

Thermal adaptation and phenotypic plasticity in a warming world: Insights from common garden experiments on Alaskan sockeye salmon

Morgan M. Sparks¹  | Peter A. H. Westley¹ | Jeffrey A. Falke² | Thomas P. Quinn³

¹College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, AK, USA

²U.S. Geological Survey, Alaska Cooperative Fish and Wildlife Research Unit, University of Alaska Fairbanks, Fairbanks, AK, USA

³School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA, USA

Correspondence

Morgan Sparks, Department of Biological Sciences, Purdue University, West Lafayette, IN, USA.

Email: msparks1309@gmail.com

Funding information

Western Alaska Landscape Conservation Cooperative

Abstract

An important unresolved question is how populations of coldwater-dependent fishes will respond to rapidly warming water temperatures. For example, the culturally and economically important group, Pacific salmon (*Oncorhynchus* spp.), experience site-specific thermal regimes during early development that could be disrupted by warming. To test for thermal local adaptation and heritable phenotypic plasticity in Pacific salmon embryos, we measured the developmental rate, survival, and body size at hatching in two populations of sockeye salmon (*Oncorhynchus nerka*) that overlap in timing of spawning but incubate in contrasting natural thermal regimes. Using a split half-sibling design, we exposed embryos of 10 families from each of two populations to variable and constant thermal regimes. These represented both *experienced* temperatures by each population, and *predicted* temperatures under plausible future conditions based on a warming scenario from the downscaled global climate model (MIROC A1B scenario). We did not find evidence of thermal local adaptation during the embryonic stage for developmental rate or survival. *Within* treatments, populations hatched within 1 day of each other, on average, and *among* treatments, did not differ in survival in response to temperature. We did detect plasticity to temperature; embryos developed 2.5 times longer (189 days) in the coolest regime compared to the warmest regime (74 days). We also detected variation in developmental rates among families *within* and *among* temperature regimes, indicating heritable plasticity. Families exhibited a strong positive relationship between thermal variability and phenotypic variability in developmental rate but body length and mass at hatching were largely insensitive to temperature. Overall, our results indicated a lack of thermal local adaptation, but a presence of plasticity in populations experiencing contrasting conditions, as well as family-specific heritable plasticity that could facilitate adaptive change.

KEYWORDS

Bristol Bay, climate change, developmental phenology, gene × environment, hatching, *Oncorhynchus nerka*, phenotypic plasticity, reaction norm

1 | INTRODUCTION

In many organisms, the timing of breeding and early life history development is closely tied to temperature, and thus changes in the thermal environment can have profound ecological and evolutionary consequences (Haugen & Vøllestad, 2000; McPhee, Noakes, & Allendorf, 2012; Merilä & Hendry, 2014; Stillwell & Fox, 2005). Often phenology, or the timing of life history events such as birth, migration, or breeding, is shaped by both environmentally induced phenotypic plasticity and heritable mechanisms (Crozier et al., 2008; Gienapp, Teplitsky, Alho, Mills, & Merilä, 2008; Gienapp et al., 2013; Reed, Schindler, & Waples, 2011). For the environmentally induced components of these life histories, theory predicts that plasticity may be lost in homogenous environments (Hutchings, 2011; Oomen & Hutchings, 2016). In order to test the relationship between the environment and life history expression, experiments quantifying local adaptation and plasticity have been conducted using many taxa (e.g., Aday, Wahl, & Philipp, 2003; Walsh & Post, 2012) and are commonly used to test thermal adaptation and plasticity within ectothermic organisms such as coldwater fishes (e.g., Haugen, 2000; Jensen et al., 2008). However, studies that explore the potential responses by coldwater-dependent populations to warming water temperatures have only recently garnered much attention (see Drinan et al., 2012; Whitney, Hinch, & Patterson, 2013, 2014) and often lack naturally variable regimes.

For salmonid fishes (i.e., salmon and trout), embryonic developmental rates and thus the timing between fertilization, hatching, and emergence are largely governed by the ambient temperature regime (Beacham & Murray, 1990; Haugen & Vøllestad, 2000; Quinn, 2005). Consequently, local, habitat-specific temperature regimes are associated with the timing of reproduction. Typically, populations in cold environments tend to spawn earlier in the season than populations in warmer environments (Brannon, 1987; Brannon, Powell, Quinn, & Talbot, 2004; Hodgson & Quinn, 2002). As with most salmonids, sockeye salmon (*O. nerka*) experience the majority of lifetime mortality between the period when eggs are fertilized and buried in the gravel to when juveniles emerge as free-swimming fish (Quinn, 2005). This period is therefore subject to selection on early life history traits and adult spawning times. Given the strong relationship between temperature, spawning timing, and embryonic development, rapid ecosystem-level temperature change could markedly affect physiological rates and survival during early life stages in salmonids (Angilletta et al., 2008; Beacham & Murray, 1990; Karjalainen, Keskinen, Pulkkanen, & Marjomäki, 2015; Steel et al., 2012; Whitney et al., 2014).

Mirroring patterns observed across the range of sockeye salmon (Hodgson & Quinn, 2002), Bristol Bay populations tend to spawn earlier in colder habitats and later in the season in warmer ones (Lisi, Schindler, Bentley, & Pess, 2013). Spawning timing for sockeye salmon is thought to reflect local adaptation to the prevailing thermal regime such that juveniles hatch and emerge when conditions are suitable the following spring, given the long-term average temperature profile of the sites (Brannon, 1987; Hodgson & Quinn, 2002;

Kinnison, Unwin, & Quinn, 2008). Additionally, spawning timing may also reflect the signature of selection acting on adults during the breeding season (Larson, Seeb, Dann, Schindler, & Seeb, 2014). Bristol Bay sockeye salmon spawn in habitats with various thermal regimes including small streams, rivers, lake and island shores, and spring-dominated ponds (Blair & Quinn, 1991; Lisi et al., 2013; Quinn, Wetzel, Bishop, Overberg, & Rogers, 2001) and these spawning habitats that drain into common juvenile salmon nursery lakes can occur in close proximity on the landscape. Yet, these sites, although being geographically close, may differ in thermal regimes and sensitivity to climate warming, given site-specific characteristics such as the extent of snow melt vs. rainwater contribution (Lisi, Schindler, Cline, Scheuerell, & Walsh, 2015; Sparks, 2016). Given site-specific responses, populations may experience abrupt change (or lack of change) in their incubation environment given a warming climate.

Fine-scale adaptation in developmental rates of populations that rear in different thermal regimes but share common nursery areas seems likely (Hendry, Hensleigh, & Reisenbichler, 1998; Quinn, Hendry, & Wetzel, 1995; Quinn et al., 2001). But, there is far more evidence for population-specific adaptation of spawning time (e.g., Brannon, 1987; Hodgson & Quinn, 2002; Kinnison et al., 2008), as opposed to developmental rates, which appears to respond less to selection (Beacham & Murray, 1990; Kinnison et al., 2008). While populations tend to exhibit less local adaptation in developmental rates than spawning time, recent work testing the effect of incubation thermal regime variability on development rate and emergence size found genetic differences at both the family (Dammerman, Steibel, & Scribner, 2016; Steel et al., 2012) and population levels (Fuhrman, Larsen, Steel, Young, & Beckman, 2017). Furthermore, studies testing these factors often lack direct comparisons of populations experiencing contrasting natal thermal regimes within shared systems, rarely take place in high latitude habitats experiencing more rapid and extreme change, and poorly account for plausible predictions of climate change because of the use of thermal treatments that lack natural variability or represent temperatures unlikely to be experienced in nature.

The overarching goal of this study was to test for the presence and extent of thermal adaptation and plasticity in developmental rates and larval morphology for two high latitude, spatially proximate populations of sockeye salmon that experience very different thermal regimes (one a descending variable and initially warmer regime, and the other initially cooler and constant regime). The primary goal was to assess potential responses to water temperatures under experienced temperature regimes and plausible scenarios of global change. Using a common garden experimental approach that incorporated both natal thermal regimes and specific predictions for these regimes given global climate scenarios, our specific objectives were to: (i) quantify population- and family-level heritable (plasticity) differences in developmental rates (i.e., hatching time) within and among temperature regimes, (ii) test for local adaptation to incubation temperature by comparing embryo survival between natal and foreign temperature regimes, and (iii) quantify population- and

family-specific responses in size at hatching (length and mass) across temperature treatments. Given presumptions of thermal adaptations, we expected that populations and families would have the highest survival in natal temperature regimes and lower survival in regimes of the foreign environment for treatments representing experienced conditions. Similarly, we expected the population from the warmer and more variable environment to be better adapted (higher survival, more plastic development) to future warming scenarios given its natal thermal environment. Furthermore, we expected population- and family-specific differences in time needed to hatch to be indicative of heritable developmental rates. Additionally, we expected to observe greater plasticity in hatch timing and size at hatching (length and mass) from the population that spawns in a variable thermal habitat (Hutchings, 2011; Oomen & Hutchings, 2016). Finally, we expected that larvae would be smaller at warmer temperatures owing to increased metabolic costs at higher temperatures (Beauchamp, 2009; Quinn, 2005) from physiological processes such as reduced yolk conversion efficiency (sensu Atkinson, 1994; Atkinson & Sibly, 1997).

2 | MATERIALS AND METHODS

2.1 | Study populations and experimental animals

The many large lake systems of Bristol Bay, Alaska support the world's most abundant wild sockeye salmon populations—for example, 59.1 million adult salmon returned to the nearshore waters in 2015 (Jones et al., 2016). Populations of salmon within Bristol Bay watersheds generally overlap in their timing of entry to freshwater (Doctor, Hilborn, Rowse, & Quinn, 2010; Jensen & Mathisen, 1987), but spawn asynchronously over several months (Lisi et al., 2013; Schindler et al., 2013). The two focal populations of sockeye salmon in this study both spawn in early to mid-August only a few kilometers from each other, but in starkly contrasting thermal regimes. The Woody Island population spawns along beaches in the wind-driven surface waters of Iliamna Lake (Leonetti, 1997; Olsen, 1964), resulting in a thermal regime that is warm (~13°C) during the spawning season but then rapidly cools as the lake cools and (in most years) freezes during the incubation period (Adkison, Ward, & Quinn, 2013; Sparks, 2016). In contrast, the Pedro Bay Pond population (8.5 km away straight line distance from Woody Island) spawns in a series of small spring-fed ponds and streams, flowing into Iliamna Lake. These embryos develop in water that remains at a near constant temperature (~4°C during the incubation period), thus is cooler initially, and then milder in the middle of the winter than the Woody Island population. The “Pedro Ponds” experimental families for our study were created from parents collected in one of these ponds (referred to as ‘Big Pond’ in Quinn, Rich, Gosse, and Schtickzelle (2012)), but referred to as Pedro Ponds hereafter for simplicity and because it is a representative spawning habitat in this pond network (Quinn, Volk, & Hendry, 1999; Quinn et al., 2012).

Despite temporal overlap in spawning period and geographical proximity, the two populations are largely reproductively isolated

owing to natal homing behavior (Blair & Quinn, 1991; Quinn et al., 1999). Spatial isolation, coupled with presumed differences in selection pressures on the spawning grounds, likely explains observed phenotypic (Blair, Rogers, & Quinn, 1993) and genetic differences between these populations (Gomez-Uchida et al., 2011).

On August 12, 2015, gametes from 10 females and 20 males from each of the Woody Island and Pedro Bay Ponds populations were stripped and fertilized in the field (Table 1). A single female was stripped of eggs into a fertilization basin and then two males were stripped of milt concurrently, creating a half-sib family. Hereafter we refer to each half-sibling unit simply as a “family” and abbreviate them as W1-W10 for Woody Island families and P1-P10 for Pedro Ponds families in our experiment. All families were transported separately and incubated in isolation from other families in the experiment from that point on. Our experimental design of mating two males with a single female (half-sibling families) emulated the breeding system of sockeye salmon, where multiple males frequently mate with a single female (Esteve, 2005), and also reduced the chances of fertilization failures. Additionally, this mating strategy can result in sperm competition, which leads to some unknown within-family variability. Fertilized ova were disinfected with a 100:1 ovadine solution, and allowed to water harden for 60 min before being individually bagged by family and put in chilled coolers (to maintain ~10°C). Fertilized eggs were flown directly to the University of Alaska Fairbanks.

2.2 | Thermal laboratory experiments

Within 12 h of fertilization, the 10 families from each population were placed into vertical incubators and exposed to a suite of five temperature treatments (see details in next section). Each incubator was supplied by a recirculating supply of 375 L of oxygen-saturated water at an average flow of 18 L/s (Table 2). Approximately, 100–150 fertilized ova per family were placed into each of four replicate (per experimental apparatus) 7.62 cm diameter × 6.35 cm tall PVC containers with screened bottoms. Each of the four replicated containers were then haphazardly placed into four trays at different levels of the incubator (one in each tray) such that all families from all populations experienced every tray to control for any subtle variation in temperature as water flowed from top to bottom of the apparatus. Embryos were maintained in constant darkness and sampled under red light.

TABLE 1 Average male and female length (*SD*), and egg mass (*SD*) specific to the two populations of Bristol Bay, Alaska sockeye salmon used in this study, each represented by 10 families (10 males, 20 females for each population). Length was measured from mid-eye to hypural plate. Egg weight was measured postfertilization and water-hardening

Population	Male length (mm)	Female length (mm)	Egg mass (g)
Woody Island	443.1 (29.5)	436.1 (22.3)	0.138 (0.013)
Pedro Ponds	453.1 (26.6)	465.4 (16.6)	0.113 (0.009)

TABLE 2 Summary environmental characteristics for five experimental temperature treatments. Observed mean temperature, coefficient of variation, median and predicted days to hatch^a, conductivity, dissolved oxygen, and flow are shown. Average temperature and coefficient of variation were measured to the treatment-specific median day to hatch

Treatment	Mean temp °C	CV	Median days to hatch	Predicted days to hatch ^a	Conductivity (uS)	DO (mg/L)	Flow (L/s)
WI_MIROC	10.14	0.20	74	65	42.8	9.36	0.14
WI_AVG	9.10	0.28	82	68	18.9	9.66	0.17
PP_MIROC	7.26	0.02	100	87	19.0	10.27	0.23
WI_Cold	5.42	0.58	118	97	36.1	10.54	0.14
PP_AVG	2.83	0.03	189	160	14.5	11.34	0.22

^aPredictions were made using a model from Beacham and Murray (1990).

2.3 | Temperature treatments

We exposed developing embryos to five either constant or variable (variability measured as CV of temperature) temperature treatments (summarized in Table 2, Figure 1) that reflected conditions that the two populations would have experienced in their local natal sites (home conditions), if individuals had strayed among sites (foreign conditions, Sheridan, 1962), and might experience under a scenario of climate warming at each site. Specifically, the following five treatments were: (i) WI_AVG: the long-term averages of observed data (1990–1992, 2000–2010) experienced by the Woody Island population during each day over incubation; (ii) WI_Cold: the 2004 temperature regime, which was the coldest experienced by the Woody Island population over the same period and allowed for a broader range of variable temperatures, as WI_MIROC (see below) and WI_AVG were somewhat similar; (iii) PP_AVG: the average temperature (constant 4°C, although the treatment actually averaged 2.8°C based on the ability the chiller unit was able to cool water) experienced by the Pedro Ponds population; (iv) WI_MIROC: a regime representative of downscaled climate change predictions in the warmest year of the 2090s for the 0.5 × 0.5 degree grid centered around the Woody Island region of Iliamna Lake generated using the MIROC global climate model (A1B emissions scenario, Sparks, 2016); and (v) PP_MIROC: a simplistic climate change scenario for the Pedro Ponds population that predicts water temperature in the Ponds will approximately double to a constant 8°C based on projections (approximate average annual air temperature for the region) from the MIROC model (Table 2, Figure 1) (Sparks, 2016).

The model used to predict future scenario for Woody Island was a generalized additive model created using the relationship between the 3-day rolling average of observed daily maximum air temperature and observed daily lake temperature (1990–1992, 2000–2010), which had the best fit of any rolling average model we tested (GAM; $R^2_{adj} = 0.814$). Lake temperatures for 2099 were forecasted using the same model but based on 0.5 × 0.5 degree resolution daily maximum air temperature predictions under the MIROC A1B scenario, which reflected the most extreme regime forecasted among many climate models and scenarios (CIG, 2015). In turn, the future scenario for the Pedro Ponds was created using approximate average annual air temperature for the region using those same predictions.

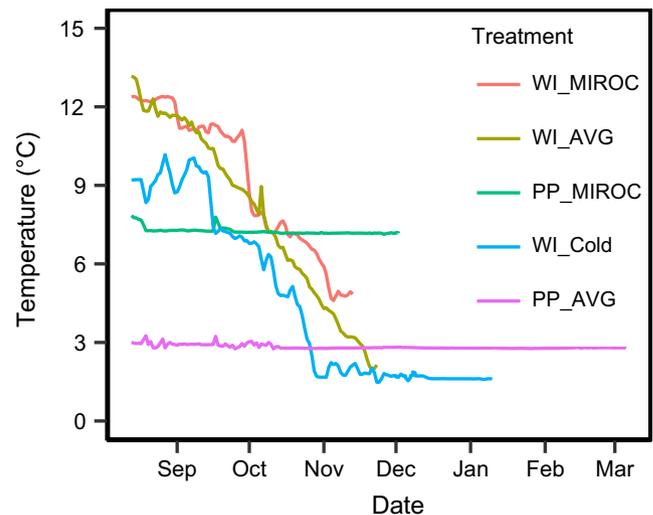


FIGURE 1 Mean daily temperatures for five experimental treatments in which two Bristol Bay, Alaska sockeye salmon populations were reared over the course of the study. Regimes ended after all fish in each treatment hatched. See text for details regarding treatments.

This was a more simplistic assumption of future temperatures in the Pedro Ponds, as the spring and groundwater dynamics have not been studied, and meant to be a more general characterization for groundwater systems throughout the region. For a more specific discussion of exact methods, see Sparks (2016).

Temperatures in the experiment were recorded by HOBO Tid-Bit recorders (15-min intervals, accurate to 0.2°C) placed in the bottom tray of the apparatus and a hand thermometer was used to measure daily temperature in each tray. Temperatures in the WI_AVG, WI_Cold, and WI_MIROC treatments were adjusted each day at 09:00 hr as needed to match the relative average daily temperature for each treatment. Apparatuses were held in temperature-controlled rooms approximately 2°C above the warmest treatment temperature.

2.4 | Experimental data collection

Dead embryos were removed from all treatments the first day after transportation (these were considered transportation mortalities),

after which all mortalities were recorded for analysis. Dead embryos from treatments were removed on a weekly basis to avoid algal or bacterial growth, except during periods of known developmental sensitivity during the critical state of development between 80 and 100 ATUs (accumulated thermal units, sum of daily average temperature; Quinn, 2005).

Hatching larvae, hereafter termed alevins, were removed from the treatment and sacrificed in an overdose of tricaine methanesulfonate (MS-222) the day they hatched. On each day of sampling, the first 25 individuals from each family in each treatment were weighed to the nearest 0.001 g and then photographed using a Canon Rebel T5i with a macro 50 mm lens in a standardized fashion. Photographing and weighing of alevins continued daily until 150 individuals per family per treatment were sampled or all fish had hatched, after which remaining hatching fish from that family and treatment were sacrificed and preserved. Photographs were analyzed using ImageJ software (<https://imagej.nih.gov/ij/>) to quantify mid-eye to hypural length (0.001 mm). Measurements were made by using the same scale in each photo (a ruler of 10 mm) that was used to translate pixels to millimeters, this measurement was then reset for each photograph (most photographs had multiple fish) so as to account for any movement of the photographic apparatus. All photographs of sacrificed alevins were taken immediately after they were sacrificed to avoid preservation changing the shape of fish. To explore measurement error, two measurers quantified body length of the same 50 images and revealed an error of <3%, measurements were repeated by individuals a second time and revealed intrameasurer error of <1.5%.

2.5 | Data analysis

We used a well-established statistical model (Beacham & Murray, 1990) developed through experimental rearing of a number of different populations of sockeye salmon in British Columbia, Canada to estimate the number of days to hatch given the experimental thermal regimes, and then compared them with the observed data in each treatment (Table 2). The comparison was used to draw inferences on the utility of using such a model outside of populations for which it was developed and also to elucidate potential genetic differences in development among populations from different regions of sockeye salmon habitat.

We fit a linear mixed effects model (Bolker, 2008; Bolker et al., 2009) to quantify the contribution of population and family-level effects on time until hatching following the general form:

$$y_i = \alpha + T_j + P_k + L_l + a_{m(k)} + T_{j,m(k)} + \varepsilon_i \quad (1)$$

where y was the number of days until a given embryo (i) hatched, α is the intercept, T was the fixed effect of temperature treatment j , P was the fixed effect of population k , and L was the fixed effect of the of the incubator level l (tray 1–4). Random effects included $a_{m(k)}$ as the random intercept for family m (nested within population k) and was included to quantify how the treatment effect differs among families, and $T_{j,m(k)}$ was a random treatment effect for family m (nested within population k) and was included to represent how a

given treatment affects the response among families and populations to detect any underlying $G \times E$ response (gene \times environment; a differential heritable plastic response among families or populations). Given the confounded effect of population and egg size (i.e., Woody Island fish had larger eggs than Pedro Pond fish; Table 1), we included only the former factor in analyses as previous work has shown little influence of egg size on developmental rate (Beacham & Murray, 1990).

This modeling approach was similarly used to analyze differences in alevin mass and length among populations, families, and temperature treatments. All three models were fit assuming independent Gaussian distributions for the residuals and for each of the random effects after data were graphically confirmed to be normally distributed. Variability in survival was analyzed using the same form as Equation (1), but with a logit link and binomial error distribution given the binomial nature of the response variable (fish were coded 0 if they died and 1 if they lived to hatch). We fit 11 models of varying complexity for each response variable, using all combinations of fixed and random effects (using Equation 1 as the parent equation) and determined the most parsimonious models, based on BIC (stats package, R Core Team, 2015). We considered models for which the BIC exceeded that of the best model (lowest BIC) by more than 4 to have had substantially lower evidence and thus limited interpretation accordingly (Bolker, 2008; Burnham & Anderson, 2002). All analyses were done in Program R (R Core Team, 2015) and mixed models were analyzed in the package lme4 (Bates, Maechler, Bolker, & Walker, 2015).

3 | RESULTS

3.1 | Population and family-specific hatch timing

Developmental rates (i.e., number of days needed to hatch) were predominantly determined by temperature and did not vary between populations. A model including fixed effects for temperature treatment and tray level in the incubator, combined with a random treatment effect for family nested within population, had the strongest support in describing the observed patterns (Table S1). All populations and families exhibited plasticity in response to temperature, evidenced by the fastest development in the warmest treatment (WI_MIROC mean = 10.14°C, Table 3), and progressively slower development as temperature decreased (Figures 2 and 3). The difference between average days to hatch between the two populations was ≤ 1 d among treatments, indicating no difference in developmental time between the populations. Mean number of days to hatch across both populations was 74 days ($SD = 3.87$) in the warmest treatment (as measured by mean, WI_MIROC) and 189 d ($SD = 5.45$) in the coldest treatment (PP_AVG) (Figure 2). The number of days needed to hatch in the warmest treatment (WI_MIROC) was 8 d less than the next warmest treatment (WI_AVG) and was 115 d less than the coolest temperature treatment (PP_AVG).

Families differed in developmental rates both *within* and *among* treatments (Figure 3). We detected evidence suggestive of a $G \times E$

response in developmental rates based on the inclusion of the random treatment effect in the best model (Table S1). However, the influence of the $G \times E$ effect was one or two orders of magnitude less than the fixed temperature effect, in which variance ranged from 1.5 to 3.3 d among families within treatments (Figures 3 and

TABLE 3 Parameter estimates for the best-supported linear mixed effects model based on BIC estimates predicting days to hatch for two populations of sockeye salmon from Bristol Bay, Alaska

Random effects	Name	Variance	SD
Family within population	TreatmentPP_AVG	4.93	2.22
	TreatmentPP_MIROC	2.15	1.47
	TreatmentWI_AVG	4.94	2.22
	TreatmentWI_Cold	10.71	3.27
	TreatmentWI_MIROC	3.31	1.82
Population	TreatmentPP_AVG	0.00	0.00
	TreatmentPP_MIROC	0.01	0.07
	TreatmentWI_AVG	0.04	0.19
	TreatmentWI_Cold	2.33	1.53
	TreatmentWI_MIROC	0.02	0.16
Residual		9.90	3.15
Fixed effects	Estimate	SE	t value
(Intercept)	189.4	0.5	369.9
TreatmentWI_MIROC	-115.3	0.4	-257.5
TreatmentWI_AVG	-106.4	0.5	-197.8
TreatmentPP_MIROC	-88.5	0.4	-246.8
TreatmentWI_Cold	-70.7	1.3	-53.8
Tray2	-0.3	0.1	-3.6
Tray3	-0.8	0.1	-11.2
Tray4	-0.9	0.1	-12.5

4). We also detected evidence that increasing thermal regime variability may be related to hatching variability across families (Table 3, see random effects), as the variance of both random effects tended to be largest in the most variable temperature treatments (Table 2, see CV). Despite its inclusion in the top model, the estimated effect of the incubator level was less than 1 day (our measurement scale for development) and temperature varied by $<0.3^{\circ}\text{C}$ between the topmost and lowermost incubator trays (cooler in the upper trays), indicating almost no tray effect on the developmental time in this experiment.

3.2 | Population and family-specific survival

Survival did not vary among temperature treatments, but differed markedly among families and populations. The top ranked model included treatment as both a fixed effect and a random effect of treatment for families nested within populations, combined with population and family terms (the primary descriptors of survival; Table S2, Table 4). Population-specific survival was 0.69 ($SD = 0.24$) for the Pedro Bay Ponds population and 0.36 ($SD = 0.34$) for the Woody Island population. Survival among families varied substantially, ranging from 0.02 to 0.96 with a mean of 0.53, but was largely consistent for a given family across treatments (Table 5). The highest surviving family from the Pedro Ponds population was P5 (0.96, $SD = 0.04$) and the lowest was P9 (0.06, $SD = 0.02$). Of the Woody Island families, the W2 family experienced the highest survival (0.85, $SD = 0.09$) and the W6 and W8 families experienced the lowest survival at (0.02, $SD = 0.03$ and 0.02, respectively).

3.3 | Responses in alevin mass and length

Based on the plots (Figure 5), alevin mass was primarily influenced by family and population (Woody Island eggs were consistently

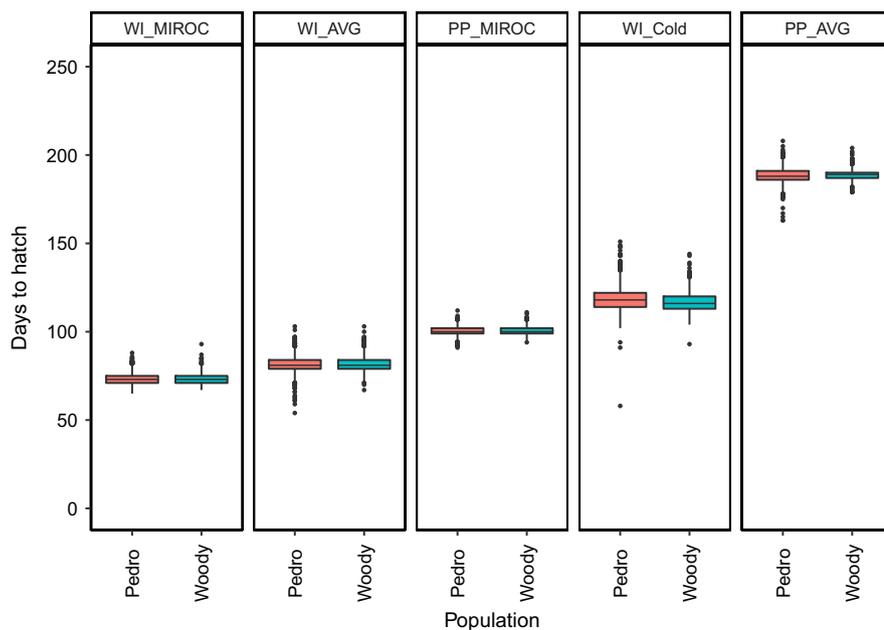


FIGURE 2 Box plots of days to hatch by population across five temperature treatments for two sockeye salmon populations from Bristol Bay, Alaska. See text for description of treatments. Treatments are arranged in order from warmest to coolest mean temperature. Within boxes, dark bars represent the median, solid lines the 25% and 75% quantiles, whiskers the 5th and 95th percentiles, and dots are outliers.

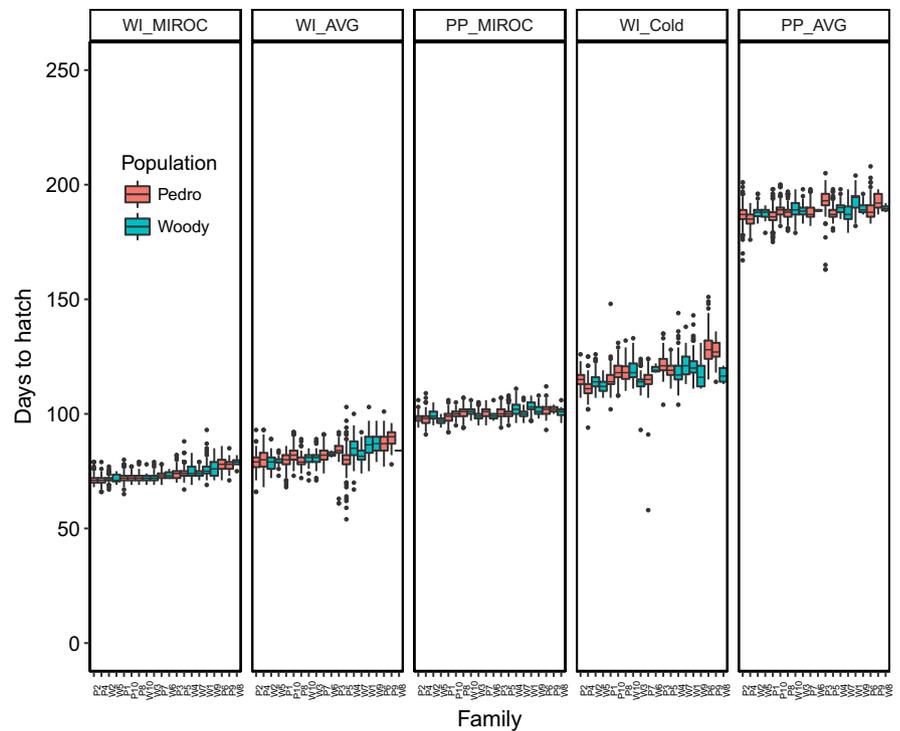


FIGURE 3 Box plots of days to hatch by families across five temperature treatments for two sockeye salmon populations from Bristol Bay, Alaska. See text for description of treatments. Treatments are arranged in order from warmest to coolest mean temperatures and families are arranged in order of median hatch date from the WI_MIROC treatment. Within boxes, dark bars represent the median, solid lines the 25% and 75% quantiles, whiskers the 5th and 95th percentiles, and dots are outliers.

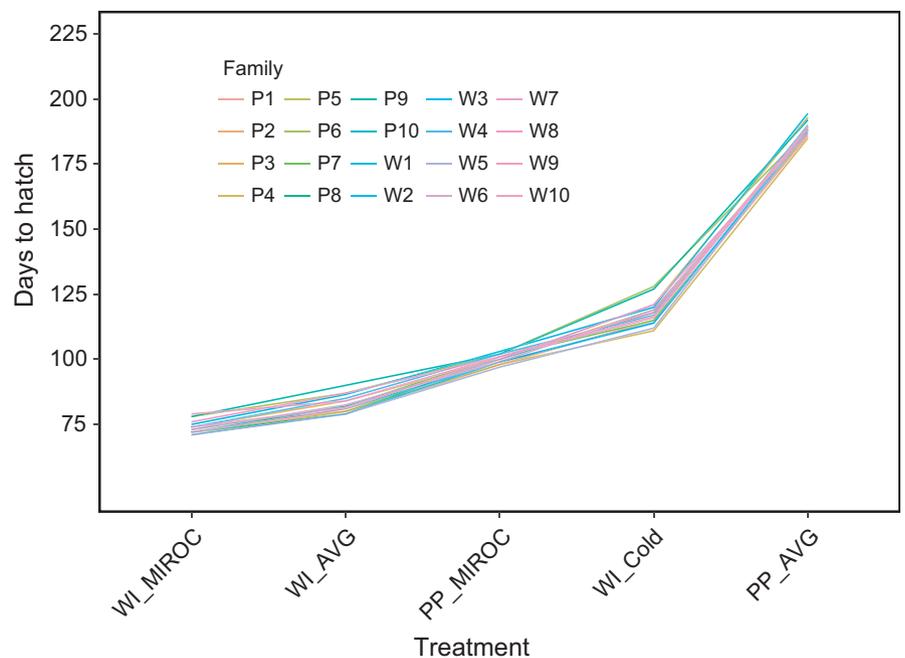


FIGURE 4 Family-specific reaction norms for median days to hatch for two populations of sockeye salmon from Bristol Bay, Alaska. Treatments are arranged in descending order of temperature (warmest to coolest means).

larger across families, but variation among families caused some overlap between populations, Table 1, Figure 5a) and varied negligibly among temperature treatments. The best-supported model for alevin mass included treatment as the fixed effect and family (egg weight) and treatment as the random effect (Table S3), although the next best-supported model's ΔBIC was <4 and included the fixed population term, indicating some support for a population effect. Given the rule of parsimony, results suggest the population term is not contributing markedly to parameter estimates based on inclusion or

exclusion of this factor. The outliers observed in Figure 5 may account for why the population means are different, but not significantly. Across all treatments and families, weight averaged 0.105 g (Pedro Ponds was 0.097 $SD = 0.012$ and Woody Island was 0.106 $SD = 0.014$) and the random variation attributed to population (variance = 0.000233) was an order of magnitude greater than random variation among families (variance = 0.000042), indicating that differences in alevin weight were largely attributable to populations but not treatment effects (Table 6, Figure 5b). The PP_AVG treatment had

the strongest, albeit very small, effect on mass across treatments (-0.003 g) and fish tended to be marginally lighter as treatments grew colder.

TABLE 4 Parameter estimates for best-supported generalized linear mixed effects model based on BIC estimates predicting survival for two populations of sockeye salmon from Bristol Bay, Alaska

Random effects	Name	Variance	SD	
Groups	Family:population (intercept)	3.00	1.73	
	TreatmentPP_MIROC	0.59	0.77	
	TreatmentWI_AVG	0.78	0.89	
	TreatmentWI_Cold	0.77	0.88	
	TreatmentWI_MIROC	0.98	0.99	
	Population (Intercept)	1.30	1.14	
	TreatmentPP_MIROC	0.12	0.34	
	TreatmentWI_AVG	0.12	0.34	
	TreatmentWI_Cold	0.09	0.30	
	TreatmentWI_MIROC	0.04	0.21	
Fixed effects	Estimate	SE	z value	Pr(> z)
(Intercept)	0.30	0.77	0.39	0.70
TreatmentPP_MIROC	-0.39	0.26	-1.47	0.14
TreatmentWI_AVG	-0.32	0.28	-1.11	0.27
TreatmentWI_Cold	-0.40	0.26	-1.51	0.13
TreatmentWI_MIROC	-0.42	0.25	-1.69	0.09

TABLE 5 Mean proportional survival for each family of two populations of Bristol Bay, Alaska sockeye salmon exposed to a suite of five temperature treatments over incubation. See text for details regarding treatments

Family	PP_AVG	PP_MIROC	WI_AVG	WI_Cold	WI_MIROC
P1	0.76 (0.04)	0.65 (0.08)	0.67 (0.08)	0.70 (0.05)	0.67 (0.03)
P2	0.78 (0.04)	0.68 (0.09)	0.73 (0.08)	0.67 (0.06)	0.71 (0.08)
P3	0.79 (0.07)	0.69 (0.05)	0.67 (0.03)	0.69 (0.08)	0.72 (0.05)
P4	0.75 (0.04)	0.73 (0.01)	0.73 (0.04)	0.78 (0.06)	0.80 (0.03)
P5	0.92 (0.03)	0.97 (0.03)	0.96 (0.03)	0.99 (0.01)	0.99 (0.02)
P6	0.75 (0.06)	0.83 (0.04)	0.73 (0.26)	0.84 (0.03)	0.83 (0.04)
P7	0.80 (0.07)	0.79 (0.04)	0.74 (0.11)	0.78 (0.06)	0.82 (0.02)
P8	0.65 (0.02)	0.54 (0.04)	0.55 (0.05)	0.57 (0.03)	0.62 (0.05)
P9	0.06 (0.04)	0.06 (0.02)	0.06 (0.02)	0.05 (0.01)	0.07 (0.02)
P10	0.76 (0.09)	0.81 (0.04)	0.88 (0.01)	0.83 (0.03)	0.87 (0.03)
W1	0.07 (0.03)	0.89 (0.08)	0.91 (0.02)	0.93 (0.05)	0.96 (0.02)
W2	0.74 (0.07)	0.81 (0.03)	0.87 (0.11)	0.95 (0.04)	0.88 (0.03)
W3	0.72 (0.08)	0.78 (0.04)	0.86 (0.04)	0.86 (0.02)	0.78 (0.02)
W4	0.23 (0.06)	0.23 (0.02)	0.33 (0.05)	0.33 (0.04)	0.33 (0.08)
W5	0.09 (0.02)	0.13 (0.04)	0.08 (0.02)	0.10 (0.04)	0.09 (0.04)
W6	0.02 (0.04)	0.04 (0.03)	0.01 (0.02)	0.01 (0.01)	0.02 (0.03)
W7	0.40 (0.24)	0.31 (0.05)	0.39 (0.11)	0.26 (0.06)	0.28 (0.04)
W8	0.02 (0.00)	0.03 (0.02)	0.01 (0.01)	0.02 (0.02)	0.01 (0.01)
W9	0.06 (0.05)	0.13 (0.04)	0.12 (0.07)	0.10 (0.01)	0.09 (0.03)
W10	0.29 (0.05)	0.37 (0.05)	0.40 (0.04)	0.37 (0.06)	0.39 (0.04)

Similar to mass, differences in alevin body length were influenced by population (egg weight) and treatment, as well as to a lesser extent by tray level. The best-supported model included treatment and tray as fixed effects and treatment as the random effect (Table S4). The global average length was 19.2 mm with the random effects of population ($SD = 0.46$) and family ($SD = 0.36$). The average length among all individuals was 18.99 mm ($SD = 0.75$), and the Pedro Ponds population was shorter on average (18.64 mm, $SD = 0.74$) than the Woody Island population (19.12 mm, $SD = 0.72$). Treatment effect ranged from -0.5 to 0.08 , where the trend was for treatments with a colder mean to have shorter lengths (Table 7, Figure 5a). On average, body length was 6.5% longer in the warmest mean treatment (WI_MIROC) compared to the coolest mean treatment (PP_AVG), but fish were longest (by 0.08 and 0.05 mm, respectively) in the two intermediary treatments (WI_AVG and PP_MIROC). Finally, the tray effect ranged from 0.03 to 0.15, where fish tended to be longer in lower (slightly warmer) trays.

3.4 | Thermal variability and hatch timing

We detected a positive relationship between increasing thermal regime variability (CV) and increasing variability in hatch timing (number of days from 10% to 90% hatched). The least variable treatments (PP_AVG and PP_MIROC, $CV = 0.03, 0.02$) were among the lowest in number of days between 10% and 90% hatched (10 and 7 d, respectively), whereas the most variable

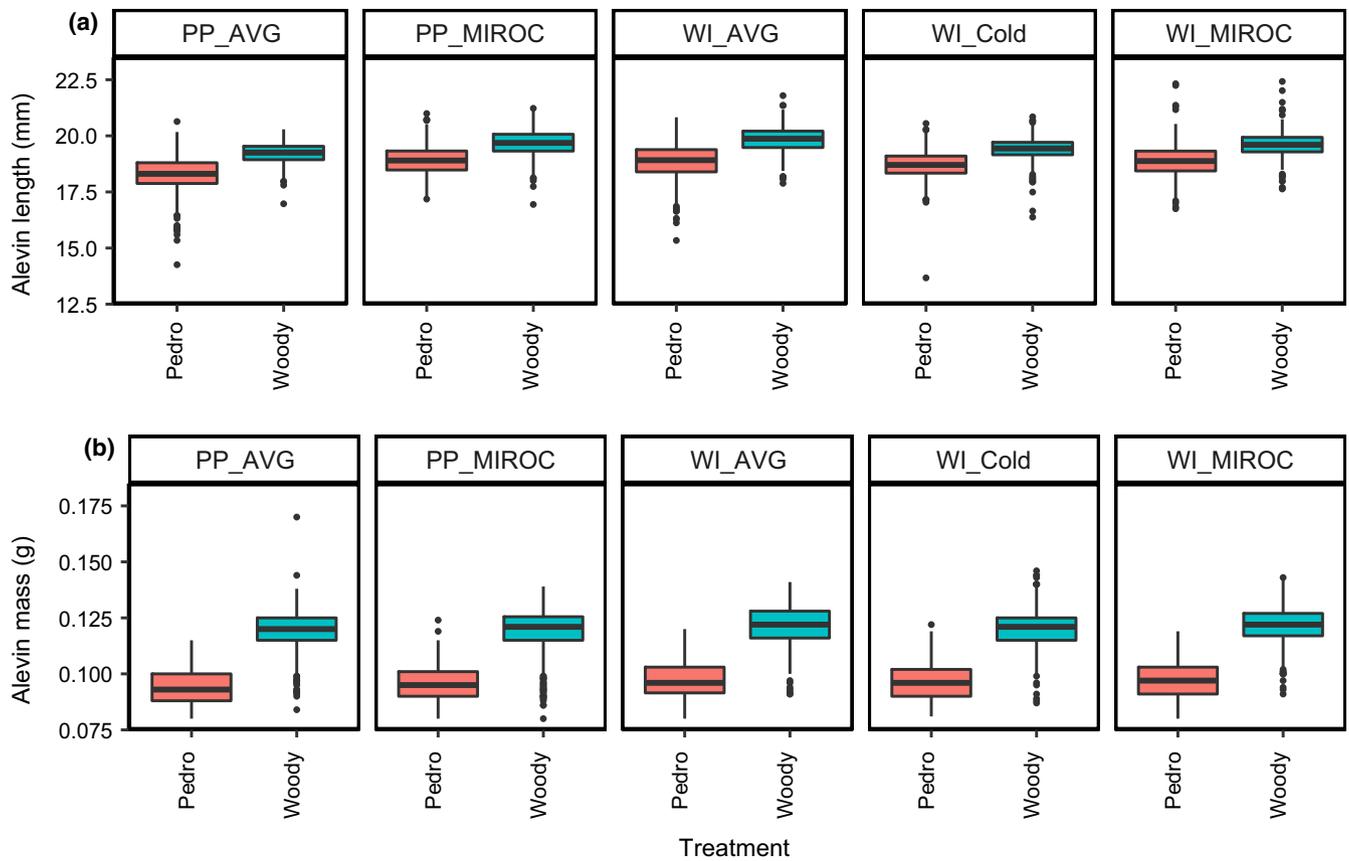


FIGURE 5 Alevin length (a) and mass (b) as a function of population and treatment. Treatments are arranged from warmest to coolest mean temperatures. Within boxes, dark bars represent the median, solid lines the 25% and 75% quantiles, whiskers the 5th and 95th percentiles, and dots are outliers.

TABLE 6 Parameter estimates for the best-supported linear mixed effects model based on BIC estimates predicting alevin mass (g) for two populations of sockeye salmon from Bristol Bay, Alaska

Random effects	Name	Variance	SD
Groups	Family:Population (Intercept)	4.20E-05	0.007
	TreatmentWI_AVG	1.00E-06	0.001
	TreatmentPP_MIROC	5.00E-06	0.002
	TreatmentWI_Cold	1.00E-06	0.001
	TreatmentPP_AVG	1.00E-06	0.001
	Population (Intercept)	2.33E-04	0.015
	TreatmentWI_AVG	0.000	4.00E-05
	TreatmentPP_MIROC	1.00E-06	0.001
	TreatmentWI_Cold	0.000	7.00E-05
	TreatmentPP_AVG	0.000	0.001
	Residual		2.80E-05
Fixed effects	Estimate	SE	t value
(Intercept)	0.108	0.011	9.940
TreatmentWI_AVG	0.000	0.000	-0.207
TreatmentPP_MIROC	-0.002	0.001	-2.285
TreatmentWI_Cold	-0.001	0.000	-3.538
TreatmentPP_AVG	-0.003	0.000	-7.520

treatment (WI_Cold, CV = 0.69) needed 16 d for the same hatching metric, and the next most variable treatment (WI_AVG, CV = 0.43) needed 12 d. The correlation of these variables, albeit with only five points of data ($\alpha = 0.05$), resulted in the value of $r = .86$ (Pearson's correlation, $P = 0.061$). This trend was observed in both populations.

3.5 | Hatching model predictions vs. observed values

Despite similarity in shapes of development curves (Figure 6), we found that the Beacham and Murray (1990) model consistently underestimated the number of days to hatch and performed increasingly worse between the warmest treatment (WI_MIROC = 9 days difference between observed and predicted timing) and coolest treatment (PP_MIROC = 29 days).

4 | DISCUSSION

This study revealed a lack of differences in developmental rates and almost identical patterns of phenotypic plasticity in two contrasting populations of Alaskan sockeye salmon under scenarios of already experience temperatures and in the face of a warming climate

TABLE 7 Parameter estimates for the best-supported linear mixed effects model based on BIC estimates predicting alevin length (mm) for two populations of sockeye salmon from Bristol Bay, Alaska

Random effects	Name	Variance	SD
Groups	Family:Population (Intercept)	0.13	0.36
	TreatmentWI_AVG	0.05	0.21
	TreatmentPP_MIROC	0.05	0.22
	TreatmentWI_Cold	0.03	0.16
	TreatmentPP_AVG	0.07	0.27
	Population (Intercept)	0.22	0.47
	TreatmentWI_AVG	0.01	0.09
	TreatmentPP_MIROC	0.00	0.01
	TreatmentWI_Cold	0.00	0.00
	TreatmentPP_AVG	0.00	0.00
	Residual	0.23	0.48

Fixed effects	Estimate	SE	t value
Intercept	19.20	0.34	56.62
TreatmentWI_AVG	0.08	0.08	0.90
TreatmentPP_MIROC	0.05	0.05	0.87
TreatmentWI_Cold	-0.19	0.04	-4.55
TreatmentPP_AVG	-0.52	0.07	-7.81
Tray2	0.04	0.02	2.42
Tray3	0.09	0.02	6.39
Tray4	0.15	0.02	10.18

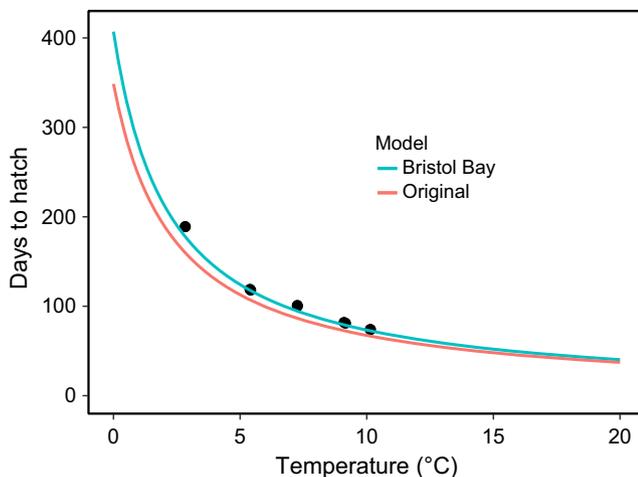


FIGURE 6 Comparison of model predictions of days to hatch (D) as a function of mean temperature (T) based on a widely cited model (Original: where $a = 6.727$ and $b = -2.394$; Beacham & Murray (1990); red line) and our refit of that model using data from this experiment (Bristol Bay: where $a = 6.796$ and $b = -1.917$; blue line). Points represent the observed average days to hatch for each population under each of the five treatments.

system. Counter to expectations, we found no evidence that populations spawning at the same time in very different temperature regimes exhibited population-specific developmental rates or differential survival in response to temperatures that would have indicated

thermal local adaptation during the embryonic stage. Rather, we observed marked plasticity in developmental rates at the population level, and differences in hatching timing across half-sibling families within and among temperature treatments, indicating a heritable basis for development rate. Furthermore, we observed a small yet significant positive relationship between temperature and body size at hatching, which is contrary to the commonly reported pattern. Taken as a whole this study indicates that phenotypic plasticity in developmental rates may buffer these populations and families in the face of warming temperatures while also serving as a heritable template on which selection may occur.

Given that the Woody Island and Pedro Ponds populations spawn at overlapping times but under very different thermal regimes, it would be expected that if their development was shaped by selection to accessing a shared nursery habitat at approximately the same time, the populations' embryos would need to develop at different rates to accommodate the thermal differences during development. For example, eggs that were fertilized on the shared peak spawning date of August 18 are predicted (based on Beacham & Murray, 1990; Sparks, 2016) to hatch and emerge after 147 d (January 12) and 242 d (April 17), respectively, for the Pedro Ponds population and after 77 d (November 3) and 188 d (February 22) for the Woody Island population. This prediction estimates nearly a 2-month difference in emergence time assuming no population-level differences in developmental rates. As such, we expected to see population-specific differences in developmental rates when reared in common garden conditions. Moreover, we expected that population-level plastic responses would be associated with the degree of thermal heterogeneity of the natal incubation temperature regime (i.e., higher plasticity in the Woody Island population) (Hutchings, 2011).

Counter to expectations, we found no support that populations differed in the number of days to hatch neither within treatments nor across treatments. Other studies (Beacham & Murray, 1989; Haugen & Vøllestad, 2000; Kinnison, Unwin, Hershberger, & Quinn, 1998; Wood & Fraser, 2015) that focused on population-level differences also found a similar lack of genetic differences in hatch timing in regimes representing natural conditions (but see Jensen et al., 2008; Whitney et al., 2014). We expected to observe population differences while others did not because of the inclusion of fluctuating thermal regimes, which has produced significant population (Fuhrman et al., 2017) and family-level differences (Dammerman et al., 2016; Steel et al., 2012; Tillotson, 2015). Furthermore, we expected this because we used populations that use a shared rearing environment later during their early life history and we expected their phenology, even with very different developmental thermal regimes, to generally synchronize given their shared recipient environment. We estimate that developmental rates between these distinct populations would need to be approximately 17% faster for the Pedro Ponds population and 21% slower for the Woody Island population in order to synchronize hatching. These differences are markedly higher than values reported in previous studies (e.g., Hendry et al., 1998), suggesting constraints on the evolution of developmental rate.

Although the temperature regimes used in our study reflected plausible natural regimes and variability, the treatments may have not been stressful enough to reveal cryptic population variation that is expressed under abnormal conditions (Gibson & Dworkin, 2004; Schlichting, 2008). We also acknowledge that temperature and oxygen are correlated and our study controlled for this by using flowing oxygen-saturated water during incubation, which may differ from conditions experienced in the wild (Martin et al., 2017). Additionally, it is possible that by creating families from individuals spawning in the early portion of the spawning season of each population, we missed some of the within population variation. Indeed, later spawning fish can compensate with faster developmental rates (Boatright, 2003; Hendry et al., 1998). An alternative model for this experiment might have included more populations with different spawn dates from a wider range of thermal environments (e.g., glacial fed rivers, smaller lakes), where selection on development could have been even more intense, and we might have observed stronger divergence in developmental rates (e.g., Whitney et al., 2014) using these methods.

Populations are hypothesized to be shaped by selection to match spawning timing to the temperature during embryonic development, such that colder rearing temperatures are compensated by earlier spawning (Brannon, 1987; Hodgson & Quinn, 2002). While this hypothesis may hold true, recent work suggests the relationship between spawning timing and emergence timing may be less influenced by incubation temperature over the course of development than widely thought (Sparks, 2016). Moreover, work by another group also revealed variation in MHC expression among ecotypes of sockeye salmon in the Wood River system consistent with pathogen-mediated selection that may in part be influenced by temperatures adults experience on the spawning grounds (Larson et al., 2014), which could help explain temperature-based selection on adult spawn time.

In contrast to the limited population-level differences, we detected appreciable family-level differences within temperature treatments consistent with a heritable component to developmental rates and differences among temperature regimes suggestive of gene by environment interactions ($G \times E$). These findings reinforce other studies that report $G \times E$ interactions between hatch timing and incubation regime at the family-level (Burt, Hinch, & Patterson, 2012; Kinnison et al., 2008; Steel et al., 2012). This past work and other developmental studies of salmonids have shown that while spawning date can be plastic (Brannon, 1987; Karjalainen et al., 2015; Schindler et al., 2013; Sparks, 2016), embryonic development may be highly conserved (Brannon, 1987; Schindler et al., 2013; Sparks, 2016) and have low heritability (Kinnison et al., 2008; Quinn et al., 2015). Taken as two sides to the same coin, this would suggest that plasticity may help buffer populations against environmental change if the heritability of embryonic development is low, whereas the near canalization but high heritability of spawning timing is the heritable mechanism underpinning the evolution of hatching timing.

Given our assumption of local adaptation, we expected that survival would be highest in the natal regimes relative to regimes of the foreign population. Counter to this expectation, population-specific

survival did not change relative to experienced temperature regime, indicating that these populations are not thermally adapted at the developmental stage we measured or are both specifically adapted to the experimental thermal regimes used (Table 4). Furthermore, depending on ambient temperature, it may take many days or weeks for fish to start feeding exogenously (Quinn, 2005) and population-specific variation in energy use or efficiency could contribute to differential responses at this life history period (Kavanagh, Haugen, Gregersen, Jernvall, & Vøllestad, 2010), but were not tested for in this experiment. Additionally, we expected populations to be thermally locally adapted in hatch timing, yet populations were plastic in this trait; populations hatched at the same time among all treatments. These populations use a common nursery lake following emergence, and could be adapted to fine-scale local conditions given their disparate expected emergence timing based on our experimental results (Abrey, 2005; Sparks, 2016). In other words, the ecological agents of selection in the wild are likely much broader than the basic effect of temperature on survival and development that we measured in the laboratory (MacColl, 2011; Martin et al., 2017).

Populations and families did survive at different rates, and fish in the Pedro Ponds population had higher overall survival than those from the Woody Island population, which we suggest may reflect transport effects from the field to the laboratory. However, there was substantial variation around survival in populations, which was largely driven by differential survival of families. Families consistently survived at similar levels across thermal treatments, but varied substantially from family to family within the populations (Table 5). These results mostly contradict findings from similar experiments where populations that did not share nursery habitats were locally adapted for survival to hatch (Drinan et al., 2012; Haugen, 2000; Whitney et al., 2013). Another explanation might be that by chance, the populations performed well in the other's environment, and that comparisons between more than two sockeye salmon populations would have led to different results (Kawecki & Ebert, 2004). In this study, we traded off population number with number of treatments and compared populations that spawn at the same time but incubate in contrasting thermal regimes. Similar studies in fishes often deal with this tradeoff by either using more populations that spawn at different periods and rearing them in constant environments (e.g., Whitney et al., 2014) or rearing them to a given ATU threshold—where it is not a true common garden until after the threshold is reached—and then using variable thermal regimes (e.g., Steel et al., 2012). Regardless, we acknowledge the inherent difficulty in scaling results from controlled laboratory studies to patterns observed in nature.

The lack of survival differences relative to other studies may also relate to our choice of temperature regimes that were generally more realistic and less stressful than those used in most previous studies that reared fish in constant regimes (Burt et al., 2012; Drinan et al., 2012; Haugen, 2000; Whitney et al., 2013), and under climate change scenarios where conditions were quite extreme (Whitney et al., 2013, 2014). Many of these studies (Drinan et al., 2012; Whitney et al., 2013, 2014) had similar ranges, yet much higher temperature treatment means (about 6°C mean difference), but found local

adaptation in survival. Alternatively, a recent study of brown trout (*Salmo trutta*) found no thermal local adaptation during juvenile development, but correlative evidence for a relationship to a precipitation gradient across Norway (Bærum, Vøllestad, Kiffney, Rémy, & Haugen, 2016). The authors inferred that physical factors impacted by climate change like streamflow instead of temperature may be important selective agents for consideration. This inference is further backed up by recent work (Siepielski et al., 2017) that suggests the strongest forces of selection across species and biomes was local and regional precipitation and transpiration rather than global climate forces.

Alevin mass and length varied by population, family, and treatment and differed between populations as a function of egg size (Table 1). Egg size did not seem to have an appreciable effect on timing to hatch, consistent with previous results (Beacham & Murray, 1989), and the difference between populations (Woody Island eggs being larger) was consistent with past studies (Blair et al., 1993; Quinn et al., 1995). While the treatment effects were significant (fish were smaller in the coldest treatments), treatment effects were an order of magnitude less (≤ 0.003 for mass) than the population effect, which may be a marginal phenotypic difference of little biological significance (Figure 5). These results were similar to other studies that found differences in alevin mass were largely driven by family or population, as opposed to temperature treatment (Burt et al., 2012; Hendry et al., 1998; Whitney et al., 2014). Our findings were inconsistent with other studies (Burt et al., 2012; Drinan et al., 2012; Haugen & Vøllestad, 2000; Hendry et al., 1998), in which fish were shorter in warmer treatments. A potential explanation of this observed difference could be that the warmest temperatures in our study were generally much cooler than the warmest temperatures in other studies, which in some cases were beyond what fish would have experienced in the wild. Instead, our experiment's warmest treatments were based on best predictions of climatic warming, which were closer to thermal optima for sockeye salmon (Beauchamp, 2009) than prior studies. Rearing experiments at abnormally high temperatures may reveal cryptic plasticity (Gibson & Dworkin, 2004) but may not be as useful in determining actual responses to expected temperature change.

There is increasing interest in understanding the role of the timing of temperature delivery to developing embryos beyond consideration of average temperatures (Dammerman et al., 2016; Fuhrman et al., 2017; Steel et al., 2012; Tillotson, 2015). In a series of common garden experiments, Murray and Beacham (1987) found that chum (*O. keta*) and Chinook salmon (*O. tshawytscha*) development was mediated by the *average* temperature more than the thermal regime's *shape* (warm leading to cool vs. cool leading to warm). In contrast, recent common garden experimental evidence with Chinook salmon suggests that varying thermal regime delivery (i.e., same average temperature over the course of development, but highly fluctuating temperatures on the day or week scale), resulted in fish in the most variable regimes accumulating significantly more thermal units (TUs) before emerging, as well as more fish emerging partially developed (yolk-sac visible) (Fuhrman et al., 2017; Steel et al., 2012;

Tillotson, 2015). In a similar common garden study with lake sturgeon (*Acipenser fulvescens*), Dammerman et al. (2016) found that embryos reared at warmer and more variable temperatures were 6–10 times more variable in developmental traits. While our study was not designed to explicitly test how regimes with the same average but different variability may affect days needed to hatch, we did find a strong positive relationship ($r = .86$) between thermal regime and hatch timing variability. In fact, the time between 10% and 90% hatching was 1.6 to 2.3 times larger in the most variable treatment (WI_Cold, CV = 0.69, days = 16) than in the least variable treatments (PP_AVG and PP_MIROC, CV = 0.3 and 0.2, days = 10 and 7). The only instance where this trend did not hold was in the intermediate variability treatment (WI_MIROC, CV=0.29), which needed 8 days for the middle 80% of fish to hatch. A likely explanation for this anomaly is that WI_MIROC was a more thermally variable treatment but incubation was much shorter relative to other treatments. In other words, as incubation time grew increasingly longer in the less variable treatments, the variation around mean incubation time is expected to increase. As such, even though the thermal regime in MIROC was more variable, mean incubation time was much shorter, which likely decreased variation in hatching relative to the longer, less thermally variable treatments, PP_AVG and PP_MIROC.

Similar to the findings of Steel et al. (2012), our results reveal shortcomings in the utility of a widely used empirical model in salmonids, including sockeye salmon, to predict the timing of hatching or emergence given temperature (Beacham & Murray, 1990). Because we included temperature regimes ranging from an average of 2.8 to 10.14°C, we were able to confirm the nonlinear relationship between hatch timing and temperature found by other studies (Beacham & Murray, 1990). Our results indicated that the Beacham and Murray model, developed using British Columbian populations, is a useful general tool but it should be applied with caution, especially to more northerly populations. We refit the hatch model using the average population response for each treatment and predicted as much as 40 days difference (at very cold temperatures) between the predictions of the two models in regimes that might be expected in natural settings (Figure 6). These results indicate that regional differences of populations should be taken into account when using models to predict time to hatch.

Because our climate change treatments were informed by appropriate downscaled projections of temperature change specific to study populations, we were able to make informed inferences about the potential impacts of climate change to our populations. In particular, survival was not reduced as a direct effect of the warmest treatments, even for the Pedro Ponds population, which experiences a very cold and stable natal incubation regime. While survival during this narrow time period may not be impacted as a result of temperature per se, changing temperatures could create a mismatch between the recipient nursery environment and timing of development (Abrey, 2005; Schindler, Rogers, Scheuerell, & Abrey, 2005; Visser, 2008; Visser & Both, 2005). That being said, a dire mismatch seems unlikely for the Woody Island population as the future warming scenario (WI_MIROC) changed hatch timing by only 8 days from the

observed average temperature regime (WI_AVG) over the last decade-and-a-half. This is well within the range of predicted hatch timing over the last half-century (Sparks, 2016) and mismatch dynamics are dependent on rates of change in both development and the recipient nursery environment for young fish. If the lake is increasingly hospitable early in the season then earlier hatching and emergence may not impact survival. Indeed the trend over the past decades has been for ice to leave the lake earlier and the temperatures to be warmer, facilitating growth of juvenile sockeye salmon (Rich, Quinn, Scheuerell, & Schindler, 2009; Tillotson & Quinn, 2016). For the Pedro Ponds population, the climate change regime was expected to double the temperature in the ponds from approximately 4 to 8°C (PP_AVG to PP_MIROC) and imparted an 89-day difference from the experienced natal incubation regime. This would be a significant shift in the embryonic phenology for this population and could lead to mismatches with the recipient lake environment. This potential for mismatch though should be taken with caution because, although shallow groundwater temperatures are highly correlated with mean annual air temperature for a given region (Hayashi & Rosenberry, 2002), specific climate change impacts in the Pedro Ponds are highly uncertain as the groundwater-surface water dynamics are not known. Finally, given the small magnitude of the effect of temperature on body size and substantial time for compensatory growth, it seems unlikely that temperature would reduce the fitness of sockeye salmon populations through alterations in alevin body size.

The results of this study indicated a lack of thermal local adaptation between populations in developmental rates and embryonic survival, and strong evidence for heritable plastic phenotypic shifts among families in relation to climate scenarios. For example, the Pedro Pond population hatched nearly 3 months earlier between the natal regime and the climate change scenario for that environment, without a significant shift in survival. Considered together, these patterns suggest that plasticity may sufficiently buffer populations to cope with realistic predicted water temperature changes at least during this narrow phase of the life history. Furthermore, because of the genetic underpinnings of plasticity revealed among families, there is potential for a transgenerational response to selection in nature (Ghalambor, McKay, Carroll, & Reznick, 2007; Hutchings, 2011; Reed et al., 2011). Our results reinforce the strength of temperature as a driver of embryonic development, but it remains unclear how the responses observed here may propagate through other stages of the life history as juvenile growth and survival is primarily governed by temperature and intraspecific competition (Rich et al., 2009; Schindler et al., 2005; Tillotson & Quinn, 2016). Despite this uncertainty, what is clear is that maintenance of these heritable plastic responses by maintaining diversity across families and populations will be important for adaptation to warming or more variable water temperatures caused by climate change.

ACKNOWLEDGEMENTS

This work was supported by the Western Alaska Landscape Conservation Cooperative and completed in partial fulfillment of a Master's degree of Fisheries at the University of Alaska Fairbanks (UAF). Milo

Adkison provided helpful study design and editorial input. Thanks to Curry Cunningham, Jason Ching, Krista Oke, Rachel Hovel, and Martini Arostegui for aid in collecting gametes. Additional thanks to Curry Cunningham for advice on mixed effects models. Furthermore, thanks to Lyric St. John, Jolie Billings, Anyssa Interante, and Christine Terzi, as well as other staff from the UAF Biological Research and Diagnostics Facility, for their diligent work monitoring the experiment. Similarly, Monroe Morris and Evan Mchenry were instrumental in sampling alevins and photograph analysis. We also thank three anonymous reviewers for their helpful recommendations and comments on an earlier version of this manuscript. The staff and facilities of the Alaska Cooperative Fish and Wildlife Research Unit, College of Fisheries and Ocean Sciences, and the Institute of Arctic Biology at UAF were significant in the success of this project. Collection of long-term data on the sockeye salmon populations at Iliamna Lake has been supported by many entities but we especially thank the Pacific salmon seafood industry, the Gordon and Betty Moore Foundation, and the National Science Foundation programs on Biocomplexity and on Coupled Natural and Human Systems. This work was conducted under UAF Institutional Animal Care and Use Committee protocol # 719625-2 and ADFG fish resource permits # CF-16-028 and P-15-010. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

REFERENCES

- Abrey, C. A. (2005). Variation in the early life history of sockeye salmon (*Oncorhynchus nerka*): Emergence timing, an ontogenetic shift, and population productivity. PhD dissertation, University of Washington, USA.
- Aday, D. D., Wahl, D. H., & Philipp, D. A. (2003). Assessing population-specific and environmental influences on bluegill life histories: A common garden approach. *Ecology*, *84*, 3370–3375.
- Adkison, M. D., Ward, M. B., & Quinn, T. P. (2013). Nest site preference and intrasexual competition in female sockeye salmon, *Oncorhynchus nerka*. *Environmental Biology of Fishes*, *97*, 385–399.
- Angilletta M. J., Steel E. A., Bartz K. K., Kingsolver J. G., Scheuerell M. D., Beckman B. R., & Crozier L. G. (2008). Big dams and salmon evolution: Changes in thermal regimes and their potential evolutionary consequences. *Evolutionary Applications*, *1*, 286–299.
- Atkinson, D. (1994). Temperature and organism size: A biological law for ectotherms? *Advances in Ecological Research*, *25*, 61–74.
- Atkinson, D., & Sibly, R. M. (1997). Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends in Ecology & Evolution*, *12*, 235–239.
- Bærum, K. M., Vøllestad, L. A., Kiffney, P., Rémy, A., & Haugen, T. O. (2016). Population-level variation in juvenile brown trout growth from different climatic regions of Norway to an experimental thermal gradient. *Environmental Biology of Fishes*, *99*, 1–10.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.
- Beacham, T. D., & Murray, C. B. (1989). Variation in developmental biology of sockeye salmon (*Oncorhynchus nerka*) and Chinook salmon (*O. tshawytscha*) in British Columbia. *Canadian Journal of Zoology*, *67*, 2081–2089.
- Beacham, T. D., & Murray, C. B. (1990). Temperature, egg size, and development of embryos and alevins of five species of Pacific salmon: A comparative analysis. *Transactions of the American Fisheries Society*, *119*, 927–945.

- Beauchamp, D. A. (2009). Bioenergetic ontogeny: Linking climate and mass-specific feeding to life-cycle growth and survival of salmon. *American Fisheries Society Symposium*, 70, 1–19.
- Blair, G. R., & Quinn, T. P. (1991). Homing and spawning site selection by sockeye salmon (*Oncorhynchus nerka*) in Iliamna Lake, Alaska. *Canadian Journal of Zoology*, 69, 176–181.
- Blair, G. R., Rogers, D. E., & Quinn, T. P. (1993). Variation in life history characteristics and morphology of sockeye salmon in the Kvichak River system, Bristol Bay, Alaska. *Transactions of the American Fisheries Society*, 122, 550–559.
- Boatright, C. (2003). Timing of migration, spawning and juvenile emergence by sockeye salmon in Bear Lake, Alaska. MS Thesis. University of Washington, USA.
- Bolker, B. M. (2008). *Ecological Models and Data in R*. Princeton: Princeton University Press.
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H., & White, J. S. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution*, 24, 127–135.
- Brannon, E. L. (1987). Mechanisms stabilizing salmonid fry emergence timing. *Canadian Special Publication of Fisheries and Aquatic Sciences*, 96, 120–124.
- Brannon, E. L., Powell, M. S., Quinn, T. P., & Talbot, A. (2004). Population structure of Columbia River basin Chinook salmon and steelhead trout. *Reviews in Fisheries Science*, 12, 99–232.
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. New York: Springer.
- Burt, J. M., Hinch, S. G., & Patterson, D. A. (2012). Parental identity influences progeny responses to incubation thermal stress in sockeye salmon *Oncorhynchus nerka*. *Journal of Fish Biology*, 80, 444–462.
- CIG. (2015). *North Pacific region hydroclimate scenarios*. Seattle, Washington: Climate Impacts Groups.
- Crozier L. G., Hendry A. P., Lawson P. W., Quinn T. P., Mantua N. J., Battin J., ... Huey, R. B. (2008). Potential responses to climate change in organisms with complex life histories: Evolution and plasticity in Pacific salmon. *Evolutionary Applications*, 1, 252–270.
- Dammerman, K. J., Steibel, J. P., & Scribner, K. T. (2016). Increases in the mean and variability of thermal regimes result in differential phenotypic responses among genotypes during early ontogenetic stages of lake sturgeon (*Acipenser fulvescens*). *Evolutionary Applications*, 9, 1258–1270.
- Doctor, K. K., Hilborn, R., Rowse, M., & Quinn, T. P. (2010). Spatial and temporal patterns of upriver migration by sockeye salmon populations in the Wood River system, Bristol Bay, Alaska. *Transactions of the American Fisheries Society*, 139, 80–91.
- Drinan, D. P., Zale, A. V., Webb, M. H., Taper, M. L., Shepard, B. B., & Kalinowski, S. T. (2012). Evidence of local adaptation in westslope cutthroat trout. *Transactions of the American Fisheries Society*, 141, 872–880.
- Esteve, M. (2005). Observations of spawning behaviour in *Salmoninae*: *Salmo*, *Oncorhynchus* and *Salvelinus*. *Reviews in Fish Biology and Fisheries*, 15, 1–21.
- Fuhrman, A. E., Larsen, D. A., Steel, E. A., Young, G., & Beckman, B. R. (2017). Chinook salmon emergence phenotypes: Describing the relationship between temperature, emergence timing and condition factor in a reaction norm framework. *Ecology of Freshwater Fish*, 1–13.
- Ghalambor, C. K., McKay, J. K., Carroll, S. P., & Reznick, D. N. (2007). Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Functional Ecology*, 21, 394–407.
- Gibson, G., & Dworkin, I. (2004). Uncovering cryptic genetic variation. *Nature Reviews Genetics*, 5, 681–690.
- Gienapp, P., Lof, M., Reed, T. E., Mcnamara, J., Verhulst, S., & Visser, M. E. (2013). Predicting demographically sustainable rates of adaptation: Can great tit breeding time keep pace with climate change?. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 368, 20120289.
- Gienapp, P., Teplitsky, C., Alho, J. S., Mills, J. A., & Merilä, J. (2008). Climate change and evolution: Disentangling environmental and genetic responses. *Molecular Ecology*, 17, 167–178.
- Gomez-Uchida, D., Seeb, J. E., Smith, M. J., Habicht, C., Quinn, T. P., & Seeb, L. W. (2011). Single nucleotide polymorphisms unravel hierarchical divergence and signatures of selection among Alaskan sockeye salmon (*Oncorhynchus nerka*) populations. *BMC Evolutionary Biology*, 11, 48.
- Haugen, T. O. (2000). Early survival and growth in populations of grayling with recent common ancestors—field experiments. *Journal of Fish Biology*, 56, 1173–1191.
- Haugen, T. O., & Vøllestad, L. A. (2000). Population differences in early life-history traits in grayling. *Journal of Evolutionary Biology*, 13, 897–905.
- Hayashi, M., & Rosenberry, D. O. (2002). Effects of ground water exchange on the hydrology and ecology of surface water. *Ground Water*, 40, 309–316.
- Hendry, A. P., Hensleigh, J. E., & Reisenbichler, R. R. (1998). Incubation temperature, developmental biology, and the divergence of sockeye salmon (*Oncorhynchus nerka*) within Lake Washington. *Canadian Journal of Fisheries and Aquatic Sciences*, 55, 1387–1394.
- Hodgson, S., & Quinn, T. P. (2002). The timing of adult sockeye salmon migration into fresh water: Adaptations by populations to prevailing thermal regimes. *Canadian Journal of Zoology*, 80, 542–555.
- Hutchings, J. A. (2011). Old wine in new bottles: Reaction norms in salmonid fishes. *Heredity*, 106, 421–437.
- Jensen, L. F., Hansen, M. M., Pertoldi, C., Holdensgaard, G., Mensberg, K. L., & Loeschcke, V. (2008). Local adaptation in brown trout early life-history traits: Implications for climate change adaptability. *Proceeding of the Royal Society. Series B, Biological Sciences*, 275, 2859–2868.
- Jensen, K. A., & Mathisen, O. A. (1987). Migratory structure of the Kvichak River sockeye salmon (*Oncorhynchus nerka*) escapement, 1983. *Canadian Special Publication of Fisheries and Aquatic Sciences*, 96, 101–109.
- Jones, M., Sands, T., Elison, T., Salomone, P., Brazil, C., Buck, G., ... Lemons, T. (2016). 2015 Bristol Bay area annual management report. Alaska Department of Fish and Game, Fishery Management Report No. 16-13, Anchorage.
- Karjalainen, J., Keskinen, T., Pulkkanen, M., & Marjomäki, T. J. (2015). Climate change alters the egg development dynamics in cold-water adapted coregonids. *Environmental Biology of Fishes*, 98, 979–991.
- Kavanagh, K. D., Haugen, T. O., Gregersen, F., Jernvall, J., & Vøllestad, L. A. (2010). Contemporary temperature-driven divergence in a Nordic freshwater fish under conditions commonly thought to hinder adaptation. *BMC Evolutionary Biology*, 10, 350.
- Kawecki, T. J., & Ebert, D. (2004). Conceptual issues in local adaptation. *Ecology Letters*, 7, 1225–1241.
- Kinnison, M. T., Unwin, M. J., Hershberger, W. K., & Quinn, T. P. (1998). Egg size, fecundity and early development rate of two New Zealand Chinook salmon (*Oncorhynchus tshawytscha*) populations, with a comparison to their ancestral Sacramento River population. *Canadian Journal of Fisheries and Aquatic Sciences*, 55, 1946–1953.
- Kinnison, M. T., Unwin, M. J., & Quinn, T. P. (2008). Eco-evolutionary vs. habitat contributions to invasion in salmon: Experimental evaluation in the wild. *Molecular Ecology*, 17, 405–414.
- Larson, W. A., Seeb, J. E., Dann, T. H., Schindler, D. E., & Seeb, L. W. (2014). Signals of heterogeneous selection at an MHC locus in geographically proximate ecotypes of sockeye salmon. *Molecular Ecology*, 23, 5448–5461.
- Leonetti, F. E. (1997). Estimation of surface and intragravel water flow at sockeye salmon spawning beaches in Iliamna Lake, Alaska. *North American Journal of Fisheries Management*, 17, 194–201.
- Lisi, P. J., Schindler, D. E., Bentley, K. T., & Pess, G. R. (2013). Association between geomorphic attributes of watersheds, water temperature, and salmon spawn timing in Alaskan streams. *Geomorphology*, 185, 78–86.
- Lisi, P. J., Schindler, D. E., Cline, T. J., Scheuerell, M. D., & Walsh, P. B. (2015). Watershed geomorphology and snowmelt control stream thermal sensitivity to air temperature. *Geophysical Research Letters*, 42, 3380–3388.

- MacColl, A. D. (2011). The ecological causes of evolution. *Trends in Ecology and Evolution*, *26*, 514–522.
- Martin, B. T., Pike, A., John, S. N., Hamda, N., Roberts, J., Lindley, S. T., & Danner, E. M. (2017). Phenomenological vs. biophysical models of thermal stress in aquatic eggs. *Ecology Letters*, *20*, 50–59.
- McPhee, M. V., Noakes, D. L., & Allendorf, F. W. (2012). Developmental rate: A unifying mechanism for sympatric divergence in postglacial fishes? *Current Zoology*, *58*, 21–34.
- Merilä, J., & Hendry, A. P. (2014). Climate change, adaptation, and phenotypic plasticity: The problem and the evidence. *Evolutionary Applications*, *7*, 1–14.
- Murray, C. B., & Beacham, T. D. (1987). The development of Chinook (*Oncorhynchus tshawytscha*) and chum salmon (*Oncorhynchus keta*) embryos and alevins under varying temperature regimes. *Canadian Journal of Zoology*, *65*, 2672–2681.
- Olsen, J. C. (1964). Studies of sockeye salmon lake spawning grounds in Iliamna Lake, Bristol Bay, Alaska. MS Thesis, University of Washington, USA.
- Oomen, R. A., & Hutchings, J. A. (2016). Genetic variation in plasticity of life-history traits between Atlantic cod (*Gadus morhua*) populations exposed to contrasting thermal regimes. *Canadian Journal of Zoology*, *94*, 257–264.
- Quinn, T. P. (2005). *The behavior and ecology of Pacific salmon and trout*. Seattle, WA: University of Washington Press.
- Quinn, T. P., Hendry, A. P., & Wetzel, L. A. (1995). The influence of life history trade-offs and the size of incubation gravels on egg size variation in sockeye salmon (*Oncorhynchus nerka*). *Oikos*, *74*, 425–438.
- Quinn, T. P., McGinnity, P., & Reed, T. E. (2015). The paradox of “premature migration” by adult anadromous salmonid fishes: Patterns and hypotheses. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*, 1015–1030.
- Quinn, T. P., Rich, H. B. Jr, Gosse, D., & Schtickzelle, N. (2012). Population dynamics and asynchrony at fine spatial scales: A case history of sockeye salmon (*Oncorhynchus nerka*) population structure in Alaska, USA. *Canadian Journal of Fisheries and Aquatic Sciences*, *69*, 297–306.
- Quinn, T. P., Volk, E. C., & Hendry, A. P. (1999). Natural otolith microstructure patterns reveal precise homing to natal incubation sites by sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Zoology*, *77*, 766–775.
- Quinn, T. P., Wetzel, L., Bishop, S., Overberg, K., & Rogers, D. E. (2001). Influence of breeding habitat on bear predation and age at maturity and sexual dimorphism of sockeye salmon populations. *Canadian Journal of Zoology*, *79*, 1782–1793.
- R Core Team. (2015). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. URL <https://www.R-project.org/>
- Reed, T. E., Schindler, D. E., & Waples, R. S. (2011). Interacting effects of phenotypic plasticity and evolution on population persistence in a changing climate. *Conservation Biology*, *25*, 56–63.
- Rich, H. B. Jr, Quinn, T. P., Scheuerell, M. D., & Schindler, D. E. (2009). Climate and interspecific competition control the growth and life history of juvenile sockeye salmon (*Oncorhynchus nerka*) in Iliamna Lake, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, *66*, 238–246.
- Schindler, D. E., Armstrong, J. A., Bentley, K. T., Jankowski, K., Lisi, P. J., & Payne, L. X. (2013). Riding the crimson tide: Mobile terrestrial consumers track phenological variation in spawning of an anadromous fish. *Biology Letters*, *9*, 20130048.
- Schindler, D. E., Rogers, D. E., Scheuerell, M. D., & Abrey, C. A. (2005). Effects of changing climate on zooplankton and juvenile sockeye salmon growth in southwestern Alaska. *Ecology*, *86*, 198–209.
- Schlichting, C. D. (2008). Hidden reaction norms, cryptic genetic variation, and evolvability. *Annals of the New York Academy of Sciences*, *1133*, 187–203.
- Sheridan, W. L. (1962). Relation of stream temperatures to timing of pink salmon escapements in Southeast Alaska. In N. J. Wilimovsky (Ed.), *Symposium on Pink Salmon* (pp. 87–101). Vancouver, BC: Institute of Fisheries, University of British Columbia, Vancouver.
- Siepielski A. M., Morrissey M. B., Buoro M., Carlson S. M., Caruso C. M., Clegg S. M., . . . Hereford, J. (2017). Precipitation drives global variation in natural selection. *Science*, *355*, 959–962.
- Sparks, M. M. (2016). Climate, embryonic development, and potential for adaptation to warming water temperatures by Bristol Bay sockeye salmon. MS Thesis. University of Alaska Fairbanks, USA.
- Steel, E. A., Tillotson, A., Larsen, D. A., Fullerton, A. H., Denton, K. P., & Beckman, B. R. (2012). Beyond the mean: The role of variability in predicting ecological effects of stream temperature on salmon. *Ecosphere*, *3*, art104.
- Stillwell, R. C., & Fox, C. W. (2005). Complex patterns of phenotypic plasticity: Interactive effects of temperature during rearing and oviposition. *Ecology*, *86*, 924–934.
- Tillotson, A. E. (2015). Temperature-induced plasticity of emergence phenotypes in Chinook salmon (*Oncorhynchus tshawytscha*). MS Thesis. University of Washington, USA.
- Tillotson, M. D., & Quinn, T. P. (2016). Beyond correlation in the detection of climate change impacts: Testing a mechanistic hypothesis for climatic influence on sockeye salmon (*Oncorhynchus nerka*) productivity. *PLoS ONE*, *11*, e0154356.
- Visser, M. E. (2008). Keeping up with a warming world; assessing the rate of adaptation to climate change. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *275*, 649–659.
- Visser, M. E., & Both, C. (2005). Shifts in phenology due to global climate change: The need for a yardstick. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *272*, 2561–2569.
- Walsh, M. R., & Post, D. M. (2012). The impact of intraspecific variation in a fish predator on the evolution of phenotypic plasticity and investment in sex in *Daphnia ambigua*. *Journal of Evolutionary Biology*, *25*, 80–89.
- Whitney, C. K., Hinch, S. G., & Patterson, D. A. (2013). Provenance matters: Thermal reaction norms for embryo survival among sockeye salmon *Oncorhynchus nerka* populations. *Journal of Fish Biology*, *82*, 1159–1176.
- Whitney, C. K., Hinch, S. G., & Patterson, D. A. (2014). Population origin and water temperature affect development timing in embryonic sockeye salmon. *Transactions of the American Fisheries Society*, *143*, 1316–1329.
- Wood, J. L. A., & Fraser, D. J. (2015). Similar plastic responses to elevated temperature among different-sized brook trout populations. *Ecology*, *96*, 1010–1019.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Sparks MM, Westley PAH, Falke JA, Quinn TP. Thermal adaptation and phenotypic plasticity in a warming world: Insights from common garden experiments on Alaskan sockeye salmon. *Glob Change Biol.* 2017;00:1–15. <https://doi.org/10.1111/gcb.13782>