Vol. 741: 203–216, 2024
https://doi.org/10.3354/meps14521

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published July 30[§]

Contribution to the Theme Section 'Small pelagic fish: new research frontiers'

Growth of spring- and autumn-spawned larvae of Atlantic herring *Clupea harengus*: a long-term experiment mimicking seasonal light conditions

Florian Berg[1,2,*], Gaute Seljestad[2], Arild Folkvord[1,2]

[1]Institute of Marine Research (IMR), PO Box 1870 Nordnes, 5018 Bergen, Norway
[2]University of Bergen, Department of Biological Sciences, PO Box 7803, 5020 Bergen, Norway

ABSTRACT: Atlantic herring *Clupea harengus* populations differ in their spawning time, and spring- and autumn-spawning populations are genetically distinct. Offspring of these populations encounter seasonal variations in productivity. We conducted a fertilization experiment using spring-spawning Atlantic herring. Offspring were reared for 3 yr with seasonal varying light cycles starting either in spring or autumn, using 2 fixed temperature levels and food provided in excess. Such long-term experiments from hatching to maturation in small pelagic fish are very rare. We hypothesized that longer daylengths early in life would provide an overall growth advantage resulting in larger size after 1 yr (same amount of light) compared to those experiencing prolonged daylight later in life due to higher size-dependent growth rates at smaller sizes. Larvae with initial spring conditions initially grew faster. However, contrary to our expectations, offspring with initial autumn conditions had caught up to similar size after 1 yr. Herring at higher temperatures grew faster, even when correcting for the amount of degree-days. After the first year, individuals hatched in spring showed higher growth at the higher temperature while herring hatched under autumn light conditions consistently had higher growth rates at lower temperatures. The somatic condition of herring followed the daylength, with best conditions during summer and poorest during winter. This was the first long-term experiment conducted on herring with varying light conditions from hatching to maturation. Our novel results indicate that herring display considerable growth plasticity, reflecting the wide range of environmental conditions and life histories sustaining herring populations.

KEY WORDS: Hatching time · Long-term rearing · Temperature · Growth plasticity · *Clupea harengus* · Light manipulation

1. INTRODUCTION

Successful spawning and the following recruitment of offspring is essential for the survival and sustainability of any given population (Iles & Sinclair 1982). Fine-tuning the spawning time to match the most favourable environmental conditions is particularly important for high-latitude marine organisms due to the relatively short duration of seasonal peaks in prey abundance (Durant et al. 2007). The timing of spawning is primarily defined by an interaction between water temperature and photoperiod. While the photoperiod at a given latitude changes seasonally within a year, it does not vary annually, and is therefore not affected by climate change. This seasonal change in photoperiod follows a latitudinal gradient, where

*Corresponding author: florian.berg@hi.no

[§]Advance View was available March 28, 2024

Publisher: Inter-Research · www.int-res.com

days and nights are equally long near the equator throughout the year but diverge towards the poles. This latitude gradient requires special adaptations to the seasonal photoperiod regardless of temperature (Varpe 2017). Especially in times of climate change, species need to adapt to new environmental conditions or migrate to avoid extinction (Moritz & Agudo 2013, Gienapp 2020).

This interaction between photoperiod and temperature will become more important under projected changes in climate where directional shifts in distribution of marine populations are expected (Barange et al. 2009, Pecl et al. 2017). Climate-driven poleward shifts have already been documented for several species (Perry et al. 2005, Fossheim et al. 2015, Kortsch et al. 2015), leading to changes in experienced photoperiod and light intensity. However, photoperiod will also constrain poleward distribution of pelagic species which, as visual foraging fish, are dependent on sufficient amounts of light (Sundby et al. 2016, Ljungström et al. 2021, Langbehn et al. 2022). Thus, it is essential to reveal the mechanisms underlying the production cycle of marine fish at high latitudes and the growth and survival of their offspring.

Several studies have documented temperature and photoperiod effects on growth and maturation of marine fish. Manipulation of photoperiod and also temperature has long been a common method to offset maturation and gamete production in aquaculture (e.g. Roberts et al. 1978). An experimental study on Atlantic cod showed that extended light periods when fish were fed in excess enhanced growth at all temperature regimes used (7, 10, 13°C) during the early juvenile stage (Imsland et al. 2007). The long-term growth benefits of differences in initial temperature and photoperiod were also observed to persist after 17 mo under subsequent common culture conditions. In herring larvae, increased growth at high temperatures and longer day lengths have also been documented (Folkvord et al. 2009a,b), but no long-term temperature experiments have previously been carried out for this species. A long-term experiment on herring with different photoperiod regimes (natural and 6 mo offset) revealed clear differences in gonadal development at an age of 2.5 yr, but this was not accompanied by differences in final size (dos Santos Schmidt et al. 2022). The combined effects of temperature and photoperiod conditions are of particular concern in the climate-driven changes in fish population distributions, since any poleward shifts will also be accompanied by changes in seasonal light regimes (Saikkonen et al. 2012).

In general, the spawning season of fish at high latitudes is restricted to specific time periods, mostly linked to seasonal changes in photoperiod and light intensity. The duration of these periods may range over several months within the same season, such as spring or autumn. However, there is one clear exception: Atlantic herring *Clupea harengus*, which, as a species, spawns throughout the entire year (dos Santos Schmidt et al. 2021), with spawning time varying markedly between genetically differentiated populations (Han et al. 2020) and within populations. As a result, and for management purposes, herring are predominately split into either spring or autumn spawners which can be clearly discriminated by a few genes linked to spawning time (Lamichhaney et al. 2017). Genetically distinct herring spawning types, mainly spring and autumn, have been identified (Bekkevold et al. 2016, Han et al. 2020). Historical shifts in dominance of either spawning type are likely linked to overfishing and/or climate change (MacKenzie & Ojaveer 2018, Atmore et al. 2022). Notably, interbreeding between genetically divergent spawning types has also been documented (Berg et al. 2021). However, the underlying mechanisms determining the spawning time, especially autumn vs. spring, remain unknown, as do the long-term consequences for the growth and survival trajectories of their offspring.

Although the gap between autumn and spring spawning is several months, both spawning types start their vitellogenesis near the spring equinox (McPherson & Kjesbu 2012). Therefore, while autumn spawners will reproduce within the same year that vitellogenesis is initiated, spring spawners will reproduce in the year after (dos Santos Schmidt et al. 2017). Typically, the water temperature is higher during autumn spawning than during spring spawning. A challenge for offspring and the newly hatched larvae is that during autumn, the days become shorter and food more limited, while during spring, the days become longer and the productivity of plankton increases. Comparing the growth trajectories of wild autumn- and spring-hatched larvae originating from the same genetic populations is not feasible because they will never experience the same environmental conditions. Therefore, we conducted an experiment over a long time period to investigate the growth trajectories of offspring of genetically spring-spawning herring hatched either under autumn or spring conditions. The experimental design was 2-factorial with treatments of temperature and photoperiod. Parameters investigated during the experiment were growth (defined as changes in length at age), mortality, and somatic condition.

We hypothesized that longer daylengths experienced by larvae early in life would provide an overall growth advantage resulting in larger size after 1 yr (same amount of light) compared to larvae that experienced prolonged daylengths later in life due to higher size-dependent growth rates at smaller sizes. Thus, larvae reared under spring conditions should have a prolonged larger size at age compared to larvae reared under autumn conditions. We also expected this effect to be enhanced under relatively higher temperature conditions when food was not limiting.

2. MATERIALS AND METHODS

2.1. Parental population and fertilization experiment

Norwegian spring-spawning herring (N = 108) were collected on 20 February 2019 from gillnets set overnight on a local spawning ground (60° 34′ 11″ N, 5° 0′ 19″ E), northwest of Bergen, Norway. Live herring were terminally anaesthetized (>0.5 g l^{-1} Metacain/Finquel®), stored in individual plastic bags, and transported in a cooling box to the experimental laboratory within approximately 2 h after retrieval from gillnets.

Experimental protocols were reviewed and approved by the Norwegian Food Safety Authority (ID-8459 and 19426). Three full-sibship crosses, each consisting of 1 fully mature female and fully mature male, were used as the starting point for this experiment (Table 1); another cross was dismissed due to fertilization rates <50% (data not shown). The parental fish were selected based on their spawning condition (i.e. running sperm and eggs) to secure high fertilization rates. Fertilizations were conducted at a salinity of 16 psu and water temperature of approximately 9°C to achieve high fertilization rates (Berg et al. 2019). Eggs were gently stripped onto replicate glass plates in 25 × 35 cm trays and sperm, activated by seawater, was poured over the settled eggs. The water in the trays was gently circulated to ensure proper fertilization. After 30 min, the egg plates were rinsed with running seawater and transferred into flow-through incubation trays. The salinity was 34 psu and water temperature was 8.5 ± 0.15°C during the incubation. Fertilization rates were estimated 24 h post fertilization (for details, see Berg et al. 2019, Mueller et al. 2023). Light intensity and photoperiod fluctuated according to the seasonal and daily cycle in Bergen (60° N). The hatching date, defined as the median day of hatching (i.e. when 50% of larvae had hatched), was 6 March 2019.

Table 1. Overview of adult herring (sex, total length [TL], weight, and gonadosomatic index [GSI] = gonad weight/somatic weight×100) used for the crosses. Fertilization rates of individual crosses are presented

Cross	Sex	TL (cm)	Weight (g)	GSI	Fertilization rate (%)
1	F	34.3	320.9	38.72	90.1
	M	30.5	233.4	30.46	
2	F	34.7	385.0	43.27	98.8
	M	34.0	335.7	26.18	
3	F	34.2	353.1	38.28	98.6
	M	33.2	314.5	28.90	

2.2. Experimental design and larval rearing

The experimental design was 2-factorial with treatments of temperature (7°C or 10°C) and light (natural or offset) resulting in 4 experimental treatments: '7 nat', '7 off', '10 nat', and '10 off'. For the initial larval rearing, 8 black round tanks (1 m diameter) containing 300 l of water were initially used and split into 2 replicates of the 4 experimental treatments. The temperature regimes were achieved by using 2 separate climate-controlled rooms set at 7°C and 10°C, respectively. The tanks were covered with double-layered black cloth to allow different light regimes in tanks in the same room. The water flow was initially semi-stagnant and replenished manually with 5–10 l daily. Natural light refers to light intensities and photoperiod fluctuating according to the seasonal and daily light cycle at the sampling location of the parental herring population (60° N). The offset light refers to light cycle out of phase by 6 mo (Fig. 1). Light intensity and photoperiod were regulated by an OxyGuard Dali® light control system, where the light intensity is expressed by the degree of the sun above the surface. During mid-summer, the light intensity was approximately 10 times higher compared to mid-winter. At the hatching date of larvae (6 March), the natural light regime was adjusted to that of 3 April (12.9 h daylength at 60° N), whereas the offset light regime was adjusted to 26 September (12.5 h daylength at 60° N). The water temperatures for the experimental groups were stable at either 7 or 10°C. The water salinity was constant at 34 psu.

After hatching, 500 larvae from each of the 3 crosses were transferred to each of the 8 tanks, resulting in an initial larval stocking density of 1500 larvae per tank (Fig. 1). Larvae were fed daily with natural filtered zooplankton ad libitum (see below). The natural zoo-

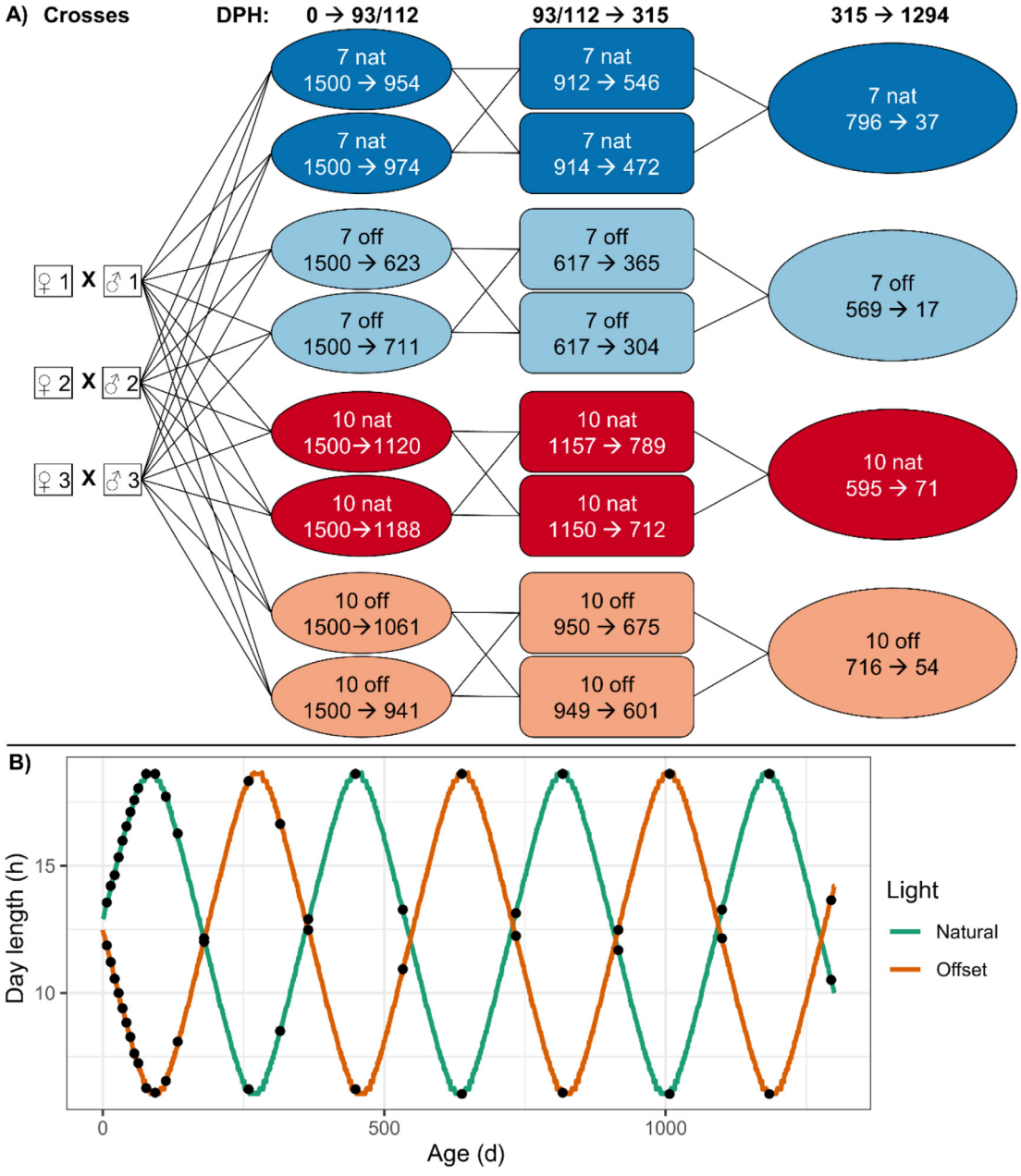

Fig. 1. (A) Experimental design of the 3 phases for herring reared from 0–1294 d post hatching (DPH). Constant temperatures of 7°C (red) and 10°C (blue) and different light regimes (nat: natural; off: offset) were used. Start and end points of each phase are indicated, as are the initial and final numbers of herring per tank. Initially, 500 larvae of 3 different crosses were combined per tank. (B) Depiction of the fluctuating light regimes following the natural light cycle in Bergen (60° N) or out of phase by 6 mo (offset) over a period of 3.5 yr. Points indicate sampling events of herring (see Table 2 for details)

plankton consisted mainly of different copepod species and their nauplii stages. Each day, an estimate of the density of the remaining plankton was made for each tank, and plankton were added to reach 2000 prey l^{-1}. After the reallocation of larvae (see below), herring were weaned onto dry feed (AgloNorse 600–900 µm; 58–60% protein, 17–20% fat). The size of the dry feed was increased over the experimental period and was fed in excess based on previously observed growth rates.

At 93 and 112 d post hatching (DPH), herring from the replicates at 10 and 7°C, respectively, were moved in new square tanks (1 × 1 m) with flow-through water to allow more effective water exchange (Fig. 1). Larvae at 7°C were transferred later due to their slower development until reaching an appropriate size to

handle the flow-through water system. During this transfer, larvae from each replicate were split into 2 different tanks (50% in each) and mixed with larvae from the second replicate of the same treatment. Again, 8 tanks were used, 2 replicates per experimental treatment. This reallocation was done to minimize tank effects in the new time period of the experiment. Tanks with the same light regimes were allocated in the same room, and water temperature was maintained by regulation of individual water flow of each tank. In total, 1826, 1234, 2307, and 1899 herring were transferred from '7 nat', '7 off', '10 nat', and '10 off' groups, respectively (Fig. 1).

At 315 DPH, herring from replicate tanks were merged into 1 of 4 green circular tanks (2 m diameter) to accommodate more space for the larger juveniles (Fig. 1). For logistic reasons, no replicates were possible thereafter, but the environmental conditions of the treatments were left unchanged. In total, 796, 569, 595, and 716 herring were transferred from '7 nat', '7 off', '10 nat', and '10 off' groups, respectively (Fig. 1). The experiment was terminated on 20 September 2022, and the herring were thus reared over a period of 3.5 yr. This experimental design allowed for direct comparison of the impacts of temperature and light conditions on larval and juvenile growth.

2.3. Sampling procedure

At the beginning of the experiment, weekly samples of N = 10 larvae from each of the different tanks were routinely taken and photographed (Leica MZ7.5) throughout the larval period (up to 77 DPH, Table 2). This N was based on the prior experienced level of variability in somatic traits between individuals within a replicate (2 × 10, i.e. 20 per treatment), and the considerations regarding animal welfare to

Table 2. Overview of ages (in days post hatching) and rearing conditions at which herring length samples were taken during the first 3.5 yr of life. Numbers of larvae (N) sampled at 7 and 10°C (N7 and N10, respectively), the daylength (in hours) on the sampling date (DayL), the cumulative sum of hours of daylength (SumL), and the season for the 2 different light regimes (natural and offset) are presented. The offset light regime is 6 mo out of phase compared to the natural light regime. Note that the season refers to the starting point, i.e. summer/winter refer to the time of the solstices, whereas spring/autumn refers to the time of the equinox

Date	Age	Natural light					Offset light				
(yr-mo-d)		N7	N10	DayL	SumL	Season	N7	N10	DayL	SumL	Season
2019-03-13	7	20	20	13.6	106	Spring	20	19	11.9	97	Autumn
2019-03-20	14	20	20	14.2	203	Spring	20	20	11.2	178	Autumn
2019-03-27	21	20	20	14.6	304	Spring	20	20	10.6	254	Autumn
2019-04-03	28	20	20	15.3	409	Spring	20	20	10.0	326	Autumn
2019-04-10	35	20	20	16.0	519	Spring	20	20	9.4	393	Autumn
2019-04-17	42	20	20	16.5	634	Spring	20	20	8.8	456	Autumn
2019-04-24	49	20	20	17.1	751	Spring	20	20	8.3	516	Autumn
2019-05-01	56	20	20	17.6	873	Spring	20	20	7.6	571	Autumn
2019-05-08	63	20	20	18.0	998	Spring	20	20	7.2	623	Autumn
2019-05-22	77	20	20	18.6	1254	Summer	20	20	6.3	716	Winter
2019-06-07	93	20	125	18.6	1552	Summer	20	100	6.1	814	Winter
2019-06-26	112	94	20	17.7	1897	Summer	94	20	6.5	932	Winter
2019-07-17	133	31	30	16.3	2253	Summer	34	34	8.1	1085	Winter
2019-09-02	180	100	100	12.2	2916	Autumn	90	90	12.0	1556	Spring
2019-11-20	259	100	100	6.2	3608	Winter	100	100	18.3	2781	Summer
2020-01-15	315	48	48	8.5	3988	Winter	48	48	16.6	3794	Summer
2020-03-05	365	60	60	12.9	4523	Spring	60	71	12.5	4523	Autumn
2020-05-28	449	50	50	18.6	5889	Summer	50	50	6.2	5277	Winter
2020-08-20	533	50	50	13.3	7275	Autumn	50	50	10.9	5929	Spring
2020-12-03	638	50	20	6.0	8210	Winter	50	20	18.6	7545	Summer
2021-03-09	734	20	20	13.1	9086	Spring	20	20	12.2	9083	Autumn
2021-05-31	817	15	15	18.6	10455	Summer	15	15	6.1	9805	Winter
2021-09-07	916	15	15	11.7	12009	Autumn	15	15	12.5	10652	Spring
2021-12-07	1007	15	15	6.0	12745	Winter	15	16	18.6	12130	Summer
2022-03-10	1100	12	12	13.3	13610	Spring	12	12	12.2	13606	Autumn
2022-06-02	1184	12	12	18.6	15003	Summer	6	12	6.0	14328	Winter
2022-09-20	1294	37	71	10.5	16663	Autumn	14	54	13.6	15333	Spring
Sum		**929**	**963**				**893**	**926**			

reduce the number of animals used for experimentation. For larvae up to 77 DPH, standard length (SL) was measured from photos using ImageJ. Photographed larvae were stored in either ethanol or at −80°C after being flash frozen in liquid nitrogen for potential later genetic analyses (not part of this study). On days of reallocation or transfer to new tanks, 50 or more individuals were sampled per tank. The time between samples increased after the larval period because the growth of herring slowed down and weekly sampling was not necessary (Table 2). At the juvenile to adult phase, herring were sampled quarterly near solar equinox or solstice, respectively. At each sampling, individual fish were measured for total length (TL) and weight (from 93 DPH onwards) using a length measuring board and a Sartorius® balance (ED3202S-0CE). For adult fish, sex and maturity stage were determined for each sampled fish to follow the gonadal development. For each sampled individual, tissue samples were collected for later genetic analyses.

2.4. Statistical analysis

To allow for direct comparison between SL and TL, we used a factor of 1.15 to estimate the SL when TL was measured by dividing the TL by 1.15 (R^2 = 0.87, F. Berg et al. unpublished). Note that throughout the paper, we only use SL for consistency even though the TL was measured.

In general, all of the described modelling followed a backward selection approach incorporating all fixed and random effects where necessary (mixed-effects models). Only the final selected model is presented; non-significant model terms were excluded. First, the optimal structure of the random effects was tested using a likelihood ratio test based on the models fitted by restricted maximum likelihood estimations (REML) (Zuur et al. 2009). Also based on REML fits, the fixed-effects structure was optimized using marginal *F*-statistics (Pinheiro & Bates 2000). For all models, both the random effect a and the residual ε are assumed to be normally distributed with mean of zero and variance σ^2_{treat}. This structure allows for different residual variances depending on the experimental treatment. The assumptions of normality (both for the response variable and residuals), homogeneity of variances, and independence of errors were inspected graphically and tested using Shapiro-Wilk, Levene's, and Durbin-Watson tests, respectively. For all models, assumptions were not violated. Furthermore, the 'DHARMa' package in R (Hartig 2022) was used to examine model diagnostics where possible. Diagnostic plots (see Figs. S7–S10) and statistical result tables are provided in the Supplement at www.int-res.com/articles/suppl/m741p203_supp.pdf.

For the first 93 d of the experiment, we used a linear model to estimate the growth rate of larvae from measured length at age for the 4 experimental groups. A linear mixed-effects model was applied to investigate the effect of the different temperature ($Temp_{ij}$) and light ($Light_{ij}$) regimes and their interaction on the SL (SL_{ij}) of larvae:

$$\begin{aligned} SL_{ij} = {} & \alpha + \beta_1 \times DPH_i + \beta_2 \times Temp_{ij} + \beta_3 \times \\ & Light_{ij} + \beta_4 \times DPH_i \times Temp_{ij} + \beta_5 \times DPH_i \times \\ & Light_{ij} + \beta_6 \times Temp_{ij} \times Light_{ij} + \beta_7 \times DPH_i \times \\ & Temp_{ij} \times Light_{ij} + a_j + \varepsilon_{ij} \end{aligned} \quad (1)$$

where DPH is the age of larvae i in days post hatching; $Temp_i$ and $Light_i$ are factorial covariates representing the temperature (7 vs. 10°C) and light (natural vs. offset) regimes, respectively; and the term a_j is the random effect for each tank j. The mixed-effects model was fitted using the 'lme' function within the R package 'nlme' (Pinheiro & Bates 2000).

The daily mortality of larvae within each tank was estimated in the period from hatching until the first transfer (reallocation) of herring (92 or 111 DPH for the 7 and 10°C tanks, respectively). For all tanks, the initial and final stocking numbers were known as well as number of larvae removed for sampling; consequently the total survival and average daily mortality rates were determined manually by iteration. The estimated daily mortality is the average daily mortality accounting for the timing and extent of sampling. Furthermore, the mortality rates between the first and second reallocation were estimated. Differences in the daily mortality rates ($Mortality_i$) between the 2 periods ($Period_i$; start to first reallocation, and first to second reallocation) and the different temperature and light regimes were tested with an ANOVA:

$$\begin{aligned} Mortality_i = {} & \alpha + \beta_1 \times Period_i + \beta_2 \times Temp_i + \\ & \beta_3 \times Light_i + \beta_4 \times Period_i \times Temp_i + \beta_5 \times \\ & Period_i \times Light_i + \varepsilon_i \end{aligned} \quad (2)$$

No replicates were available after the last reallocation, and consequently no statistical tests of mortality were performed for this period.

The effects of light regime on the length of fish after a full year in the experiment (365 d, and a complete annual light cycle) were tested with Student's *t*-test for each temperature treatment. In addition, results of a 2-factorial ANOVA are provided in Table S1. A sim-

ilar test was conducted for the length at ages 2 and 3 (Fig. S1).

To follow size over time, we plotted the SL from each sampling date against the age of larvae, the sum of daylength, and the experienced degree-days. The experienced degree-days were estimated as the sum of daily mean temperatures, e.g. after 3 d, the experienced degree-days at 7 and 10°C were 21 and 30, respectively. Similarly, the 'sum of daylength' was estimated as cumulative experienced daylength. The growth trends (defined as changes in length over time) for the first year were fitted to generalized additive models (GAMs), since they allow flexible nonparametric effects of covariates (Hastie & Tibshirani 1990). Model selection was based on the generalized cross validation score. Isotropic smoothing functions $s()$, uniform in all orientations, were used to define smooth terms (thin-plate regression spline, Wood 2003). Three different GAMs were fitted to investigate the log-transformed (natural logarithm) SL against age (DPH_i):

$$\ln(SL_i) = \alpha + \beta_1 \times Temp_i + \beta_2 \times Light_i + \beta_3 \times Temp_i \times Light_i + \beta_4 \times s_{Temp}(DPH_i) + \beta_5 \times s_{Light}(DPH_i) + \varepsilon_i \quad (3)$$

against the sum of daylength ($Dayl_i$):

$$\ln(SL_i) = Temp_i + \beta_2 \times Light_i + \beta_3 \times Temp_i \times Light_i + \beta_4 \times s_{Temp}(Dayl_i) + \beta_5 \times s_{Light}(Dayl_i) + \varepsilon_i \quad (4)$$

and against the experienced degree-day (DD_i):

$$\ln(SL_i) = \alpha + \beta_1 \times Temp_i + \beta_2 \times Light_i + \beta_3 \times Temp_i \times Light_i + \beta_4 \times s_{Temp}(DD_i) + \beta_5 \times s_{Light}(DD_i) + \varepsilon_i \quad (5)$$

For all models, an interaction between the smoother and the temperature and light regime was included. Growth for the entire 3.5 yr experimental period was calculated in the same way and visualized by a locally weighted smoothing (loess) line (Figs. S2–S4).

Residuals of the following linear length–weight model were used as proxy for individual somatic condition:

$$\ln(Weight_i) = \alpha + \beta_1 \times \ln(SL_i) + \beta_2 \times Temp_i + \beta_3 \times Light_i + \varepsilon_i \quad (6)$$

where $\ln(Weight_i)$ is the natural logarithm of the wet weight, and $\ln(SL_i)$ is the natural logarithm of the SL. Only post-metamorphic fish (SL >55 mm) were included in this calculation of somatic condition. The mean of somatic condition was estimated for each of the 4 seasons (Table 2). The use of season allows a direct comparison of seasonal variability between the light regimes. To close the seasonal cycle, the estimated values for the winter season were duplicated and added as second winter at the end of the seasonal cycle. The data were fitted using a GAM to explore the seasonal variation ($Season_i$) of somatic condition ($Cond_i$) in relation to the different temperature and light regimes:

$$Cond_i = \alpha + \beta_1 \times Temp_i + \beta_2 \times Light_i + \beta_3 \times Temp_i \times Light_i + \beta_4 \times s_{Temp}(Season_i) + \beta_5 \times s_{Light}(Season_i) + \varepsilon_i \quad (7)$$

An interaction between the smoother and the temperature and light regime was included.

All statistical analyses and plotting were conducted in the R software (R Core Team 2022). For all tests, we used a significance level of $\alpha = 0.05$.

3. RESULTS

3.1. Larval rearing during the first three months

During the first 3 mo of the experiment, larval growth was linear for all 4 experimental groups (ANOVA, $p < 0.001$; Fig. 2; Table S2). Both temperature and light influenced the growth trajectories of larvae, and their interaction was significant (ANOVA,

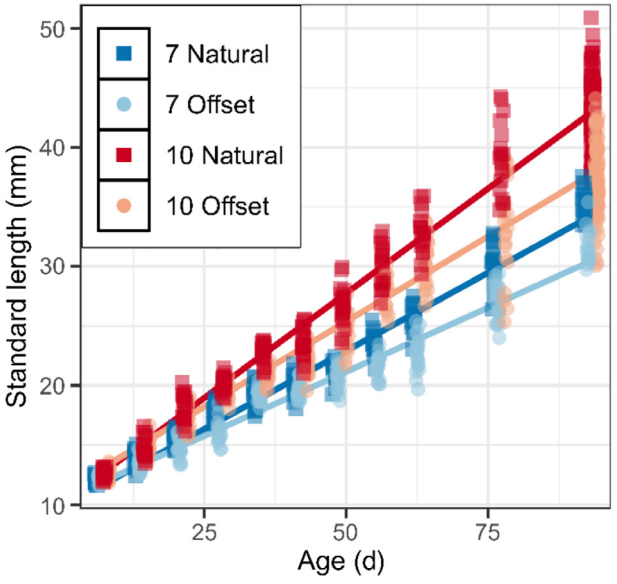

Fig. 2. Standard length at age for herring larvae for the first 93 d of the experiment (from equinox to solstices) reared under different light and temperature regimes (constant temperatures of 7 and 10°C and different light regimes, where nat: natural; off: offset). Modelled linear trend lines are shown

$p < 0.01$; Table 3). The intercept of the model (i.e. length at age 0) did not vary between groups (ANOVA, $p = 0.102$). Larvae reared at 10°C and under natural light had the highest growth rates (0.36 mm d^{-1}; slope of the model), whereas larvae reared at 7°C and in the offset light regime had the lowest growth rates (0.22 mm d^{-1}). In general, temperature had a higher impact (0.09 mm d^{-1} difference) on larval growth than light regime (0.07 mm d^{-1} difference).

The overall daily mortality was 0.34% during the first 3 mo. In general, daily mortality rates were lower under the natural light regime at the same temperature, and lower at 10°C within the same light regime (Table 4). Thus, the highest daily mortality was observed under the offset light regime and 7°C water temperature (0.6%), whereas the lowest daily mortality rates occurred under the natural light regime at 10°C (0.14%, Table 4).

Table 3. Estimated growth rates (mm d^{-1}) of herring larvae based on a linear fixed-effects model for the first 93 d of the experiment (from equinox to solstices) reared under different light and temperature regimes

Temperature (°C)	Light	Growth rate
7	Natural	0.263
7	Offset	0.215
10	Natural	0.352
10	Offset	0.286

3.2. Growth during the first year

After 1 yr and the same amount of daylight, the SL of herring reared under natural (131.1 mm) and offset (128.5 mm) light conditions did not differ between fish in the 10°C temperature regime (*t*-test, $p = 0.152$, Fig. 3). Herring reared at 7°C and under natural light conditions (95.3 mm) were slightly smaller than individuals from the offset light regime (99.4 mm; *t*-test, $p = 0.010$). Herring reared at 10°C were, on average, 32.4 mm longer than individuals reared at 7°C.

Herring growth during the first year varied with age, daylength, and temperature (Fig. 4). The overall trend was that individuals reared at 10°C were consistently longer than those from the corresponding light regime at 7°C (Tables S3–S5). For the length at age, there were relatively small but significant differences between fish from the 2 light regimes, but for both temperatures, those fish reared under natural light conditions were larger, except for the last sample at age 1 (Fig. 4A; Table S3). For the length at experienced cumulative daylengths, individuals in the offset group were always larger than herring in the natural light regime after the same amount of light (Fig. 4B), i.e. fish in the offset group had a higher growth rate per available hour of light (Table S4). This trend changed in the second half of the year, when the growth rate increased for the natural light. Thus, the growth rate per light hour was highest during autumn and winter (shorter daylength; Table S5). The general pattern was not as clear for the comparison of

Table 4. Overview of the overall estimated survival and average daily mortality (in percent) of herring for each tank within the first period of the experiments (upper section, from Day 0 until 93/112 d post hatching) and the second period (lower section, from Day 93/112 until the second reallocation at 315 d post hatching). Initial number, remaining, and sampled herring are indicated for the respective time periods, 315 d in total

Tank	Temp (°C)	Light	Days	Initial number	Remaining	Sampled	Survival	Daily mortality
1	7	Natural	112	1500	954	148	71.6	0.30
2	7	Natural	112	1500	974	155	73.4	0.28
3	7	Offset	112	1500	623	150	47.8	0.66
4	7	Offset	112	1500	711	158	54.6	0.54
9	10	Natural	93	1500	1220	139	90.0	0.11
10	10	Natural	93	1500	1188	116	86.3	0.16
6	10	Offset	93	1500	1061	139	78.7	0.26
7	10	Offset	93	1500	941	122	69.2	0.40
22	7	Natural	203	912	546	115	70.4	0.17
23	7	Natural	203	914	472	115	61.5	0.24
32	7	Offset	203	617	365	112	74.8	0.14
33	7	Offset	203	617	304	112	63.7	0.22
24	10	Natural	222	1157	789	125	77.7	0.11
25	10	Natural	222	1150	712	125	71.0	0.15
34	10	Offset	222	950	657	122	80.6	0.10
35	10	Offset	222	949	601	122	74.4	0.13

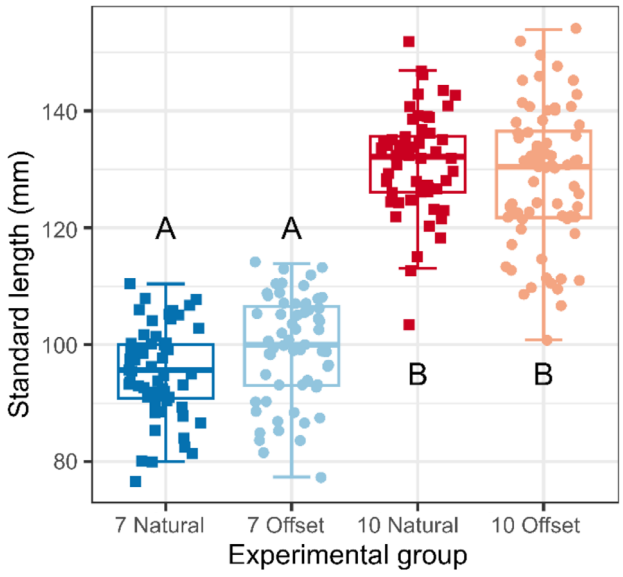

Fig. 3. Standard length of individual age-1 herring reared under different light (natural and offset) and temperature (7 and 10°C) regimes. Horizontal lines represent medians, boxes represent the interquartile range (IQR), and whiskers represent the lowest and highest observations within 1.5× IQR. Individual points indicate raw data. Compact letter displays of all pairwise comparisons based on the 2-way ANOVA (Table S1) are provided to demonstrate statistical differentiation

length at sum of degree-days, but eventually the herring from the 10°C groups were larger (Fig. 4C). However, there were significant differences between fish from the different temperature and light regimes (Table S5).

3.3. Growth during three and a half years

The pattern of growth observed for Year 1 continued, but with less clarity in Years 2 and 3 (Figs. S1–S4). In addition, a stunting effect occurred in fish from all tanks after the first year. The slope of the length–weight relationship of herring reared over 3.5 yr was constant after metamorphosis at approximately 55 mm (overall slope = 3.28; Fig. 5) and was not influenced by light or temperature as seen from the growth trajectories. The slope was slightly steeper for smaller fish, and this observed growth stanza after metamorphosis was expected. In general, the length–weight relationship of fish >55 mm reared under different temperature conditions followed the same trend, but fish reared in colder water were 3.7% heavier at any given length (ANOVA, $p < 0.001$). The light regime had no effect on the length–weight relationship (ANOVA, $p = 0.171$), but was not omitted from the model when estimating the residuals. The residuals from the linear length–weight model were used as proxy to investigate seasonal effects among the 4 experimental groups.

The residuals from the length–weight relationship clearly followed a seasonal pattern induced by different light regimes among all 4 experimental groups (Fig. 6). As expected, all groups had their highest somatic condition in summer or autumn. Under the natural light regime, the lowest somatic condition was observed during winter, whereas it was observed during spring for herring reared under 7°C and offset light conditions. For herring reared under offset light conditions and 10°C, the season with lowest somatic conditions was not conclusive because a drop in somatic condition was observed during summer. However, when considering the raw data (Fig. S5), this drop might be due to the low variation in somatic condition between individuals sampled during summer.

The daily mortality rates decreased after the first reallocation at solstices (Table 4). This drop was more prominent in the offset light regime compared to the natural light regime, where it was already at very low levels during the first part of the experiment (ANOVA, period×light interaction, $p = 0.001$; Table S8). The daily mortality within the offset light groups was always lower within respective temperature regimes compared to the natural light groups (Table 4). Average daily mortality was lower in the 10°C groups compared to the 7°C groups prior to the last reallocation (ANOVA, $p = 0.030$). In the last unreplicated part of the experiment, there was a tendency for mortality to be higher during winter and spring, following a similar pattern as the somatic condition (data not shown).

4. DISCUSSION

To our knowledge, this is the first study where viable offspring of Atlantic herring have been reared in captivity for 3.5 yr under simulated natural and offset light regimes at different temperatures. The results of our study clearly reject the initial hypothesis that longer daylengths early in life would provide an overall growth advantage compared to those experiencing this later in life. After 1 yr, herring reared under the offset light regime were either of equal size or even larger compared to herring under the natural light regime in colder temperatures. As expected, herring were larger at age at higher temperatures, while the overall and seasonal patterns observed followed the same trends between the 2 temperature regimes.

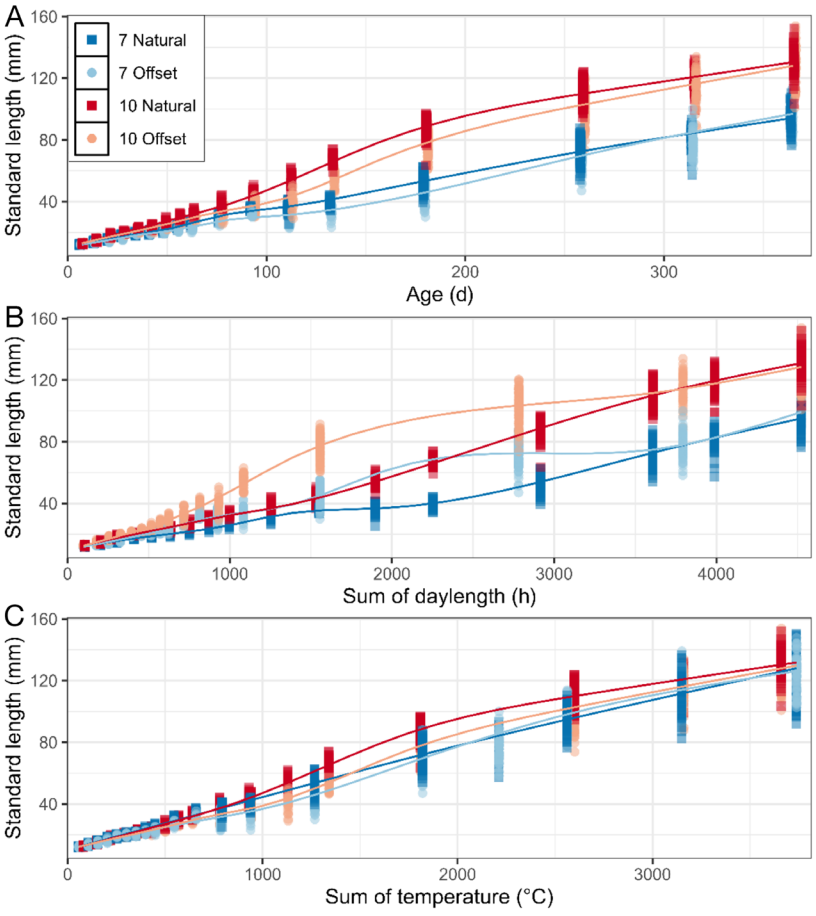

Fig. 4. Growth development of herring during the first year of the experiment displayed as changes in standard length at (A) age, (B) sum of daylength, and (C) sum of temperature (degree-days) reared under different light (natural and offset) and temperature (7 and 10°C) regimes. Note that for the sum of temperature, additional data for the 7°C groups were added until they reached the same number of degree-days as the 10°C groups at age 1. Generalized additive model prediction lines (Tables S3–S5) are shown

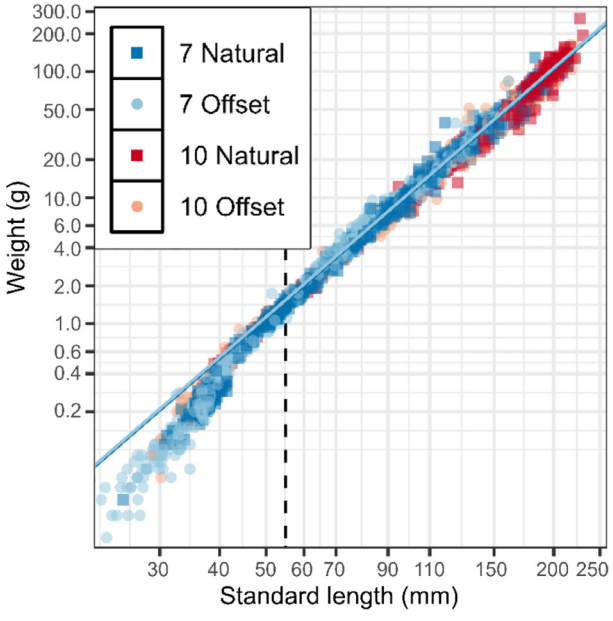

Fig. 5. Length–weight relationship of herring reared under different light (natural and offset) and temperature (7 and 10°C) regimes over the entire experimental period. Prediction lines from a linear model of fish >55 mm (dashed line) are presented (differences almost not visible). See Table S6 for estimated length–weight relationship equations

Herring larvae display considerable growth plasticity and are able to cope with severe environmental conditions. It is surprising that larvae from genetically spring-spawning adults not only survived well under autumn-hatching light conditions, but later compensated for the lower growth experienced the first months of life. Furthermore, the higher mortality at colder temperatures is in contrast to a previous study by Folkvord et al. (2009a), where the daily mortality on average was twice as high at 10°C compared to 6°C (0.36 vs. 0.16% d^{-1}). This pattern is expected to be more common as most processes, such as growth and mortality, typically are elevated at higher temperatures (Houde 1989). The difference in larval daily mortality rates between experiments mainly occurred in the 10°C groups (0.36 in the previous study vs. 0.14% d^{-1} in this study), but in both cases, the mortality rates can be considered very low and suggestive of a low direct selection related to temperature. In both experiments, the parental fish were Norwegian spring-spawning herring, but effects of genetic differences cannot be ruled out, as population differences in temperature-related markers have been suggested (Han et al. 2020).

Experimental studies are limited to testing only one or several factors, each at a few levels. In nature, multiple interacting factors are expected to impact fish production. In field and experimental studies, environmental and genotypic influences on growth trajectories, mortality rates, and other phenotypic traits are confounded (Conover 1992). Variability between offspring from 3 parental crosses can be neglected because larvae had the same size at hatching, the phenotypes of parents were comparable, very low mortality occurred, and crosses contributed equally to all tanks initially. One shortcoming of the current experiment is the lack of genetic varia-

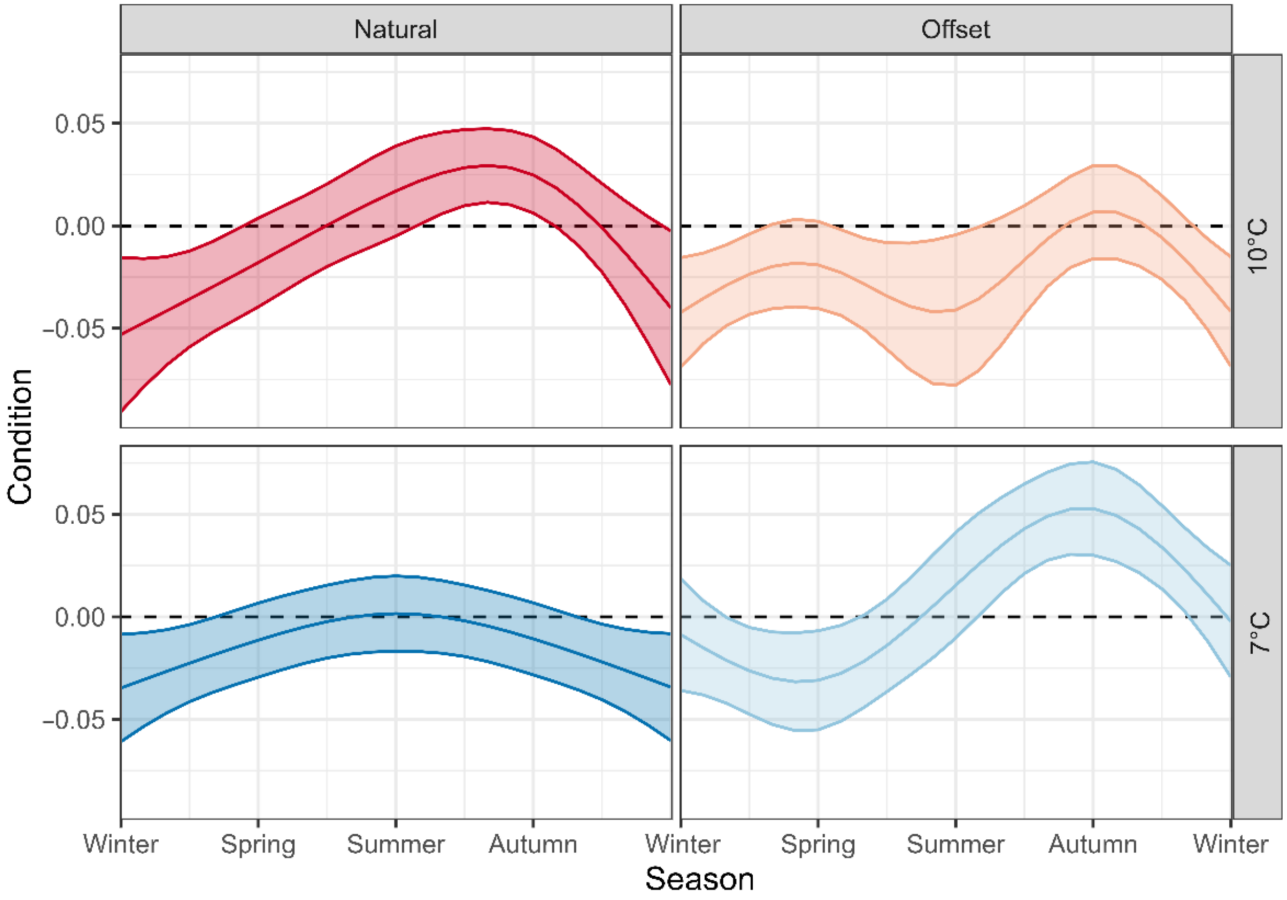

Fig. 6. Residuals of the linear length–weight model are used as proxy for the somatic condition of individual herring (>55 mm) reared under varying light regimes (natural vs. offset) and temperature (7 vs. 10°C). Generalized additive model prediction lines (Table S7) and their 95% confidence intervals are shown to indicate the seasonal variation in the somatic condition among herring from the 4 experimental groups. Raw data are presented in Fig. S5. Note that season refers to the starting point of the season, i.e. summer/winter refer to the time of the solstices, whereas spring/autumn refer to the time of the equinoxes

tion between spring- and autumn-spawning herring. It would have been beneficial to co-rear both genetically spring- and autumn-spawning herring, or at least hybrids of these distinct genetic spawning types. Thus, further common garden experiments are recommended to help identify the underlying mechanisms determining the timing and associated trade-offs linked to spawning in herring.

For this experiment, we chose constant temperature regimes to focus on the temperature effect per se and its potential interaction with seasonal light regime, not attempting to mimic natural temperature conditions. Having seasonally fluctuating temperature conditions on top of potential ontogenetic and size-dependent temperature relations would render the temperature effects dependent on season itself, something that would obscure the validity of the season vs. temperature interaction. With the current design, the temperature effect as such was independent, and did not co-vary with the light regime effect. The temperatures are within what is experienced for both autumn- and spring-spawned herring larvae in Norwegian waters, with 7°C being on the lower end, and 10°C being on the mid to higher end of the experienced temperature range (Berg et al. 2017, Tiedemann et al. 2021). The temperature ranges were mostly defined by larval temperature preferendum, since larvae typically have narrower ranges compared to juveniles (Pörtner & Peck 2010). The unique experimental design allowed direct comparison of young Atlantic herring of the same age that experienced either spring or autumn light conditions during their first few months of life. That herring offspring had similar average body lengths after a year suggests that the size-at-age differences between wild herring populations with different spawning times cannot solely be explained by the differences in seasonal light regimes. It has been demonstrated that the

spring light regime accelerates larval growth (Johannessen et al. 2000). Further, in a study with an experimental design similar to that used here, offspring of autumn-spawning herring achieved higher growth rates during the larval stage using a spring light regime versus an autumn light regime (Folkvord et al. 2009b). Data reported here suggest that the growth benefit achieved during the first 3 mo of life is subsequently lost. Still, higher initial growth rates under spring conditions and a longer growing season before the first winter are expected to result in reduced size-dependent winter mortality (Conover 1992).

Wild autumn-hatched larvae are unlikely to feed *ad libitum*. This is supported by analysis of daily increments of larval herring otoliths (e.g. Fossum & Moksness 1993, Brophy & Danilowicz 2002). Suboptimal feeding conditions further constrain winter survival of larvae. Herring growth and survival are likely more sensitive to prey abundance than light regimes (Folkvord et al. 2009b). Typically, an interaction of temperature and food level is found, where growth is relatively suppressed in the high-temperature, low-ration group since relatively more of the available energy is funneled into respiration rather than growth (Folkvord et al. 2009a,b).

The herring reared under autumn light conditions in this rearing experiment probably showed compensatory growth, as prey was not an additional limiting factor. In salmon, for example, compensatory growth can occur after various conditions for poor growth, such as low food (Stefansson et al. 2009) and low temperatures (Handeland et al. 2000), but also reduced light (Mortensen & Damsgård 1993, Pino Martinez et al. 2023). Compensatory growth occurs for herring after periods with reduced prey abundance (Pedersen et al. 1990, Pedersen 1993), but our study is the first demonstrating compensatory growth of herring related to light conditions. The advantages of compensatory growth are mainly related to size-dependent mechanisms such as mortality or fecundity (Ali et al. 2003).

The seasonal pattern observed for the somatic condition and daily mortality rates indicated that autumn-hatched larvae endure challenging environmental conditions. These challenges for herring larvae will be even greater in the natural environment than implemented in our experimental setup. In nature, temperatures will vary, and prey abundance will decline during late autumn to winter. A direct comparison of wild autumn-spawned herring larvae and spring-spawned ones would be desirable, but they cannot be sampled at the same time or even at the same age due to unknown hatching dates. Ideally, larvae of genetically spring- and autumn-spawned herring and their hybrids could be reared in the same experiment. Hybrids have been shown to have a growth advantage (Folkvord et al. 2009b), which might be linked to underlying genetic differences (Berg et al. 2018). Originally, it was planned to cross spring-spawning females with cryopreserved sperm of autumn-spawning males and co-rear the resulting spring–autumn hybrids with pure spring-spawning larvae. Such an experiment including purebreds and hybrids could display the adaptability between spring- and autumn-spawning herring to their actual spawning time. With this experimental design, it would be possible to investigate the daily mortality rate of different genetic spawning types, which would be essential to understand the mechanism driving the spawning time.

Reared herring do not reach their maximum adult length compared with their wild relatives (Smoliński & Berg 2022, Stenevik et al. 2022). This is likely a tank-size effect on survival and growth performance (Blaxter 1968). When data reported here were compared to a previous long-term experiment (Berg et al. 2018, Tonheim et al. 2020), adult herring had a larger size at age in larger tanks (Fig. S6). Therefore, the observed stunting effect is most likely due to the limiting tank size. Our data do not indicate that tank size affected seasonal patterns in somatic condition or daily mortality.

Our novel results about growth trajectories of Atlantic herring larvae reared under different light and temperature regimes indicate that Atlantic herring display considerable growth plasticity, reflecting the wide range of environmental conditions and life history traits that herring populations experience. Linking the feeding, growth, somatic condition, and mortality of herring reared under controlled environments provides new insights into the adaptability and plasticity of this species. The consequences of a northerly shift in marine taxa due to climate change might benefit populations at the northern end of the geographic range (Kjesbu et al. 2022). To what extent growth or mortality might be affected by food limitations due to light intensity or daylength requires further examination. Therefore, finding the correct spawning time and location will be crucial at higher latitudes because of the natural boundaries limiting shifts in time and space (Conover 1992).

Acknowledgements. We are grateful to Christel Krossøy, Frank Midtøy, Heikki Savolainen, and Julie Skadal at UiB for their efforts in the common garden experiments and rearing of herring over more than 3 years. We also acknowledge

Silje Marie Ryland for assistance with the larval rearing. This work was funded by RCN project 254774 (GENSINC). We dedicate this work to the long-time champion of experimental herring research, Dr. John H.S. Blaxter, who sadly passed away in April 2023.

LITERATURE CITED

Ali M, Nicieza A, Wootton RJ (2003) Compensatory growth in fishes: a response to growth depression. Fish Fish 4: 147–190

Atmore LM, Martínez-García L, Makowiecki D, André C, Lõugas L, Barrett JH, Star B (2022) Population dynamics of Baltic herring since the Viking Age revealed by ancient DNA and genomics. Proc Natl Acad Sci USA 119: e2208703119

Barange M, Bernal M, Cergole MC, Cubillos LA and others (2009) Current trends in the assessment and management of stocks. In: Roy C, Checkley D, Alheit J, Oozeki Y (eds) Climate change and small pelagic fish. Cambridge University Press, Cambridge, p 191–255

Bekkevold D, Gross R, Arula T, Helyar SJ, Ojaveer H (2016) Outlier loci detect intraspecific biodiversity amongst spring and autumn spawning herring across local scales. PLOS ONE 11:e0148499

Berg F, Husebø Å, Godiksen JA, Slotte A, Folkvord A (2017) Spawning time of Atlantic herring (*Clupea harengus*) populations within a restricted area reflects their otolith growth at the larval stage. Fish Res 194:68–75

Berg F, Almeland OW, Skadal J, Slotte A, Andersson L, Folkvord A (2018) Genetic factors have a major effect on growth, number of vertebrae and otolith shape in Atlantic herring (*Clupea harengus*). PLOS ONE 13:e0190995

Berg F, Slotte A, Andersson L, Folkvord A (2019) Genetic origin and salinity history influence reproductive success of Atlantic herring. Mar Ecol Prog Ser 617-618:81–94

Berg F, Østgaard HD, Slotte A, Andersson L, Folkvord A (2021) A combination of genetic and phenotypic characterization of spring- and autumn-spawning herring suggests gene flow between populations. ICES J Mar Sci 78: 694–703

Blaxter JHS (1968) Rearing herring larvae to metamorphosis and beyond. J Mar Biol Assoc UK 48:17–28

Brophy D, Danilowicz BS (2002) Tracing populations of Atlantic herring (*Clupea harengus* L.) in the Irish and Celtic Seas using otolith microstructure. ICES J Mar Sci 59:1305–1313

Conover DO (1992) Seasonality and the scheduling of life history at different latitudes. J Fish Biol 41:161–178

dos Santos Schmidt TC, Slotte A, Kennedy J, Sundby S and others (2017) Oogenesis and reproductive investment of Atlantic herring are functions of not only present but long-ago environmental influences as well. Proc Natl Acad Sci USA 114:2634–2639

dos Santos Schmidt TC, Hay DE, Sundby S, Devine JA and others (2021) Adult body growth and reproductive investment vary markedly within and across Atlantic and Pacific herring: a meta-analysis and review of 26 stocks. Rev Fish Biol Fish 31:685–708

dos Santos Schmidt TC, Berg F, Folkvord A, Pires AMA, Komyakova V, Tiedemann M, Kjesbu OS (2022) Is it possible to photoperiod manipulate spawning time in planktivorous fish? A long-term experiment on Atlantic herring. J Exp Mar Biol Ecol 552:151737

Durant JM, Hjermann DØ, Ottersen G, Stenseth NC (2007) Climate and the match or mismatch between predator requirements and resource availability. Clim Res 33: 271–283

Folkvord A, Fiksen Ø, Høie H, Johannessen A, Otterlei E, Vollset KW (2009a) What can size distributions within cohorts tell us about ecological processes in fish larvae? Sci Mar 73:119–130

Folkvord A, Høie H, Johannessen A, Solbakken T (2009b) Effects of prey concentration, light regime, and parental origin on growth and survival of herring larvae under controlled experimental conditions. ICES J Mar Sci 66: 1702–1709

Fossheim M, Primicerio R, Johannesen E, Ingvaldsen RB, Aschan MM, Dolgov AV (2015) Recent warming leads to a rapid borealization of fish communities in the Arctic. Nat Clim Change 5:673–677

Fossum P, Moksness E (1993) A study of spring-and autumn-spawned herring (*Clupea harengus* L.) larvae in the Norwegian Coastal Current during spring 1990. Fish Oceanogr 2:73–81

Gienapp P (2020) Opinion: Is gene mapping in wild populations useful for understanding and predicting adaptation to global change? Glob Change Biol 26:2737–2749

Han F, Jamsandekar M, Pettersson ME, Su L and others (2020) Ecological adaptation in Atlantic herring is associated with large shifts in allele frequencies at hundreds of loci. eLife 9:e61076

Handeland SO, Berge Å, Björnsson BT, Lie Ø, Stefansson SO (2000) Seawater adaptation by out-of-season Atlantic salmon (*Salmo salar* L.) smolts at different temperatures. Aquaculture 181:377–396

Hartig F (2022) DHARMa: residual diagnostics for hierarchical (multi-level / mixed) regression models. R package version 0.4.6. https://CRAN.R-project.org/package=DHARMa

Hastie TJ, Tibshirani RJ (1990) Generalized additive models. Chapman & Hall, London

Houde ED (1989) Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. Fish Bull 87:471–495

Iles TD, Sinclair M (1982) Atlantic herring: stock discreteness and abundance. Science 215:627–633

Imsland AK, Foss A, Koedijk R, Folkvord A, Stefansson SO, Jonassen TM (2007) Persistent growth effects of temperature and photoperiod in Atlantic cod *Gadus morhua.* J Fish Biol 71:1371–1382

Johannessen A, Blom G, Folkvord A (2000) Differences in growth pattern between spring and autumn spawned herring (*Clupea harengus* L.) larvae. Sarsia 85:461–466

Kjesbu OS, Sundby S, Sandø AB, Alix M and others (2022) Highly mixed impacts of near-future climate change on stock productivity proxies in the North East Atlantic. Fish Fish 23:601–615

Kortsch S, Primicerio R, Fossheim M, Dolgov AV, Aschan M (2015) Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. Proc R Soc B 282:20151546

Lamichhaney S, Fuentes-Pardo AP, Rafati N, Ryman N and others (2017) Parallel adaptive evolution of geographically distant herring populations on both sides of the North Atlantic Ocean. Proc Natl Acad Sci USA 114: E3452–E3461

Langbehn TJ, Aksnes DL, Kaartvedt S, Fiksen Ø, Ljungström G, Jørgensen C, Bates A (2022) Poleward distribution of

mesopelagic fishes is constrained by seasonality in light. Glob Ecol Biogeogr 31:546–561
Ljungström G, Langbehn TJ, Jørgensen C (2021) Light and energetics at seasonal extremes limit poleward range shifts. Nat Clim Change 11:530–536
MacKenzie BR, Ojaveer H (2018) Evidence from the past: exploitation as cause of commercial extinction of autumn-spawning herring in the Gulf of Riga, Baltic Sea. ICES J Mar Sci 75:2476–2487
McPherson LR, Kjesbu OS (2012) Emergence of an oocytic circumnuclear ring in response to increasing day length in Atlantic herring (*Clupea harengus*). Mar Biol 159:341–353
Moritz C, Agudo R (2013) The future of species under climate change: resilience or decline? Science 341:504–508
Mortensen A, Damsgård B (1993) Compensatory growth and weight segregation following light and temperature manipulation of juvenile Atlantic salmon (*Salmo salar* L.) and Arctic charr (*Salvelinus alpinus* L.). Aquaculture 114: 261–272
Mueller J, dos Santos Schmidt TC, Seljestad G, Gröger J, Clemmesen C, Berg F (2023) Analysis of reproductive traits reveals complex population dynamics on a small geographical scale in Atlantic herring. Front Mar Sci 10: 978694
Pecl GT, Araújo MB, Bell JD, Blanchard J and others (2017) Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. Science 355: eaai9214
Pedersen BH (1993) Growth and mortality in young larval herring (*Clupea harengus*); effects of repetitive changes in food availability. Mar Biol 117:547–550
Pedersen BH, Ugelstad I, Hjelmeland K (1990) Effects of a transitory, low food supply in the early life of larval herring (*Clupea harengus*) on mortality, growth and digestive capacity. Mar Biol 107:61–66
Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. Science 308:1912–1915
Pinheiro JC, Bates DM (2000) Mixed-effects models in S and S-PLUS. Springer, New York, NY
Pino Martinez E, Imsland AKD, Hosfeld ACD, Handeland SO (2023) Effect of photoperiod and transfer time on Atlantic salmon smolt quality and growth in freshwater and seawater aquaculture systems. Fishes 8:212
Pörtner HO, Peck MA (2010) Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. J Fish Biol 77:1745–1779
R Core Team (2022) R: a language and environment for statistical computing (version 4.2.2). R Foundation for Statistical Computing, Vienna. http://www.R-project.org
Roberts DE Jr, Harpster BV, Henderson GE (1978) Conditioning and induced spawning of the red drum (*Sciaenops ocellata*) under varied conditions of photoperiod and temperature. J World Aquacult Soc 9:311–332
Saikkonen K, Taulavuori K, Hyvönen T, Gundel PE and others (2012) Climate change-driven species' range shifts filtered by photoperiodism. Nat Clim Change 2:239–242
Smoliński S, Berg F (2022) Varying relationships between fish length and scale size under changing environmental conditions — multidecadal perspective in Atlantic herring. Ecol Indic 134:108494
Stefansson SO, Imsland AK, Handeland SO (2009) Food-deprivation, compensatory growth and hydro-mineral balance in Atlantic salmon (*Salmo salar*) post-smolts in sea water. Aquaculture 290:243–249
Stenevik EK, Hølleland S, Enberg K, Høines Å and others (2022) Predicting density-dependent somatic growth in Norwegian spring-spawning herring. ICES J Mar Sci 79: 1340–1352
Sundby S, Drinkwater KF, Kjesbu OS (2016) The North Atlantic spring-bloom system — where the changing climate meets the winter dark. Front Mar Sci 3:28
Tiedemann M, Nash RDM, Stenevik EK, Stiasny MH, Slotte A, Kjesbu OS (2021) Environmental influences on Norwegian spring-spawning herring (*Clupea harengus* L.) larvae reveal recent constraints in recruitment success. ICES J Mar Sci 78:640–652
Tonheim S, Slotte A, Andersson L, Folkvord A, Berg F (2020) Comparison of otolith microstructure of herring larvae and sibling adults reared under identical early life conditions. Front Mar Sci 7:529
Varpe Ø (2017) Life history adaptations to seasonality. Integr Comp Biol 57:943–960
Wood SN (2003) Thin plate regression splines. J R Stat Soc Ser B Stat Methodol 65:95–114
Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York, NY

Editorial responsibility: Susana Garrido (Guest Editor), Lisbon, Portugal
Reviewed by: 3 anonymous referees

Submitted: April 27, 2023
Accepted: December 27, 2023
Proofs received from author(s): March 11, 2024