Evidence of hatch-time based growth compensation in the early life history of two salmonid fishes

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Abstract
Initial body size can indicate quality within-species, with large size increasing the likelihood of survival. However, some populations or individuals may have body size disadvantages due to spatial/temporal differences in temperature, photoperiod, or food. Across-populations, animals often have locally adapted physiology to compensate for relatively poor environmental influences on development and growth, while within-population individual behavioral adjustments can increase food intake after periods of deprivation and provide opportunities to catch up (growth compensation). Previous work has shown that growth compensation should include within-population differences related to short growing seasons due to delayed hatch time. We tested the hypothesis that individual fish that hatch later grow faster than those that hatch earlier. The relative magnitude of such a response was compared with growth variation among populations. We sampled young of the year Arctic charr and brook trout from five rivers in northern Labrador. Daily increments from otoliths were used to back-calculate size to a common age and calculate growth rates. Supporting the hypothesis, older fish were not larger at capture than younger fish because animals that hatched later grew faster, which may indicate age-based growth compensation.

Keywords
back-calculation, counter-gradient variation, developmental plasticity, hatch phenology, Salvelinus

1 INTRODUCTION
Early phenotype can establish individuals on trajectories towards alternative life histories, and influences factors such as morphology, growth, and reproduction (Clarke et al., 2016; Jonsson & Jonsson, 2014; Rohde et al., 2015; Taborsky, 2006; Walsh et al., 2015). In turn, the phenology (timing) of reproductive events such as germination, hatch, or birth affects early phenotypes (Beer & Anderson, 2001; Brännäs, 1995; Einum & Fleming, 2000; Sternecker et al., 2014). Therefore, there is often strong selective pressure to reproduce at an optimal time (McNamara et al., 2011; Morgan & Christy, 1994; Morin et al., 1990). For example, phenology has been shown to affect reproductive success in plants (Satake et al., 2001), corals (Guest et al., 2008; Mercier et al., 2011), insects (Maino et al., 2017), amphibians (Morin et al., 1990), fishes (Morbey & Ydenberg, 2003), birds (Reed et al., 2009; Shoji et al., 2015), and...
mammals (Rotella et al., 2016). The fitness outcomes of variable timing of reproductive events are connected to subsequent growth conditions that offspring are likely to encounter.

Intra-specific variation in growth rate is ubiquitous and occurs at population (e.g., Carlson et al., 2004; McCairns, 2004; Yamahira & Conover, 2002) and individual levels (e.g., Mortensen & Damsgård, 1993; Nicieza & Metcalfe, 1997). Among-population growth differences often exist due to latitudinal (and elevational) gradients in temperature and photoperiod, with individuals at higher latitudes experiencing shorter growing seasons (Campos et al., 2009; Sinnatamby et al., 2014). If phenotypic optima are similar across such conditions, disadvantaged populations can evolve a greater genetic capacity for growth to mitigate some negative environmental effects on size via plasticity (Arendt & Wilson, 1999; Campos et al., 2009; Conover & Present, 1990; Pearson & Warner, 2018; Purchase & Brown, 2000). There is predictable latitudinal variation in temperature and photoperiod that contribute to counter-gradient variation in growth potential among populations, where higher latitude populations evolve faster growth rates at equivalent temperatures to that of those at lower latitudes (Campos et al., 2009; Lapolla, 2001; Sinnatamby et al., 2014). Such among-population patterns in local adaptation are termed counter-gradient variation and occur via genetic changes across generations (Figure 1).

Within-populations, some individuals may experience relatively disadvantaged conditions. For example, a period of depressed feeding opportunities can result in diminished growth rates; however, compensatory behaviors can allow them to catch up by the end of the growing season (Metcalfe & Monaghan, 2001). Whereas counter-gradient variation is genetic adaptation across-populations, within-population growth compensation (Figure 1) may be considered an intrinsic plastic response (of the same individual) to changes in the environment (Carlson et al., 2004; Zhu et al., 2003) that is triggered by environmental cues (Gotthard, 2008), depletion of energy stores (Ali et al., 2003), or timing of hatch (Gotthard, 2000; Hirose et al., 2012; Mikolajewski et al., 2015; Orizaola et al., 2010; Simonin et al., 2016; Stoks et al., 2006). Compensatory growth can have positive effects on individuals, through an increased likelihood of survival (associated with larger body size); however, growth compensation is associated with bolder foraging behaviors, which put these individuals at a greater risk of predation (Biro et al., 2004; Damsgård & Dill, 1998; Nicieza & Metcalfe, 1997).

Among-populations, in addition to growth potential, counter-gradient variation in local adaptation has been associated with developmental timing (Figure 1); the concept is easily transferable. Both are influenced by temperature, and locally adapted physiology can produce common phenotypes despite substantial plasticity. Salmonid fishes provide a useful illustration. Salmonids are poikilo-thermic meaning their developmental rate is linked to temperature, hatching faster in warmer water. However, at colder temperatures, they need fewer accumulated thermal units (ATU) to hatch (Brannon, 1987; Quinn, 2005), and there is evidence of counter-gradient variation of ATUs to hatch, across-populations (Sparks et al., 2019).

Within-population hatch or birth timing is affected by environmental conditions (McNamara et al., 2011; Rooke et al., 2019), mating timing (Sternecker et al., 2014), parental genetics (Solberg et al., 2014), maternal condition (Berejikian et al., 2014), and investment in offspring (Beacham et al., 1985; Maino et al., 2017). Sub-optimal hatching phenology can result in a mismatch in trophic dynamics with prey (Brännäs, 1995), whereby food is unavailable to newly hatched offspring. Optimal hatching timing is stochastic year to year but may be relatively stable across generations. Hatch too early and there may be no food and/or sub-optimal environmental conditions. However, late hatching is at a competitive disadvantage for feeding territories compared with early hatchers due to dominance hierarchies (Cutts et al., 1999; Metcalfe & Thorpe, 1992). Thus, sub-optimal hatch timing can result in slower growth rates and lower chances of survival (Borcherding et al., 2010; Einum & Fleming, 2000; Skoglund et al., 2012; Snucins et al., 1992).

Previous work has established that subsequent growth rate is related to hatch time across-populations (e.g., Lapolla, 2001), and within-individuals, periods of slow growth due to limited food will be compensated by periods of faster growth when food availability increases (Metcalfe & Monaghan, 2001). In this study, we focus on growth compensation within-populations related to shorter growing seasons due to delayed hatch time (Figure 1). An individual may compensate for hatching late, where they are disadvantaged by a shorter growing season, by growing faster than other individuals (within their population) that hatched earlier, thereby making the best of a bad situation. Such work has been supported by both theory (Abrams et al., 1996) and data from insects (see: Gotthard, 2000; Mikolajewski et al., 2015; Stoks et al., 2006), fish (Simonin et al., 2016), amphibians (Orizaola et al., 2010), and birds (Hirose et al., 2012; Lindholm et al., 1994). We tested this hypothesis in two salmonid species (Salvelinus spp.) where the relative magnitude of such a response was compared with growth variation within each species and across their populations (five rivers) in northern Labrador, Canada.

2 | MATERIALS AND METHODS

2.1 | Environmental information

Sampling occurred on secondary and tertiary streams of five river systems in northern Labrador, Canada: Hebron River, Kamanatsuk Brook, Fraser River, Anaktalik Brook, and Igluvialruk Brook (Figure 2; Appendix S1). Temperature loggers (n = 4, HOBO TidbiT v2, UTBI-001) were installed during the spawning season in October 2012 and removed during the June 2013 sampling period at two sampling sites, Fraser and Anaktalik rivers; and one additional river: Iklivilik Brook (Appendix S1). Loggers were fastened to rebar and firmly placed in riverbeds (Appendix S2). Salmonids often spawn in groundwater seeps having relatively steady flows of water at stable temperatures. The temperature loggers placed in Fraser River were in a spawning aggregation where redds were observed.
while the loggers in Anaktalik River and Ikadlivik Brook were placed in the main flow of the river. However, the temperature estimates from our loggers are likely underestimates (through winter) compared to those experienced in the redds because the loggers were in the water column and not in the gravel (where salmonids lay their eggs, and when in the presence of groundwater seeps, tend to have more stable temperatures). Average temperatures per day were plotted (Appendix S2). Temperatures below 0°C were not included in the overall monthly averages because the loggers were assumed to be in ice.

2.2 | Fish collection

We collected young of the year Arctic charr and brook trout (Salvelinus alpinus and S. fontinalis) using a Smith-Root LR24 backpack electrofisher between June 24 and June 29, 2013. Potential collection sites were viewed from a helicopter with each tributary selectively sampled by electrofishing upstream. Areas where we were unlikely to find young of the year, such as sandy substrate, turbulent water, or water that was deeper than ~1 m, were not surveyed. The minimum stretch of water sampled was ~100 m long by at least 1 m wide per stream (minimum area 100 m² per river), and we only sampled two or three individuals from any one group of fish to minimize the risk of collecting multiple siblings from a family. After capture, the fish were euthanized, measured (fork length), and a tissue sample was taken and placed in 95% ethanol for genetic species identification. The fish were then frozen (at −20°C) for later otolith extraction.

All animals were handled in accordance with the Guide to the Care and Use of Experimental Animals (Memorial University Animal care permit: 12-08-CP) and permitting from Fisheries and Oceans Canada.

2.3 | Genetic identification of species

The small physical size of the newly emerged hatchlings made morphological species identification difficult. Therefore, we used genetic barcoding to identify the species of each individual (brook trout or Arctic char; n = 436). We extracted DNA from tissue samples using a Qiagen DNeasy Blood and Tissue Kit according to the manufacturer’s protocol (Qiagen). A 520 base pair fragment of the cytochrome c oxidase 1 (CO1) gene was amplified by PCR using standard COI barcoding primers (Cox1-1F AAGCTATTGTCACCGCAGCATG and Cox1-1R CACCTCGAGGTGTCCGAAG-AAT). We purified the PCR products with an Exo-SAP clean-up method and sent them to Genome
Quebec (McGill University, QC) for sequencing using standard dideoxy methods. We aligned the sequences in MEGA v6.0 (Tamura et al., 2013) and species identification was unambiguously determined for all 436 fish.

2.4 | Otolith work and hatch date

Sagittal otoliths were extracted from young of the year fish using an established methodology (Radtke et al., 1996). Each otolith was fixed to a glass slide and polished using 3 and 30 μm lapping film. In salmonids a layer of calcium carbonate is deposited every day; this forms an increment that can be used to interpret fish age (see Radtke, 1989; Radtke et al., 1996; and Adams et al., 1992 for methods). When a band appears darker and thicker than the others, it is considered a check. Checks can occur for a variety of reasons including stress due to hatch, emergence, or environmental change such as a storm, lack of food, or handling stress in aquaculture settings (Adams et al., 1992; Campana & Neilson, 1985). The result of this stress is slower growth, and therefore two or more daily rings merge into one thicker ring (Adams et al., 1992). In this study, we were interested in both hatch and emergence checks. The hatch check is a thick ring that encircles all of the primordia (nuclei upon which the otolith is built) near the core of the otolith. The emergence check occurs when hatchlings leave their gravel nest and begin exogenous feeding (Appendix S3). After the establishment of the emergence check, growth often accelerates and therefore subsequent rings are further apart and more translucent (Campana, 2001; Campana & Neilson, 1985). Other work has shown that hatch and emergence times can be inferred in wild salmonids based on otolith microstructure (Fitzgerald et al., 2021).

Of the original 436 individuals, only fish from rivers with a sample size $n \geq 10$ young of the year fish of a species and for which we could obtain daily age readings were included in further analyses (324 fish: 206 Arctic charr; 118 brook trout; see Appendix S4 for details). We were unable to age 112 fish due to otolith loss or breakage during processing. Based on the number of daily increments present and the date of capture, each fish’s hatch date was back-calculated (Table 1). Photographs of otoliths were taken using a compound microscope under 100x magnification. The photographs were cropped and gray-scaled, and the color range of grays was reduced to make ring visualization easier using Photoshop.

Each otolith was assigned a blind code and read without knowledge of species or river origin. We reintepreted age on a random subset of 50 fish to determine precision. Precision estimates were based on the coefficient of variation (CV) values (Chang, 1982). A
Table 1. Information for species in each site collected June 24 to June 29, 2013, in Labrador, Canada.

| Species        | Site          | N  | Mean ± SD age (days)       | Mean ± SD hatch date | Mean ± SD estimated fork length at 25 days (mm) | Mean ± SD estimated fork length at 50 days (mm) | Mean ± SD Otolith radius at hatch (mm) | Mean ± SD Otolith radius at capture (mm) | Median fork length at 50 days (mm) |
|----------------|---------------|----|---------------------------|----------------------|-----------------------------------------------|-----------------------------------------------|--------------------------------------|--------------------------------------|---------------------------------|
| Arctic charr   | Hebron        | 83 | 60 ± 10                   | Apr 28               | 27.8 ± 2.2                                    |                                                | 0.13 ± 0.03                         | 0.17 ± 0.03                         | 21.7 ± 1.8                     |
|                | Fraser        | 19 | 60 ± 9                    | Apr 22               | 27.6 ± 1.2                                    |                                                | 0.14 ± 0.05                         | 0.16 ± 0.03                         | 21.5 ± 1.4                     |
|                | Anaktalik     | 92 | 61 ± 12                   | Apr 24               | 27.9 ± 1.6                                    |                                                | 0.13 ± 0.04                         | 0.17 ± 0.02                         | 21.7 ± 1.0                     |
|                | Igluvigaluk   | 12 | 60 ± 8                    | Apr 20               | 27.6 ± 1.0                                    |                                                | 0.12 ± 0.02                         | 0.17 ± 0.00                         | 21.9 ± 1.2                     |
| Brook trout    | Kamanatsuk    | 100| 58 ± 10                   | Apr 27               | 25.2 ± 2.2                                    |                                                | 0.05 ± 0.05                         | 0.13 ± 0.03                         | 23.8 ± 2.3                     |
|                | Igluvigaluk   | 12 | 59 ± 11                   | Apr 30–May 17        | 25.2 ± 2.2                                    |                                                | 0.13 ± 0.03                         | 0.17 ± 0.02                         | 21.0 ± 1.8                     |

Note: Site number refers to locations in Figure 1. Descriptive statistics for: Mean age (in days, on June 24—First day of electrofishing), mean and median hatch date, mean otolith radius at capture (mm), otolith radius at hatch (mm), mean fork length at capture (mm), and estimated fork length at 25 and 50 days old (mm). Only samples from species in rivers that had a sample size of at least 10 individuals were included.  

2.5 | Growth rate and back-calculated lengths

We used the ObjectJ plugin for ImageJ (Schneider et al., 2012) to calculate the fish’s daily growth rate (fork length in mm/day) based on the width of the daily otolith rings. The total radius of the otolith was measured from the hatch line to the last visible increment. Absolute daily growth was then calculated based on the total growth of the fish (fork length at capture minus estimated hatch size; defined below) compared with the width of each daily otolith ring. We back-calculated hatching length to 25 and 50 days post-hatch (Table 1) using the biological intercept model (1) (Campana, 1990; Vigliola & Meekan, 2009).

\[
L_a = L_c + \frac{(O_c - O_a)(L_c - L_o)}{(O_o - O_a)}
\]  

Where \( L_a \) was fish fork length (size, mm), \( O_a \) was otolith radius (μm), \( L_c \) and \( O_c \) were sizes at capture, \( L_o \) and \( O_o \) were sizes at hatch. One of the weaknesses of this model was that fork length needs to be estimated in order to estimate posthatch lengths. We used a hatch fork length (\( L_c \)) of 18 mm based on previous work on brook trout (Penney et al., 2018). Additionally, we conducted a sensitivity analysis with an assumed hatch size of 16 and 20 mm and it made no difference in the overall conclusions.

We calculated each fish’s size (fork length in mm) each day based on the width of each otolith ring. Next, an average daily growth rate (average fork length increase, mm/day) was calculated based on the total absolute growth of the fish (length at capture minus estimated hatch size, mm, see model 1) compared with the width of each daily otolith ring. We compared growth rates (mm/day) for three different time periods. First, we examined the first 25 days of life to compare age effects on growth, next we examined a set time period (from June 1 to 21) to compare growth rates during standardized environmental conditions (photoperiod, and temperature), and finally, we looked at overall growth rates (posthatch to time of capture). For each of these instances, we used model (1) to estimate the growth rate.

2.6 | Data analyses and statistics

For descriptive purposes and to determine whether we could examine our hypothesis at a species level, we tested whether the river
TABLE 2  Results of analysis of variance (ANOVA) for hatch date and overall posthatch growth rate (mm/day) between fish species (Salvelinus alpinus and S. fontinalis) for samples collected among five rivers June 24 to June 29, 2013, in Labrador, Canada.

| Factor   | Factor       | F   | df | p   | F   | df | p  |
|----------|--------------|-----|----|-----|-----|----|----|
| Species  | Hatch date   | 0.21| 1,318 | .65 | 4.21 | 1,318 | .04 |
| River    | Growth rate  | 0.16| 4,318 | .96 | 1.99 | 4,318 | .10 |

Abbreviations: df, degrees of freedom; F, calculated F statistic; p, probability. Significance for bold value is p < 0.05.

We did not test for the interaction between species and river for model (2) because we did not have representatives from both species in each river. There was no effect of the river on hatch date (above), or overall growth rate (Tables 1 and 2), so the populations were pooled for further analyses. Therefore, we conducted linear regressions for each species (regardless of the river) to determine: (1) whether there was an association between fork length at capture and age and (2) whether there was an association between hatch date and growth rate. For all analyses, α was set at .05. Residuals were examined to test for normality and heteroscedasticity, and no deviations were observed. The map was created in ArcGIS. All graphs (ggplot2), data processing, and statistics were done in R version 4.1.2 (R Core Team, 2021; using packages car, ggpmisc, Hmisc, lme4, and lubridate).

3 | RESULTS

The hatch dates (Table 1) for brook trout (mean: April 26; range: March 30 to May 17) and Arctic char (mean: April 24; range: March 21 to May 17) did not differ between species, or among rivers (Table 2). Brook trout (26.5 ± 3.7 SD) were slightly shorter than Arctic char (27.7 ± 1.8 SD, Table 2, Figure 3).

Subsequent to pooling populations, we conducted linear regressions and found no relationship between age and fork length at capture (mm) for Arctic char ($R^2 = .003, p = .42$) or brook trout ($R^2 = .007, p = .38$; Figure 4). Older fish were not bigger than younger fish. To better understand the absence of a relationship between age and body size at the same capture time, we conducted additional tests regressing hatch date to the daily growth rate (fork length increase, mm/day) at three time points. We found significant relationships with all three time points (first 25 days posthatch, June 1 to 21, and entire posthatch life) for both Arctic charr ($R^2 = .09, p < .001; R^2 = .19, p < .001; R^2 = .12, p < .001$, respectively) and brook trout ($R^2 = .08, p < .001; R^2 = .19, p < .001; R^2 = .13, p < .001$, respectively; Figure 5), whereby, fish with earlier hatch dates had slower growth rates than fish that had later hatch dates.

4 | DISCUSSION

The objective of this paper was to test the hypothesis that hatch time affects growth rate, where individuals that hatch later are disadvantaged by a shorter growing season than those that hatch earlier and therefore would grow faster to compensate, potentially making the best of a bad situation. We found support for our hypothesis in two species of salmonids. Overall, there was more variation in growth rate among individuals within-populations, than across-populations. There was no relationship between age (in days) and size of young of the year char ($>75$ days old, sampled in late June), which means that older hatchlings were not larger than younger ones. We found that this occurred because fish that hatched later grew faster, potentially as a form of growth compensation. Interestingly, this finding is contrary to work conducted on Northern pike (Esox lucius) and common triplefin (Festorygion lapillum) where early harters grew faster (Moginie & Shima, 2018; Trabelsi et al., 2013, respectively); and work on congeneric white-spotted charr (S. leucomaenis) where early hatchers were consistently larger than late hatchers (Yamamoto et al., 1997).

However, growth compensation has been found in other studies and has been linked to initially poor environmental conditions such as drought (Oesterheld & McNaughton, 1991), high density (Sundström et al., 2013), or low food availability (Metcalfe & Monaghan, 2001; Walling et al., 2007). Thus, differences in growth rates due to hatch timing may be an adaptive response to a shorter growing season experienced by late harters, as shown in insects (see: Gotthard, 2000; Nikolajewski et al., 2015; Stoks et al., 2006), fish (Simion et al., 2016), amphibians (Orizaola et al., 2010), and birds (Hirose et al., 2012; Lindholm et al., 1994).

Individuals may have poor resource stores if they have few opportunities to gather resources. This situation can arise through a food shortage brought on by a competitive disadvantage from not establishing feeding territories before others in their cohort (Cutts et al., 1999; Metcalfe & Thorpe, 1992), or shorter growing seasons (Arendt & Wilson, 1999; Campos et al., 2009). A period of faster (compensatory) growth often occurs after depletion of resources causes a period of slow growth (Ali et al., 2003; Metcalfe & Monaghan, 2001).

Individuals counteract or compensate for this disadvantage by growing faster, which allows them to reach a similar size at a later time point, to individuals that were not stunted. This has been shown in juvenile Atlantic salmon, where there was a negative relationship.
FIGURE 3  Box plot comparisons of fork length at (a) capture, and back-calculated fork lengths for (b) 50 and (c) 25 days old for Arctic charr and brook trout (Salvelinus alpinus and S. fontinalis) and river (only rivers with a sample size greater than 10 were included) sampled June 24 to June 29, 2013, in northern Labrador, Canada. The boxplot shows the median (line) interquartile range (IQR, 25% and 75%), whiskers represent the next quartile of the data (1.5*IQR), and outliers are represented by dots. Open circles represent the mean for each group.

FIGURE 4  Plots showing the lack of a relationship between age (days) and fork length (mm) at capture for (a) Arctic charr and (b) brook trout among five rivers in northern Labrador, Canada.
between size at the end of the final winter before smolting and growth rate up to the smolt migration (Nicieza & Brana, 1993).

To investigate this process in response to hatch timing instead of food, we examined growth rates at three time points: during initial growth, for the entire life posthatch, and for the first 3 weeks of June. We found that during all three time periods individuals that hatched later grew faster than early hatchers. This phenomenon was observed in daily otolith growth increments, where incremental growth of late-hatching individuals tended to be larger than that of early-hatching individuals. The June growth comparisons indicate that late hatchers grow faster even under the same abiotic conditions and food availability (discussed below).

Previous work in other salmonid species has shown that larger eggs tend to produce bigger offspring, and larger offspring may emerge from the nest (i.e., ready to begin exogenous feeding) earlier than smaller offspring (e.g., Cogliati et al., 2018; Solberg et al., 2014). The probable difference in resource availability (both diminished fat stores and yolk resources) in early life may be enough to trigger a growth compensation response in the late-hatching fish. Additionally, individuals that are larger have a higher absolute growth rate but a lower relative or proportional growth rate (Van Buskirk et al., 2017). Cogliati et al. (2018) found that when comparing early and late hatchers there was no difference in growth rate but did find that fish from small eggs had a significantly larger increase in size.

**FIGURE 5** Plots showing simple linear regression models for the relationship between hatch date and average daily growth rate (fork length increase, mm/day) regardless of river for (a) the first 25 days of life; (b) the time period of June 1 to 21; and (c) for their entire life posthatching (average mm/day, based otolith estimation) for Arctic charr (left) and brook trout (right) (Salvelinus alpinus and S. fontinalis) among five rivers in northern Labrador, Canada.
over time. In our case, the older fish grew slower, therefore the potential bias is in a conservative direction because the small fish had a higher absolute growth rate and a higher proportional growth rate.

We do not know whether there was differential survival based on size or growth rate, therefore it is possible that individuals that hatched late but grew slow may have had higher mortality. Additionally, it is unknown with certainty whether intrinsic effects such as hatch time, or extrinsic environmental conditions experienced at different hatch times, were the main causes for differences in growth rate. There are likely notable differences in food supply (e.g., insect abundance increases through the spring) and photoperiod in the experiences of the early and late hatchers, which might explain the differences in growth rates. One could also assume that temperature would be an extrinsic explanation for the pattern of increased growth rate later in the season. However, when comparing the first 25 days posthatch experienced by early hatchers (early April, −1°C) and late hatchers (mid-May, −2°C), the temperature profiles were likely not different enough to explain the difference in growth rates. Most importantly, the comparison during the first 3 weeks of June controls for differences in both abiotic and biotic effects, and showed that not only was the pattern the same but also it had the strongest relations in both abiotic and biotic effects, and showed that not only was the pattern the same but also it had the strongest relationship (highest $R^2$ values). Due to prior residence advantage for early hatchers (O’Connor et al., 2000), we speculate that in order for late hatchers to grow faster, they possibly had to feed longer and/or more aggressively which is contrary to previous work that generally showed that early emergers tend to be bolder (Laakkonen & Hirvonen, 2007; Vaz-Serrano et al., 2011).

Our estimated hatch timing (based on accumulated thermal units, ATU) fits with estimated temperatures (~1 to 2°C) because Labrador populations spawn in mid-October to early November (DFO, 2001), and we would expect a hatch range of late March to mid-May (~160–190 days at 1–2°C). Previous work has shown that Arctic char hatch between 331 and 416 ATU (at 8.5°C, 39–49 days; Yanik et al., 2002) and brook trout between 477 and 483 ATU (at −10−11°C, 43–48 days; Penney et al., 2018, Witzel & MacCrimmon, 1983). We found relatively similar results in lab experiments conducted on Arctic char embryos from the Fraser River, Labrador (400 ± 34.9 ATU; Penney and Purchase unpublished data).

The results of this study show that the timing of hatch affects growth rate, providing more evidence that hatch phenology can play an important role in early life history. Growth rate and size are two important early life-history traits in fishes and understanding the nuances of factors that affect early growth can help explain how different early phenotypes project into different adult life-history strategies (Clarke et al., 2016). Future work designed to empirically test specifically how hatch phenology affects growth rate and survival through the first year of life, and how that translates into differences in fitness for salmonids is recommended. Furthermore, predicted changes in climate are likely to affect hatch phenology (Rooke et al., 2019), and therefore, more research should be done to understand the consequences of changes in complex northern ecosystems.

AUTHOR CONTRIBUTIONS
Heather D. Penney: Conceptualization (lead); data curation (lead); formal analysis (lead); funding acquisition (equal); methodology (equal); visualization (lead); writing – original draft (lead); writing – review and editing (lead). Donald G. Keefe: Conceptualization (supporting); methodology (supporting); resources (equal); writing – review and editing (supporting). Robert C. Perry: Conceptualization (supporting); methodology (supporting); resources (equal); writing – review and editing (supporting). Craig F. Purchase: Conceptualization (lead); formal analysis (supporting); funding acquisition (lead); methodology (equal); project administration (lead); resources (equal); supervision (lead); writing – review and editing (supporting).

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DATA AVAILABILITY STATEMENT
Data will be archived on Dryad upon publication.

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REFERENCES
Abrams, P. A., Leimar, O., Nylin, S., & Wiklund, C. (1996). The effect of flexible growth rates on optimal sizes and development times of flexible growth rates on optimal sizes and development times in a seasonal environment. The American Naturalist, 147(3), 381–395.
Adams, C. E., Murray, K. R., & Huntingford, F. A. (1992). The periodicity of primary increment formation in the otoliths of Arctic char Salvelinus alpinus (L.). Journal of Fish Biology, 41(4), 515–520. https://doi.org/10.1111/j.1095-8649.1992.tb02679.x
Ali, M., Nicieza, A., & Wootton, R. J. (2003). Compensatory growth in fishes: A response to growth depression. Fish and Fisheries, 4(2), 147–190. https://doi.org/10.1046/j.1467-2979.2003.00120.x
Arendt, J. D., & Wilson, D. S. (1999). Countergradient selection for rapid growth in pumpkinseed sunfish: Disentangling ecological and evolutionary effects. Ecology, 80(8), 2793–2798. https://doi.org/10.2307/177259
Beacham, T. D., Withler, F. C., & Morley, R. B. (1985). Effect of egg size on incubation time and alevisn and fry size in chum salmon (Oncorhynchus keta) and coho salmon (Oncorhynchus kisutch). Canadian Journal of Zoology, 63(4), 847–850. https://doi.org/10.1139/z85-125
Beer, W. N., & Anderson, J. J. (2001). Effect of spawning day and temperature on salmon emergence: Interpretations of a growth model for Methow River Chinook. *Canadian Journal of Fisheries and Aquatic Sciences*, 58(5), 943–949. https://doi.org/10.1139/f01-049

Berejikian, B. A., Bush, R. A., & Campbell, L. A. (2014). Maternal control over offspring life history in a partially anadromous species, *Oncorhynchus mykiss*. *Transactions of the American Fisheries Society*, 143(2), 369–379. https://doi.org/10.1080/00205887.2013.862181

Biro, P. A., Abrahams, M. V., Post, J. R., & Parkinson, E. A. (2004). Predators select against high growth rates and risk-taking behavior in domestic trout populations. *Proceedings of the Royal Society of London – Series B: Biological Sciences*, 271(1554), 2233–2237. https://doi.org/10.1098/rspb.2004.2861

Borchering, J., Beeck, P., DeAngelis, D. L., & Scharf, W. R. (2010). Match or mismatch: The influence of phenology on size-dependent life history and divergence in population structure. *The Journal of Animal Ecology*, 79(5), 1101–1112. https://doi.org/10.1111/j.1365-2656.2010.01704.x

Brännäs, E. (1995). First access to territorial space and exposure to strong competitors acting on body size, growth rate and compensatory growth: An empirical test in a wild trout population. *Proceedings of the Royal Society B: Biological Sciences*, 262, 174–180. https://doi.org/10.1098/rspb.1995.0064

Bucx, C. F., & Penney, J. A. (2012). Adaptation in a partially anadromous salmonid species. *Canadian Journal of Fisheries and Aquatic Sciences*, 69(12), 2717–2726. https://doi.org/10.1139/ac12-032

Bulter, W. L., Cunjak, R. A., & Smith, H. D. (2005). Latitudinal variation in growth of *Crangon crangon* (Gosline, 1855) measured from otolith microstructure. *Journal of Fish Biology*, 66(5), 943–959. https://doi.org/10.1111/j.1095-8649.1992.tb03848.x

Cutts, C. J., Metcalfe, N. B., & Taylor, A. C. (1999). Competitive asymmetries in territorial juvenile Atlantic salmon, *Salmo salar*. *Oikos*, 86, 479–486. https://doi.org/10.2307/3546652

Damsgård, B., & Dill, L. M. (1998). Risk-taking behavior in weight-compensating coho salmon, *Oncorhynchus kisutch*. *Behavioral Ecology*, 9(1), 26–32. https://doi.org/10.1093/beheco/9.1.26

DFO. (2001). *North Labrador Arctic Charr*. DFO Stock Status Rep. D2-07.

Einum, S., & Fleming, I. A. (2000). Selection against late emergence and small offspring in Atlantic salmon (*Salmo salar*). *Evolution*, 54(2), 628–639. https://doi.org/10.1111/j.0014-3820.2000.tb00664.x

Fitzgerald, K. A., Haworth, M. R., Bestgen, K. R., Farrall, C. J., Utsumi, S., Kishida, O., Uno, H., & Kanno, Y. (2021). Hatch timing of two subarctic salmonids in a stream network estimated by otolith increments. *Fisheries Management and Ecology*, 28(6), 507–515. https://doi.org/10.1111/fme.12504

Gotthard, K. (2000). Increased risk of predation as a cost of high growth rate: An experimental test in a butterfly. *The Journal of Animal Ecology*, 69(5), 896–902. https://doi.org/10.1046/j.1365-2656.2000.00432.x

Gotthard, K. (2008). Adaptive growth decisions in butterflies. *Bioscience*, 58(3), 222–230. https://doi.org/10.1641/B580308

Guest, J. R., Baird, A. H., Clifton, K. E., & Heyward, A. J. (2008). From molecules to moonsbeams: Spawning synchrony in coral reef organisms. *Invertebrate Reproduction and Development*, 51(3), 145–149. https://doi.org/10.1080/07924259.2008.9652264

Hirose, F., Kazama, K., Ito, M., & Watanuki, Y. (2012). Accelerated growth rates in late-hatched rhinoceros auklet *Cerorhinca monocerata* chicks depend on food conditions and growth stage: An experimental approach. *Ibis*, 154(2), 296–306. https://doi.org/10.1111/j.1474-919X.2011.01205.x

Jonsson, B., & Jonsson, N. (2014). Early environment influences later performance in fishes. *Journal of Fish Biology*, 85(2), 151–188. https://doi.org/10.1111/jfb.12432

Laakkonen, M. V., & Hirvonen, H. (2007). Is boldness towards predators related to growth rate in naïve captive-reared Arctic char (*Salvelinus alpinus*)? *Canadian Journal of Fisheries and Aquatic Sciences*, 64(4), 665–671. https://doi.org/10.1139/f07-041

Lapolla, A. E. (2001). Bay anchovy *Anchoa mitichilli* in Narragansett Bay, Rhode Island. II. Spawning season, hatch-date distribution and young-of-the-year growth. *Marine Ecology Progress Series*, 217, 103–109. https://doi.org/10.3354/meps217103

Lindholm, A., Gauthier, G., & Desrochers, A. (1994). Effects of hatch date and food supply on Gosling growth in Arctic-nesting greater snow geese. *The Condor*, 96(4), 898–908. https://doi.org/10.2307/1369100

Maino, J. L., Pirtle, E. I., & Kearney, M. R. (2017). The effect of egg size on hatch time and metabolic rate: Theoretical and empirical insights on developing insect embryos. *Functional Ecology*, 31, 227–234. https://doi.org/10.1111/1365-2435.12702

McCa irns, R. S. J. (2004). Adaptive variability in response to differences in seasonality: A study of countergradient variation in the growth of Brook trout *Salvelinus fontinalis*, from western Newfoundland (MSc.). Dalhousie University, Halifax, NS.

McNamara, J. M., Barta, Z., Klaassen, M., & Bauer, S. (2011). Cues and the optimal timing of activities under environmental changes. *Ecology Letters*, 14(2), 1183–1190. https://doi.org/10.1111/j.1461-0248.2011.01686.x

Mercier, A., Sun, Z., & Hamel, J.-F. (2011). Reproductive periodicity, spawning and development of the deep-sea scleractinian coral *Flabellum angulare*. *Marine Biology*, 158(2), 371–380. https://doi.org/10.1007/s00227-010-1565-7

Metcalfe, N. B., & Monaghan, P. (2001). Compensation for a bad start: Grow now, pay later? Trends in *Ecology & Evolution*, 16(5), 254–260. https://doi.org/10.1016/S0169-5347(01)02124-3

Metcalfe, N. B., & Thorpe, J. E. (1992). Early predictors of life-history events: The link between first feeding date, dominance and seaward migration in Atlantic salmon, *Salmo salar*. *Journal of Fish Biology*, 41, 93–99. https://doi.org/10.1111/j.1095-8649.1992.tb03871.x
Mikolajewski, D. J., Block, M. D., & Stoks, R. (2015). The interplay of adult and larval time constraints shapes species differences in larval life history. Ecology, 96(4), 1128–1138. https://doi.org/10.1890/14-0262.1

Moginie, B. F., & Shima, J. S. (2018). Hatch date and growth rate drives reproductive success in nest-guarding males of a temperate reef fish. Marine Ecology Progress Series, 592, 197–206. https://doi.org/10.3354/meps12506

Morvey, Y. E., & Ydenberg, R. C. (2003). Timing games in the reproductive phenology of female Pacific salmon (Onchorhynchus spp.). The American Naturalist, 161(2), 284–298. https://doi.org/10.1086/ an.2003.0161.issue-2

Morgan, S. G., & Christy, J. H. (1994). Plasticity, constraint, and optimality in reproductive timing. Ecology, 75(8), 2185–2203. https://doi.org/10.2307/1940876

Morin, P. J., Lawler, S. P., & Johnsen, E. A. (1990). Ecology and breeding phenology of larval Hyla andersonii: The disadvantages of breeding late. Ecology, 71(4), 1590–1598. https://doi.org/10.2307/1938294

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(3), 261–272. https://doi.org/10.1016/0044-8486(93)90301-E

Nicieza, A. G., & Brana, F. (1993). Compensatory growth and optimum size in one-year-old smolts of Atlantic salmon (Salmo salar). In R. J. Gibson & R. E. Cutting (Eds.), Production of juvenile Atlantic salmon, Salmo salar, in natural waters (pp. 225–237). Canadian Special Publication of Fisheries and Aquatic Sciences 118 p.

Nicieza, A. G., & Metcalfe, N. B. (1997). Growth compensation in juvenile Atlantic salmon: Responses to depressed temperature and food availability. Ecology, 78(8), 2385–2400. https://doi.org/10.1890/0012-9658(1997)078[2385:GCJAS]2.0.CO;2

O’Connor, K. I., Metcalfe, N. B., & Taylor, A. C. (2000). The effects of prior residence on behavior and growth rates in juvenile Atlantic salmon (Salmo salar). Behavioral Ecology, 11(1), 13–18. https://doi.org/10.1093/beheco/11.1.13

Oesterheld, M., & McNaughton, S. J. (1991). Effect of stress and time for recovery on the amount of compensatory growth after grazing. Oecologia, 85(3), 305–313. https://doi.org/10.1007/BF00302064

Orizaga, G., Dahl, E., & Laurila, A. (2010). Compensating for delayed hatching across consecutive life-history stages in an amphibian, Oikos, 119(6), 980–987.

Pearson, P. R., & Warner, D. A. (2018). Early hatch enhancement survival despite beneficial phenotypic effects of late-season developmental environments. Proceedings of the Royal Society B, 285(1874), 20180256. https://doi.org/10.1098/rspb.2018.0256

Penney, H. D., Beirão, J., & Purchase, C. F. (2018). Phenotypic plasticity during external embryonic development is affected more by maternal effects than multiple abiotic factors in brook trout. Evolutionary Ecology Research, 19, 171–194.

Purchase, C. F., & Brown, J. A. (2000). Interpopulation differences in growth rates and food conversion efficiencies of young grand banks and gulf of Maine Atlantic cod (Gadus morhua). Canadian Journal of Fisheries and Aquatic Sciences, 57(11), 2223–2229. https://doi.org/10.1139/H10-204

Quinn, T. P. (2005). The behavior and ecology of Pacific salmon & trout. American Fisheries Society.

R Core Team. (2021). R: A language and environment for statistical computing. Version: 4.1.2. R Foundation for Statistical Computing. http://www.R-project.org/

Radkte, R. L. (1989). Larval fish age, growth, and body shrinkage: Information available from otoliths. Canadian Journal of Fisheries and Aquatic Sciences, 46(11), 1884–1894. https://doi.org/10.1139/F89-237

Radkte, R. L., Fey, D. P., DeCicco, A. F., & Montgomery, A. (1996). Otolith microstructure in young-of-the-year Dolly Varden, Salvelinus malma, from American and Asian populations: Resolution of comparative life history characteristics. Arctic, 49(2), 162–169. https://doi.org/10.14430/arctic1194

Reed, T. E., Warzybok, P., Wilson, A. J., Bradley, R. W., Wanless, S., & Sydeman, W. J. (2009). Timing is everything: Flexible phenology and shifting selection in a colonial seabird. The Journal of Animal Ecology, 78(2), 376–387. https://doi.org/10.1111/j.1365-2656.2008.01503.x

Rohde, K., Dreher, E., & Hochkirch, A. (2015). Sex-specific phenotypic plasticity in response to the trade-off between developmental time and body size supports the dimorphic niche hypothesis. Biological Journal of the Linnean Society, 115(1), 48–57. https://doi.org/10.1111/bij.12460

Rooke, A. C., Palm-Flawd, B., & Purchase, C. F. (2019). The impact of a changing winter climate on the hatch phenology of one of North America’s largest Atlantic salmon populations. Conservation Physiology, 7(1), coz015. https://doi.org/10.1093/comphys/coz015

Rotella, J. J., Paterson, J. T., & Garrett, R. A. (2016). Birth dates vary with fixed and dynamic maternal features, offspring sex, and extreme climatic events in a high-latitude marine mammal. Ecology and Evolution, 6(7), 1930–1941. https://doi.org/10.1002/ece3.1985

Satake, A., Sasaki, A., & Iwasa, Y. (2001). Variable timing of reproduction in unpredictable environments: Adaption of flood plain plants. Theoretical Population Biology, 60(1), 1–15. https://doi.org/10.1006/tpbi.2001.1528

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH image to ImageJ: 25 years of image analysis. Nature Methods, 9(7), 671–675. https://doi.org/10.1038/nmeth.2089

Shoji, A., Aris-Brosou, S., Culina, A., Fayet, A., Kirk, H., Padget, O., Juarez-Martinez, I., Boyle, D., Nakata, T., Perrins, C. M., & Guilford, T. (2015). Breeding phenology and winter activity predict subsequent breeding success in a trans-global migratory seabird. Biology Letters, 11(10), 20150671. https://doi.org/10.1098/rsbl.2015.0671

Simonin, P. W., Parrish, D. L., Rudstam, L. G., Pientka, B., & Sullivan, P. J. (2016). Interactions between hatch dates, growth rates, and mortality of age-0 native rainbow smelt and nonnative alewife in Lake Champlain. Transactions of the American Fisheries Society, 145(3), 649–656. https://doi.org/10.1080/00028487.2016.1143401

Sinнатамби, R. N., Dempson, J. B., Reist, J. D., & Power, M. (2014). Latitudinal variation in growth and otolith-inferred field metabolic rates of Canadian young-of-the-year Arctic charr: Ecology of Freshwater Fish, 24(3), 478–488. https://doi.org/10.1111/eff.12166

Skoglund, H., Einum, S., Forseth, T., & Barlaup, B. T. (2012). The penalty for arriving late in emerging salmonid juveniles: Differences between species correspond to their interspecific competitive ability. Functional Ecology, 26(1), 104–111. https://doi.org/10.1111/j.1365-2435.2011.01901.x

Snucins, E. J., Curry, R. A., & Gunn, J. M. (1992). Brook trout (Salvelinus fontinalis) embryo habitat and timing of alevin emergence in a lake and a stream. Canadian Journal of Zoology, 70(3), 423–427. https://doi.org/10.1139/cz92-064

Solberg, M. F., Fjelldal, P. G., Nilsen, F., & Glover, K. A. (2014). Hatching time and alevin growth prior to the onset of exogenous feeding in farmed, wild and hybrid Norwegian Atlantic salmon. PLoS ONE, 9(12), e113697. https://doi.org/10.1371/journal.pone.0113697

Sparks, M. M., Falke, J. A., Quinn, T. P., Adkison, M. D., Schindler, D. E., Bartz, K. K., Young, D. B., & Westley, P. A. H. (2019). Influences of spawning timing, water temperature, and climatic warming on early life history phenology in western Alaska sockeye salmon. Canadian Journal of Fisheries and Aquatic Sciences, 76(1), 123–135. https://doi.org/10.1139/cjfas-2017-0468

Sterner, K., Denic, M., & Geist, J. (2014). Timing matters: Species-specific interactions between spawning time, substrate quality, and recruitment success in three salmonid species. Ecology and Evolution, 4(13), 2749–2758. https://doi.org/10.1002/ece3.1128
Stoks, R., Block, M. D., & McPeek, M. A. (2006). Physiological costs of compensatory growth in a damselfly. *Ecology, 87*(6), 1566–1574. [https://doi.org/10.1890/0012-9658(2006)87[1566:PCOCG]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[1566:PCOCG]2.0.CO;2)

Sundström, L. F., Kaspersson, R., Näslund, J., & Johnsson, J. I. (2013). Density-dependent compensatory growth in brown trout (*Salmo trutta*) in nature. *PLoS ONE, 8*(5), e63287. [https://doi.org/10.1371/journal.pone.0063287](https://doi.org/10.1371/journal.pone.0063287)

Taborsky, B. (2006). The influence of juvenile and adult environments on life-history trajectories. *Proceedings of the Royal Society of London – Series B: Biological Sciences, 273*(1587), 741–750. [https://doi.org/10.1098/rspb.2005.3347](https://doi.org/10.1098/rspb.2005.3347)

Tamura, K., Stecher, G., Peterson, D., Filipski, A., & Kumar, S. (2013). MEGA6: Molecular evolutionary genetics analysis version 6.0. *Molecular Biology and Evolution, 30*(12), 2725–2729. [https://doi.org/10.1093/molbev/mst197](https://doi.org/10.1093/molbev/mst197)

Trabelsi, A., Gardeur, J.-N., Teletchea, F., Brun-Bellut, J., & Fontaine, P. (2013). Hatching time effect on the intra-spawning larval morphology and growth in northern pike (*Esox lucius* L.). *Aquaculture Research, 44*(4), 657–666. [https://doi.org/10.1111/j.1365-2109.2011.03070.x](https://doi.org/10.1111/j.1365-2109.2011.03070.x)

Van Buskirk, J., Cereghetti, E., & Hess, J. (2017). Is bigger really better? Relative and absolute body size influence individual growth rate under competition. *Ecology and Evolution, 7*, 3745–3750.

Vaz-Serrano, J., Ruiz-Gomez, M. L., Gjøen, H. M., Skov, P. V., Huntingford, F. A., Øverli, Ø., & Höglund, E. (2011). Consistent boldness behaviour in early emerging fry of domesticated Atlantic salmon (*Salmo salar*): Decoupling of behavioural and physiological traits of the proactive stress coping style. *Physiology and Behavior, 103*(3-4), 359–364. [https://doi.org/10.1016/j.physbeh.2011.02.025](https://doi.org/10.1016/j.physbeh.2011.02.025)

Vigliola, L., & Meekan, M. G. (2009). The back-calculation of fish growth from otoliths. In B. S. Green, B. D. Mapstone, G. Carlos, & G. A. Begg (Eds.), *Tropical fish otoliths: Information for assessment, management and ecology* (pp. 174–211). Springer Netherlands. [https://doi.org/10.1007/978-1-4020-5775-5_6](https://doi.org/10.1007/978-1-4020-5775-5_6)

Walling, C. A., Royle, N. J., Metcalfe, N. B., & Lindström, J. (2007). Early nutritional conditions, growth trajectories and mate choice: Does compensatory growth lead to a reduction in adult sexual attractiveness? *Behavioral Ecology and Sociobiology, 61*(7), 1007-1014. [https://doi.org/10.1007/s00265-006-0333-7](https://doi.org/10.1007/s00265-006-0333-7)

Walsh, M. R., Cooley, F., Biles, K., & Munch, S. B. (2015). Predator-induced phenotypic plasticity within- and across-generations: A challenge for theory? *Proceedings of the Royal Society B: Biological Sciences, 282*(1798), 20142205. [https://doi.org/10.1098/rspb.2014.2205](https://doi.org/10.1098/rspb.2014.2205)

Witzel, L. D., & MacCrimmon, H. R. (1983). Embryo survival and alevin emergence of brook char, *Salvelinus fontinalis* and brown trout, *Salmo trutta*, relative to redd gravel composition. *Canadian Journal of Zoology, 61*(8), 1783–1792. [https://doi.org/10.1139/z83-230](https://doi.org/10.1139/z83-230)

Yamahira, K., & Conover, D. O. (2002). Intra- vs. interspecific latitudinal variation in growth: Adaptation to temperature or seasonality? *Ecology, 83*(5), 1252-1262. [https://doi.org/10.1890/0012-9658(2002)083[1252:IVILV]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[1252:IVILV]2.0.CO;2)

Yamamoto, S., Shinomi, H., & Goto, A. (1997). The effect of birth date on growth of juvenile white-spotted char *Salvelinus leucomaenis*. *Fisheries Science, 63*(6), 931–933. [https://doi.org/10.2331/fishsci.63.931](https://doi.org/10.2331/fishsci.63.931)

Yanik, T., Hisar, S. A., & Bölükbası, C. (2002). Early development and growth of arctic char (*Salvelinus alpinus*) and rainbow trout (*Oncorhynchus mykiss*) at a low water temperature. *The Israeli Journal of Aquaculture = Bamidgeh, 54*(2), 73–78.

Zhu, X., Wu, L., Cui, Y., Yang, Y., & Wootton, R. J. (2003). Compensatory growth response in three-spined stickleback in relation to feed-deprivation protocols. *Journal of Fish Biology, 62*(1), 195-205. [https://doi.org/10.1046/j.1095-8649.2003.00019.x](https://doi.org/10.1046/j.1095-8649.2003.00019.x)

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