Journal of FISH BIOLOGY
Published for the Fisheries Society of the British Isles

Journal of Fish Biology (2013) **82**, 1159–1176
doi:10.1111/jfb.12055, available online at wileyonlinelibrary.com

Provenance matters: thermal reaction norms for embryo survival among sockeye salmon *Oncorhynchus nerka* populations

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(Received 16 June 2012, Accepted 19 December 2012)

Differences in thermal tolerance during embryonic development in Fraser River sockeye salmon *Oncorhynchus nerka* were examined among nine populations in a controlled common-garden incubation experiment. Forcing embryonic development at an extreme temperature (relative to current values) of 16° C, representing a future climate change scenario, significantly reduced survival compared to the more ecologically moderate temperature of 10° C (55% *v*. 93%). Survival at 14° C was intermediate between the other two temperatures (85%). More importantly, this survival response varied by provenance within and between temperature treatments. Thermal reaction norms showed an interacting response of genotype and environment (temperature), suggesting that populations of *O. nerka* may have adapted differentially to elevated temperatures during incubation and early development. Moreover, populations that historically experience warmer incubation temperatures at early development displayed a higher tolerance for warm temperatures. In contrast, thermal tolerance does not appear to transcend life stages as adult migration temperatures were not related to embryo thermal tolerance. The intra-population variation implies potential for thermal tolerance at the species level. The differential inter-population variation in thermal tolerance that was observed suggests, however, limited adaptive potential to thermal shifts for some populations. This infers that the intergenerational effects of increasing water temperatures may affect populations differentially, and that such thermally mediated adaptive selection may drive population, and therefore species, persistence.

Key words: adaptation; climate change; early life history; embryonic development; incubation; temperature.

INTRODUCTION

There is an increasing need to understand how various taxa, species and populations will respond to shifts in their thermal environment (Taylor, 1991; Baumann & Conover, 2011) with both the continued threat of anthropogenic climate change to natural systems (IPCC, 2007) and the poorly understood fitness consequences

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of those regime changes (Crozier *et al*., 2008). Adaptive differences in response to the current environmental conditions among fish populations (Eliason *et al*., 2011) suggest that different populations will display unequal suitability to future environmental states. A response to an altered thermal environment through phenotypic changes could result in a functional improvement in survival, reproduction or growth (Beacham, 1988; Stearns, 1992). Exploring variation in thermal tolerance among populations can be used to highlight the potential for different populations to adapt to climate change (Jensen *et al*., 2008).

The cumulative effects of climatic shifts will affect all taxa, but aquatic species that exist within freshwater ecosystems are particularly at risk because of changes in both hydrology (*e.g*. frequency of stochastic flood events) and thermal regimes (*e.g*. shifting cyclical thermal patterns) (Pike *et al*., 2008). The life-history diversity, distinct spawning population structure and prior research connecting survival to temperature effects make sockeye salmon *Oncorhynchus nerka* (Walbaum, 1792) a good species to study population-level variation in thermal tolerance. *Oncorhynchus nerka* is an anadromous poikilothermic fish that remains immobile during incubation in a variety of freshwater streams, rivers and lakes for 4–10 months, making developing embryos especially vulnerable to increasing freshwater temperatures (Bryant, 2009; Healey, 2011; Martins *et al*., 2012). Within British Columbia, Canada, millions of *O. nerka* representing hundreds of genetically and geographically distinct populations spawn in the Fraser, Skeena and Columbia River catchments, as well as smaller coastal systems, from June to December every year (Groot & Margolis, 1991; Beacham *et al*., 2004*a*, *b*). Unique environmental conditions experienced by each population have been linked to distinct life-history strategies employed by different groups in order to maximize fitness (Ricker, 1972; Quinn, 2005; Eliason *et al*., 2011). These may be due, in part, to local adaptation to thermal environments (Berg & Moen, 1999; Angilletta *et al*., 2002). Predicted increases in incubation temperatures within the region (Walker & Sydneysmith, 2008) could affect fish survival differentially across populations of *O. nerka* if the current traits associated with thermal adaptation vary in response to future temperature change (Bradshaw & Holzapfel, 2008; Healey, 2011).

While morphological differences among populations are well documented (Beacham & Murray, 1989, 1990, 1993; Groot & Margolis, 1991), there has been limited experimental research on whether broad differences in population-level adaptive thermal tolerance are due to genetic differences or phenotypically plastic responses to environmental variation, known as phenotypic plasticity (Burt *et al*., 2011). This variable response among populations can be represented by reaction norms (Schlichting & Pigliucci, 1998), where, assuming maternal effects have been minimized, phenotypic variation in response to the environment can be visually depicted by crossed reaction norms. Reaction norms can represent a suite of traits, but in terms of lifetime fitness, reaction norms for survival are one of the best means of assessing adaptive differences among populations (Hutchings, 2004, 2011). Several studies have used these methods to assess thermal tolerance in salmonids *via* survival under varying conditions in a common-garden trial (Hendry *et al*., 1998; Jensen *et al*., 2008; Hutchings, 2011). Hendry *et al*. (1998) found significant differences in survival from hatching among four recently differentiated *O. nerka* populations from Lake Washington, although the sample sizes were small and the chosen populations did not represent a wide range of environmental conditions. Within British Columbia, Beacham & Murray (1989) observed two populations and found that an interior-spawning population of Fraser River *O. nerka* (Adams River) had better survival under decreased incubation temperatures than a coastal-spawning population (Weaver Creek). They proposed that this was attributable to adaptation to lower historical incubation temperatures in the interior of the province, but did not suggest how populations might respond to elevated temperatures as would be expected with climate change. Further afield, Jensen *et al*. (2008) found local adaptation in early developmental traits by conducting common-garden trials among populations of brown trout *Salmo trutta* L. 1758 in Denmark, and although they used only moderately elevated experimental temperature treatments, potential differences in adaptive variation to climate change were suggested. Thus, thermal tolerance may be found to differ within a species through evidence of phenotypic plasticity (Gienapp *et al*., 2008).

In *O. nerka*, there has been a large focus on the effect of high migration temperatures during adult migration, specifically related to population-specific thermal tolerance (Martins *et al*., 2012) and the ability to adapt to future climate change (Eliason *et al*., 2011; Hague *et al*., 2011; Reed *et al*., 2011). There is some evidence that salmonids may be able to quickly adjust to environmental change (Angilletta *et al*., 2002) and adapt to new thermal regimes within 10–20 generations (Hendry *et al*., 1998; Hendry & Kinnison, 1999). This work has suggested that evolutionary responses to climate change will probably be driven by a combination of behavioural changes in reproductive timing [*e.g*. migration timing; Reed *et al*. (2011)], and by physiological adaptation to environmental conditions [*e.g*. thermal tolerance; Eliason *et al*. (2011)]. It is not known, however, whether populations that currently have a high thermal tolerance during the adult stage will also tolerate higher temperatures during early life stages. This would imply that the physiological basis for thermal tolerance exhibited by adults may extend to include the non-motile embryo stages.

Embryonic thermal sensitivity was explored in nine populations of *O. nerka* from British Columbia, Canada, using a common-garden incubation study. As thermal tolerance among populations can reflect local adaptation by natural selection (Haugen & Vollestad, 2000), the following predictions were made: (1) populations would differ in their embryonic survival response to increased temperature and (2) thermal tolerance would reflect historical incubation temperatures from natal spawning grounds. Two additional expectations were as follows: that intra-population variation in thermal tolerance would vary, indicative of within-population plasticity to temperature changes and future potential to adapt, and upstream migration temperatures would also be positively related to embryo thermal tolerance, suggesting that thermal tolerance can cross life-history stages.

MATERIALS AND METHODS

FISH CAPTURE AND GAMETE COLLECTION

Populations of *O. nerka* were examined from the Fraser ($n = 8$) and Columbia ($n = 1$) Rivers (Fig. 1). The Fraser River populations are geographically distinct within the watershed, reflect a range of spawning ground and adult migration thermal conditions and exhibit a range of life-history characteristics (Table I). Okanagan River *O. nerka* from the Columbia River system were included in the study because their spawning adults are some of the most thermally tolerant among all *O. nerka* populations (Hodgson & Quinn, 2002; Hyatt *et al*.,

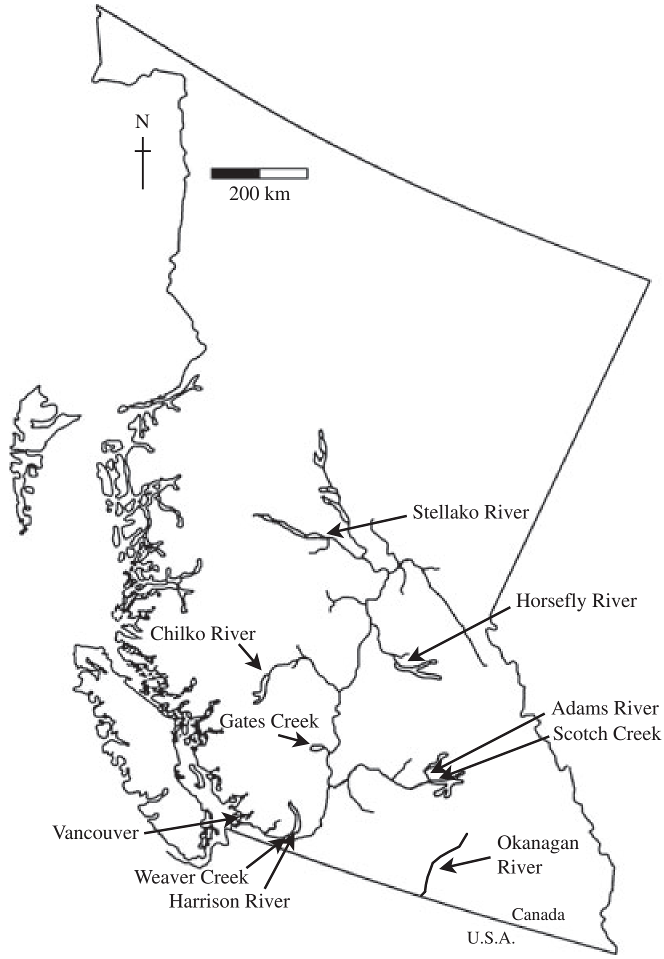

Fig. 1. Map of the study populations within the Fraser River catchment and the upper Columbia River, within British Columbia, Canada. Embryos and adult samples from each group were transported back to laboratory facilities at the University of British Columbia, Vancouver, British Columbia, for fertilization, incubation and husbandry throughout early development. Fertilization was standardized at *c*.24 h post-collection to ensure that transportation time did not affect the results.

2003) and are comparable in terms of migration distance and challenge to several of the upper-river Fraser River populations (Table I).

Reproductively mature adult *O. nerka* ($n = 12$–20 unique pairs) were captured from spawning grounds during peak spawning using a hand-held beach seine. All adults used in this study were sacrificed immediately by concussion to the head. Eggs and milt were hand expelled and collected in clean, dry plastic containers that were immediately oxygenated (with 100% O_2) and placed on ice for transport to laboratory facilities at UBC. Previous work has shown that transporting unfertilized gametes results in higher survival than transporting activated, developing eggs (Jensen & Alderice, 1983), and that salmonid eggs and sperm will remain viable with a 95–100% fertilization potential for up to 5 days as long as temperatures are low and sufficient oxygen levels are maintained within the containers (Jensen & Alderice, 1984). Nevertheless, as some populations were geographically isolated and transport to UBC took

TABLE I. Environmental characteristics and ecology for nine populations of *Oncorhynchus nerka*, eight from the Fraser River and one from the Columbia River (CR). Peak spawning date, mean, maximum and minimum spawning temperatures (mean ± S.D.) for Fraser River populations are reported from a 10 day period encompassing the estimated mean peak spawning date during the years 1990–2010. Peak river entry and mean migration temperatures are reported for historical averages, but for Adams, Weaver and Harrison, recent shifting run timings to earlier river entry are reported in parentheses. Sources: Fraser River populations, Pacific Salmon Commission – Department of Fisheries and Oceans PSC-DFO, pers. comm.; Okanagan River, Hodgson & Quinn (2002), Hyatt *et al*. (2003), K. Hyatt, pers. comm. and S. Folks & R. Bussanich, pers. comm.

Population	Gates Creek	Scotch Creek	Chilko River	Horsefly River	Stellako River	Okanagan Lake (CR)	Adams River	Weaver Creek	Harrison River
Run timing group (Fraser River)	Early summer	Early Summer	Summer	Summer	Summer	Columbia River	Late	Late	Late
Peak river entry	31 July	31 July	11 August	11 August	11 August	15 June	27 September (12 September)	27 September (27 August)	27 September (27 August)
Migration distance from river entry (km)	400	484	642	796	1100	1200	484	161	121
Elevation (m)	280	366	1174	728	716	276	366	10	10
Collection date (2010)	31 August	8 September	21 September	27 September	1 October	14 October	18 October	25 October	10 November
Unique families per population	18	20	12	14	15	20	20	20	16
Mean ± S.D. 10 egg dry mass (g)	0·43 ± 0·03	0·35 ± 0·03	0·42 ± 0·02	0·36 ± 0·04	0·34 ± 0·03	0·38 ± 0·04	0·41 ± 0·06	0·52 ± 0·04	0·73 ± 0·07
Mean ± S.D. female L_S (cm)	53·2 ±1·3	52·7 ± 1·6	52·1 ± 2·1	51·4 ± 2·3	50·8 ± 1·7	42·9 ± 2·5	56·5 ± 1·8	54·1 ± 2·7	53·9 ± 2·4
Historical peak spawn date	3 September	September	28 September	10 September	28 September	17 October	11 October	19 October	12 November
Mean spawning temperature (° C)	9·59 ± 0·76	10·84 ± 2·75	9·95 ± 1·39	12·72 ± 1·92	10·95 ± 2·33	12·10 ± 0·82	11·81 ± 1·96	10·43 ± 1·41	8·50 ± 1·13
Maximum spawning temperature (° C)	10·22 ± 0·90	11·92 ± 2·79	10·83 ± 1·16	14·06 ± 1·98	11·97 ± 2·44	14·2 ± 2·91	13·07 ± 2·01	11·57 ± 1·48	9·09 ± 1·29
Minimum spawning temperature (° C)	8·90 ± 0·70	9·46 ± 3·02	8·45 ± 2·75	11·21 ± 1·91	9·81 ± 2·27	11·1 ± 1·23	9·95 ± 2·66	9·42 ± 1·52	7·73 ± 1·40
Adult migration temperature (median; ° C)	17·6	17·6	16·6	16·6	16·2	17·5	14·2 (16·9)	14·9 (17·4)	14·8 (17·4)

L_S, standard length.

much longer than others (Fig. 1 and Table I), all groups were fertilized at 24 h post-collection, standardized in order to avoid confounding survival estimates.

FERTILIZATION PROTOCOL AND INCUBATION METHODS

Gametes were crossed by a randomized mating design wherein each male was paired once with each female, resulting in 12–20 unique families per population. For each cross, three replicates of 15 g of eggs (*c*. 80–140 eggs) were fertilized with 0·3 ml of milt and activated with 30 ml of water at either 10, 14, or 16° C, according to their planned incubation temperature. After 1 min to allow fertilization, an additional 100 ml of water was added to each jar to increase dissolved oxygen levels, and the jars were left undisturbed for 45 min (Jensen, 1988) to allow the eggs to fully harden. This dry fertilization method has been used in various studies on Fraser River *O. nerka* and been shown to result in >90 to 95% survival during embryonic development at ideal temperatures (Patterson *et al*., 2004). Family baskets were then randomly distributed in vertical stack incubators, with single replicates of each family at 10, 14, or 16° C. Parentally mediated effects are certainly a significant aspect of early developmental plasticity (Janhunen *et al*., 2010; Burt *et al*., 2012*a*), but as the focus of this study was on inter-population differences, the logistical constraints of the study design did not allow full investigation of the parental effects by including replication at the family level.

Incubation temperatures were chosen to characterize a range of elevated temperatures observed during peak spawning among the chosen populations (D. Patterson, unpubl. data). Additionally, long-term data on the thermal range for the species suggested 10° C as approximating the upper thermal optima for incubation, 16° C a stressful temperature likely to result in *c*. 50% mortality from fertilization to hatch and 14° C an appropriate intermediate, albeit still high, temperature (Beacham & Murray, 1990; McCullough *et al*., 2001). Populations were selected to represent a range of geographic locations and spawning timing, and thereby capture a range of spawning and incubation-ground thermal conditions (Table I).

Eggs were left undisturbed in the incubation stacks for the first 24–48 h, and thereafter were checked every 48 h for mortality and hatching. Stacks were covered to reduce light exposure, except while checking the eggs (<5 min day^{-1} family^{-1}). Dissolved oxygen concentrations were held constant above 85%, water flow was maintained at *c*.10 l min^{-1} through all Heath trays and temperature was held constant (daily fluctuations ± 0·3° C) using a system of small aquarium heaters, chillers and temperature control computers. All dead eggs were promptly removed and cleared in Stockard's Solution [5% formaldehyde (40%), 4% glacial acetic acid, 6% glycerine and 85% water] (Rugh, 1952) for a minimum of 24 h and visually assessed for fertilization. When groups had reached 430–450 accumulated thermal units (*i.e. c*. 43–45 days at 10° C, 31–32 days at 14° C and 27–28 days at 16° C), successfully eyed eggs [estimated according to Jensen (1988)] were counted and any surviving un-eyed eggs were discarded. Once hatching was observed for any family in a population at a given temperature, newly hatched alevin mortality and survival were recorded during daily observations. Alevins were maintained within Heath stacks until emergence and subsequent husbandry in the laboratory.

DATA ANALYSIS

All statistical analyses were based on population means (*i.e*. population averages of the values for each family) at each temperature treatment to evaluate the population response as determined by family replicates (see Table I; families numbered 12–20, depending on population; equal sample sizes across temperature treatments). Survival to hatch from fertilization (S_H) was used rather than total egg numbers in order to separate the effects of incubation treatment from the potential effects of temperature on fertilization or other pre-existing issues that could affect egg viability (Brooks *et al*., 1997; Vladic & Jarvi, 1997). There were no significant differences in fertilization success observed between temperature treatments, suggesting that variation in egg viability among populations prior to fertilization was due to other factors [*i.e*. parental effects on egg maturation; Jeffries *et al*. (2012)].

Proportional survival data (% of fertilized eggs) were logit transformed to meet the normality and homoscedasticity assumptions of parametric tests (Warton & Hui, 2011). Temperature and population differences were tested using mixed-effect ANOVAs (type III sum of squares) to determine the statistical significance of fixed effects, and subsequent Tukey's HSD *post hoc* multiple comparisons tests for survival and hatch timing analysis. All analyses were conducted using R language (R Foundation; www.r-project.org).

The survival response was assessed using a linear mixed model with population and temperature treatment as the fixed effects, and family and incubation stack as the random effects. Population variation was assessed using a base model with the form: $y_{jk} = \mu + T_j \times N + F(N_k) + \varepsilon_{jk}$, where y is the response variable (S_{H}), T represents the temperature treatment (three levels, represented by j), N is the population and F is the family identity (full-sib families, levels represented by k). For all analyses, temperature and population were considered fixed effects, varying by the random effect of family. The effect of distinct Heath stacks within the incubation design as well as egg size were evaluated as a metric for maternal investment, but these were found to be non-significant as related to embryo survival and were thus removed from the current model. Differences among fixed effects (temperature treatments and population) were tested using Tukey's HSD tests.

For each population, embryos experience the warmest water temperatures during the initial egg deposition and early development period, as all populations spawn on the descending limb of the thermograph, incubate during cold winter conditions and fry emerge during cool spring temperatures. Therefore, it was surmised that the initial spawning period would represent the most critical thermal stress period for developing embryos. Historical water temperatures recorded during peak spawn periods (D. Patterson, unpubl. data) were used to calculate mean temperatures during the spawning season for each Fraser River population, and peak spawning temperatures were selected from observational data for peak spawning activity at each location. Using these estimates of spawning duration with the temperature data, mean, maximum and minimum temperatures during peak spawning over the last two decades (1990–2010) were calculated for each population. For the Columbia River population (Okanagan River), average migration temperatures were taken from an analysis of Columbia River spawning temperatures (Hodgson & Quinn, 2002), and spawning temperatures from Hyatt *et al*. (2003) and with assistance from K. Hyatt (pers. comm.) as well as the Okanagan Nation Alliance (S. Folks & R. Bussanich, pers. comm.). Although the Columbia River population was included in the overall model, it is quite difficult to predict the link between temperatures and salmonid thermal tolerance in this highly manipulated river system (Quinn *et al*., 1997), and, as such, the Fraser River populations were analysed separately.

Using historical temperature as a proxy for population within an adjusted version of the same base model, the relationship between historical spawning temperatures and thermal tolerance was tested for within the incubation study. A mixed-model ANOVA was used overall to test for the interaction of incubation temperature and historical spawning temperature: $y_{jk} = \mu + T_j \times H_k + N_k + F(N_{kl}) + \varepsilon_{jk}$, where y is offspring survival to hatch, H represents historical temperature during peak spawn and T, N and F are the same as defined within the original model. Within this adjusted model, temperature and historical temperature were considered fixed effects, while population and family were nested random effects. Again, the effects of Heath stack and egg mass were not significant and were subsequently removed from this final model. A simplified version of this model was used separately within each temperature treatment. Tukey's HSD *post hoc* tests were used to explore significant relationships within groups.

Additionally, Pearson correlations were calculated to assess the relationship between population-level offspring survival and historical spawning temperatures for each population, and the requisite r-values were stated. The significance level for all tests was set at $\alpha = 0.05$.

RESULTS

EMBRYONIC SURVIVAL

Survival varied significantly owing to the interaction of population and temperature treatment (ANOVA, $F_{16,422} = 2.17$, $P < 0.01$; Fig. 2). Mean ± S.D. survival to

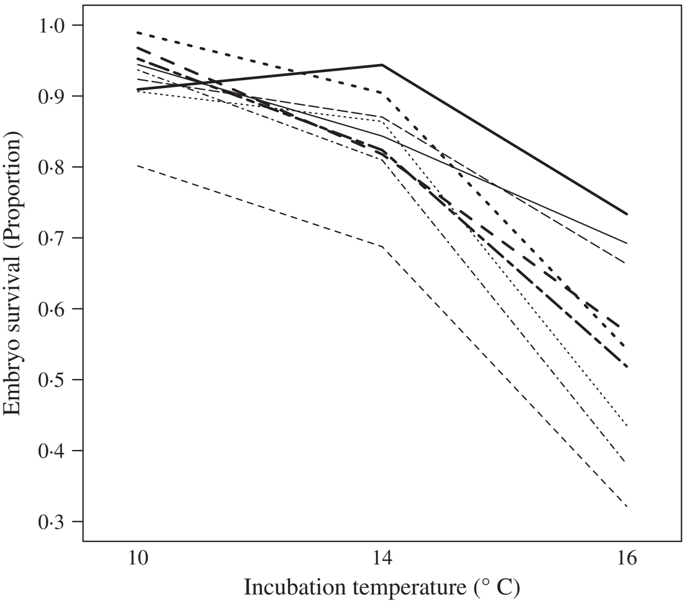

FIG. 2. Reaction norms showing mean *Oncorhynchus nerka* population survival to hatch at incubation temperatures of 10, 14 and 16° C. Reaction norms show the mean response per group at a given incubation temperature. The interaction of temperature and population shows a significant interaction of genotype by environment by crossing reaction norms. Spawning river populations: ——, Adams; - - -, Chilko; ......, Gates; .-.-., Harrison; - - -, Horsefly; — —, Okanagan; ——, Scotch; — —, Stellako; . . ., Weaver.

hatch for fertilized eggs was highest across all populations within the 10° C treatment (93 ± 16%), declined at 14° C (85 ± 20%) and decreased more rapidly at 16° C (55 ± 27%; a 41% decline compared to 10° C) (Fig. 3). The relative variation among mean survival estimates increased with temperature, and was three times higher among stocks at 16 than 10° C (C.V. = 17·1% at 10° C, 23·3% at 14° C and 48·9% at 16° C). While maternal effects (egg size) were different among groups (ANOVA, $F_{9,456} = 377{\cdot}83$, $P < 0{\cdot}001$), they did not significantly affect population mean offspring survival to hatch, and were therefore not included in the base model.

Tukey's HSD *post hoc* comparisons of the model estimates showed that there were no differences among population-level survival at the coolest temperature (10° C). Although Chilko Lake embryos did exhibit reduced survival even at this temperature, the response was not significant, it occurred gradually throughout the incubation period, and could not be attributed to a thermal event. At the intermediate treatment (14° C), population response to temperature differed significantly (ANOVA, $F_{8,94} = 4{\cdot}08$, $P < 0{\cdot}001$). Specifically, Tukey's HSD *post hoc* tests showed that Scotch Creek offspring survived better than the Okanagan ($P < 0{\cdot}05$), Harrison River ($P < 0{\cdot}05$) and Chilko River populations ($P < 0{\cdot}01$). Chilko Lake alevin survival was significantly poorer than the Weaver Creek population ($P < 0{\cdot}01$); indeed, Chilko fish performed the worst at 14° C compared to all other populations. At the highest temperature (16° C), population differences in survival were strongly evident (ANOVA, $F_{8,92} = 5{\cdot}35$, $P < 0{\cdot}001$), and the Scotch Creek families again outperformed all others, especially the late-run Harrison River ($P < 0{\cdot}01$), Chilko

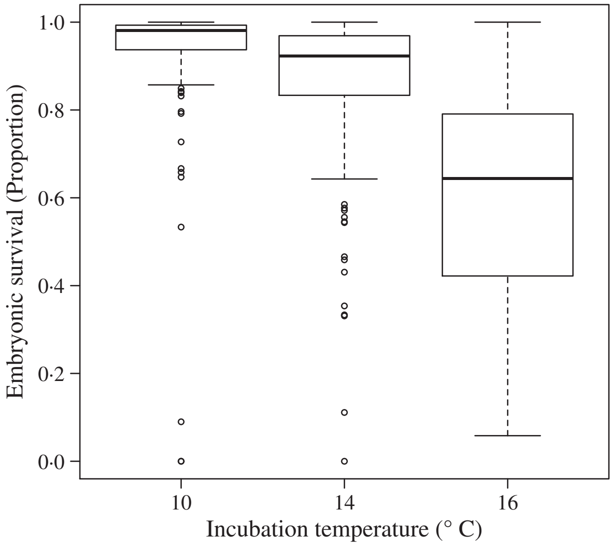

FIG. 3. The effect of temperature on embryonic *Oncorhynchus nerka* survival across incubation temperatures of 10, 14 and 16° C, showing averages across all populations. —, median; □, 25th and 75th quartiles; ⌶, range of data; ○, extremes.

Lake ($P < 0.01$) and Gates Creek ($P < 0.05$) populations. Chilko Lake fish survival was consistently lower than the other summer-run populations (Horsefly River; $P < 0.01$) and even a late-run Adams River population ($P < 0.01$). Similarly, the latest timed group, the Harrison River eggs also responded poorly to warm incubation temperatures, with lower survival than the other late timed Adams ($P < 0.05$) population.

Population variation and within-population variation increased with increasing temperature, but the magnitude of this shift was dependent on population (Fig. 4). The relative variation among family means within a population was up to 50·8 times higher at 16° C than at 10° C (*e.g*. Weaver Creek alevin, c.v. = 1% at 10° C, 18% at 14° C and 56·7% at 16° C). Relative variation within populations ranged from 0·4 times higher to 50·8 times higher at 16° C than at 10° C. Interestingly, those populations with the highest survivorship at 16° C (high thermal tolerance) were more often to have the lowest inter-population variation, while the populations with an average thermal tolerance had high plasticity among families (especially Okanagan, Weaver and Stellako).

CONNECTION WITH HISTORICAL TEMPERATURES

In general, populations with higher historical spawning temperatures had higher embryonic survival to hatch at warmer temperatures. Mean peak spawning temperatures for all populations represented population differences as related to offspring survival in the overall model (ANOVA, interaction of the effects of incubation treatment and mean historical spawning temperatures, all populations, $F_{2,308} = 13.36$, $P < 0.001$), as did maximum peak spawning temperatures

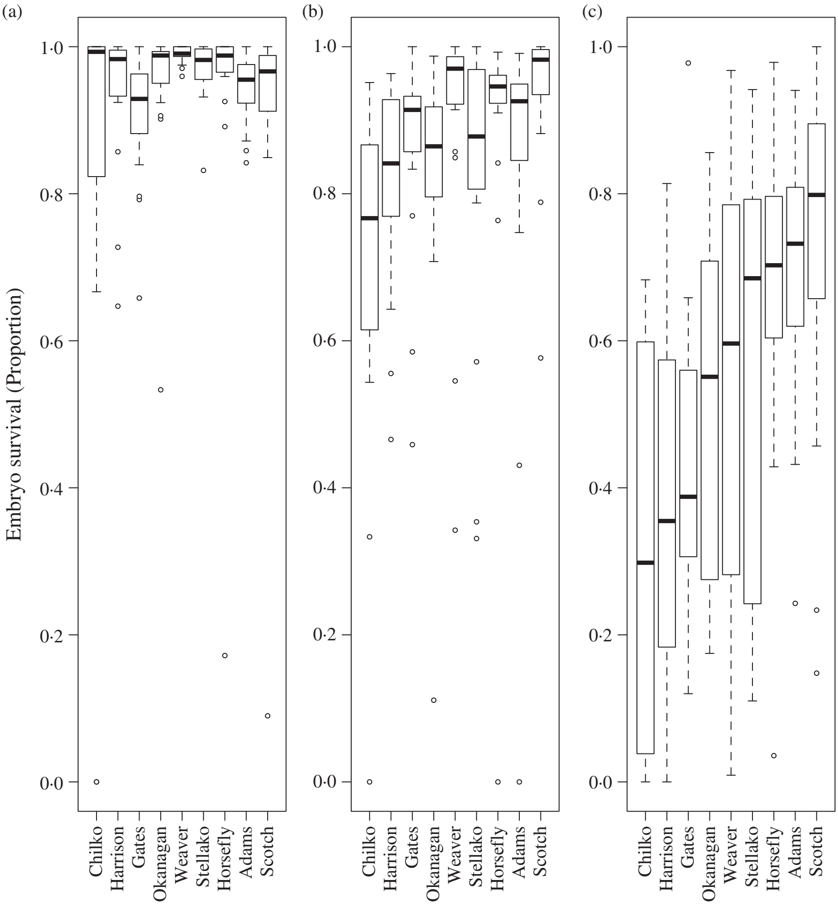

FIG. 4. The effect of temperature on *Oncorhynchus nerka* populations across incubation temperatures of (a) 10° C, (b) 14° C, (c) 16° C. Populations are ranked in all temperatures by their survival at 16° C. The effects of provenance and temperature treatment during embryonic development on survival to hatch, showing family variation within populations. —, median; □, 25th and 75th quartiles; ⌶, range of data; ○, extremes.

($F_{2,308} = 13·43$, $P < 0·001$). This relationship was much stronger at the high temperature treatment (mean peak spawning temperature correlated with survival at 16° C, $r = 0·32$, $P < 0·001$; maximum peak spawning temperature, $r = 0·29$, $P < 0·001$), especially when this relationship was tested among only Fraser River populations (mean spawning temperature, $r = 0·393$, $P < 0·001$). The correlation was not significant for either all populations or just Fraser River populations at 14° C ($r = 0·05$, $P > 0·05$; $r = 0·09$, $P > 0·05$) or 10° C ($r = 0·06$, $P > 0·05$; $r = 0·05$, $P > 0·05$). All three metrics of spawning temperatures examined, maximum, mean and minimum, provided similar results for Fraser River stocks. Interestingly, there was no relationship between adult migration temperatures and thermal embryo tolerance for both Fraser River and Columbia River populations ($r = −0·04$, $P > 0·05$).

DISCUSSION

Exposure to high temperatures through embryo development until hatching resulted in a decreased, but differential, survival across nine genetically distinct populations of *O. nerka* in a common-garden trial. The magnitude of thermal effects varied among populations in a manner that suggested adaptation to long-term environmental conditions. Population differentiation through local adaptation means that native populations have a higher fitness within their natal environment than other populations of the same species. Additionally, inter-population phenotypic plasticity in survival increased with increasing temperatures, as previously shown at the family level (Beacham, 1988; Burt *et al*., 2012*a*). Considering both inter and intra population variability in thermal tolerance suggests that forming predictions for future population adaptation to warming waters is not as simple as identifying current tolerance limits; it will be important to consider population-specific thermal scope for activity and to understand the large-scale ecological drivers of thermal tolerance (Sunday *et al*., 2011).

POPULATION-SPECIFIC RESPONSES TO HIGH TEMPERATURES

The observed differences in embryonic survival among populations were substantial, and the interaction of genotype and environment observed by crossing survival reaction norms suggested that there was no clear additive effect of temperature across populations. Genotypes responded differentially, with some populations exhibiting a greater magnitude of survival response between 10 and 14° C, while for other populations the increase in temperature between 14 and 16° C resulted in a significant decrease in survival (Fig. 2). The fact that several populations exhibited only slightly reduced survival at 14° C, and even (to a lesser extent) at 16° C, suggests that plasticity to temperature within *O. nerka* may be relatively high in this early life stage (Hutchings *et al*., 2007; Hutchings, 2011).

Considering the adaptive implications of observing differences in thermal tolerance in a common-garden study, a long-term temperature database was used to assess historical thermal regimes among groups. This study was able to suggest a link between experimental embryonic survival and historical thermal conditions. Indeed, it appears that populations that have historically experienced cool spawning temperatures (*e.g*. Gates Creek, Chilko River and Harrison River; Table I) were less able to cope with increased temperature within the experimental context, whereas populations that spawn during warmer conditions were better able to cope with the higher 16° C incubation temperatures. More specifically, the populations with the lowest embryonic survival in this study were all populations that spawn in cool-adapted spawning regions. Chilko River flows from a glacially fed lake, so the water consequently remains cool throughout most of the year. Harrison River *O. nerka* may also be cool-adapted as this population spawns in the late autumn, when river temperatures have notably decreased. While Gates Creek is an early summer-run stock, water temperatures are cooler in comparison to the other stocks within this run timing group, as the inflow to the spawning area derives from high mountain streams. Conversely, the best survivors were those derived from populations that have historically had higher probability of experiencing near 16° C water temperatures during spawning, and therefore may be better adapted to warm incubation temperatures.

An exception to this trend was the upper Columbia River population, the Okanagan River fish, which had only moderate experimental thermal tolerance yet experienced the highest migration and spawning temperatures (Stockwell *et al*., 2001; Hodgson & Quinn, 2002; Hyatt *et al*., 2003; Table I). This thermal regime is, however, a product of intensive management of the river for hydroelectric power production and has led to warming of the river in recent decades (Quinn & Adams, 1996; Quinn *et al*., 1997). Given that the thermal consequences of dams are likely to affect thermally sensitive late spawning populations more than heat-tolerant early spawning groups (Quinn *et al*., 1997), the anthropogenic effects of such development may affect the speed of development and growth more than the thermal tolerance. Certainly, it will take time to change thermal adaptation for these populations (Angilletta *et al*., 2008).

While variation in inter-population survival response implies a breadth of thermal tolerance for the species, intra-population variation suggests phenotypic plasticity within a genotype. Consistent to the original prediction, among-family variation in survival to hatch increased with temperature, especially when comparing the 16 and 10° C treatments (Fig. 4). This trend has been observed in other studies of salmonids, which noted that variation among families increases as thermal conditions diverge from environmental norms or thermal optima (Beacham & Murray, 1985, 1989; Hendry *et al*., 1998; Burt *et al*., 2012*a*). Adaptive differences suggest that different populations display unequal suitability to specific environmental states, resulting in phenotypic changes that form a functional improvement in survival, reproduction or growth (Beacham, 1988; Stearns, 1992). Phenotypic plasticity thus allows populations and species to accommodate environmental variation; greater plasticity will allow population survival in the short term without necessitating selection for genetic change. Among-population plasticity for thermal tolerance, however, does not necessarily pair with within-population thermal tolerance; these data show that those populations with the highest thermal tolerance were also those with the lowest intra-population variation (Fig. 4). This may indicate less plasticity for thermal scope in those groups, although without elevating experimental temperatures further, this is merely a suggestion. Certainly, current tolerance for elevated temperatures does not necessarily reflect the potential to withstand additional warming; for populations that already experience warm temperatures, the species-level critical thermal maxima still indicate that such populations will become compromised (Crozier & Zabel, 2006). Therefore, it is important to understand the climate change at a regional scale that is relevant to the spatial structure of the salmonid population under investigation, and not just provide broad predictions.

Previous experimental research has found evidence of broad differences in population-level adaptive thermal tolerance using survival responses (Beacham & Murray, 1989; Hendry *et al*., 1998; Hutchings *et al*., 2007; Jensen *et al*., 2008; Hutchings, 2011). In general, such research has found that populations tend to be best suited to temperatures that most closely resemble the historical thermal regime of their natal habitat (Taylor, 1991; Hutchings, 2011). Warming temperatures may, however, soon push certain groups to or beyond their thermal range (Hague *et al*., 2011; Reed *et al*., 2011). This suggests that those populations with the greatest thermal tolerance at present may not be those groups that respond favourably in the future. Current thermal tolerance is not necessarily indicative of future thermal tolerance, as those populations may already be at or near the limit of their thermal scope (Stillman, 2003). This is important at a species level, as variation amongst populations will drive species-level resistance, resilience and subsequent selective response to climate change (Hutchings *et al*., 2007; Bradshaw & Holzapfel, 2008; Lyon *et al*., 2008).

An interesting aspect of this study is that, and contrary to the original expectation, thermal tolerance varies greatly with life stage (Beacham & Murray, 1987; Healey, 2011), suggesting it will be important to avoid generalizing from studies on other life stages, such as those on adults (Eliason *et al*., 2011) or fry (Beacham & Murray, 1989). For example, while Chilko Lake adults have been identified as thermally tolerant during their up-river migration (Eliason *et al*., 2011), Chilko embryos were the least tolerant of warming temperatures within this study (Fig. 2). Similarly, adult Okanagan *O. nerka* experience the warmest upstream migration conditions (Hyatt *et al*., 2003; Table I), but did not have the highest thermal tolerance as embryos (Fig. 2). Indeed, adult migration temperatures were not correlated with offspring survival in this study, as opposed to the positive correlation found with spawning ground temperatures. Moreover, this study only looked at the sessile embryonic development stage during incubation, the portion of the life history where increasing spawning ground water temperatures may have a direct effect (Healey, 2011), and did not consider the latent effects of supraoptimal temperature regimes. Carry-over effects of elevated temperature during incubation have been shown to affect later life stages, even if high temperature is removed (Beacham & Murray, 1987; Burt *et al*., 2012*a*, *b*). For this reason, it is important to consider these differences in population viability under thermal stress with additional precaution, considering that the effects of temperature on developmental pathways may significantly affect future competitive behaviours, including swimming ability and lifetime fitness.

Rapidly changing thermal regimes will certainly affect species distribution of both terrestrial and aquatic species, shifts particularly driven by the increasing frequency of extreme climatic events (Jentsch *et al*., 2007). In birds, reproductive timing has been found to shift as temperature increases, implying that sufficient phenotypic plasticity in reproductive traits will be critical for population persistence (Lyon *et al*., 2008). In terms of climate change adaptation, seasonal timing shifts may have the greatest influence on species persistence as populations have evolved synchronous events within their life history in response to natal environmental norms (Brannon, 1987; Bradshaw & Holzapfel, 2008; Charmantier *et al*., 2008). Changes in reproductive timing have the capacity to severely affect species like *O. nerka*, which have clearly adapted to differential environments among populations (Eliason *et al*., 2011; Hague *et al*., 2011). In addition, increasing water temperatures will also affect reproductive maturation and ovulation of the parents (Pankhurst *et al*., 1996; King *et al*., 2007), and in some cases may relate to spawning failure (Crozier *et al*., 2008). Warming in-river temperatures can negatively affect both the ability of some returning adults to successfully migrate to spawning areas (Macdonald *et al*., 2010; Eliason *et al*., 2011) and alter the maturation of eggs (Jeffries *et al*., 2012), thus increasing the survival cost of maturation and reproduction (Kuparinen *et al*., 2012). Intergenerational temperature effects may also persist from early development and deleteriously affect lifetime success of their offspring (Burt *et al*., 2012*a*, *b*; Salinas & Munch, 2012). As shown here, a successful spawning event at warm temperatures does not presume offspring survival (Pankhurst & Munday, 2011). Life stage-specific thermal tolerance may affect specific survival of developing eggs, alevin or fry, and the cumulative effects of warming waters across life stages will probably have severe deleterious consequences for lifetime fitness.

FUTURE RESEARCH AND MANAGEMENT IMPLICATIONS

Temperature is known to affect survival and development of Pacific salmon *Oncorhynchus* spp. throughout their life cycle. This is, however, the first study of such scale that investigates the thermal tolerance of wild *Oncorhynchus* embryos across many populations of the same species, and links this response to differences in historical thermal experience. This analysis supports recent work on population-level physiological differences in this species at the adult life stage (Eliason *et al*., 2011; Martins *et al*., 2011), and augments the preceding work on *O. nerka* that focused on only two populations during early development (Beacham & Murray, 1989). The populations studied differ in their ability to develop under alternative thermal regimes, suggesting phenotypic plasticity and potentially genetic heritability for thermal tolerance. Embryonic response to environmental change can have serious repercussions for subsequent life stages and lifetime fitness (Murray & Beacham, 1986, 1987; Burt *et al*., 2012*a*), highlighting the importance of plasticity in response to environmental regimes during early development. The results imply that some *O. nerka* populations may have a greater ability to survive and, potentially, to adapt to warming climate regimes than others. In these cases, the fitness consequences of temperature and potentially adaptive responses by populations can be predicted, especially when using survival as a fitness-related trait (Hutchings *et al*., 2007; Hutchings, 2011).

Future work should focus on fully evaluating the genetic basis of phenotypic plasticity by using a quantitative genetics approach to estimate the heritability of thermal tolerance (*i.e*. quantify additive genetic variance), knowledge that would serve population viability models for *O. nerka* (Reed *et al*., 2011). While thermal tolerance may suggest adaptive potential, it is probably not enough; sufficient heritable variation in phenotypic responses to thermal conditions is required in order for potential adaptation to exist (Angilletta *et al*., 2002; Bryant, 2009). Variation in temperature-related survivorship is a serious conservation concern, and fisheries management could certainly benefit from incorporating this knowledge when setting population-specific spawning escapement targets (Holt & Peterman, 2006; Macdonald *et al*., 2010). In addition, improving habitat management of spawning areas by protecting cool water flow and controlling water levels where possible may help offset the effects of climate warming in some areas (Healey, 2011; Macdonald *et al*., 2012). Overall, when considering the long-term viability of this important resource, it will remain important to retain genotypic and phenotypic variability within the species, especially considering the unpredictable effects of environmental stochasticity and climate change.

This research was conducted with the approval of the Animal Ethics Committee of the University of British Columbia, according to the principles of the Canadian Council on Animal Care (Animal Care #A08-0388). C.K.W. was supported by an NSERC Canada Graduate Scholarship and a VanDusen Graduate Fellowship from the Faculty of Forestry. Thanks to R. Bussanich and S. Folks of the Okanagan Nation Alliance for field and data assistance, and to K. Hyatt for access to thermal data. Many thanks for training and project support to the DFO Environmental Watch programme, and all members of the Pacific Salmon Conservation and Ecology Laboratory, especially to A. Lotto, J. Burt, E. Vogt and A. Haas for field and laboratory assistance, and E. Martins for statistical advice.

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