Intra-population variation in reproductive timing covaries with thermal plasticity of offspring performance in perch *Perca fluviatilis*

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### Abstract

1. Life history theory posits that organisms should time their reproduction to coincide with environmental conditions that maximize their fitness. Population-level comparisons have contributed important insights on the adaptive value of reproductive timing and its association to environmental variation. Yet, despite its central role to ecology and evolution, the causes and consequences of variation in reproductive timing among individuals within populations are poorly understood in vertebrates other than birds.

2. Using a combination of observational field studies and a split-brood experiment, we investigated whether differences in breeding time were associated with changes in hatching success, reproductive allocation and reaction norms linking offspring performance to temperature within an anadromous Baltic Sea population of perch *Perca fluviatilis*.

3. Field observations revealed substantial variation in reproductive timing, with the breeding period lasting almost 2 months and occurring in temperatures ranging from 10 to 21°C. The hatching success of perch decreased as the reproductive season progressed. At the same time, the reproductive allocation strategy changed over the season, late breeders (the offspring of which were introduced into a high resource environment and increased predation pressure) produced more and smaller eggs that resulted in smaller larvae, compared with early breeders.

4. The split-brood experiment in which eggs were incubated in different temperatures (10, 12, 15, 18°C) showed that differences in reproductive timing were associated with a change in the shape of the reaction norm linking offspring performance to water temperature indicative of adaptive phenotypic plasticity, with the offspring of early breeders performing best in low temperatures and the offspring of late breeders performing best in high temperatures.

5. The seasonal changes in reproductive traits and the shape of the thermal performance suggest time-dependent adaptive differences among individuals within populations.
1 | INTRODUCTION

Reproductive timing is an important component of the life history of individuals with potential to influence the survival of their offspring (Einum & Fleming, 2000; Schultz, 1993; Verhulst & Nilsson, 2008). According to life history theory, organisms should time their reproduction to coincide with environmental conditions that maximize their fitness (Ims, 1990; McNamara et al., 2011; Miller-Rushing et al., 2010; Singer & Parmesan, 2010). Insights regarding the adaptive value of reproductive timing, and its association with life history trait diversity, have been provided by comparisons among populations subjected to different environmental conditions along latitudinal and altitudinal gradients (Forrest & Miller-Rushing, 2010; Hut et al., 2013; Marrot et al., 2018; Sunde et al., 2019), and by longitudinal studies of populations and species in temporally changing environments (de Villemereuil et al., 2020; Marrot et al., 2018; Phillimore et al., 2016; Radchuk et al., 2019). Reproductive timing often varies considerably also among individuals within populations and breeding seasons, such that reproduction at a population-specific breeding location extends throughout a season under varying environmental conditions (e.g. Hendry et al., 2004; Lowe et al., 2009; Møller et al., 2011; Morley et al., 2014; Tibblin et al., 2016; Yamamoto & Sota, 2009). Such variation in reproductive timing may contribute to the origin (via genetic accommodation and assimilation) and maintenance of genetic and phenotypic variability in other traits, which could ultimately impact the capacity of populations to cope with and adapt to environmental modifications associated with climate change and habitat exploitation (Bolnick et al., 2003; Forsman & Wennersten, 2016; Kelly, 2019; Lande & Shannon, 1996; Schwander & Leimar, 2011). Yet, for most organisms other than birds, we have a limited understanding of the drivers that shape reproductive timing, and little is known about whether and how variation in reproductive timing influences adaptive trait diversity within populations (Hendry & Day, 2005; Lowerre-Barbieri et al., 2011; McNamara et al., 2011; Taylor & Friesen, 2017).

The reproductive timing of individuals can influence the survival of their offspring by affecting the range of environmental conditions to which they are exposed, such as abiotic conditions during egg development, resource abundances and the type and intensity of interactions within and among species (Gienapp et al., 2014; Miller-Rushing et al., 2010; Persson & Greenberg, 1990; Singer & Parmesan, 2010). The resulting temporal change in the selective regime imposed by these drivers has potential to modify the optimal solution to trade-offs among reproductive traits over the breeding season, such that the combination of trait values that confers the highest fitness is not the same in the early, intermediate and late season (Brinkhof et al., 2002; Roff, 1992). This is likely of particular importance in temperate regions with pronounced seasonal cycles in the biotic (e.g. resource availability and trophic interactions) and abiotic factors (e.g. temperature and light) to which the early life stages are exposed (Brodersen et al., 2011; George & Harris, 1985; Singer & Parmesan, 2010; Straile, 2002; Ushio et al., 2018). This raises the intriguing and largely overlooked question whether differences in reproductive timing within a population are accompanied by shifts in associated reproductive traits, and in the optimal solution to life history trade-offs, driven by the changes in environmental conditions and selection pressures across the breeding season (Devaux & Lande, 2010; Hendry & Day, 2005; Tamario et al., 2019; Taylor & Friesen, 2017).

One way to investigate the causes and potential consequences of variation in reproductive timing in seasonal environments is to examine whether and how the shape of the reaction norms that link phenotypic expression to changes in environmental conditions vary among individuals (genotypes) within the population (i.e. genotype by environment interactions, see Box 1 in Voelkl et al., 2020) and differ over the breeding season (Forsman, 2015; Via et al., 1995). A graphical model that illustrates hypothetical adaptive seasonal variation in the reaction norms that link performance to temperature in the offspring produced by parents that breed at different times of the season (early and cold vs. late and warm) is provided in Figure 1a.b. Changes in the shape of the predominating reaction norm(s) over the season might be expected if there are underlying genetic differences between early and late breeders (Ghalambor et al., 2007; Merilä & Hendry, 2014). Insofar as changes in the shape of reaction norms over the season contribute to increased performance and fitness of individuals, this would constitute a rare example of time-dependent, adaptive phenotypic plasticity (Abbey-Lee & Dingemanse, 2019; Chevin & Lande, 2015; Chevin et al., 2010; Qvarnström et al., 2000). In the context of ongoing climate change, increased knowledge of thermal performance curves (reaction norms) is crucial to a better
understanding of how temperature change will impact the performance of individuals, populations and species (Dahlke et al., 2020; Deutsch et al., 2008). Yet, whether the shape of reaction norms covary with reproductive timing, and its potential adaptive value, remains largely unknown.

Here we explore whether and how individual differences in reproductive timing influenced hatching success, reaction norms and reproductive allocation within an anadromous Baltic Sea population of perch *Perca fluviatilis* that inhabits a seasonally changing environment. Perch is a keystone predatory fish species that is widely distributed in temperate fresh and brackish water systems (Craig, 2000; Donadi et al., 2017). It is suitable for studies of causes and consequences of variation in reproductive behaviour by being a total breeder (all eggs released in a single egg strand) that generally deposits the eggs in shallow water (Craig, 2000; Tibblin et al., 2012). This allows for robust quantification of breeding activity across time in natural settings through visual inspection (Tibblin et al., 2012).

Moreover, many perch populations have an extensive breeding period in spring when environmental conditions continuously change in a directional manner (Craig, 2000), such that the early life stages will experience different conditions (e.g. temperature, resource abundances (zooplankton) and species interactions) depending on when reproduction occurs.

The overall aim of this study was to examine whether and how variation in reproductive timing exposes young life stages to varying environmental conditions and different selective regimes throughout the breeding season, and to understand how environmental conditions thereby impact adaptive trait diversity. To that end, we combined observations under natural conditions in the wild with a split-brood common garden experiment (Figure 1). Specifically, we assessed: (a) how the reproductive timing of perch was related to temporal variation in temperature, resource abundance (zooplankton density) and predation pressure estimated by the relative abundance of the main larvae predator, the three-spined

![Field study](image1.png)

**FIGURE 1** Graphical model of adaptive seasonal variation in reaction norms and study design. (a) Adaptive landscape illustrating hypothetical seasonal variation in the relationship linking performance (e.g. hatching success) to temperature in offspring produced by parents that breed early, intermediate and late in the season. (b) Hypothetical variation in reaction norms among offspring born to parents sampled in the beginning (blue), middle (brown) and end (red) of the breeding season. (c) Schematic illustration of the study design to investigate environmental correlates to spawning intensity in the field across the breeding season in combination with experimental evaluation of hatching success and thermal performance in offspring. Quantification of breeding intensity and environmental correlates (temperature, abundances of zooplankton and sticklebacks) thereof occurred between the 3rd of April and 24th of June. Egg strands used in the laboratory experiment were sampled between the 22nd of April and 19th of June.
stickleback (Gasterosteus aculeatus, hereafter sticklebacks; Byström et al., 2015; Eklöf et al., 2020); and (b) whether and how intra-population variation in reproductive timing and the associated temporal changes in environmental conditions influenced life history traits (hatching success, egg and larval size) and the shape of thermal performance curves (reaction norms). We tested the following three predictions: (a) perch breeding intensity should match resource peaks and/or times with little predation pressure on juveniles (Lowerre-Barbieri et al., 2011; Morgan & Christy, 1995; Verhulst & Nilsson, 2008); (b) there should be a seasonal shift in reproductive allocation strategy, with individuals producing more but smaller offspring (i.e. less investment in each) at times with predator presence (Walsh & Reznick, 2000) and/or high resource abundance (Einum & Fleming, 2000; Hutlings, 1991; Sibly & Calow, 1983); and (c) there should be seasonal differences in the shape of the reaction norm linking hatching success to incubation temperature, with the temperature optima for hatching success increasing during the course of the breeding season as an adaptive response to increasing water temperatures.

2 | MATERIALS AND METHODS

2.1 | Quantifying the timing and intensity of reproduction and its relation to environmental conditions

We studied the reproduction of anadromous perch in Hossmoån, a small stream (mean annual discharge ~1.5–2 m³/s, width >10 m) that discharges to the southwestern Baltic Sea (Figure 2), throughout the breeding season of 2019 (3 April–24 June). Previous studies have shown that Hossmoån harbours a thriving population of anadromous perch that migrates from the Baltic Sea to the lower river stretches to reproduce in spring (Tibblin et al., 2012). To facilitate accurate repeated and representative quantifications of the timing and intensity of perch reproduction, we set eight transects (end-start marked with buoys; total length of transects: 900 m, width of each transect: ~5 m, total covered area: ~4,500 m²; Figure 2) covering putative breeding habitats (depth of <2 m with reed belts and/or macrophytes) within the previously identified breeding area (Tibblin et al., 2012). The number and location of newly deposited egg strands were estimated every second workday (Monday–Wednesday–Friday) during a period of 80 days covering the full reproductive period (i.e. our survey started before any egg strands were deposited and ended when no newly deposited egg strands had been recorded for 5 days). Egg strands were located visually using a combination of polarizing glasses and bathyscope. The position of each egg strand (N_{tot} = 511) was marked with a red cellulose tape (tied to the nearest reed straw) and recorded on a map to avoid double counting. In addition, we also monitored a subset of the egg strands (N = 12) until hatching to obtain an estimate of incubation time in the natural habitat, information that was subsequently used to back-calculate the estimated hatching date in the natural habitat (Supporting Information).

To address the role of seasonal environmental variation in shaping the timing and intensity of breeding, we monitored water temperature, zooplankton abundances and the presence of sticklebacks in the breeding habitat throughout the breeding season. Temperature data were recorded (every hour) with temperature loggers (HOBO Pendant), placed at six locations within the study area (Figure 2) at a depth of 15–30 cm. Once perch breeding begun, zooplankton samples were collected on a weekly basis (each Monday) at six fixed locations in the breeding area (Figure 2) by sampling 1.7 L of water at 30 cm of depth using a Ruttner sampler. These samples were immediately filtered through a 20-µm-pore size filter and fixed with Lugol’s...
solution and kept at 4°C in the laboratory until processing. Using a stereomicroscope (Olympus SX7), we identified and quantified the abundances of rotifers, copepods, copepod nauplii and cladocerans (Supporting Information; Table S1), with later analyses focusing on the abundances of nauplii and rotifers which are the primary food resource for the early life stages of perch (Craig, 2000; Nunn et al., 2007). On each occasion when breeding intensity was quantified (Monday–Wednesday–Friday), we quantified the presence and relative abundance (daily capture/total capture across season) of sticklebacks using minnow traps (Promar, model TR-501), an established method for capturing sticklebacks (Merilä, 2015), at six locations (Figure 2).

### 2.2 | Split-brood temperature tolerance experiment

To evaluate whether and how reproductive timing influenced reproductive allocation, hatching success and the temperature dependence of the latter (reaction norms), we collected three to six newly deposited egg strands (occasionally fewer when low breeding activity) each day that breeding intensity was quantified along the transects (Figure 1). These egg strands (N = 69) were gently loosened from the substrate and transferred intact to a water-filled bucket (10-L) using a thin-meshed net after which a subsample (~10 cm) was taken and transported in a 0.8-L container with stream water to the Linnaeus University laboratory. Upon arrival, we split each egg strand sample in four subsamples that were placed in four constant rooms set with fixed temperatures (10.0 ± 0.4 S.D., 11.6 ± 0.5 S.D., 15.4 ± 0.7 S.D. and 17.7 ± 0.6 S.D. °C, hereafter 10, 12, 15 and 18°C treatments) that comprised the expected natural variation in breeding temperature (Craig, 2000). After acclimatization for ~1 hr, we randomly sampled two replicates (weight of replicate, 1.23 g ±0.18 S.D.) for each family and temperature treatment, transferred them to 0.8-L flow-through containers filled with aerated tap water, and randomly positioned them in custom-made racks (details on the flow-through containers in Sunde et al., 2018). At this point, we photographed (Nikon D5600, F/7.1, 1/60 s, ISO-400, focal length 50 mm) each replicate to determine the initial number of viable eggs, the total number of eggs, and the number of eggs/gonad weight (g). Complete water exchanges were conducted regularly in all samples (daily, in 15 and 18°C, and about every second day in 10 and 12°C treatments) by gently overflowing the containers with temperature-specific water, to remove biological by-products and maintain a consistently high oxygen concentration within the samples.

After the viable eggs had hatched (in early stages, dead eggs were easily identified by becoming opaque, whereas in later stages the embryo ceased moving and became grey), we took a final standardized photograph (Nikon D5600, F/11, 1/80 s, ISO-400, focal length 50 mm) that was used to quantify hatching success (number of hatched larvae/number of viable eggs) using the multipoint tool in ImageJ (Schneider et al., 2012). At termination of each replicate, we transferred a subsample (~10, Ntot = 4,439) of hatched larvae onto a measuring board, and photographed the larvae using a macro lens (F/3.8, 1/80 s, ISO-100, Tamron SP 90 mm). We used this photograph to estimate the length of the larvae using ImageJ, by first scaling the image to the measuring board, and then estimating the length of the juveniles using the segmented line and ROI tool. Larvae with clear motion blur and/or a hard to detect outline of their body were excluded from the length estimates.

### 2.3 | Statistics

All statistical analyses were performed using R v. 3.5.2 with Rstudio v. 1.1.46 (R Core Team, 2018; RStudio Team, 2016).

#### 2.3.1 | Timing and intensity of breeding and its relation to seasonal (a)biotic changes

To examine whether and how breeding intensity was associated with seasonal changes in stream temperature and abundances of zooplankton and sticklebacks, we conducted a multiple linear regression using the lm function in R. As a response variable, we used the number of hatching egg strands (time of hatching for egg strands estimated by applying the in situ observed average degree days until hatch, Supporting Information), rather than newly deposited egg strands, to link the external environmental conditions to the timing of emerging larvae. We set the number of hatching egg strands at the day of zooplankton collection ±3 days (+5 days in the final week of sampling) in relation to the corresponding average stream temperature, abundances of zooplankton (nauplii + rotifers) and relative stickleback abundances (mean number of the relative capture of sticklebacks across three sampling occasions in each week) across the six sampling locations (Figure 2). The variance inflation factors (VIFs) suggested relatively low collinearity among variables (temperature: 2.95; zooplankton: 2.2; sticklebacks: 4.76; Dormann et al., 2013; Graham, 2003).

#### 2.3.2 | Experimental evaluation of temperature dependence of hatching success over the reproductive season

To evaluate whether and how hatching success and the temperature dependence of hatching success (reaction norms) changed across the reproductive period, we analysed data with two complementary approaches treating the reproductive timing (season) as either continuous (ordinal date) or categorical such that the reproductive season was divided into three stages: early, intermediate and late season. Grouping to season was based on the distribution of breeders along the season and the stream water temperature at the time of egg deposition (Figure 3; early breeders below 15, intermediate 15-18, and late above 18°C), and in relation to expected breeding temperatures (~10–18°C) according to the literature (Craig, 2000; Gillet & Dubois, 2007).

Hatching success and its relationship with reproductive timing and experimental incubation temperature was analysed with generalized linear mixed models (GLMMs) with a binomial error structure using...
the glmer function in the lme4 package (Bates et al., 2014). Here, temperature treatment was set as a continuous fixed effect, season as a categorical or continuous fixed effect (models were conducted with both settings, see above), and the family-by-temperature interaction was included as a random effect to account for among family variation in temperature-dependent reaction norms (slopes). To evaluate whether reproductive timing influenced the thermal performance curves (reaction norms), the model also included the fixed effect of season-by-temperature interaction. In the model with season set as a continuous fixed effect, ordinal date was rescaled (divided by 100) to improve the model fit. Significance of fixed effects was assessed with a type II Wald’s Chi-square test.

### 2.3.3 Seasonal shifts in reproductive allocation strategies

Using data from the split-brood laboratory incubation experiment, we examined whether and how reproductive allocation strategies (the number of eggs per gonad weight and the larvae length) changed across the reproductive season, using linear mixed-effects models. These data were analysed with two approaches (as above) treating reproductive timing as either a continuous (ordinal date) or a categorical explanatory variable. We ran separate models for each response variable (number of eggs per gonad weight and larvae length), setting season as a fixed continuous or fixed categorical effect respectively, and family as a random effect. Significance of fixed effects was evaluated with a type II Wald’s Chi-square test.

### 3 RESULTS

#### 3.1 Breeding intensity, zooplankton abundance and stickleback presence in the stream

Perch breeding commenced on 22 April (ordinal date 112) at a temperature of ~10°C and lasted until 19 June (ordinal date 170) with temperatures reaching 21°C. In total, 511 unique egg strands were detected across the breeding season with peak intensity occurring in late May–early June when temperatures were above 15°C (Figure 3). Zooplankton abundances varied considerably (range of average concentrations: 3.9–153.1 nauplii+rotifers L⁻¹, Table S1) and had two seasonal peaks, early
May and early June with the later peak followed by consistently high abundances (Figure 3). Sticklebacks arrived at the breeding area in the end of May and remained until the breeding season ended (Figure 3). The number of hatching egg strands was positively associated with increasing abundances of zooplankton and stream temperatures, but not significantly associated with the relative abundance of sticklebacks (multiple linear regression: $F_{3,5} = 23.92$, $R^2 = 0.93$, $p = 0.002$; zooplankton: $F_{1,5} = 11.62$, $p = 0.019$; temperature: $F_{1,5} = 11.50$, $p = 0.019$; sticklebacks: $F_{1,5} = 0.22$, $p = 0.66$; Figure 3; Table S3).

### 3.2 Experimental evidence on seasonal- and temperature-dependent hatching success

The hatching success of perch changed throughout the breeding season ($\chi^2 = 19.17$, $df = 2$, $p < 0.001$), such that later reproductive timing was associated with impaired hatching success (estimated marginal means, hatching success ±SE: early $0.74 ± 0.11$, intermediate $0.52 ± 0.11$, late breeders $0.26 ± 0.12$; Figure 4). Temperature did not have an overall effect on hatching success ($\chi^2 = 2.56$, $df = 1$, $p = 0.11$). However, the effect of temperature on hatching success changed over the breeding season indicative of adaptive thermal plasticity (temperature × season interaction, $\chi^2 = 10.16$, $df = 2$, $p = 0.006$; Figure 4); the hatching success of late breeders increased with increasing temperature (slope ±SE = 0.0090 ± 0.0058) whereas the hatching success of early and intermediate breeders instead declined with increasing temperature (slope early season = −0.0095 ± 0.0052, intermediate = −0.0074 ± 0.0040; Figure 4). Reassuringly, these results were robust to the choice of analytical approach; treating reproductive timing as a continuous (ordinal date) rather than categorical (grouping to early–intermediate–late) explanatory variable rendered qualitatively the same results with a gradual
change over the season in hatching success and in the effects of temperature on hatching success (ordinal date: $\chi^2 = 17.40$, df = 1, $p < 0.001$; temperature: $\chi^2 = 2.50$, df = 1, $p = 0.11$; temperature × ordinal date interaction: $\chi^2 = 6.14$, df = 1, $p = 0.013$).

3.3 | Seasonal differences in eggs per gonad weight and larval size

The reproductive allocation strategy, estimated as eggs per gonad weight and size of the larvae in the laboratory experiment, changed across the season (season as categorical variable: eggs/gonad weight: $\chi^2 = 54.04$, df = 2, $p < 0.001$; larvae length: $\chi^2 = 33.75$, df = 2, $p < 0.001$; Season as ordinal date: eggs/gonad weight: $\chi^2 = 29.70$, df = 1, $p < 0.001$; larvae length: $\chi^2 = 10.85$, df = 1, $p < 0.001$; Figure 4). The number of eggs per gonad weight increased as the season progressed (eggs/gram weight: early 6.07, ±0.07; intermediate 6.52, ±0.05; late 6.69, ±0.05; Figure 4). However, the size of the larvae in the laboratory experiment, changed across the season (season as categorical variable: larvae size: early 96.3, ±3.91; intermediate 130.4, ±5.07; late 141.4, ±6.73; Figure 4). The number of eggs per gonad weight increased as the season progressed (eggs/gram weight: early 6.07, ±0.07; intermediate 6.52, ±0.05; late 6.69, ±0.05; Figure 4). However, the size of the larvae in the laboratory experiment, changed across the season (season as categorical variable: larvae size: early 96.3, ±3.91; intermediate 130.4, ±5.07; late 141.4, ±6.73; Figure 4).

4 | DISCUSSION

Previous research on the relationship between environmental variation, reproductive timing and adaptive trait diversity has in vertebrates other than birds generally focused on comparisons among spatially and/or temporally separated populations, while largely overlooking the potential for these processes to also influence the ecology and evolution within populations (Bolnick et al., 2003; de Villeneuve et al., 2020; Hendry & Day, 2005; Taylor & Friesen, 2017). Here, we add to the current body of knowledge of the causes and consequences of intraspecific trait variation by combining results from field observations and experimental studies that reveal that reproductive intensity, hatching success and reproductive allocation were related to seasonal changes in temperature and resource abundance, but not predator presence, within an anadromous population of perch. Importantly, we also provide rare experimental evidence that the within population variation in reproductive timing was associated with a change over the season in the shape of the predominating reaction norm linking offspring performance to water temperature, pointing to time-dependent adaptive phenotypic plasticity.

Our results revealed a substantial variation in reproductive timing among individuals within the population with the breeding period lasting almost 2 months (22 April–19 June). During this period, the environmental conditions in the breeding habitat changed dramatically with a continuous increase in water temperature (10–21°C), highly varying resource (zooplankton) abundances and the arrival of predators (sticklebacks) feeding on perch larvae. In accordance with predictions (from theory), the intense breeding activity coincided with high resource abundances, such that the timing of breeding and subsequent hatching matched suitable resources (zooplankton) to the early life stages. The arrival of predators (sticklebacks) that feed on perch larvae coincided with perch breeding. Still, the changes in the relative abundance of sticklebacks were not associated with the number of hatching egg strands. Temperature was positively associated with the number of hatching egg strands, with hatching of egg strands peaking above 15°C which is at the upper end of what is reported in previous studies on perch (Craig, 2000; Gillet & Dubois, 2007). Interestingly, the upper temperature range at which breeding and egg incubation occurred exceeded the previously described upper thermal tolerance of perch recruitment (20°C; Craig, 2000), indicating an unexpectedly high thermal tolerance within the population studied here.

The associations (or lack thereof) between breeding intensity and environmental factors implicate resource abundance and temperature as key drivers in shaping the timing of reproduction, similarly to what previously has been shown in many bird species (Burger et al., 2012; Charmantier et al., 2008; Martín, 1987; Visser et al., 2006). Yet, breeding occurred during a prolonged period with varying environmental conditions. Based on the assumption that individuals time their reproduction to maximize their fitness, this indicates that alternative strategies (i.e. other than matching peak resource levels) may be viable and contribute to the maintenance of variation in reproductive timing (Lms, 1990; Miller-Rushing et al., 2010; Roff, 1992). The reproductive success of individuals is determined by trade-offs among early life history traits, and the optimal solution to these trade-offs is likely modified by seasonal changes in temperature, resource abundance and predation pressure (Gienapp et al., 2014; Singer & Parmesan, 2010; Varpe, 2017). Interestingly, our laboratory experiment uncovered that hatching success was lower, regardless of temperature treatment, in the relatively large proportion of individuals that reproduced in the later stages of the season at high natural temperatures. The reproductive allocation strategy also changed over the season, with individuals reproducing in later stages (high resource environment) producing more eggs per gonad weight and smaller offspring. Although the observational nature of these data calls for caution regarding inference of causality, these patterns suggest an ongoing temporal trade-off between hatching success (breeds early) and survival of early life stages (breeds late in a high resource environment). The seasonal shift in life history traits, with increased resource investment per offspring in a low resource environment early in the season, and vice versa in late breeders, might represent an adaptive response to seasonally changing environmental conditions and selection regimes (Abbey-Lee & Dingemanse, 2019; Chevin & Lande, 2015; Qvarnström et al., 2000). This pattern coheres to the hypothesis that selection favours an increased resource investment in individual offspring with reductions in resource abundance (Sibly & Calow, 1983), which previously in fish mainly have received empirical support in studies of salmonid species (Einum & Fleming, 1999; Hutchings, 1991). In line with our prediction, this indicates the coexistence of alternative reproductive strategies within the population (Fournier-Level et al., 2016; Hendry & Day, 2005), although potential
Our temperature manipulation experiment adds further support to the above conclusion that intra-population variation in reproductive timing was associated with (adaptive) differences in life history traits, potentially driven by seasonally changing selective regimes. We uncovered seasonal shifts in the temperature dependence of offspring performance (shape of reaction norms), with the offspring of early breeders (i.e. reproducing at low temperatures) performing best in low temperatures and the offspring of late breeders performing best in high temperatures. The association of reproductive timing with the shape of the thermal performance curves provides an example of time-dependent, adaptive phenotypic plasticity that may enable individuals and the population to cope with the prevailing and seasonally changing thermal conditions (Figure 1a,b). There is ample evidence from inter-population comparisons that organisms reproduce in thermal conditions to which they are adapted (Hut et al., 2013; Marrot et al., 2018; Sunde et al., 2019). However, our findings represent rare evidence on adaptive variation in thermal performance within populations (Brans et al., 2017; Fournier-Level et al., 2016; Marrot et al., 2018; Salinas & Munch, 2012; Tamario et al., 2019).

The seasonal differences in life history traits and thermal performance curves within our study population may reflect genetic divergence between temporally separated breeders (adaptation by time, hereafter ABT) or environmentally induced maternal effects (e.g. transgenerational plasticity; Brans et al., 2017; Hendry et al., 1999; Salinas & Munch, 2012). Although previously overlooked, ABT has recently been proposed as an important process in shaping adaptive variation, but empirical support as to whether and how this process also acts within a reproductive season and location remain exceedingly scarce (Hendry & Day, 2005; Taylor & Friesen, 2017). In short, ABT relies on the, across taxon documented, heritable components involved in reproductive timing that could cause assortative mating within and across generations, and subsequently reduce gene flow within a reproductive period. This could promote the evolution of genetically distinct reproductive groups (e.g. late and early breeders) within a population (Hendry & Day, 2005). Breeding in a seasonal environment may result in that reproductive groups are exposed to divergent selective regimes, potentially leading to adaptive divergence in life history traits and reaction norms, that is, ABT, similar to that of local adaptations to spatial environmental variation (Hendry & Day, 2005; Kawecki & Ebert, 2004; Tibbitt et al., 2015).

To conclude, within population variation in reproductive timing was associated with changes in life history traits and the thermal dependence of offspring performance, and these changes may reflect adaptations that match phenotype-dependent optimal environmental conditions at the time of reproduction. This is a key finding from an ecological and evolutionary point of view, and exemplifies how seasonal environmental variation may generate and maintain adaptive trait diversity within populations (Fournier-Level et al., 2016). Our findings of time-dependent adaptive variation in reproductive traits, life history trade-offs and thermal performance curves within a population have implications for management and conservation, especially at times of increasing environmental stresses due to climate change and increasing anthropogenic pressure through harvesting and habitat exploitation (Bellard et al., 2012; Newbold, 2018). Warmer and more variable temperatures associated with ongoing climate change constitute major threats to biodiversity with vast consequences for fish recruitment (Bellard et al., 2012; Dahlke et al., 2020; Newbold, 2018). Preserving and restoring variation in the timing of reproductive events, solutions to life history trade-offs, and thermal performance curves reported in the present study can render populations better able to cope with such environmental challenges (Forsman & Wennersten, 2016; Kelly, 2019; Meyers & Bull, 2002).

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AUTHORS’ CONTRIBUTIONS
M.H. and P.T. conceived the study; M.H., O.N., P.L., A.F. and P.T. designed the study; M.H., O.N. and P.T. conducted the field and laboratory work; M.H. analysed the data with support from P.T., O.N. and A.F.; All authors contributed to interpretation of results; P.T. and M.H. wrote the manuscript, with input from O.N., P.L. and A.F. All authors commented and agreed to the final version of the manuscript.

DATA AVAILABILITY STATEMENT
Analyses reported in this article can be reproduced using the data archived in Dryad Digital Repository https://datadryad.org/stash/dataset/doi:10.5061/dryad.dbvr15f1g (Hall et al., 2021).

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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