Developmental temperature stress and parental identity shape offspring burst swimming performance in sockeye salmon (*Oncorhynchus nerka*)

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Abstract – The persistent effects of embryonic temperature stress and individual parentage on fry swimming performance were examined in a cross-fertilisation experiment using sockeye salmon (*Oncorhynchus nerka*). A fixed-velocity test of burst swimming was used to assess the endurance capacity and behavioural performance of individual fry from 10 offspring families incubated at 12, 14 or 16 °C to hatch and then reared through yolk absorption and exogenous feeding stages in a common posthatch environment (average 6.9 °C). Fry burst swim time (BST) was influenced by an interaction between incubation temperature and family identity. Average BST was longer for fry from the 12 °C prehatch treatment compared to 14 and 16 °C, although differences were largely attributable to temperature effects on average fry size. Behavioural observations revealed that fish incubated at 16 °C performed more poorly, having a larger proportion of individuals that required stimulation to swim, fatigued more frequently or were classified as ‘nonswimmers’. Within all three incubation temperature treatments, mean BST varied significantly among offspring families, independent of fry mass and length. An interesting relationship was observed within the 16 °C treatment, whereby families with higher survivorship were characterised with lower mean BSTs. Collectively, these findings demonstrate that exposure to high temperatures in early sockeye salmon development can result in persistent, parentally mediated effects on fry performance. As such, these results provide important insight into how elevated temperature events during egg incubation may affect early life history selection processes and survival in stages beyond when the stressor is experienced.

Key words: early life history; thermal stress; maternal influence; paternal influence; family effects

**Introduction**

In Pacific salmon (*Oncorhynchus* spp.), the period directly following fry emergence is critical to survival and has an important influence on population dynamics (Elliott 1989). During this transition from endogenous to exogenous feeding in sockeye salmon (*Oncorhynchus nerka*), performance-linked traits such as size and swimming ability are highly important as individual fry migrate to natal lakes, forage for food and interact with competitors and predators (Burgner 1991). Fry-to-smolt mortality rates are high (Bradford 1995) due primarily to predation, and initial selection during this period will depend on individuals’ performance capacity and behaviour (Eggers 1978). Intrinsically, variation in size or performance at this postlarval emergence stage is derived from two sources: environmental and parental influences during

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Temperature and parentage influence sockeye fry swim performance

development. Whereas many studies have examined the influence of these factors on embryonic and larval phenotypes, few have investigated the persistence of both the embryonic environment and parental influences on performance-linked traits beyond yolk-feeding stages (Beacham 1990; Heath et al. 1993; Green & McCormick 2005).

Water temperature is a critical regulator of physiological processes in aquatic poikilotherms and is an especially poignant factor affecting the developmental rates and survival of eggs (Blaxter 1992). The thermal regime during embryogenesis can also influence the development and expression of important phenotypic traits (e.g., size – Atkinson 1996; meristics – Fowler 1970; muscle cellularity – Johnston & McLay 1997). Concurrently, there is increasing evidence that thermally induced phenotypic plasticity in early ontogeny can affect subsequent performance at later life stages (Elphick & Shine 1998; Pechenik et al. 1998; Watkins 2000; Albokhadaim et al. 2007; Koumoundouros et al. 2009). For example, an increase of 2 ˚C in the water temperature during embryonic development in fishes is enough to alter the proliferation and differentiation of myogenic progenitor cells and protein synthesis necessary for skeletal muscle growth, consequently affecting the muscle phenotype of posthatch larvae (Johnston 2006; Martell & Kieffer 2007). These temperature effects can remain imprinted in later juvenile stages and result in decreased swim performance (Koumoundouros et al. 2009). At developmental temperatures that approach upper tolerance limits, thermal stress can result in the disturbance of cellular/genetic pathways with potential consequences for offspring morphology, physiology and behaviour (Takle et al. 2004; Wargelius et al. 2005; Turner et al. 2007). Whereas thermal stress during development is shown to have latent effects on locomotor performance in herpetofaunal studies (Brana & Ji 2000), similar experiments examining the latent impacts of supra-optimal embryonic temperatures in fish populations have not been conducted.

Along with environmental effects, individual metabolic and performance capacities are determined by genetic and nongenetic parental influences. In many species of fish, embryonic and larval characteristics such as size, meristics, metabolism, muscle cellularity and growth are shown to vary among offspring families as a function of either female or male parental identity (Beacham 1990; Chambers & Leggett 1996; Heath et al. 1999; Trippel et al. 2005; Pakkasmaa et al. 2006; Morasse et al. 2008; Rossignol et al. 2010). Whereas the majority of these studies are limited to assessing phenotypes during egg and hatching stages, there is increasing evidence to suggest that parental influences can show considerable temporal persistence. In experiments that investigated offspring beyond the onset of exogenous feeding, substantial parentally mediated variation has been detected in offspring size (Nadeau et al. 2009), muscle fibres and growth (Albokhadaim et al. 2007; Macken et al. 2008), stress response (Heath et al. 1993), and swim performance (Garenc et al. 1998; Tierney et al. 2009).

Experimental tests of swimming capacity have been used in many species of fish as a quantitative assessment of performance linked to fitness (Beamish 1979). In studies specific to salmonid fry and juveniles, differences in swim performance have been assessed between species (Hawkins & Quinn 1996; McDonald et al. 1998; Hale 1999) and between populations (Taylor & McPhail 1985a,b; Taylor & Foote 1991; Pon et al. 2007), but rarely between offspring families or as a function of their developmental environment. Despite evidence that exposure to incubation thermal stress can affect survival, morphology and physiology in salmonid fry (Finn 2007; Turner et al. 2007), the potential for elevated developmental temperatures to have latent effects on fry swim performance has not been examined. Similarly, although several studies have shown considerable among-family variation in the enzymatic correlates of locomotor activity (Garenc et al. 1998; Patterson et al. 2004; Rossignol et al. 2010), we found only one study that has investigated parental identity as a potential source of variation in salmonid swimming capacity (Nadeau et al. 2009).

In the context of climate change, predicted increases in mean temperatures and the frequency of extreme temperature events in salmonid freshwater habitat (Hague et al. 2011) may result in incubation environments surpassing thresholds for optimal development. As such, understanding the persistence of parental and temperature influences will be essential in gaining a more comprehensive view of how environmental change may influence early life history selection processes and survival. The objective of this experiment was to determine whether exposure to developmental high-temperature stress results in latent effects on fry swim performance and whether swim performance differs between offspring families. To do this, we tested the burst swim endurance of individual, 3-week-old fry from 10 offspring families that had been exposed to three levels of temperature stress between fertilisation and hatch. We predicted that (i) burst swim performance would be lower in the fish that experienced higher thermal stress during incubation and (ii) differences in fry burst swim endurance within temperature treatments would be attributable, at least in part, to offspring parental identity. While investigating these predictions, we sought to determine whether any variation in fry swimming performance (among temperature treatments, among families and at
the individual level) could be explained by differences in fry size attributes or selective processes resulting from exposure to high temperatures during development.

**Methods**

**Fish collection and incubation design**

The study population consisted of sockeye salmon from Weaver Creek (49°32’N; 121°88’W), one of the major stocks in the lower Fraser River of southern British Columbia, Canada. Gametes were collected as described in the study of Burt et al. (in press). Briefly, sockeye salmon were captured by beach seine in the Harrison River on 15–18 September 2008 on Chehalis First Nations territory 117 km from the mouth of the Fraser and 5 km downstream from their spawning grounds. Upon capture, fish were immediately transported to the Fisheries and Oceans Canada Cultus Lake Laboratory (49°07’N; 121°98’W), where an adipose fin clip was taken to confirm stock identification (Beacham et al. 2005) and adults were randomly placed in holding tanks (~20,000 l) until the fish reached sexual maturity, confirmed by gentle abdominal pressure extruding either eggs or sperm.

Eggs and milt were collected from six mature females and six mature males on 10 October 2008 and then transferred on ice to Simon Fraser University (<2 h transport time) for fertilisations. Ten offspring families were created using a dry fertilisation technique described by Nadeau et al. (2009). The eggs of five females (numbered 1–5) were crossed with the milt of a single male (male A) to create five paternally linked half-sib families (1A, 2A, 3A, 4A and 5A). Similarly, the eggs of a single female (female 6) were crossed using the milt of different males (letters B–F) to create five maternally linked half-sib families (6B, 6C, 6D, 6E and 6F). A full-factorial cross-design was not possible because of limitations associated with gamete (egg) quantities and the desire to replicate families within temperature treatments. Nine individual fertilisations were performed for each of the ten gamete combinations, so that three replicates of each family cross could be incubated within three separate temperature treatments (total n = 90 family replicates). Fertilised eggs were allowed to water-harden for 45 min, during which time they were transported to the University of British Columbia (<1 h transport time) for incubation at the Forest Sciences Aquatic Laboratory.

Each replicate from each family cross was transferred into a separate netted cylindrical egg capsule and placed in a flow-through Heath stack fed by recirculating dechlorinated city water at one of three incubation temperatures (12, 14 and 16 °C). Each family was represented once in a single tray, in a single Heath stack (three Heath stacks per temperature treatment). Incubation temperatures were selected based on existing data for sockeye salmon (Beacham & Murray 1990) to encompass a thermal range that included a treatment within the species’ upper incubation optima (12 °C), a thermally stressful temperature associated with an approximate 50% fertilisation-to-hatch mortality (16 °C) and an intermediate treatment (14 °C). All egg capsules were initially incubated at 12 °C and incrementally elevated to treatment temperatures over 3 days. Once at treatment temperatures, recorded actual treatment means (±SD) were 11.8 ± 0.4, 13.8 ± 0.4, 15.7 ± 0.4 °C. Egg capsules were checked regularly until hatch and daily thereafter, and dead eggs were recorded and removed. Mortality between fertilisation and hatch was significantly higher within families exposed to the 16 °C incubation treatment (39.9% ± 23.2 SD), moderate for families incubated at 14 °C (16.2% ± 18.7 SD) and low for families incubated at 12 °C (5.4% ± 4.6 SD) (see details and analysis in the study of Burt et al. in press).

**Posthatch incubation and rearing**

After families in a temperature treatment reached 95% hatch, the water temperature was slowly lowered (1 °C per day) to the ambient temperature of the laboratory water supply (10 °C in early December and declining to 5 °C by February, average = 6.9 °C). All 90 family crosses/replicates therefore experienced identical ambient posthatch temperatures up to, and during, fry swim trials. Alevins were checked every 2 days, and mortalities were recorded. Posthatch alevin mortality in fish from the 12 and 14 °C treatments was low (0.4% and 2.3%, respectively); however, some latent mortality occurred for alevins that had been exposed to 16 °C (13.7% ± 14.0 SD).

Families were determined to have reached ‘emergence’ stage by visual inspection, when the yolk sacs of the fish were entirely covered by chromatophores (‘buttoned up’). At this stage in the wild, fish would emerge from their incubation gravel, migrate to their nursery lake and begin exogenous feeding. Visual inspections revealed that families from the three temperature treatments reached emergence stage in approximately same time period, likely due to the fact that the 12 °C families required a lower number of accumulated thermal units (~1086 ATUs) to ‘button up’ compared to the 16 °C families (~1230 ATUs). This mechanism for stabilising emergence timing to compensate for differences in thermal regimes has been documented in salmon populations in the wild (Brannon 1987). For assurance, we obtained confirmation that the total number of ATUs attained by our
12 °C emergent fry was close to the value attained by sockeye fry upon emergence from the Weaver Creek spawning channel (~1000 ATUs; R. Stitt, Weaver Creek Spawning Channel, Department of Fisheries and Oceans, personal communication).

Over 9 consecutive days, all family replicates were transferred from their Heath stack egg capsules into individual netted 10-l rearing enclosures (n = 90). Transferred fry were placed in rearing enclosures at equal stocking densities (30 fish/10-l enclosure), and enclosures were randomly positioned within multiple 1000 l flow-through troughs. Rearing densities were slightly lower (15–28 fry) for several 16 °C exposed families that experienced high mortality during incubation. Fry were fed powdered fishmeal (EWOS Canada Ltd., Surrey, BC, Canada) in two daily instalments of ~1% total body mass for a period of just over 3 weeks, at which point swim trials began following 24 h of fasting. During rearing, lighting conditions were adjusted regularly to reflect the natural photoperiod (49°18’N). Mortality during this exogenous feeding stage was generally low (0% in 12 °C group, 0.1% in 14 °C group and 1.5% in 16 °C group).

Burst swimming protocol and measurements

A fixed-velocity test of burst swimming was performed on individual fish to assess endurance capacity as a component of overall fitness. Burst swimming is defined here as a maximal swimming effort that can be sustained for only a short period (usually ≤ 20 s; Beamish 1979), but for a longer duration than a startle response (usually <1 s) for which the term burst swimming has also been used (Taylor & McPhail 1985b). Burst swim trials have successfully been used to evaluate intra- and interspecific differences in anaerobic capacity in juvenile salmonids (McDonald et al. 1998; Pon et al. 2007; Nadeau et al. 2009) and are advantageous in comparison with other measures of prolonged swimming (i.e., U_{crit}) in that they do not take long and many individuals can be tested in a short period of time.

Burst swim trials were conducted in an open-top rectangular flume (230 length × 17 cm width, described in detail by Pon et al. 2007) within a sectioned off swimming channel measuring 30 long and 6.9 cm wide (water depth = 1.8 cm). To maintain laminar flow, fresh flowing water was passed through two honeycomb flow straighteners before entering the swim channel, which was gated with wire mesh at either end. The swim channel was illuminated with incandescent light from above, apart from a dark-shaded region at the head of the channel, intentionally provided to encourage fry to remain actively swimming against the incoming current and avoid falling back. Encountered flow velocity was calculated from discharge/cross-sectional area. Flow velocity was maintained constant at 23.0 (±0.7 cm s^{-1}) throughout duration of swim tests, equating to an average fry swimming speed of 8.0–8.6 BL s^{-1} (dependent on fry length). Preliminary trials established that fry could maintain position swimming at maximal effort against this current speed for approximately 30 s before fatiguing and falling back to the rear gate of the swim area. Water temperature for all trials was 5.8 °C (±0.2 °C).

A maximum of 10 fry from each independently reared family replicate (n = 90 family replicates) were subjected to a burst endurance swim trial between 12 and 18 February 2009. Families were swum in corresponding order to the day they were transferred to rearing enclosures, thus ensuring all fish had experienced a similar number of feeding days (22 or 23) prior to the test. To avoid any effects of specific dynamic action on swim performance, families were not fed for 24 h prior to their swim trial, ensuring complete food evacuation.

To begin each trial, one fry was randomly scooped from its rearing enclosure (fry scooped and transported in water to minimise exertion and stress) and introduced directly into the flowing current of the swim channel. Most fry would immediately initiate burst swimming, holding position under the shaded area at the head of the swim channel until fatigued. Fish that did not initially burst were stimulated using a blunt probe, which, in most cases, promoted immediate bursting. If fish were not able to initiate bursting or swim against the current for >5 s, these fish were recorded as ‘nonswimmers’ and sampled for length and weight. In the event of a ‘nonswimmer’, another fish was randomly selected from the same rearing enclosure to perform the trial with the aim of obtaining 10 valid swim trials for each family replicate.

Burst swimming time was calculated as the interval between the initiation of burst swimming (T_0) and the point when fatigued fish fell back beyond the line marked by the shaded region (T_F). Upon fall back, fish were immediately stimulated with a blunt probe to confirm complete fatigue. If fish reinitiated burst swimming, this swimming duration and successive bursting episodes were incorporated into the calculation of cumulative burst swim time (BST):

\[
BST = \sum_{i=1}^{n} (T_F - T_0)
\]

where \( n \) is the number of bursting episodes. Individual BSTs were obtained by video analysis of swimming trials recorded by two wide-angle lens video cameras (Panasonic WV-BP312; 4.5 mm focal length) connected to a time-lapse VCR (Panasonic AG-6124, Panasonic, Secaucus, NJ, USA). Upon trial completion, fish were removed from the channel, sacrificed by
overexposure to MS-222, blotted dry and measured for length (±0.1 mm) and mass (±0.0001 g). Video data from one of the three 14 °C family 4B replicates were corrupted and subsequently excluded.

Data and statistical analysis

Data from 858 individual burst swim trials were analysed using SAS 9.1 (SAS Institute: http://www.sas.com). Because body size can influence salmonid swim performance (Taylor & McPhail 1985a,b; McDonald et al. 1998), analyses were carried out to examine the influence of size on BST. We confirmed that both fry mass and length had small, but significant, influences on individual fry BST by calculating regressions using a logarithmic transformation (Fig. 1). Subsequently, we generated both mass-independent and length-independent BSTs according to the methods described by Packard & Boardman (1988). BST values for individual fry were adjusted to the overall average fry mass or fry length and scaled using the coefficients obtained from the logarithmic regressions. No significant differences were detected in the slopes of the 12, 14 and 16 °C fry mass-by-BST logarithmic regressions (ANCOVA, $F_{2,852} = 2.28$, $n = 858$, $P > 0.05$) or fry length-by-BST logarithmic regressions (ANCOVA, $F_{2,852} = 1.63$, $n = 858$, $P > 0.05$), so single scaling coefficients from the slope of the common regression line were used (Fig. 1). Mass-adjusted BSTs (BSTM) and length-adjusted BSTs (BSTL) were obtained by the following equations:

$$\text{BST}_{\text{M}} = \frac{\text{BST}}{(\overline{M}/M)^{b_1}} \quad \text{or} \quad \text{BST}_{\text{L}} = \frac{\text{BST}}{(\overline{L}/L)^{b_2}}$$

where BST is the unadjusted BST of an individual fry, $\overline{M}$ is the grand mean for fry mass, $\overline{L}$ is the grand mean for fry length, $b_1$ is the slope of the mass versus BST regression ($b_1 = 0.932$) and $b_2$ is the slope of the length versus BST regression ($b_2 = 2.77$).

To examine the first hypothesis and test for a difference in swimming performance between temperature treatments, in addition to the interaction between temperature and parentage (family identity), a nested mixed model ANOVA was used:

$$y_{ijkl} = \mu + T_j + P_k + F(P)_{l(k)} + T \times P_{jk} + T \times F(P)_{j(l(k))} + \varepsilon_{ijkl}$$

where $y =$ burst swim time (BST, BSTM or BSTL), $T_j =$ temperature for treatment $j$, $P_k =$ parent spawner used to generate half-sibs ($k =$ ‘female’ or ‘male’ parent spawner), $F_l =$ family identity nested within male or female spawner ($l = 1–5$ within ‘male’ or $6–10$ within ‘female’) and $\varepsilon$ is the random error term. Heath stack effects (family replicates) were included in the original model but were found to be nonsignificant and were subsequently removed from the current model. For all analyses, $T$ and $P$ were considered fixed effects, while all other variables, including family identity, were considered to be random effects. Differences between temperature treatments were assessed using pairwise $t$-tests and a Bonferroni alpha correction (Whitlock & Schluter 2009). In all analyses, BSTs were square-root-transformed to meet the assumptions of normality (Kolmogorov–Smirnov test) and homoscedasticity required for parametric tests.

To examine our second hypothesis and test for differences in swimming performance between families, a simplified mixed-model ANOVA was used separately within the 12, 14 and 16 °C treatment groups:

$$y_{ik} = \mu + P_k + F(P)_{i(k)} + \varepsilon_{ik}$$

where $y =$ burst swim time (BST, BSTM or BSTL) and the variables $P$ and $F$ are defined the same as in the model above. Again, the effect of Heath stack (family
replicate) was not significant in the analysis of BST within each temperature treatment and was subsequently removed from the model. To compare female versus male spawner influence on BST (using BST\(_M\)), we subdivided the data within temperature treatments into maternal half-sib crosses and paternal half-sib crosses. One-way ANOVAs were used to test the significance of the variation among families differing in maternal identity or paternal identity.

We conducted contingency analyses on several behavioural observations recorded for each swim trial (\(n = 858\) fry). Pearson’s chi-square tests were performed to compare the proportions of fry among temperature treatments with regard to whether they (i) needed physical stimulation to initiate swimming (1 = yes, 0 = no), (ii) were able to complete swim trials in one continuous burst (1 = yes, 0 = no) and (iii) fatigued frequently during swim trial (proportion of fry demonstrating \(\geq 3\) or \(\geq 5\) fall-backs). The proportion of ‘nonswimmers’ (unable to burst swim and hold against current for \(>5\) s) from each temperature treatment was also compared using a Pearson’s chi-square test (total \(n = 922\), ‘nonswimmer’ fry added to the number of fry with valid swim times).

Finally, owing to the high mortality experienced in the families exposed to the 16 °C treatment, we used a linear regression to examine whether mean family survivorship (\% offspring survived) was predictive of mean fry swimming performance (BST\(_M\)).

### Results

#### Developmental temperature effects

The range (2 SD) in length of fry that were swim-tested was 24.9–30.5 mm, while the range in mass was 0.134–0.276 g. Significant differences were found between temperature treatments for mean fry length (12 > 14 > 16 °C) and mass (12 ≈ 14 > 16 °C, Fig. 2). Overall, fry mass and length explained a relatively small amount of the variation in individual fry BST. Individual fry mass explained slightly more of the variation (15.4%) compared to fry length (10.6%) (Fig. 1).

Without adjustment for size, the BST of 3-week-old fry was significantly affected by developmental temperature treatment (ANOVA, \(F_{2,16} = 6.4, n = 858, P < 0.01\), Fig. 3a). Specifically, fry exposed to the 12 °C incubation were able to maintain burst swimming for a longer time (37.4 s ± 13.9 SD) than fry exposed to 14 °C (31.9 s ± 11.9 SD) and 16 °C (32.1 s ± 14.7 SD) prehatch temperatures (Fig. 3a). Among-treatment differences in BST were partly attributable to temperature effects on fry size. When individual BSTs were scaled to account for differences in fry mass, only the 12 and 14 °C treatment means remain significantly different (Fig. 3b). Analysis using length-adjusted BSTs revealed no differences in swim performance between temperature groups (Fig. 3c).

Observations involving physical stimulation or fatiguing fry during swim trials showed that fish incubated at 16 °C performed more poorly (Table 1). A larger proportion of individuals from the 16 °C treatment needed stimulation to promote initial burst swimming (\(\chi^2 = 83.2, n = 858, P < 0.0001\)). Fish from the 16 °C group were less able to burst for a single continuous duration (\(\chi^2 = 24.6, n = 858, P < 0.0001\)), showing a higher occurrence of swim trials during which fry fell back \(\geq 3\) times (\(\chi^2 = 25.3, n = 858, P < 0.0001\)) or fell back \(\geq 5\) times (\(\chi^2 = 29.3, n = 858, P < 0.0001\)). Finally, a greater number of fish from the 16 °C treatment were classified as ‘nonswimmers’ (\(\chi^2 = 78.5, n = 922, P < 0.0001\)), unable to burst swim and hold against the current.

#### Family effects

Fry BST was affected by a significant interaction between incubation temperature and family (ANOVA, \(F_{16,828} = 2.95, n = 858, P < 0.0001\), indicating that the influence of family identity on fry burst swimming time was not consistent between treatments (Fig. 4). This interaction remained significant when BSTs were analysed independent of fry mass and length (ANOVA, \(F_{16,828} = 3.23\) and 3.30, respectively, \(n = 858\), both \(P < 0.0001\)). Fry mass and length were also influenced by significant temperature-by-family interactions.
Within incubation temperature treatments, mean BSTs varied significantly among offspring families (ANOVA, $F_{16,828} = 3.59$ and 4.79, respectively, $n = 858$, both $P < 0.0001$).

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Table 1. Proportion of within-temperature treatment fry that (1) needed physical stimulation to initiate swimming, (2) were able to complete swim trials in one continuous burst or (3) fatigued frequently during swim trial ($\geq 3$ or $\geq 5$ fall-backs). The number of fry from each treatment that were classified as 'nonswimmers' (not included in total $n$) is also indicated (4).

<table>
<thead>
<tr>
<th>Burst swim characteristic</th>
<th>$12^\circ$C ($n = 300$)</th>
<th>$14^\circ$C ($n = 290$)</th>
<th>$16^\circ$C ($n = 270$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1) Stimulation</td>
<td>0.20</td>
<td>0.23</td>
<td>0.47</td>
</tr>
<tr>
<td>(2) One continuous burst</td>
<td>0.40</td>
<td>0.42</td>
<td>0.24</td>
</tr>
<tr>
<td>(3) Fatigue during swim trial</td>
<td>0.27</td>
<td>0.26</td>
<td>0.44</td>
</tr>
<tr>
<td>$\geq 5$ fall backs</td>
<td>0.030</td>
<td>0.0070</td>
<td>0.10</td>
</tr>
<tr>
<td>(4) Nonswimmers</td>
<td>3</td>
<td>6</td>
<td>55</td>
</tr>
</tbody>
</table>

(ANOVA, $F_{16,828} = 3.59$ and 4.79, respectively, $n = 858$, both $P < 0.0001$).

Maternal and paternal influences on fry burst swim performance varied between temperature treatments (Fig. 4). Within the $12^\circ$C treatment, variation in mean family BST was attributable to maternal identity (ANOVA, $F_{4,145} = 8.20$, $n = 150$, $P < 0.0001$) and paternal identity (ANOVA, $F_{4,145} = 7.32$, $n = 150$, $P < 0.0001$). Within the $14^\circ$C treatment, mean BST

Fig. 4. The effects of family identity on the mass-adjusted burst swim times (BST) of 3-week-old fry within pre-hatch incubation temperature treatments. Each box plot represents the distribution of individual fry swim times within a family cross ($n = 30$). Grey boxes show the influence of female spawner identity (females 1–5 crossed to male A) and the white boxes show the influence of male spawner identity (males B–F crossed to female 6). The box displays the interquartile range, the median and mean (bold), and the 10th and 90th percentiles (error bars). The white circles represent individual fish swim times that fall outside of the 10th and 90th percentiles.
only varied among crosses differing in paternal identity (ANOVA, $F_{4,145} = 4.85$, $n = 150$, $P < 0.01$). Within the 16 °C, mean BST only varied among crosses differing in maternal identity (ANOVA, $F_{4,139} = 9.11$, $n = 144$, $P < 0.0001$).

Within the 16 °C incubation treatment group, mean family swim performance was related to mean family survivorship ($R^2 = 0.65$, $n = 10$, $P = 0.005$, Figs 4 and 5). Specifically, families that had a higher percentage of offspring survive from fertilisation to swim test day were characterised by a lower mean BST, whereas families that had a low percentage of offspring survive were capable of higher mean BSTs.

### Discussion

This study provides the first evidence in sockeye salmon that both developmental temperature and individual parentage act together to influence fry swim performance. Exposure to high-temperature stress during embryogenesis resulted in reduced endurance capacity and impaired swimming behaviour in later fry stages. As the posthatch rearing environment for all temperature treatments was controlled at a cool ambient level, we attributed these effects to temperature exposure during embryonic development.

Fig. 5. Linear regression showing only families exposed to the 16 °C incubation temperature treatment. Mean fry burst swim time (mass-adjusted BST ±SE) is shown as a function of mean family survivorship (±SE) Survivorship was measured as the % of offspring surviving from fertilization to 3-week-old fry. The 95% confidence intervals (dotted lines), $R^2$, and $P$-value are also given.

In addition to temperature, and independent of offspring size, both maternal and paternal identity was shown to influence offspring swim performance. However, a strong temperature-by-family interaction indicated that parentally mediated influences are temperature dependent.
Less than 10 studies have examined the effects of developmental temperature on later-stage swimming ability in fish, and these have been limited to marine cold-water species (Batty et al. 1993; Shepherd et al. 2000; Johnston et al. 2001; Green & Fisher 2004; Green & McCormick 2005; Guan et al. 2008; Koumoundouros et al. 2009). In general, these studies have found that differences in the swimming performance between fish from different incubation thermal regimes were primarily the result of temperature effects on muscle physiology and development. Koumoundouros et al. (2009) found that European sea bass (Dicentrarchus labrax) juveniles initially reared at 15 °C exhibited higher maximum aerobic swimming capacities than those initially reared at 20 °C. These authors attributed the increased swimming capacity of the cold-water-reared fish to having a greater relative red muscle area and increased number of red myofibres and mitochondria than that of the warmer-reared fish. In contrast, an experiment with Atlantic herring (Clupea harengus) demonstrated that fish incubated in a colder-temperature regime had reduced maximum velocities during fast-starts than warmer-incubated fish owing to their reduced development of swimming musculature, neural activity and fins (Johnston et al. 2001). In another study on larval herring, Batty et al. (1993) showed rearing temperature had no observable physiological effect on swimming performance, except through its influence on larval size.

Developmental temperature effects

Variation in juvenile salmonid swim performance has been shown to relate to body length and mass (Bams 1967; Taylor & McPhail 1985a,b; McDonald et al. 1998). However, in studies using sockeye salmon fry, there is evidence of both a strong relationship (Bams 1967) and no existing relationship (Pon et al. 2007; Nadeau et al. 2009) between body size and individual swim performance. In the present study, differences in the average fry BST between thermal treatment groups were partly explained by the effects of incubation temperature on fry size; elevated incubation treatments produced smaller fry (Beacham & Murray 1990; Kamler 2008). Consistent with findings from Bams (1967), significant differences in average fry length (12 > 14 > 16 °C) explained treatment-level differences in average swimming endurance. Nevertheless, at the individual level, fry length did not explain a large amount of variation in BST (10%), and fry mass was only slightly better (15%). When mass-adjusted BSTs were analysed, the 12 °C treated fish still swam better on average than the 14 °C group, suggesting that other inherent treatment-level effects on swim performance may be present. Overall, these results suggest that temperature plays an important role in determining average fry size and subsequent average swimming performance; however, the considerable individual variation in fry swim performance is only marginally related to individual differences in size.

Perhaps more significant than differences in total BST is the observation that when eggs were exposed to 16 °C prehatch temperatures, the resulting fry were less willing to initiate swimming and fatigued more frequently during their bursting episodes. These findings correspond with those from a study on hatching lizards (Podarcis muralis) in which individuals exposed to a stressful incubation temperature showed a more disjointed running pattern (high frequency of stops) during locomotor trials (Brana & Ji 2000). The observed differences in 16 °C exposed fish would not appear to be advantageous considering that swimming stamina and initial burst responses have been emphasised as critical swimming characteristics for predator avoidance in emergent sockeye salmon (Bams 1967). Similarly, Tierney et al. (2009) suggested that a reduced stimulus response and higher rate of fatiguing in sockeye parr were associated with poor schooling behaviour and could lead to decreased survivorship. Altogether, the reduced mass, length, BST and swimming motivation of individuals from the high-temperature exposure suggest that ecologically relevant shifts in fry fitness may result from deviations in incubation temperature above optimum.

Given that eggs in this study were incubated at temperatures approaching the upper limit of viability for embryonic development (McCullough et al. 2001), it is possible that temperature-related influences on fry swim performance were affected by selective mortality. Overall, between fertilisation and the swim test date, fish exposed to the 16 °C treatment experienced just more than 50% mortality (largely during embryogenesis), whereas fish incubated at 14 and 12 °C lost only 19% and 6%, respectively. With the possibility that surviving fish incubated at 14 and 16 °C were physiologically different to the ones that perished, conducting swim trails on these ‘survivors’ may have reduced our capacity to find even greater differences in swim performance between temperature treatments.

Family effects

Along with incubation temperature, offspring parentage had a strong effect on fry swimming ability. Within all three temperature treatments, the family with the highest mean BST was able to swim almost twice as long (1.7 times) as the family with the lowest mean swim time. Family-level differences in salmonid swim performance have only been detected in two previous studies, neither of which examined a measure of sprint/burst swimming capacity. Rossignol et al.
(2010) found that maternal and paternal identity influenced spontaneous activity (transiting from one location to another) in Atlantic salmon (*Salmo salar*), whereas Tierney et al. (2009) demonstrated sockeye parr from moribund females had reduced schooling behaviour and startle responses and fatigued more easily than offspring from spawn-ready females. Parental influences on swim performance have been detected in a limited number of studies on nonsalmonid fish (Garenc et al. 1998; Green & McCormick 2005), but overall the capacity for parentage to shape offspring performance traits is not commonly assessed (Burt et al. 2011).

Our finding that offspring families vary in their burst swim performance corresponds well with previous work on emergent and juvenile sockeye salmon. Examining the same population of Weaver Creek sockeye used for this study, Patterson et al. (2004) found significant among-family differences in the mass-specific and protein-specific levels of several enzymes, including lactate dehydrogenase (LDH), in unfed emergent fry. LDH is a critical component in the glycolytic pathways involved in sprint or burst swimming and is a frequently examined biochemical correlate of burst swim performance (Kolok 1992; Garenc et al. 1998; Gibb & Dickson 2002). Interestingly, Nadeau et al. (2009) were unable to detect maternal influences on the burst swim endurance of 4-month-old sockeye fry from the Weaver Creek population. Together with our findings, this supports the notion that parentally mediated variation in swimming capacity is considerable following emergence but fades with further feeding and growth (Garenc et al. 1998).

**Temperature–family interactions**

Our results demonstrate that embryonic incubation temperature interacts with family identity to influence fry swim performance. The dependence of parentally mediated variation on incubation temperature has been observed for a number of other life history traits (e.g., size, development rate, metabolic fingerprints, sex ratios, stress response) that are characterised by significant temperature-by-family interactions (Burt et al. 2011). Of particular interest is the variation we observed at both 12 and 16 °C. Incubation at a constant 12 °C is arguably warmer than what eggs would experience in the wild; however, this treatment is within the optimal range for development and was characterised in this experiment by very high survival. Our finding that both female and male parental identity contributed to similar levels of variation in BST within this treatment, independent of size effects, suggests that genetic factors may be important determinants of offspring performance under regular incubation conditions in the wild.

Interestingly, within the 16 °C treatment, there was a negative relationship between the thermotolerance of families (based on survivorship) and their average burst swimming capacity. One possible explanation for this relationship may be that selection occurring within families during incubation favoured individuals that were physiologically superior (better burst swimmers), which resulted in higher average swim times for the families that experienced higher mortality. This has been shown in studies on birds and insects where directional selection imposed by stressful conditions resulted in a shift in the mean value of certain morphological traits (Brown & Brown 1998; Hoffmann & Hercus 2000). An alternative explanation is that the negative relationship between family survivorship and BST could reflect a trade-off between physiological or genotypic traits that confer stress resistance and those that affect performance (Hoffmann & Parsons 1991). Selection experiments in plants and invertebrates have shown that genotypes selected for stress resistance exhibit trade-offs with other fitness-related traits (e.g., growth rate, metabolic rate – Hoffmann & Parsons 1989, 1991). In this study, a potential trade-off between surviving thermal stress and endurance capacity remains unclear and will require further research on the physiological mechanisms associated with thermotolerance in developing fish.

Collectively, our findings demonstrate for the first time that both developmental temperature stress and parental identity can shape the burst swimming performance of sockeye salmon offspring. Burst swimming performance has shown to be related to predator evasion in salmonids (Bams 1967; Taylor & McPhail 1985b) and therefore may be an important determinant of survival and fitness in sockeye salmon fry during the lake-rearing stages of their life history. This study provided evidence that exposure to high temperatures in early salmon development can result in persistent, parentally mediated effects on performance. As such, scientists and managers should have an increased awareness of the possibility that thermal stress events may have population effects in life stages beyond when the stressor is experienced. The exposure of developing eggs to temperature stress will become an increasingly important concern in the context of climate change and human developments that impact salmonid incubation thermal regimes. However, it is important to consider that this research focuses on only one performance component among a myriad of early life history factors (e.g., population density; Einum et al. 2008) that likely influence salmonid population dynamics. To build upon our findings, future studies may benefit from taking a quantitative genetics approach. This would enable researchers to partition swim performance variation
into environmental, genetic and nongenetic effects and demonstrate whether the expression of genetic variation shifts under favourable versus unfavourable incubation conditions.

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