Journal of Experimental Marine Biology and Ecology 552 (2022) 151737

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Is it possible to photoperiod manipulate spawning time in planktivorous fish? A long-term experiment on Atlantic herring

Thassya C. dos Santos Schmidt [a,1,2], Florian Berg [a,b,*,1], Arild Folkvord [a,b], Alessandra M.A. Pires [a,c], Valeriya Komyakova [a,d,e], Maik Tiedemann [a], Olav Sigurd Kjesbu [a]

[a] Institute of Marine Research, Bergen, Norway
[b] University of Bergen, Norway
[c] Departamento de Pesca a Aquicultura, Universidade Federal de Pernambuco, Recife, Brazil
[d] Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania, Australia
[e] Centre for Marine Socioecology, University of Tasmania, Hobart, Tasmania, Australia

ARTICLE INFO

Keywords:
Photoperiod
Vitellogenesis
Common garden experiment
Zeitgeber
Planktivorous

ABSTRACT

The oocyte development (vitellogenesis) of individual fish is highly dependent upon their physiology which is influenced by both intrinsic and extrinsic factors. Thus, if individuals encounter poor biophysical conditions, they will likely be unable to reproduce. The photoperiod is an external factor that is constant between years but with increasing intra-annual (seasonal) variation polewards. In high-latitude marine environments, several ecological processes are strongly photic entrained, e.g., the planktonic spring bloom. However, it is still unclear whether day length or planktonic peaks (feeding opportunity) is the main timer or regulator behind gametogenesis not only for teleost piscivores but also for planktivores living in these waters. Hence, we experimentally investigated the role of photoperiod steering vitellogenesis in the planktivorous Atlantic herring (*Clupea harengus*), rearing larvae up to the mature adult stage. We imposed a natural and 6-month offset photoperiod hypothesising that vitellogenesis is entrained by this photic *zeitgeber*. The results of our experiment clearly demonstrated that herring have a strong photic *zeitgeber* acting upon vitellogenesis according to the experienced photoperiod. Thus, the Offset Group showed a displacement in vitellogenesis of 6 months. The second hypothesis that feeding opportunities play a clear role in assisting this photic *zeitgeber* in Atlantic herring could be rejected. This clarification supports that the survival potential of the larvae is the main selection pressure in operation in these respects, i.e., rather than the extent of feeding opportunities of the adults.

1. Introduction

An organism's ability to induce spawning at the most favourable environmental time is critical for the survival and fitness of the offspring (Ims, 1990; Lowerre-Barbieri et al., 2011; Yamahira, 2004). This fine-tuning of egg release is particularly important for high-latitude marine organisms with planktonic larvae due to the relatively short duration of seasonal peaks in planktonic (prey) abundance along with the limited search potential of larvae (Durant et al., 2007). This framework is referred to as either the "critical period hypothesis" (Hjort, 1914) or, more commonly today, "the match-mismatch hypothesis" (Cushing, 1990). While spawning and resulting hatching times for many marine phyla are difficult to predict, today such attempts are further complicated by on-going ocean warming affecting reproductive processes including phenology (Alix et al., 2020; Regnier et al., 2019). Hence, understanding *zeitgeber* – cues that regulate key phenological events such as spawning time in response to photoperiod (day, month, season) as well as, potentially, more variable environmental regulators, such as temperature and food availability (Foster and Kreitzmam, 2005) – could improve our ability to project the level of recruitment success (Regnier et al., 2019; Sundby, 2000). However, in terms of teleosts the underlying information in question is largely based on aquaculture studies and thereby referring to piscivores, as exemplified below. Thus, related information on planktivores, which typically experience more seasonal

* Corresponding author at: P.O. Box 1870 Nordnes, 5817 Bergen, Norway.
E-mail address: florian.berg@hi.no (F. Berg).
[1] The two first authors equally contributed to this study.
[2] Present address: Marine and Freshwater Research Institute, Neskaupstaður, Iceland

https://doi.org/10.1016/j.jembe.2022.151737
Received 29 November 2021; Received in revised form 18 March 2022; Accepted 12 April 2022

variable prey availability, is generally lacking.

Effects of climate fluctuations and change as well as food availability on teleost reproductive phenology have received considerable attention (Alix et al., 2020; Ljungström et al., 2019; Shoji et al., 2011; Wieland et al., 2000). A particular conspicuous topic is that species may show abrupt shifts in spawning seasons (Shoji et al., 2011; Wieland et al., 2000). At high latitudes, the photoperiod defines the timing of seasonal primary and secondary plankton production (Longhurst, 2006; Sundby et al., 2016) but also, physiologically speaking, the onset of gonad maturation (including vitellogenesis) and spawning (Akhoundian et al., 2020; Hansen et al., 2001; Ishikawa and Kitano, 2020; McPherson and Kjesbu, 2012). Consequently, the application of a continuous light regime is a well-developed technique within intensive aquaculture to, as far as possible, block maturation to enhance filet production (Akhoundian et al., 2020; Good and Davidson, 2016; Hansen et al., 2001; Taranger et al., 2015). An alternative aquaculture protocol enforces either a compressed or extended photoperiod to enable "year-round production of gametes" (Norberg et al., 2004). Fundamentally speaking, the individual, temperate fish apparently relies upon specific decision windows within the photoperiod to either proceed or not with gametogenesis. So, autumn equinox (shorter days) triggers the onset of maturation in e.g. Atlantic cod (*Gadus morhua*) (Kjesbu et al., 2010b; Woodhead and Woodhead, 1965), haddock (*Melanogrammus aeglefinus*) (Migaud et al., 2010), halibut (*Hippoglossus hippoglossus*) (Methven et al., 1992), and mackerel (*Scomber scombrus*) (dos Santos Schmidt et al., 2021b), whereas spring equinox (longer days) plays the same role for salmonids (*Salmo*, *Onchorhynchus,* and *Salvelinus* spp.) (Migaud et al., 2010) and the present model species: Atlantic herring (*Clupea harengus*) (McPherson and Kjesbu, 2012).

Atlantic herring is a planktivorous (Bachiller et al., 2016), capital breeder (Kennedy et al., 2011) that depends on the spring-summer plankton production for accumulation of energy for a range of metabolic activities as well as major gonad growth (Kurita et al., 2003; Sundby et al., 2016). As a visual foraging fish targeting mesozooplankton, herring requires sufficient amount of light; any restriction may act as a barrier in terms of poleward displacement during climate change (Ljungström et al., 2021). Atlantic herring, as a species, spawns throughout the entire year, but the spawning time varies markedly between stocks (dos Santos Schmidt et al., 2021a; Parrish and Saville, 1965). As a result, herring is predominately split into either spring or autumn spawners which can be genetically discriminated (Kerr et al., 2019; Lamichhaney et al., 2017). Still, vitellogenesis of both spawning types commences near spring equinox, although on average 50 days earlier for autumn spawners (McPherson and Kjesbu, 2012). So, while autumn spawners will typically reproduce within the same year, spring spawners will reproduce the year after (dos Santos Schmidt et al., 2017). The dynamics between any sympatric spring and autumn spawning are, however, variable and the predominating type can change over time as observed in the Baltic Sea (autumn to spring (MacKenzie and Ojaveer, 2018)) or in the Northwest Atlantic (spring to autumn (DFO, 2018)). In this study, we focused on a geographical location where both spawning types co-occur during the entire year utilizing the same spawning grounds. Individuals switching between hatching and spawning season and/or genetic determined spawning season have been previously identified in that area (Berg et al., 2021). The dominating population that spawns in spring, typically from March–May (Berg et al., 2021), was selected as the present study model. However, the underlying mechanisms for any shift in spawning type (McQuinn, 1997) and how they influence the maturation development remains unknown.

When aiming at predictive models for reproductive timing, it is important to separate various environmental cues and understand the isolated importance of each prior to investigating combined effects. Therefore, the objective of this study was to evaluate how spring spawning herring, grown-up in captivity from the larval stage over 3.5 years at 60°N, respond to changes in daylength, when all other environmental effects are kept constant as far as possible. We imposed a natural and 6-month offset photoperiod expecting that the onset of maturation between these two experimental groups should show a displacement in maturation by 6 months as well. We also hypothesized that this photic *zeitgeber* might be modulated or assisted by the natural time of seasonal feeding (Foster and Kreitzmam, 2005), in herring principally restricted to summertime when the planktonic food is available in the surface layer (Bachiller et al., 2016; Bachiller et al., 2018). Any impact of the photic *zeitgeber* within that specific calendar window might be curtailed by the increasing presence of extreme long days northwards (Foster and Kreitzmam, 2005), reaching 24 h (polar day) at 66°N (Foster and Kreitzmam, 2005; Sundby et al., 2016). If so, maturing individuals in the presently established Offset Group would be challenged by either tracking the imposed photoperiod (photic *zeitgeber*) or the natural timing of prey (non-photic *zeitgeber*). Logically, a piscivorous species will not encounter this conflict between such entrainment signals as their prey is typically available throughout the whole year (Kjesbu et al., 2014).

2. Materials & methods

2.1. Ethics approval

The below-outlined larval rearing and following on-growth experiments were reviewed and approved by the FOTS Norwegian Food Safety Authority (ID-8459).

2.2. Fish rearing

For the subsequent reproductive phenology experiment, coastal adult spring spawning herring were sampled on 25 April 2016 (60°34′N and 5°0′E), west of Bergen, Norway. Individuals were caught by gillnets during the night and collected the next morning. Still alive herring were terminally anesthetized (with Finquel), stored in individual plastic bags and transported on ice in a cooling box to the experimental laboratory within approximately two hours after retrieval of gillnets.

Fertilizations were conducted at a salinity of 16 psu to achieve high fertilization rates (Berg et al., 2019). The ambient water temperature, typical for these waters, was approximately 9 °C. After 30 min, the egg plates were transferred into 35 psu for further incubation until hatching. One female was separately fertilized with two different males. The hatching date of larvae (defined as the day when 50% were hatched) was 9 May 2016. Larvae of each cross were initially reared in separate green, squared tanks (1 × 1 m) containing 300 l of water. Both tanks were exposed to a constant 12 h day/night light regime during the larval phase of the experiment.

Larval stocking density was initially 734 and 1000 larvae, respectively. Larvae were fed daily with natural filtered zooplankton in ad libitum (2000 prey/l). The natural zooplankton consisted mainly of different copepods and their nauplii stages and were stored in their original water (marine conditions) for a maximum of one day. Each day the remaining plankton was counted within each tank, and plankton was added to reach the same level of prey per litre. 133 days post hatching (DPH), the herring larvae from the two tanks ($n = 355$) were combined in a single tank and weaned onto dry feed (AgloNorse 600–900 μm, protein: 58–60%, fat: 17–20%). Herring were fed ad libitum throughout the entire experiment and the amount of food was adjusted to the size of the fish.

After autumn equinox (22 September 2016), the light regime was set to follow the natural light cycle at the sampling locations of the parental herring population (60°N). On 28 September 2016 (142 DPH), all juvenile herring were separated in two different tanks: one tank ($n = 151$) followed the natural light regime (Natural Group) whereas the light regime of the second tank ($n = 155$) was displaced by 6 months (Offset Group) (Fig. 1). In both set-ups, all individuals experienced the same temperature, from 8.5 to 9.3 °C (mean ± sd: 8.9 ± 0.2 °C) and salinity (35 psu). During the next four months only one tank per light regime was

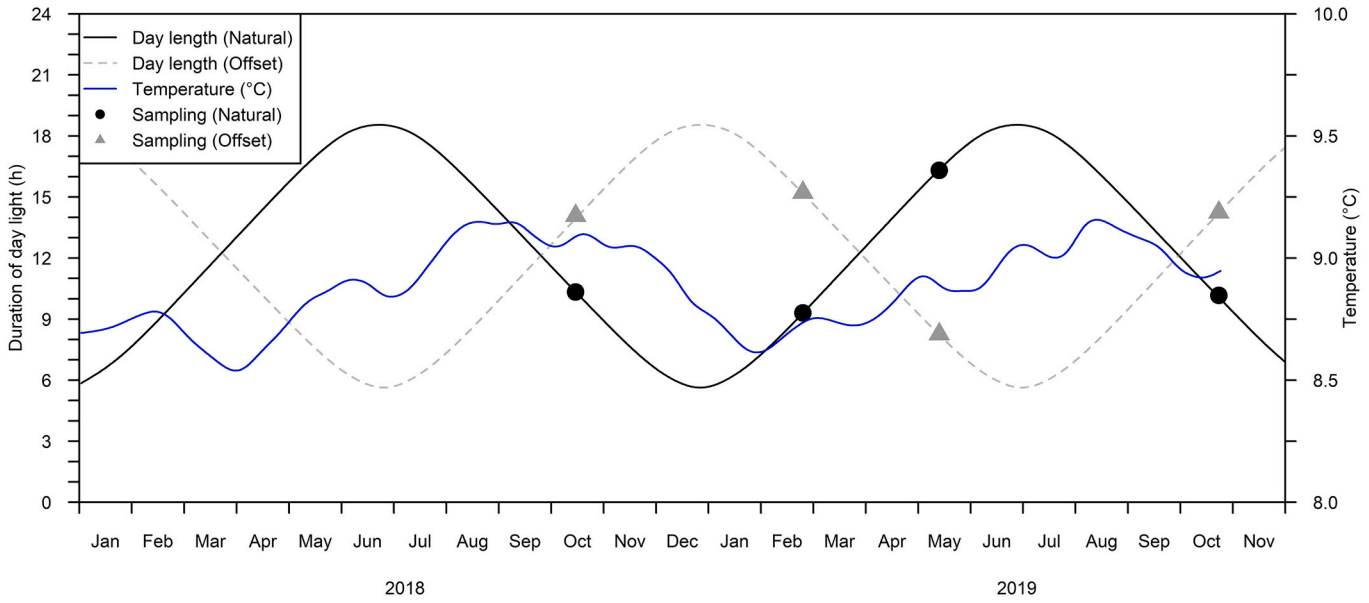

Fig. 1. Experimentally introduced natural and 6-month offset light cycle at 60°N during the latter half of the experiment, with an approximately constant water temperature. Sampling points are indicated.

used. However, as all other rearing conditions as such were almost identical, the tank effect during this limited period of four month is considered minor, i.e., not due to any physicochemical differences between these two tanks.

On 31 January 2017 (267 DPH) the herring were transported from facilities in Bergen to Matre (~85 km/~2 h distance by car; see Supplementary Information for more details about this transport). At Matre, the light regime and temperature remained the same as before transport (Fig. 1), separating the herring into two replicate tanks (2 × 2 m, ~3500 l) per light regime. The initial experimental population under the natural light regime consisted of 146 (72 + 74 per replicate) individuals and 148 (75 + 73 per replicate) under the offset light regime. The experiment ended on 14 October 2019.

2.3. Sampling procedure and statistical analyses

To track gonad maturation, we successively sampled at four time points (Table 1; Fig. 1). The first three sampling points were used to monitor health status, body condition and growth, as well as establishing oocyte development trajectories. The final sampling point (the main sample) was analysed to address our two hypotheses. Hence, the sample size in the first three instances was limited, i.e., 10 (or in one case 11) random specimens from each treatment (~5 from each replicate tank; Table 1), to assure that all tank replicates contained a sufficient number of individuals at the final sampling point. This design implied that all remaining alive specimens (n = 116; Table 1) were processed at the end of the experiment in October 2019. Hence, the main results presented below are based on the final sample. An exception is the oocyte development tracking sub-study to optimise when the experiment should be terminated in view of data relevance (cf. hypotheses), but these data also formed key baseline reproductive information. The terminally anesthetized specimens were weighted (W) to nearest 0.1 g and total length (TL) measured to nearest mm. Sex and visual maturation stage were also determined (Mjanger et al., 2020). Gonads were weighed (GW), and ovaries preserved in plentiful of phosphate-buffered 3.6% formaldehyde for further image and histological analyses. All detailed analyses were performed exclusively on females, since male herring remain in near spawning conditions for

Table 1
Overview of herring sampling scheme by period and light regime. Mean (± standard deviation [sd]) of consulted phenotypic parameters are also presented. In terms of the offset light regime the artificially experienced (experimental) month – in terms of daylength – is added as well. N = Number of observations; TL = Total length, W = Whole body weight, GSI = Gonadosomatic index, and K_n = Relative condition.

Natural date	Experimental month	Light regime	Sex	N	TL mean ± sd	W mean ± sd	GSI mean ± sd	K_n mean ± sd
11 October 2018	October	Natural	♀	3	22.20 ± 2.00	95.40 ± 34.47	0.41 ± 0.08	1.05 ± 0.06
11 October 2018	October	Natural	♂	7	23.46 ± 1.59	116.97 ± 32.11	0.23 ± 0.08	1.05 ± 0.07
11 October 2018	April	Offset	♀	3	23.17 ± 2.68	121.47 ± 74.61	1.26 ± 1.05	1.07 ± 0.25
11 October 2018	April	Offset	♂	7	22.17 ± 1.63	92.36 ± 26.39	1.15 ± 1.25	1.04 ± 0.14
18 February 2019	February	Natural	♀	9	24.26 ± 1.55	121.52 ± 17.62	1.92 ± 0.68	1.00 ± 0.17
18 February 2019	February	Natural	♂	2	23.00 ± 2.55	91.70 ± 46.53	1.05 ± 1.24	0.87 ± 0.09
18 February 2019	August	Offset	♀	4	22.48 ± 1.18	80.85 ± 8.32	0.68 ± 0.08	0.89 ± 0.09
18 February 2019	August	Offset	♂	6	22.40 ± 1.84	92.37 ± 35.11	0.25 ± 0.09	0.98 ± 0.14
7 May 2019	May	Natural	♀	6	22.95 ± 1.30	100.10 ± 19.47	2.72 ± 1.14	1.01 ± 0.11
7 May 2019	May	Natural	♂	4	23.45 ± 1.58	107.65 ± 37.43	3.63 ± 2.94	0.96 ± 0.14
7 May 2019	November	Offset	♀	5	23.16 ± 1.44	99.52 ± 20.57	1.14 ± 0.67	0.96 ± 0.05
7 May 2019	November	Offset	♂	5	23.38 ± 1.00	106.28 ± 15.98	0.64 ± 0.59	0.99 ± 0.05
14 October 2019	October	Natural	♀	28	24.53 ± 1.51	126.79 ± 35.31	1.57 ± 1.43	0.96 ± 0.12
14 October 2019	October	Natural	♂	22	23.53 ± 1.35	113.66 ± 26.44	2.41 ± 3.46	1.03 ± 0.15
14 October 2019	April	Offset	♀	37	24.29 ± 1.37	126.92 ± 28.53	4.13 ± 1.78	1.01 ± 0.08
14 October 2019	April	Offset	♂	29	23.79 ± 1.56	121.08 ± 31.39	7.43 ± 3.60	1.04 ± 0.08

several weeks (Slotte, 1999), and finer temporal scale maturation analysis was not feasible. However, GSI estimates were used to provide an indication of the reproduction development of males. Furthermore, female fecundity estimates are applicable for stock assessments which is not the case for males (Witthames et al., 2009).

The weight-at-length relationship was established for both sexes combined ($W = 5.2 \times 10^{-4} \times TL^{3.88}$, $R^2 = 0.826$, $n = 177$, $p < 0.001$, Fig. S1), due to no apparent difference attributed to sex as such ($p = 0.087$). Since the exponent of the relationship deviated from 3 (confidence interval: 3.61–4.14), we instead opted for the use of the relative condition factor (K_n). The adopted K_n formula ($K_n = W_{observed}/W_{predicted}$) calculates the difference between observed and predicted body weight (Le Cren, 1951; Wuenschel et al., 2019). The gonadosomatic index (GSI, %) was estimated as: $GSI = 100 \times GW/W$.

A general linear model was performed to test for any between-light-regime slope and intercept differences in reproductive parameters as a function of biometric (phenotypic) parameters. Two-way ANOVA was carried out to contrast potential fecundity among months (sampling time) and oocytes stages. Final TL, W, GSI, and K_n were used in a Principal Component Analysis (PCA) to investigate any phenotypic characteristics within each light regime treatment (defined as grouping variable). Even though GSI and K_n were derived from consecutive somatic measurements, they were evidently uncorrelated ($p > 0.05$) and therefore both entered in this sex-unspecific PCA (Table 1). More information about the phenotypic characteristics of both sexes and the sampling scheme can be found in the Supplementary Material. All statistical analyses and figure productions were done in R (version 4.0.4) (R Core Team, 2020).

2.4. Ovarian analyses

These samples were examined by both wholemount (whole oocyte) and histological (sectioned oocyte) techniques.

2.4.1. Wholemount

The wholemount procedure was based on the methodology described by Thorsen and Kjesbu (2001) and Anderson et al. (2020). A small subsample was transferred to a vial filled with 3.6% buffered formaldehyde, oocytes dissociated by an ultrasonic pen for around 10 s and stained in 2% toluidine blue and 1% sodium tetraborate. The surplus stain was removed by washing the samples several times in the formaldehyde solution. Oocytes of each sample were thereafter transferred into a petri dish and three random images taken. Individual oocytes were automatically measured using ImageJ and ObjectJ plug-in. An oocyte size of 100 μm was set as lower threshold value as even tinier oocytes were likely lost in cases during this sample preparation (Anderson et al., 2020). Each oocyte diameter was based on short and long axis measurements. The resulting mean oocyte diameter (OD) and leading cohort, defined as the 10% largest oocytes diameter, were then calculated.

2.4.2. Histology

Another subsample of each ovary was used for histological analyses. This tissue was dehydrated in ascending ethanol concentration (from 70% up to 100%), embedded and mounted in Technovit® 7100. The following 4-μm thickness sections were stained in toluidine blue. All slides were scanned using a slide scanner (Hamamatsu S60) with a × 40 objective and a resolution of 220 nm/pixel.

Ovaries were classified microscopically in the traditional way, i.e., based on the most advanced oocytes, split into previtellogenic (PVO), cortical alveoli (CAO), early vitellogenic (EVTO; primary and secondary vitellogenic oocytes combined), late vitellogenic (LTVO), and germinal vesicle migration oocyte (GVMO) stage (Brown-Peterson et al., 2011). Atretic oocytes were staged as early alpha (EA), late alpha residual chorion (LARC), and late alpha no chorion (LANC) (Kjesbu et al., 2010a). Relative intensity of atresia (A_{RI}, in %) was estimated as $A_{RI} = 100 \times$ N atretic oocytes/(N atretic + N normal oocytes).

2.4.3. Fecundity

Potential fecundity (F_P) was given as: $F_P = OW \times 7.474 \times 10^{10} \times OD^{-2.584}$ (dos Santos Schmidt et al., 2017), where OW is ovary weight. The F_P calculation was restricted to samples with oocytes diameter greater than 240 μm, i.e., from the CAO stage onwards (Ma et al., 1998). Hence, individuals showing PVO as the most advanced stage were excluded from this F_P work.

Realized fecundity (F_R), i.e., after correcting for atretic loss, was: $F_R = F_P - N_{es}$, where $N_{es} = F_P \times A \times D/T$, with A as the relative intensity of atresia, D number of days from sampling date until spawning, i.e. when oocytes reach the maximum diameter (1200 μm), and T the atretic turnover rate, i.e. the alpha atresia life span. The turnover rate was set at five days in this calculation exercise (Kurita et al., 2003), based on the temperature used during the experiment.

3. Results

3.1. Phenotypic traits by light regime

The PCA indicated a slight separation of phenotypic trait data points of individuals held under the two light regimes (Fig. 2). Adding sex as grouping variable did not yield any addition explanation (Fig. S2). The first two axis explained 86.2% of the variation. The noted differences were mainly attributed to GSI and K_n, with individuals from the Offset Group generally showing higher GSI and K_n (Table 1), further addressed below. TL and W did not contribute to any further separation of the two experimental groups.

3.2. Female-specific phenotypic traits by light regime

Final K_n for Natural Group females ranged from 0.70 to 1.17, and from 0.89 to 1.20 for the Offset Group. K_n regressed on the corresponding TL showed a significant difference among treatments (Linear model, slope $p = 0.017$), with a positive trend for the Natural Group whereas a negative trend for the Offset Group (Fig. 3A). A negative trend between K_n and TL was also observed in February and May 2019, but then for both groups, though sample sizes were too low to clarify if this was a robust pattern (Fig. S3).

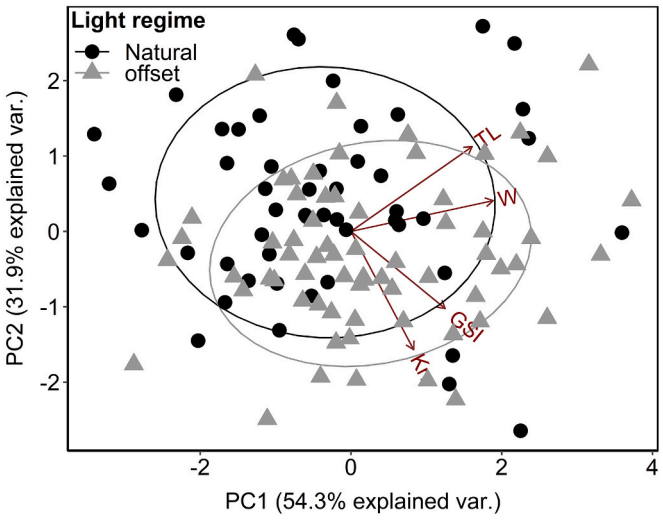

Fig. 2. Principal Components Analysis of herring phenotypic trait parameters – total length (TL), whole body weight (W), gonadosomatic index (GSI), and relative condition (K_n) – by light regime at experimental end (October 2019; $N = 116$). The ellipse shows the normal probability of 68% for each group. Loadings are given in Table S1.

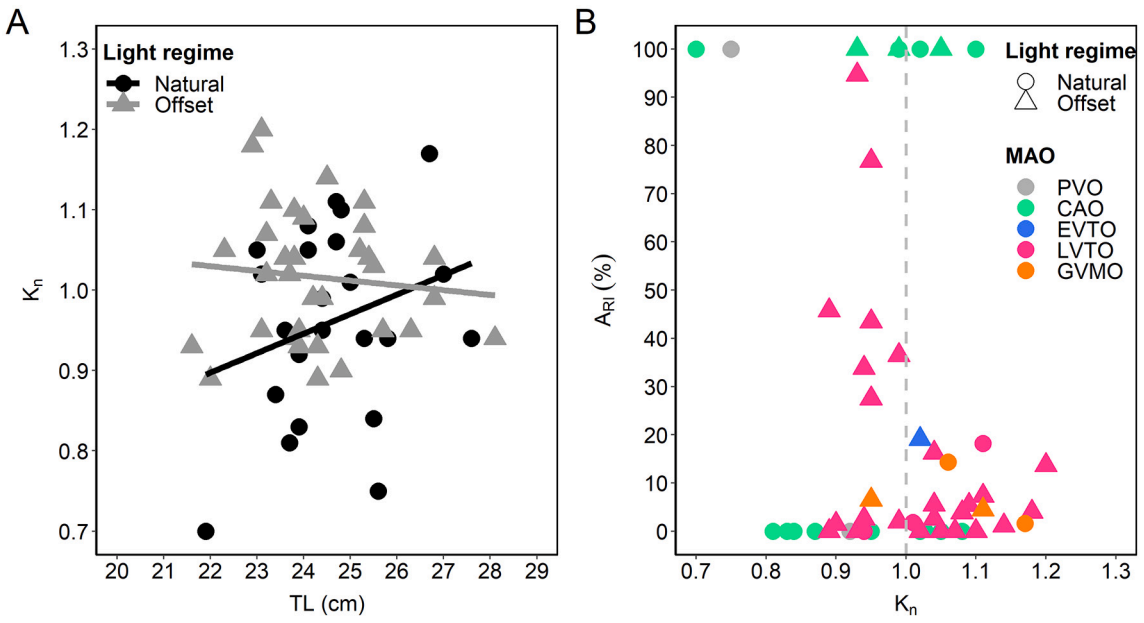

Fig. 3. Female-specific relationship at experimental end (October 2019) between (A) relative condition (K_n) and total length (TL) and (B) between relative intensity of atresia (A_{RI}) and K_n, split by light regime. Individuals were classified according to the most advanced oocyte (MAO) stage: previtellogenic (PVO), cortical alveoli (CAO), early (EVTO) and late vitellogenic (LVTO), and germinal vesicle migration (GVMO) stages. Vertical line (panel B) indicates the threshold value between individuals in good ($K_n \geq 1.0$) and poor ($K_n < 1.0$) body condition (Le Cren, 1951) (Natural Group: $N = 22$; Offset Group: $N = 37$ (Table 1)).

3.3. Prevalence and intensity of atresia by light regime

Atresia (A_{RI}) was recorded at all four sampling points (Fig. 3B; Fig. S3). At experimental end, A_{RI} generally diminished at better body condition (Fig. 3B), however, in three of these relatively fatter individuals (Natural Group: $N = 2$, Offset Group: $N = 1$) apparently all CAO were resorbed; the ovary displayed 100% atresia. A total of 10 Offset Group individuals in vitellogenesis (EVTO and LTVO stages) showed $A_{RI} > 20\%$, 9 out 10 being in bad condition ($K_n < 1.0$). In the Natural Group, five individuals were recorded with complete atresia ($A_{RI} = 100\%$) – spanning a broad range in K_n – one in the PVO stage and four in the CAO stage (Fig. 3B). This series of A_{RI} analyses included in total 65 individuals (Table 1).

3.4. Oocyte size frequency distributions by light regime

Oocytes exhibited a continuous development throughout the experiment. However, some clear differences were found between Natural and Offset Groups, using (natural) calendar day as reference (Fig. 4). At the first sampling point (11 October 2018) (Table 1), the three females examined in the Natural Group only had PVO (Fig. 4A) whilst the corresponding three females in the Offset Group showed either PVO, CAO or LVTO (Fig. 4B). Contrarily, at the second sampling point (18 February 2019) (Table 1) oocytes in the Natural Group were more advanced (Fig. 4C vs. D). At the third sampling point (7 May 2019) (Table 1), this situation still prevailed (Fig. 4E vs. F). However, at the final sampling point (14 October 2019) (Table 1), the Offset Group had generally become much more advanced (Fig. 4G vs. H). More specifically, around two-third of the females ($N = 20$) collected in the Natural Group were in PVO and CAO stages and the remaining ones ($N = 8$) in LVTO or GVMO (Fig. 4G), whereas all females collected in the Offset Group ($N = 37$) were developing, i.e. in CAO – GVMO stages (Fig. 4H). No spawning markers (postovulatory follicles) were found in any female.

Some anomalous cytoplasmic results were detected, especially at experimental end (October 2019), when 8 out 65 females (Table 1) in both light regimes showed extremely large CAO (average range 459–764 μm) (Fig. 4G and H). Evidently, these oocytes continued to grow without incorporating any vitellogenin (Fig. 5B). This pattern was especially noticeable in the Offset Group ($n = 5$, Fig. 4H). Relative condition in these specimens varied from slightly poor to good, i.e. from 0.87 to 1.05 (mean ± sd = 0.98 ± 0.06).

3.5. Fecundity

No difference was detected between light regimes in terms of the relationship between F_P and TL (Linear model, slope $p = 0.652$) (Fig. 6). Generally, females in the GVMO stage showed at that time, i.e., at experimental end, low F_P compared to other stages (Fig. 6A and B). No clear difference in F_P versus TL occurred among oocyte stages split by month (two-way ANOVA, $F = 0.571$, $df = 73$, $p > 0.05$ for both light regimes) (Fig. S5). This finding can, however, be related to the low number of observations at the first three sampling points (Table 1). In general, no significant different in F_P was recorded between light regimes and sampling months (Linear model, $p = 0.526$) (Fig. 7A). The grand mean F_P of the Natural and Offset Group was 28.7 thousand and 25.1 thousand oocytes, respectively. The F_R, on the other hand, could be markedly lower (up to one forth at a given sampling point), mainly for the Offset Group (Kruskal-Wallis, $p > 0.001$) (Fig. 7B). The peak decline in F_R for the Offset Group happened in October 2018 and 2019, and May 2019 for the Natural Group (Fig. 7B).

4. Discussion

The outcome of this long-term common garden experiment clarified that our principal hypothesis could be accepted, i.e., a 6-month offset photoperiod results in a corresponding displacement of the reproductive cycle. Hence, we found that the egg production of Atlantic spring spawning herring is closely linked to the photic timing of the spring bloom (Sundby et al., 2016). This was also the case for the male's reproduction cycle as indicated by differences in gonadosomatic index between light regimes. One can thereby assume that this reproductive trait is under high selection evolutionary pressure (Durant et al., 2007). Thus, day length appears as the main entrainment signal in line with general principles within life sciences (Foster and Kreitzmam, 2005). Using, as presently done, naïve specimens (larvae) followed by manipulation of the photoperiod appeared crucial because herring usually do

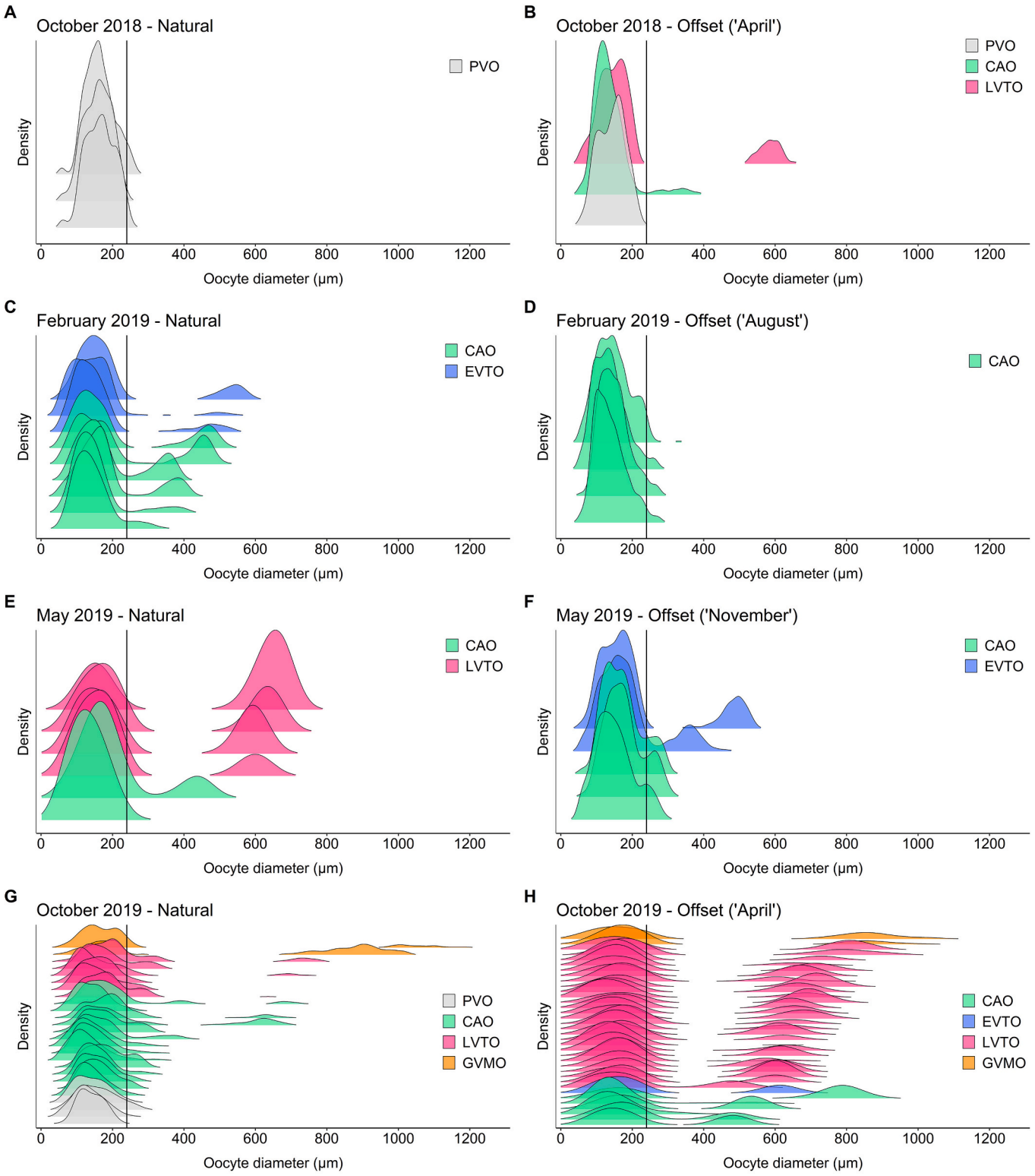

Fig. 4. Smoothed oocyte size frequency distribution by month and light regime. Samples within each panel are organized in ascending order based on maximum oocyte diameter, i.e. advancement in oogenesis: previtellogenic [PVO], cortical alveoli [CAO], early [EVTO] and late vitellogenic [LVTO], and germinal vesicle migration [GVMO]. The vertical line indicates the normal threshold value for the appearance of the CAO stage (OD = 240 µm) (Ma et al., 1998). In each panel, the calendar sampling month is presented inside parenthesis, whereas the quotation marks refer to the artificially experienced month – in terms of daylength – with reference to the Offset Group (e.g. 'April').

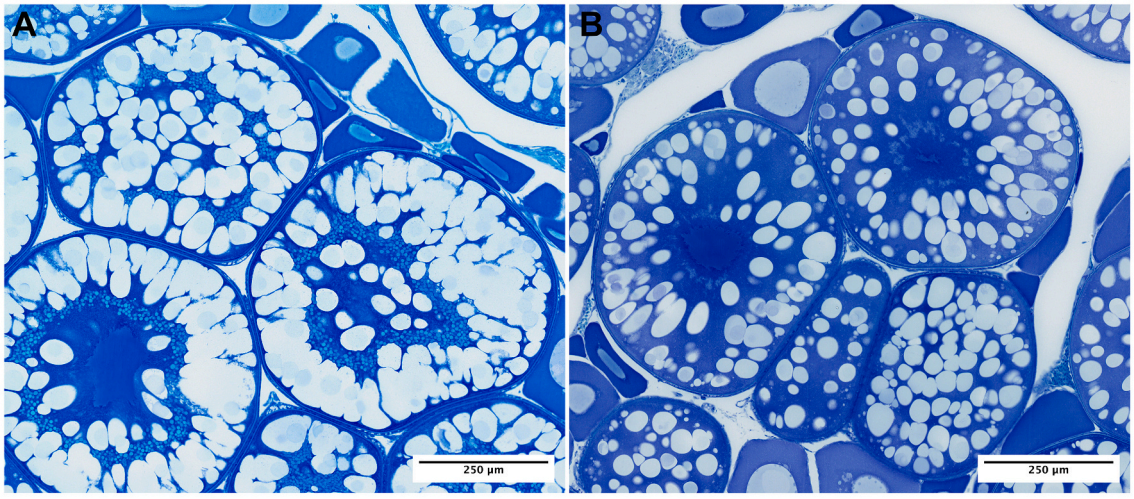

Fig. 5. Herring photomicrographs showing cytoplasmic differences between (A) oocytes in true vitellogenesis and (B) oocytes in the preceding cortical alveoli stage but of exceedingly large size. Scale bar is presented in each image.

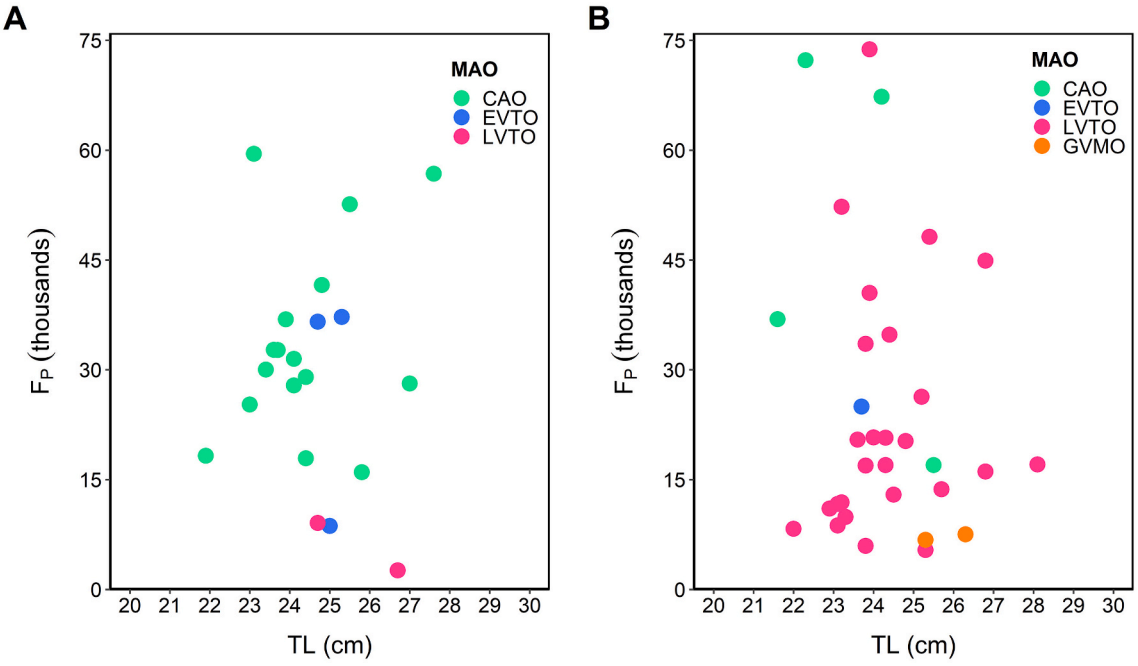

Fig. 6. Potential fecundity (F_P) in the Natural (A) and Offset Group (B) versus total length (TL) at experimental end (October 2019). The most advanced oocyte stages (MAO) (cortical alveoli [CAO], early [EVTO] and late vitellogenic [LVTO] and germinal vesicle migration [GVMO]) are annotated.

not change spawning season after first spawning (van Damme et al., 2009). When interpreting and discussing the results in the following, we focus on three main aspects; firstly, the experimental design, secondly the linkage between experiments and the wild, and thirdly in view of the broader perspective, as summarized in the Conclusion section.

4.1. Experiment design

Conducting long-term experiments are always challenging, and the results cannot be directly compared with field observations. Despite these caveats, we were able to rear spring-spawning herring under two different light regimes over 3.5-years until sexual maturation. Our experimental fish, independent of light regime, were approximately 6–8 weeks delayed in their oocyte development compared to field observations; spawning time would have been ca. 2 months after their own hatching time (see 2 Materials and Methods). This delay of oocyte development can be explained by the fact that these are experimental fish that had suboptimal growth where their maximum size was limited due to a tank size effect. Further, additional seasonal environmental factors, such as temperature, which might influence the spawning time of herring were by design excluded. The spawning time of Atlantic herring may vary noticeably from one year to the next year and might result in different reproductive success (Polte et al., 2021; Slotte et al., 2019). Thus, our results might indicate that constant environmental factors of the common garden experiment are not optimal for the reproductive development of Atlantic herring. This is in line with a previous common garden experiment but under a constant light regime where a similar trend of delayed spawning time was observed (Berg et al., 2019; Tonheim et al., 2020). However, as no reproductive (oocyte growth) information was presented no direct comparison can be made

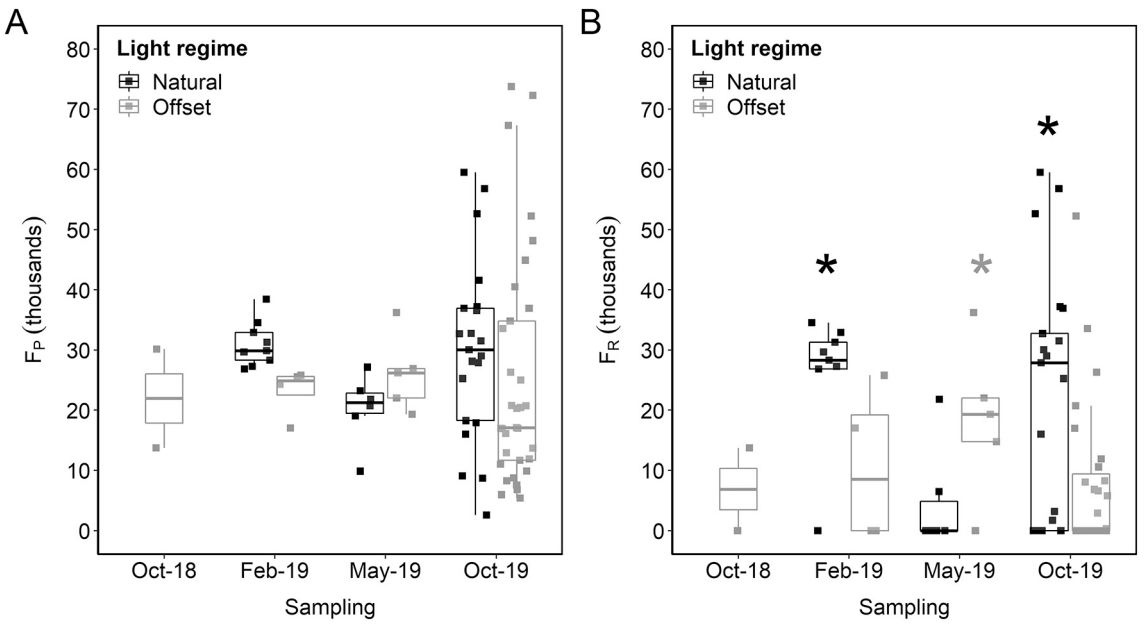

Fig. 7. Potential fecundity (F_P) (A) and realized fecundity (F_R) (B) of the Natural and Offset Group at different sampling points. Significant differences between light regimes within a sampling were marked with an asterisk (*) coloured by the light regime with higher values. Fecundity data for the Natural Group in October 2018 were excluded since all females had not progressed beyond the PVO stage (cf. Fig. S4).

with the current results.

Interestingly, the two different light regimes resulted in similar phenotypes. So, except for oocyte development trajectories, we could not find any differences between the two groups in terms of body length, weight or condition. Here it should be noted that all individuals were fed ad libitum and received the same amount of food independent of day length. Also, they reached their experimental maximum size relatively early in the experiment and thereby could divert the surplus energy into either growth in body condition and/or reproductive investment. Both in the Natural and Offset Group, individuals gathered relatively high body reserves throughout the year, even during the winter period. However, in general, it seems that the Offset Group benefited from the 6-month displacement; these individuals had 6 months more to grow prior to investing in their reproduction. All individuals lived the first half-year under a 12 h light: 12 h dark regime before the local photoperiod was entered or displaced, as previously mentioned. It can be asked if the Offset Group would have shown a similar maturation development if the light conditions had been manipulated from hatching onwards. Further experiments should also investigate if similar findings apply for autumn-spawners in view of that wild herring are able to switch between spawning seasons (Berg et al., 2021): some of the Natural Group individuals from the final October sample showed quite developed oocyte and thereby were close to spawning, indicating switching of the spawning season (McQuinn, 1997).

One limitation of this experiment is the use of a single mother and two fathers. Consequently, all individuals used in this study were full- or at least half-siblings which should be considered when interpreting the results. However, this experimental design purposely reduced the environmental parental effect, on purpose. Parental effects will affect somatic characteristics (Bang et al., 2006; Berg et al., 2019) but not necessarily the onset and development of maturation. The slight variation in experimental temperature mimicked the variation in natural temperature with reference to the nearby deep fjord. Thus, if variation in temperature would be the driving factor in terms of maturational development, both the Natural and Offset Group should have followed the same trajectories. In previous experiments, a constant temperature did not negatively affect the maturation development of Atlantic spring-spawning herring (Berg et al., 2019).

4.2. Oocyte development

Females in the Natural Group followed the expected oocyte growth trajectory for a spring spawner, though with exceptions. These special circumstances included a few females in February and May 2019 which were in a more advanced stage than, for instance, would be seen in Norwegian spring-spawning herring (NSSH) at that time in the year (dos Santos Schmidt et al., 2017). At experimental end in October 2019, a mix of oocytes stages was reported in the Natural Group, with most individuals in the previtellogenic and cortical alveoli stage, though some in the late vitellogenesis and germinal vesicle migration stage. Wuenschel and Deroba (2019) also detected adult spring spawners in previtellogenesis in October. However, most Natural Group individuals should have been in vitellogenesis as the reproduction cycle typically commenced in February – May, in line with the one of NSSH (Kurita et al., 2003; McPherson and Kjesbu, 2012). PVO- and CAO-staged females at experimental end in this Natural Group had thin ovary wall and no spawning markers (e.g., postovulatory follicles), indicating they still were sexually immature or on the way to become sexually mature, respectively. Herring oocytes are reasonably quickly reabsorbed with an atretic duration from 4.5 to 7.2 days (Kurita et al., 2003), whereas postovulatory follicles, on the other hand, can last for a long period, up to around 3 months (Wuenschel and Deroba, 2019). Therefore, due the relatively long span in time between the last two samplings (May and October 2019), we cannot firmly say whether any individuals in the Natural Group de facto spawned around summertime or not.

The applied displaced photoperiod in combination with the natural one suggests that year-round production of gametes is also feasible for planktivores in an aquaculture setting; the Natural Group showed LVO in May (2019) and the Offset Group similarly in October (2019), though the latter time corresponds to 'April' in terms of the artificially experienced day length. Thus, we can conclude that spring equinox (increasing day length) stands its advocated role as photic trigger (Kurita et al., 2003; McPherson and Kjesbu, 2012), though several of the oocyte size frequency distributions (OSFD) are difficult to interpret, e.g. the 'August' (February 2019) OSFD should have displayed more advanced oocytes (dos Santos Schmidt et al., 2017).

4.3. Condition, atresia, and fecundity

"The concept of threshold" (optimum fitness), represented by e.g. body growth and condition, feeding success, and energy availability, determining the subsequent commitment to gametogenesis (ending with sexual maturation) is key within reproductive physiology, as originally developed for *Salmo salar* (Metcalfe, 1998) and thereafter generalized to other species (Migaud et al., 2010). Thus, the projected trajectory from this sensitive window should ultimately define whether the individual in question becomes sexually mature or not (Saborido-Rey and Kjesbu, 2005). Several females in both light regimes showed poor condition ($K_n < 1$) and these poor-condition herring, in general, had high intensity of atresia. Herring in poor condition spawn later, show increased level of atresia (Óskarsson et al., 2002), and reduced fecundity (dos Santos Schmidt et al., 2017). A clear drop in realized fecundity compared to potential fecundity was noticed across the experiment. This decline was especially seen in the Offset Group. Herring in both light regimes were continuously fed during the experiment, so unsuccessful acclimation to the tank situation rather than any lack of food seems to be the underlying reason behind low-condition individuals and their high atresia.

5. Conclusion

To the best of our knowledge, this is the first experiment investigating if the onset of gametogenesis and sexual maturation of a high-latitude, planktivorous teleost can be manipulated by changing the photoperiod. The results of our experiment support our hypothesis as these findings demonstrate that the planktivorous Atlantic herring respond in very much the same way as the well-studied, piscivorous Atlantic cod (Norberg et al., 2004), both cold-temperature species. However, we would have expected that the fact that the Offset Group artificially experienced short days (experimental winter) at a time in the year when there is normally plentiful of zooplankton (prey) in the wild (natural summer) would have impacted the reported biometrics in one way or the other. Both experimental groups were fed throughout the experiment, but the term *zeitgeber* implies an imprinted "clock" running even without the evolutionary-established entrainment signal (or synchronizing agent) necessarily being in place all the time (Foster and Kreitzmam, 2005). In effect, we thus reject the second hypothesis that feeding opportunities play a clear role in assisting the photic *zeitgeber* in Atlantic herring. This clarification supports that the survival potential of the larvae is the main selection pressure in operation in these respects, i.e., rather than the extent of feeding opportunities of the adults.

Funding

The experiment and production of this manuscript was supported by the project *Recruitment Dynamics of Commercially Important Fish Species in Changing NE Atlantic ecosystems* (RECNOR, no. 14861), *Climate and Vital Rates of Marine Stocks* (CLIMRATES, no. 15205), both funded by the Norwegian Fisheries Research Sales Tax System (FFA), and *Genetic Adaptations Underlying Population Structure in Herring, Clupea harengus* (GENSINC, no. 254774), funded by the Research Council of Norway.

Author contribution

Conceptualization: OSK and AF.
Designed experiment: AF, FB, VK, and OSK.
Laboratory analyses: TCdSS, FB, AMAP, and MT.
Performed data analysis: TCdSS and FB.
Wrote the paper: TCdSS, FB, and OSK, with contribution of all authors.

Declaration of Competing Interest

The authors declare no competing interests.

Acknowledgments

The authors thank all technicians from the Institute of Marine Research in Matre and the University of Bergen being involved and conducting the experiment. The authors thank Martina H. Stiasny (University of Southampton) for her help during early discussion.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2022.151737.

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