Polte *et al.*, 2021). Overwintering is when *C. harengus* rely solely on their energy reserves and when downregulation of oocytes (atresia) takes place (dos Santos Schmidt *et al.*, 2017). A reduced atresia process could explain the somewhat lower mean *K* of the larger and earlier spawners in 2019 relative to those in 2017. Although yearly fluctuation of female *K* had also been observed in Norwegian spring-spawning herring, dos Santos Schmidt *et al.* (2017) demonstrated that a low mean *K* of females does not necessarily relate to poor reproductive output of the same year as conditions of females can affect more than one subsequent spawning seasons. Thus, comparing winter duration and differences in *K* and fecundities of the early spawners among years could shed light on the reproductive status of this population.

Egg area provided a more precise metric of size than diameter and also allowed the comparison of its variance among replicated plates, females and spawning times as areas of single eggs were quantified in the present study. Within individuals, females produced eggs of consistent size but among different females and spawning times, differences in egg size were apparent. The mean egg size recorded in this study agrees with past observation for this population (from 1.4 to 1.3 mm from April to June; Scabell, 1988). The seasonal decrease in

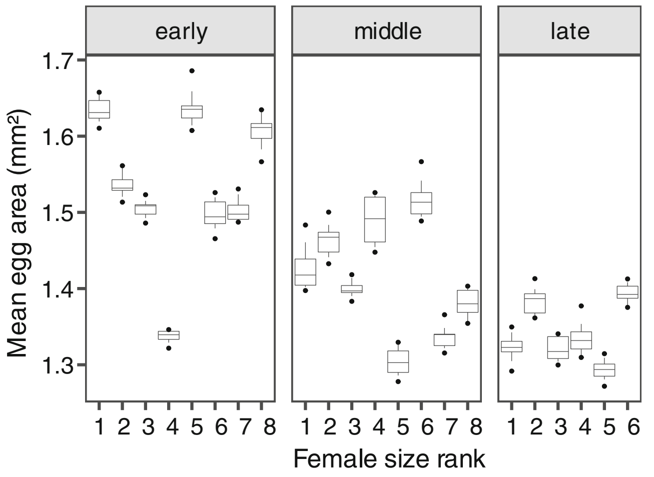

FIGURE 4 Mean egg area (mm^2) *vs.* size rank (1 = largest) of the six to eight female *Clupea harengus* for each of the three phases of the spawning season. Boxes display the 25th and 75th percentiles, and whiskers display the 10th and 90th percentiles. The dots indicate values outside the whisker range. The line displays the mean value (*n* of egg plates = 8 per female, range of eggs measured = 49–164 per egg plate). Total lengths of females are listed in Supporting Information Table S1. Frequency histograms of egg area measured per plate are shown in Supporting Information Figures S1–S3

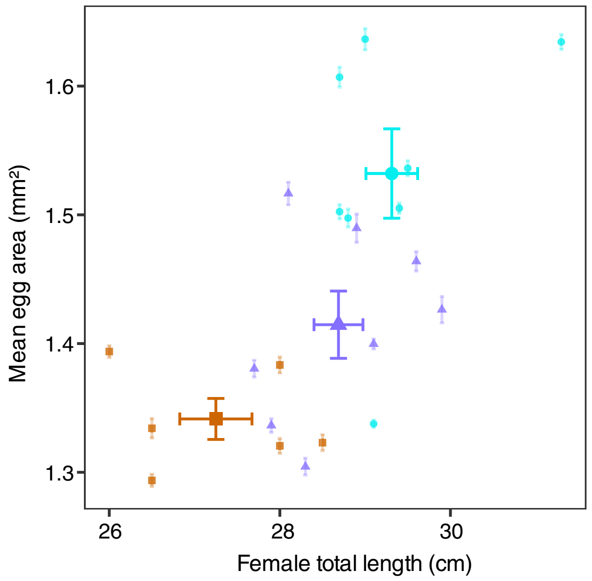

FIGURE 5 Relationship between *Clupea harengus* egg area (mm^2) and female total length (cm) at early ●, middle ▲ and late ■ phases of the spawning season. The large symbols represent the grand mean (±S.E.) for both egg area and female total length (*N* = 6 or 8) at each spawning time. The small symbols are the mean (±S.E.) egg area of each female (*n* of egg plates = 8 per female)

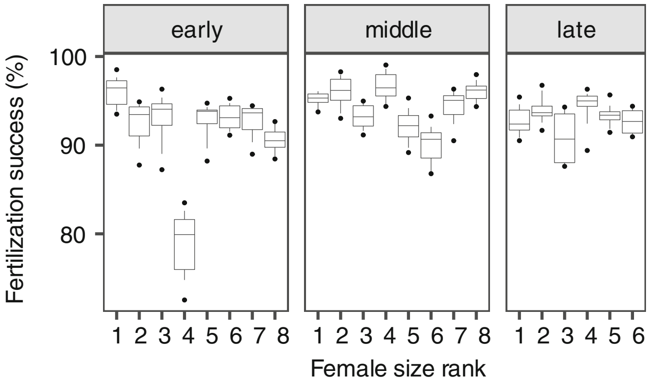

FIGURE 6 Box and whisker plots of fertilization success (%) among *Clupea harengus* females. Females are ordered by size rank (1 = largest) for each of the three phases of the spawning season. Whiskers show the 10th and 90th percentiles, whereas boxes are the 25th to 75th percentiles. The dots indicate values outside the whisker range. The mean value is displayed as a line in each box (*n* = 8 per female). Total lengths of females are listed in Supporting Information Figure S1

egg size has also been documented for many populations of *C. harengus* (Hempel & Blaxter, 1967; Rajasilta *et al.*, 1993) and has been associated with maternal differences such as size, condition and spawning experience throughout the spawning season (reviewed in Chambers & Leggett, 1996; Green, 2008). Nonetheless, this study found no significant relationship between maternal status (L_T, *K* or age) and egg size among the six or eight females sampled at the same spawning time. By separating year and age groups, Zijlstra (1973) reported only one out of the six comparisons between female size, and egg mass exhibited a positive relationship within three North Sea *C. harengus* stocks. Similarly, this positive trend was uncommon in various *C. harengus* spawning sub-groups (populations) compared by Hempel and Blaxter (1967, 12 in 27 comparisons within 16 northeast Atlantic populations) and Bradford and Stephenson (1992, 2 in 12 northwest Atlantic populations). Although much of the variation in egg size in this and other studies could be attributed to a maternal effect (Green, 2008), the results of this study are consistent with the conclusions of Chambers (1997), that egg size is unlikely to be correlated with female size.

Water temperature and salinity influence egg size both during oogenesis and at the point of spawning, after which the eggs harden within hours and the size stabilizes (Chambers, 1997). In the present study, temperature and salinity were maintained at the same condition across all trials throughout the season to eliminate their effects at the point of spawning. During oogenesis, larger and older individuals migrate further to the North Sea for feeding, whereas the smaller individuals remain mostly in the Kattegat and Skagerrak (Payne *et al.*, 2009), suggesting that the larger *C. harengus* earlier in the season experienced higher salinity than those later in the season. Higher salinity resulted in decreasing egg diameters (Dushkina, 1973; Ojaveer, 1981). Yet, the earlier spawners still produced larger eggs in the present study, and the potential salinity effect on egg size during oogenesis appeared to be small. Water temperature, on the contrary, was likely related to the linear trend of spawning time effect on egg size because the recorded *in situ* water temperatures increased linearity with the progression of the season (Tables 1 and 2) and reflected the temperature females experienced at least during the pre-spawning period. Within marine fish species, eggs produced at colder

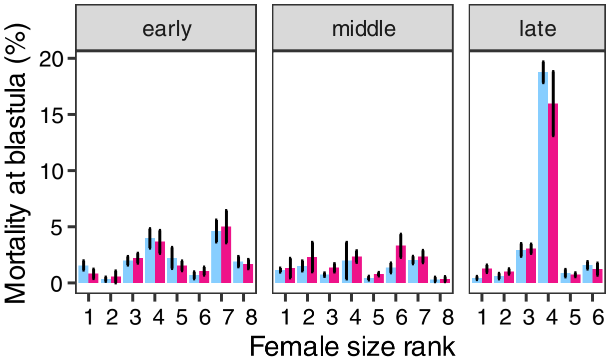

FIGURE 7 Bar plots of mean (±S.E.) percent (%) egg mortality ($n = 4$ per female per temperature treatment) at blastula stage among *Clupea harengus* females in the cold (7°C) 🟦 and warm (13°C) 🟥 treatments. Females are ordered by size rank (1 = largest) for each of the three phases of the spawning season. Total lengths of females are listed in Supporting Information Table S1

temperatures tend to be larger than those produced at warmer temperatures (Atkinson *et al.*, 2001). When six *C. harengus* populations with different spawning times in the eastern Atlantic and western Baltic were compared, mean egg mass decreased from January to June and increased from August to December (Hempel & Blaxter, 1967). This study demonstrated that egg size also changes within a population in a single spawning season. The dominant effect of temperature during oogenesis has, therefore, been overlooked in studies that showed inconsistent trends of maternal size and egg size (*e.g.*, Bradford & Stephenson, 1992; Hempel & Blaxter, 1967). Chambers (1997) suggested that the inverse relationship between egg size and temperature may be due to different magnitudes of temperature effects on growth rate and developmental rate of embryos. As temperature increases, the increase in developmental rate of embryos is faster than the increase in growth rate, resulting in a smaller size of the same developmental stage at a higher temperature. Although Chambers (1997) pointed out that the change in egg size with temperature may only be a physiological response, Marshall *et al.* (2008) suggested that this relationship could also be adaptive because food is usually scarce in colder environments where a larger size helps individuals withstand harsh conditions, as opposed to warmer environments where food is more abundant and a higher number of smaller eggs can maximize survival. Therefore, egg size is still an important trait that is linked to survival at subsequent larval stages.

During the egg stage, controlled laboratory experiments can identify key factors defining intrinsic performance such as fertilization success and developmental mortality. The range of fertilization success in the laboratory trials of this study agrees with that (70%–90%) assessed by Rosenthal *et al.* (1988) for this population. A factorial experiment of *C. harengus* female–male pairs showed that eggs of the same female could be more easily fertilized by the sperm of some males (>75% compared to <55%) and *vice versa*, but no particular female or male resulted in an overall worse fertilization success (Bang *et al.*, 2006), indicating the potential effect of genetics on fertilization success. In this study, because all eggs from all females within one spawning time were fertilized with milt from the same group of males, the lower fertilization success of the eggs (which were also relatively small) from one early spawner could be caused by genetic differences of this and other females. On the contrary, egg mortality observed in the present study occurred predominantly during the mid-blastula stage, similar to several other fish populations in the Baltic Sea (Alter & Peck, 2021; Dahlke *et al.*, 2016; Laine & Rajasilta, 1999). The blastula life stage is the period during which maternal-to-zygotic transition takes place and when embryos start to produce their own mRNA (Hill & Johnston, 1997; Tadros & Lipshitz, 2009). Before this point, the embryos have been relying on mRNA provided by their mother, which explained the significant female effect on mortality. A multi-year study on *C. harengus* from the central Baltic Sea reported a low mean mortality of eggs (1.0% and 7.5%) in two of the years but a high mortality (32.8%) in 1 year when muscle fat of females was relatively low (Laine & Rajasilta, 1999). In that same batch of eggs, fertilization success was high (>90%) indicating that mortality but not fertilization success was influenced by female condition. Although *K* showed no effect on mortality in the present study, lipid content may be a more accurate predictor. Furthermore, extrinsic factors in the wild could have higher impacts on egg survival than intrinsic factors. The highest egg mortality occurring in the laboratory trials conducted here (17.4%) is relatively low compared to the maximum mortality of 100% caused by layering of spawned eggs (Finke *et al.*, 2022). Moreover, 2.4-fold differences in egg mortality among batches were estimated to be due to predation (Kotterba *et al.*, 2017), and 1.6-fold differences in damage to eggs was documented after one storm event (Moll *et al.*, 2018). Those extrinsic factors, however, do not appear responsible for the relatively low survival of progeny early in the season as eggs at the surface layer (later-spawned) also experienced high mortality (Finke *et al.*, 2022), predation is highest late in the season (Kotterba *et al.*, 2014) and the intensity and frequency of storms at the spawning ground are similar throughout the season (Moll *et al.*, 2018).

The time to hatch in *C. harengus* embryos was not related to egg size, but, similar to other marine fishes, development was more rapid as incubation temperature increased (Peck, Huebert, & Llopiz, 2012). In the field, eggs from later in the spring season will experience warmer temperatures and develop faster to hatch, which could be an advantage as sessile eggs are more susceptible to predators (Bailey & Houde, 1989). In this study, viable eggs of all females from the same spawning time and incubated at the same temperature (7 or 13°C) hatched within the same night, irrespective of egg size. Likewise, Blaxter and Hempel (1963) compared the time required for *C. harengus* eggs to hatch among six *C. harengus* populations at temperatures between 5 and 15°C and found no effect of egg size. Compared to the results of other studies on the WBSS *C. harengus* population, the time to hatch observed here was similar to the values reported by Blaxter and Hempel (1963) and Peck, Kanstinger, *et al.* (2012). The time to hatch at 7 and 13°C still differed after normalizing the data by calculating physiological age (in degree-days) as embryos at the colder and warmer temperature hatched at greater and lesser physiological age, respectively. In the present study, the time required for embryos to hatch at both incubation temperatures slightly decreased in embryos from females spawning early, middle and late in the season. Given that egg sizes among spawning times overlapped, it is possible that water temperature experienced during oogenesis rather than egg size can exert a modest influence on the time required for eggs to hatch, but this remains to be tested.

The present study quantified the change in maternal and egg traits occurring among females captured in early, middle and late spawning waves in WBSS *C. harengus*. The fertilization success and viable hatch of eggs were relatively high, and the modest maternal effect on egg performance was unrelated to spawning time, female size, condition or egg size. In WBSS *C. harengus*, extrinsic factors such as predation (Kotterba *et al*., 2014, 2017) and/or storm events (Moll *et al*., 2018) appear to have larger impacts on egg mortality, and the "bigger is better" hypothesis does not apply during the egg stage. The results of the present study suggest that the lower survival of the early cohort observed in the wild is unlikely due to intrinsic differences in egg survival but could be due to differences in egg quality: fatty acids and other biochemical attributes were not measured in this study. After hatch, however, the larvae will not only face the same threats (from predation and storm events) as eggs but will also have the additional challenge of finding suitable food before their yolk reserves are exhausted (Houde, 1987). Differences in egg sizes among females in the present study suggest that newly hatched larvae can be provided with different amounts and/or quality of yolk reserves which, in addition to extrinsic effects, may cause differences in survival at the first-feeding stage. Further study of first-feeding larvae is needed to better understand the intra-annual differences in survival in WBSS *C. harengus*.

AUTHOR CONTRIBUTIONS

A.T.H., K.A. and M.A.P. designed the study. P.P. and M.A.P. provided materials and equipment. A.T.H., K.A. and P.P. conducted field sampling. A.T.H. and K.A performed the experiments and processed the samples. A.T.H. analysed the data and drafted the manuscript. All authors reviewed and revised the manuscript.

ACKNOWLEDGEMENTS

We would like to thank Anne Georgi, Dorothee Moll, Annegret Finke and the crew of "FSS Clupea" for their assistance with fieldwork. Special thanks to Mario Koth for otolith age reading and Martina Wichmann for managing materials for the laboratory experiments. We also thank Svenja Damm, Konstantin Kliemke, Linnea Birth, David Janßen and Emma Lefebvre for their assistance with experimental set-up and image processing. A.T.H. was supported by a 2-year Ministry of Education (MOE) Taiwan Scholarship and afterwards by a scholarship programme of the Konrad-Adenauer-Stiftung for international graduates. Open Access funding enabled and organized by Projekt DEAL.

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How to cite this article: Huang, A. T., Alter, K., Polte, P., & Peck, M. A. (2022). Disentangling seasonal from maternal effects on egg characteristics in western Baltic spring-spawning herring *Clupea harengus*. *Journal of Fish Biology*, *101*(6), 1428–1440. https://doi.org/10.1111/jfb.15210