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ORIGINAL PAPER

Swimming performance and morphology of juvenile sockeye salmon, *Oncorhynchus nerka*: comparison of inlet and outlet fry populations

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Abstract We raised two populations of sockeye salmon fry from fertilized eggs in the laboratory and tested the hypothesis that outlet fry populations, fish which must migrate upstream to reach rearing lakes after yolk-sac absorption, have better swimming ability and morphological characteristics conducive to enhanced swimming performance than inlet fry populations, fish which migrate downstream to rearing lakes. Despite being of identical age, fry from the outlet population were larger (approx. 6.7% longer, ~5 mm on average) and more laterally compressed than inlet fry at the time of our initial experiments. Using an open-top box flume, we found that the burst-swimming performance (in cm s^{-1}) of the outlet population was 31% better. We found no differences between populations in prolonged-swimming performance. We were unable to find any direct relationships between measures of swimming performance and size or shape variables, suggesting that the larger, more robust morphology of outlet fry was not responsible for the superior burst ability. Recent biochemical studies indicate outlet fry may be metabolically better provisioned for burst swimming than inlet fry. It is possible that the morphological differences between the populations of fry reflect adaptations needed by adults during their migration and spawning.

Keywords *Onchorhynchus nerka* · Morphology · Burst-swimming ability · Intra-specific variation · Local adaptation

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Introduction

Adult Pacific salmon, *Oncorhynchus* spp., return to natal streams to spawn (Quinn 1984; Quinn and Dittman 1990). During the spawning migration, some populations encounter unique environmental conditions that can serve as strong selective forces shaping inter-population differences in body morphology, fecundity, bioenergetics, and

swimming performance. For example, adults from populations with long-distance (e.g. >500 km) upriver migrations to spawning grounds start their migration with relatively higher somatic energy levels than those with short distances to traverse (Hendry and Berg 1999; Crossin et al. 2003, 2004). The former also are more energetically efficient in their swimming performance (Bernatchez and Dodson 1987; Lee et al. 2003a, b); this may be partly because their bodies are smaller and more streamlined than those of short-distance migrants (Taylor and McPhail (1985a, b; Moore 1996; Crossin et al. 2003, 2004).

Such ''energy-conserving'' morphological characteristics seem to come at a cost to reproductive fitness, however, because larger adult salmon produce more eggs and/or larger eggs than smaller salmon (Sargent et al. 1987; van den Berghe and Gross 1989; Kaeriyama et al. 1995). Indeed, fecundity and ovarian mass are usually lower for long-distance migrants (Beacham and Murray 1993; Linley 1993; Kinnison et al. 2001; Crossin et al. 2004). Spawning locale fidelity, with geographic and temporal (i.e. spawning-time) isolation, probably help to maintain these population-specific characteristics (Ricker 1972; Groot and Margolis 1991; Taylor 1991). Although much research has been conducted on the roles migration conditions can have on adult Pacific salmon body morphology and swimming performance, there are other life stages that involve energy-demanding and arduous migrations for which we know very little about how natural selection may have shaped morphology and swimming behaviour.

Juvenile Pacific salmon spend up to 2 years developing in freshwater environments (Groot and Margolis 1991) and all engage in migratory behaviour to different extents. Juvenile sockeye salmon, *O. nerka*, are noted for their migrations from natal streams to lakes in which they develop for 1–2 years (Burgner 1991). Most populations of sockeye salmon use lakes as nursery areas where fry grow rapidly, attaining sizes and energy reserves enabling them to smolt and survive a migration to ocean areas where development continues (Hinch et al. 2005). Sockeye fry are the dominant juvenile Pacific salmonid in these lakes and inter-specific competition for food is thought to be relatively low (Burgner 1991). Pronounced diel, vertical migration of fry in their pelagic feeding zones, which greatly reduces contact with predators, is also observed (Burgner 1991). Lakes are, therefore, an ideal environment for fry, in which both survival and growth rates are high. Accessing lakes is therefore an important and critical aspect of their life-history.

This ''lakeward'' migration behaviour provides opportunities for selection to act on juvenile sockeye salmon in a population-specific fashion, because rearing lakes may be located at very different distances and in different directions relative to river flow (i.e. upstream versus downstream) from natal streams (Hinch et al. 2005). Many inlet (fry that migrate downstream to lakes) and outlet (fry that migrate upstream) populations must travel several kilometres to reach rearing lakes (Burgner 1991). Migrations occur in spring when most large rivers are approaching freshet and discharge is near maximum. Local adaptation to the stock-specific migratory demands of outlet fry may be manifested as differences between morphological, swimming performance, or other behavioural traits among populations. A recent biochemical evaluation of emergent sockeye fry has identified differences between the activity of key enzymes associated with swimming performance in populations of inlet and outlet sockeye salmon (Patterson et al. 2004). Outlet fry had higher levels of the glycolytic enzyme lactate dehydrogenase relative to citrate synthase and cytochrome *c* oxidase levels, indicating they were better provisioned to engage in anaerobic activity. Outlet fry also had higher levels of oxidative enzymes, indicating greater aerobic capacity (Patterson et al. 2004). These findings suggest that outlet fry may be physiologically better provisioned than inlet fry for both burst and stamina swimming, traits which would clearly be adaptive for the upstream migration that outlet fry must undertake. There have, however, been no specific studies of swimming performance of inlet and outlet populations in sockeye salmon.

Variation in the swimming performance of juvenile Pacific salmon is related to differences between body size and shape. Larger fish are usually able to achieve faster speeds (Thomas and

Donahoo 1977; Hawkins and Quinn 1996), and deeper bodies are associated with greater burst-swimming performance (Weihs 1973; Webb 1978). Taylor and McPhail (1985a, b) observed that coho salmon, *O. kisutch*, fry with relatively large fins and deep bodies had better burst-swimming abilities than fry that were more fusiform. The latter had superior stamina swimming abilities. The authors speculated that these morphological and performance differences reflected population-specific adaptations. Specifically, the larger finned, deeper bodied fish were from coastal populations which were thought to experience higher levels of predation thus better burst abilities could be an adaptive trait for enhancing survival. Fusiform-shaped fish were from interior populations, distant from the ocean, and, although it was unclear how better stamina was an adaptation for these fry, it may be linked in an ''adaptive way'' to the morphology of the adults. Interior adult salmon have a very fusiform shape compared with coastal salmon, a trait which enhances swimming performance and conserves energy during adult migrations from the ocean to distant spawning grounds (Crossin et al. 2003, 2004).

There is, therefore, evidence that differences between swimming performance among populations of juvenile Pacific salmon may reflect physiological and morphological adaptations to local environmental conditions. In this study we examined one aspect of this issue for populations which undertake very different juvenile migrations. Specifically, we experimentally assessed swimming performance of inlet and outlet populations of sockeye salmon emergent fry from the Weaver Creek and Adams River populations and related performance to their morphology. To control for local environmental variation that may affect embryo and fry morphological development, we artificially fertilized eggs and raised embryos and fry under the same laboratory conditions before conducting swimming performance experiments. Emergent fry from these populations must swim upstream and downstream, respectively, for several kilometres in relatively large river systems (up to 1 km wide) to reach rearing lakes. Adults from these populations spawn at approximately the same time in the fall each year and fry undertake migrations in spring. On the basis of the biochemical findings of Patterson et al. (2004), and the fact that fry encounter rivers near the time they are reaching maximum discharge (i.e. spring freshet), we predict that burst and stamina-swimming performance of outlet fry will be greater than for inlet fry. We also predict that outlet fry will be characterized by larger and more robust morphology, which would facilitate better swimming performance, in particular, better burst-swimming ability (Taylor and McPhail 1985a, b).

Materials and methods

Study animals

Juvenile sockeye salmon from Weaver Creek (outlet fry) and Adams River (inlet fry) populations were used for all comparisons in this study. Both are large, wild sockeye populations within the Fraser River watershed in southwest British Columbia (Fig. 1). Adults from these populations spawn in October and emergent fry undertake their migrations from March to May each year. Beginning in March and continuing for 6–8 weeks each year, emergent Weaver Creek fry migrate 3 km downstream to the confluence with the Harrison River, and then migrate 5 km up the Harrison River to rearing grounds in Harrison Lake (David Patterson, Fisheries and Oceans Canada, personal communication). The segment of the Harrison River where fry migrate upstream ranges from 0.1 to 1.0 km wide. Because peak discharges occur between mid-May and June in the Harrison River, fry migrations are initiated immediately before freshet and continue as discharge is increasing toward its maximum. The segment of the Adams River where fry migrate downstream to their rearing lake is ~12 km long with river characteristics similar to that of the Harrison River. Peak discharges occur in June. Fry downstream migration begins in April and continues for 6–8 weeks each year (David Patterson, Fisheries and Oceans Canada, personal communication). Compared with fry migration, the opposite level of migration ''difficulty'' is experienced by adults of these two populations. Adult Weaver Creek sockeye are faced with a

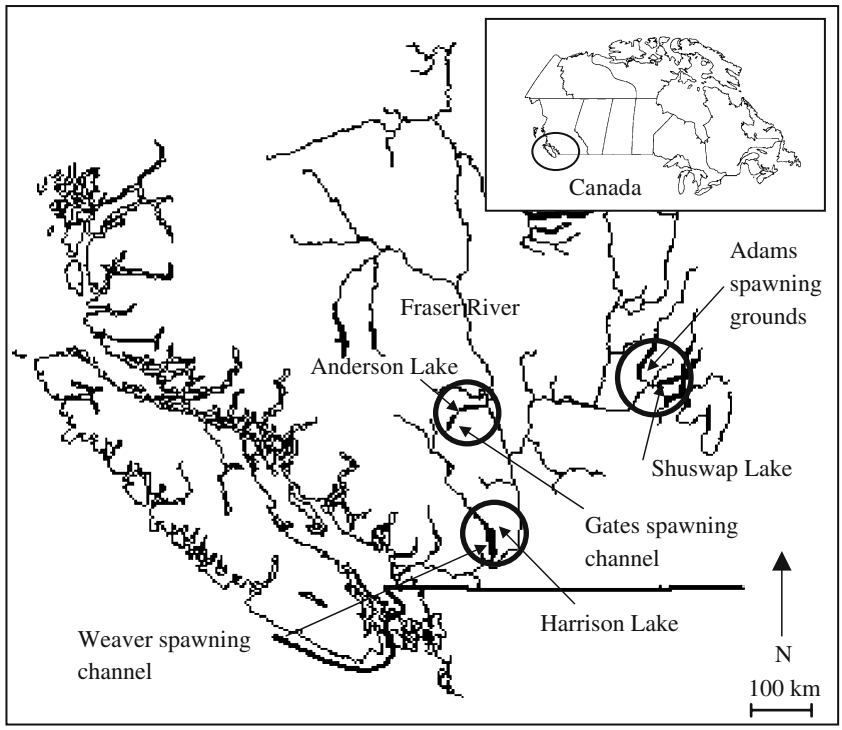


Fig. 1 Map of the Fraser River watershed, British Columbia. *Bold circles* show locations of the spawning grounds relative to the rearing lakes for the Weaver and Adams sockeye populations. The Patterson et al. (2004) study examined Gates Creek sockeye fry instead of Adams fry as their inlet population. The locations of the spawning and rearing areas of the Gates population are shown

relatively short and low-gradient freshwater migration from the ocean to their spawning grounds (distance 161 km, elevation 10 m), whereas Adams River adults encounter a much longer and more difficult migration (distance 484 km, elevation 366 m) including passage through several fast-water canyons in the Fraser and Thompson Rivers (Crossin et al. 2004).

The juveniles used in this study were reared from wild adults (10 males and 10 females from each stock) that had arrived at spawning grounds in 2003. Eggs from both populations were fertilized in the laboratory and embryos were incubated in heath trays (Alcan Aquatic Facility, Simon Fraser University, Burnaby, BC, Canada). Fry were transferred to, and raised in, 200-L oval tanks (Faculty of Forestry, The University of British Columbia (UBC), Vancouver, BC, Canada) during the summer of 2004. Fish were raised under conditions of similar within-tank densities, with minimal currents and constant water circulation for approximately 2 months. During this period fish were fed ad libitum. As fish grew, it became clear there was a divergence in average sizes with Weaver fish becoming larger than Adams fish despite being almost the same age. Before each swimming-performance trial, a subset of approximately 40 fish from each stock were randomly selected from the laboratory populations and transferred to a partitioned section of a large oval tank (partition size: 180 cm length×25 cm width×30 cm depth) to become acclimated to a slow current (<5 cm s^{-1}). Care was taken to ensure a consistent velocity throughout the partitions, and all fish seemed to actively orient into, and swim against, the current. Each fish was held in the acclimation tank for 50–60 h immediately before swimming-performance trials. In the absence of this step, fish were unable to properly orient into currents at the test velocities used. During the final 24 h before a trial fish were fed approximately half normal rations.

Experimental procedures

Swimming-performance experiments were conducted in an open-top, rectangular flume; the dimensions of the swimming area were 100 cm length×17 cm width×4 cm depth. Mesh grates (mesh size 2 mm) were placed at the front and

rear to keep fish within a discrete area and to help maintain laminar flow. Two additional honeycomb flow straighteners were positioned at the inflow end to ensure consistent flow patterns throughout the swimming area. Water was supplied from a continuously refreshed, elevated reservoir and was controlled by a hand-operated valve to maintain the desired velocities. Flow velocities were calculated by timing a round foam pellet as it travelled a known distance. Positioned above the swimming area of the flume was a wide-angle lens video camera (Panasonic WV-BP312) connected to a time lapse VCR (Panasonic AG-6124) capable of recording images at 60 frames per second. All experimental trials were conducted under controlled laboratory conditions.

We assessed two types of swimming ability, burst and prolonged swimming. Burst swimming is typically defined as the maximum speed the fish can sustain for less than 20 s (Beamish 1978; Kolok 1999). Such swim speeds predominantly involve use of anaerobic metabolism and result in large oxygen debts if their use is continuous (Hinch et al. 2005). Sockeye juveniles seem to begin accumulating oxygen debt at flow speeds in excess of four body lengths per second (BL s^{-1}) and reach maximum exertion at 10 BL s^{-1} (Brett 1964). For the burst-swimming experiment, a constant water velocity of 67 cm s^{-1} was used to test all fish. Preliminary results suggested that this velocity caused exhaustion within approximately 30 s for most individuals. Randomly drawing from the acclimatized fish, 30 individuals were tested from each stock, one at a time, and alternating between stocks. Fish were placed at a position 30 cm downstream of the top of the swim flume, approximately halfway between the two sides. Preliminary trials indicated that fish with sufficient pre-trial exposure to current would immediately begin burst swimming up to, and subsequently against, the forward mesh grate. Fish were left swimming until they were deemed to be fatigued, at which point they were removed. Fatigue was defined as a decrease in swimming speed that resulted in the fish dropping back past a preset location in the flume (30 cm from the top). Individuals were tested once only, and after removal from the swim flume were immediately and swiftly killed by cerebral percussion in preparation for subsequent measurements. All burst swimming experiments were conducted over a two-day period (29 August and 1 September 2004), with consistent water temperatures between 16.5 and 17°C. This was the same as the temperature of the water in which the fish had been reared for approximately a month before the trials and was the temperature of the reservoir water supply at that time of year. Swimming times to fatigue were assessed to the nearest 1/60th of a second with frame-by-frame playback of the recordings. All fish used in this experiment were randomly selected from our laboratory population.

Prolonged swimming speeds have been defined as those that fish can maintain for more than 20 s but less than 200 min (Beamish 1978), and reflect a measure of the fish's swimming stamina. This type of swimming usually involves both aerobic and anaerobic metabolism (Hinch et al. 2005). For the prolonged swimming trials, fish were tested in the same flume, although it was divided in half lengthwise to accommodate two fish swimming at the same time. This modification, with smaller sample sizes than for the burst-swimming experiment, was necessary to ensure that adequate numbers of fish could be tested in as short a time as possible. Drawing from a new set of fish (n=40 from each stock) that had been acclimatized to a current as described above, 20 fish from each stock were tested. Fish were tested two at a time (one from each stock), and were alternately introduced to either side of the flume divider under a nominal current. Over a 2 min period, current velocity was gradually increased by preset increments of approximately 10 cm s^{-1} every 30 s until the desired test flow velocity (42 cm s^{-1}) was obtained. This velocity was determined by pre-experiment trials as one that would typically induce fatigue in fish within a 2.5 to 15-min period, a time interval we chose that enabled all fish to be tested within a relatively short time yet would still reflect some element of swimming stamina. Fish were tested until they fatigued, which was defined by a lack of swimming response to five gentle prods with a blunt probe. After each prolonged swim test, fish were immediately killed in preparation for subsequent measurements.

Prolonged swimming trials were conducted over a two-day period (25 and 26 September 2004) at the same time each day (from 10:00 to 16:00). Water temperature was consistently between 14 and 14.5°C during prolonged swimming trials, which again was the local reservoir temperature. Because of innately faster growth rates, by the time prolonged experiments were undertaken (three weeks after the burst experiments) the largest Weaver fish (25% of the population) were too large for use in the divided swim flume (~1 cm too long). We therefore randomly selected Weaver fish from the remaining 75% of the population (n=300). To help address the issue of our ''size-selection'' we compared prolonged swimming speeds between populations using results from selected fish that reflect the population-specific size differences. These details are provided below. For both the burst and prolonged swim tests, performance measures were recorded in units of time and subsequently transformed to units of distance.

Morphological measures

Immediately after the experimental trials, several morphological measurements were made on each fish using Vernier callipers accurate to 0.1 mm (Fig. 2). Length was assessed as fork length (FL) and as post-orbital-hypural (POH) length. Pectoral fin (PEC) length (left fin only) was assessed from the forward point at which the fin connected to the body to the furthest point along the rear edge of the fin. Length of the caudal fin was assessed on both the upper and lower segments (CAUD1 and CAUD2, respectively). Caudal measures were taken from the origin of the fin to the furthest edge. Body depth was measured at two points—the distance between the origins of the dorsal and pelvic fins (DORPEL) and the distance between the origins of the adipose and anal fins (ADAN). Wet mass was measured to the nearest 0.01 g by use of a digital scale. Because the two swimming tests were conducted nearly a month apart, and fish were growing rapidly in the interim, morphological measures were made on both populations at both times specific to when swimming tests were occurring.

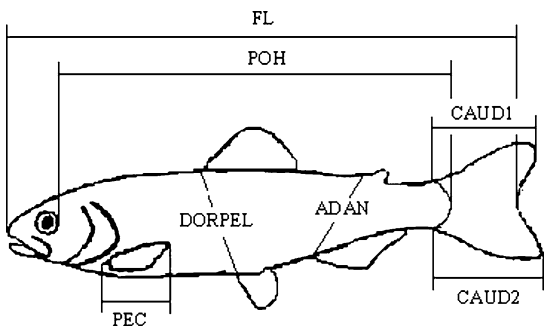


Fig. 2 Details of the morphological measurements made on all juvenile sockeye used in both the burst-swim and prolonged-swim experiments. *DORPEL* and *ADAN* are measures of body depth and *PEC*, *CAUD1*, and *CAUD2* are measures of fin length. Additional details are provided in the text

Statistical analysis

Individual fish that were deemed from the video replay to have exploited areas of low flow velocity (e.g. against the walls of the flume), were considered outliers and not included in statistical analyses. For all variables, normality was assessed by use of the Shapiro–Wilk test and equality of variance by use of Bartlett's test. Variables were log-transformed if either normality or equality of variance assumptions were not met. We did not test for multivariate normality but assumed this criterion was met if individual variables used in multivariate analyses met the equivalent univariate criterion. All analyses in this study were conducted using JMP-IN v.4.0.4 (SAS Institute, 2001). All results in this study were assessed for significance at α=0.05.

To address the prediction that outlet fry have better swimming abilities than inlet fry, we conducted two sample t-tests to compare burst and prolonged-swimming performance between the populations. We also used two sample t-tests to contrast lengths and mass of fish between groups used in these trials. Because the largest Weaver fry in the population could not be used in the prolonged swimming experiment, the average size difference between the populations that became evident as the fish grew (Weaver were ~6.5% longer in the burst experiment) was not present in the fish used in the prolonged-swimming experiment. We therefore conducted

an additional *t*-test to compare prolonged swimming measures from a subset of our fish from the two populations using fish that reflected average relative differences in the size of these two groups (i.e. we used the largest Weaver fry and the smallest Adams fry).

To address the prediction that outlet fry have larger and more robust morphologies than inlet fry, we first used principle components analysis (PCA) on the covariance matrix of log-transformed morphological variables to generate a small set of new multi-dimensional variables reflecting among-individual variability in body size and shape. Structure coefficients and their associated probabilities (correlations between the PC axes and the original morphological variables) were calculated with Pearson correlations. Separate PCAs were conducted for fish used in each of the two experiments. We then assessed morphometric differences between populations along the first two PC axes, which normally explains among-individual variability in size (PC-1) and shape (PC-2), respectively (Pimental 1979), using two sample *t*-tests.

To quantify the strength of associations among fish size, shape, and swimming performance, we conducted two further sets of analyses. First, we tested for differences between populations with regard to specific morphometric and swimming performance variables using multivariate analysis of variance (MANOVA). Specifically, MANOVA was used to identify whether populations differed with regard to the variables:

- PC-1 and burst-swimming performance,
- PC-2 and burst-swimming performance,
- PC-1 and prolonged-swimming performance, and
- PC-2 and prolonged-swimming performance.

If MANOVA identified a difference, we used canonical variate analysis (CVA), which generates a vector maximally separating the two group's centroids in multivariate space (Reyment et al. 1984), to characterize the relative contributions of the morphometric and swimming-performance variables to differentiating the populations. The magnitude and sign of the canonical variate (CV) coefficients provides this insight. Second, we used Pearson correlations to examine the general relationships between fry morphometric variation (as summarized by the PC axes) and measures of swimming performance.

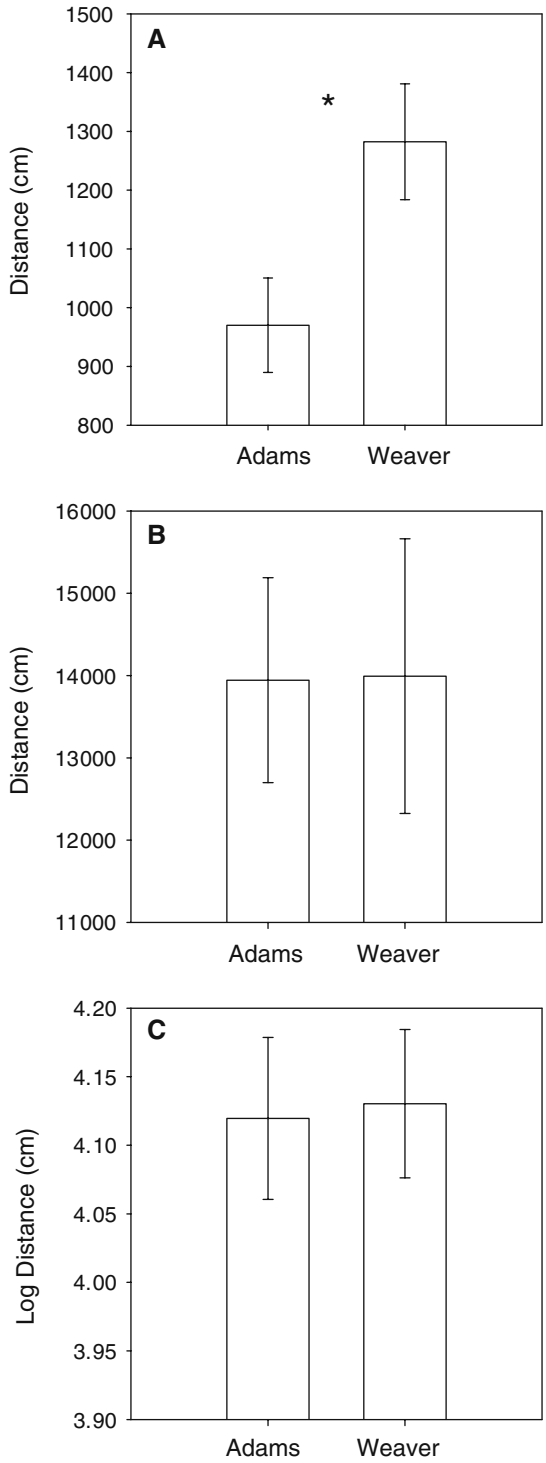
Results

Although swim-performance variables met the assumptions of normality and equality of variance, morphological and mass variables did not and were therefore log-transformed. Weaver fry (n=30) had greater burst-swimming performance than Adams fry (n=29) (t_{57}=–2.447, P=0.017; Fig. 3A). In burst-swimming trials, Weaver fry (n=30) were longer than Adams fry (n=29) ($\bar{x}\pm SE$; 79.8±0.96 mm and 74.6±0.92 mm, respectively; t_{57}=–3.918, $P<0.001$), despite being of equal age and having been reared under identical conditions. The same Weaver fry also had greater mass than Adams fry ($\bar{x}\pm SE$; 6.37±0.25 g, 4.66±0.19 g, respectively; t_{57}=–5.850, $P<0.001$).

Adams (n=17) and Weaver (n=15) fry did not differ in prolonged-swimming performance (t_{30}=–0.023, P=0.9814; Fig. 3B). Because the sample sizes were approximately one half those used in the burst experiment, we conducted a power analysis in accordance with methods in Winer (1971) to determine how doubling sample size (n=30 in both groups) would affect statistical power. On the basis of the effect size and variance observed, power would increase by 0.001, a relatively negligible amount. Our laboratory rearing observations revealed Weaver fry have faster innate growth rates, but because we excluded the largest Weaver fish from the prolonged experiment, because of flume limitations, we observed no difference in average length between the two groups of fish used in the prolonged-swim experiment (Weaver: $\bar{x}\pm SE$; 81.3±1.10 mm, Adams: $\bar{x}\pm SE$; 82.5±0.72 mm; t_{30}=–0.187, P=0.853). Nonetheless, Weaver fry in this experiment had greater mass than Adams fry ($\bar{x}\pm SE$; 7.78±0.31 g, 6.56±0.21 g, respectively; t_{57}=–3.087, P=0.004).

To examine prolonged-swimming performance in a manner which more accurately reflected

average inter-population differences in length for this particular age of fry, we selected the largest 50% of Weaver fry (n=8) and the smallest 50% of Adams fry (n=8) for a subsequent analysis. With this contrast, Weaver fry were indeed larger than Adams fry ($\bar{x}\pm SE$; 85.5±0.68 mm, 79.9±0.89 mm, respectively; t_{14}=–4.978, $P<0.001$)—a difference, on average, of 6.75% in length, which was identical with that observed between groups of fish used in the burst swimming experiment. Weaver fry also had significantly greater mass than Adams fry ($\bar{x}\pm SE$; 8.54±0.23 g, 5.99±0.27 g, respectively; t_{14}=–6.431, $P<0.001$). Using this subset of fish, we found no difference between the prolonged-swimming performances of the two populations (t_{14}=–0.134, P=0.896) (Fig. 3C). Because the sample sizes were relatively small, we conducted a power analysis in accordance with methods in Winer (1971) to determine how sample sizes similar to those we used in the burst experiment (n=30 in both groups) would affect statistical power. On the basis of the effect size and variance observed, power would increase by 0.012 only.



PCA on morphological measures from the fish used in the burst-swimming experiment (total n=59) summarized 90% of the variation in the first principle component (termed $PC1_{burst}$; Table 1). All morphological measures contributed positively and significantly to $PC1_{burst}$ indicating that this axis represented a general size trend. $PC2_{burst}$ accounted for 5% of the total variation and reflected a trend in body depth and caudal fin length. Populations differed along $PC1_{burst}$ (t_{57}= –4.961, $P<0.001$) and $PC2_{burst}$ (t_{57}=4.117, $P<0.001$), indicating that Weaver fry were larger with deeper bodies and longer caudal fins than Adams fry (Fig. 4).

PCA of morphological measures from the fish used in the prolonged swimming experiment (total n=32) summarized 77% of the variation in the first component (termed $PC1_{prolonged}$; Table 1). All morphological measures contributed positively and significantly to $PC1_{prolonged}$ indicating this axis represented a general size trend,

◀ **Fig. 3** Mean (±1 SE) distance travelled for Adams and Weaver fry for: burst-swimming performance (**A**), prolonged-swimming performance with all data (**B**), prolonged-swimming performance with largest 50% of Weaver fry and smallest 50% of Adams fry (**C**). The *asterisk* (*) indicates a significant difference

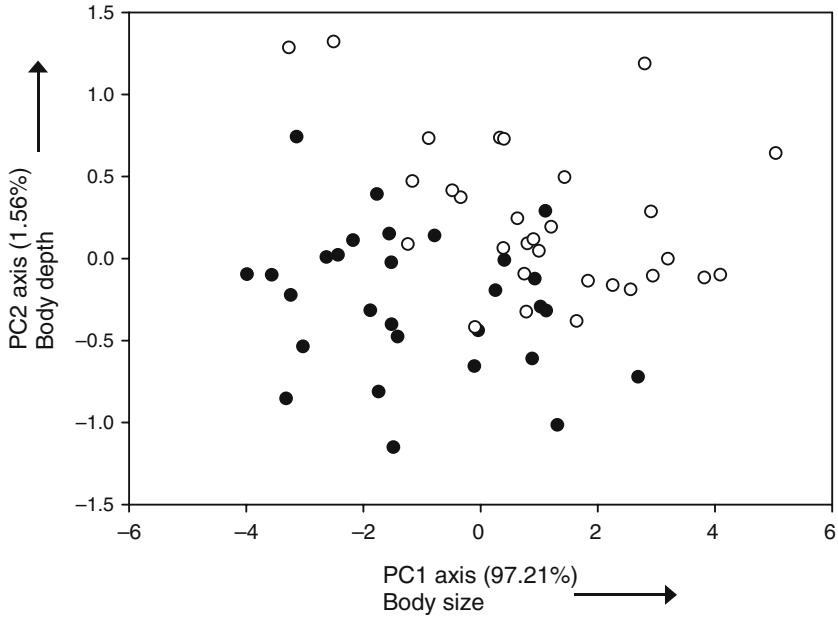


Fig. 4 PC1 scores versus PC2 scores from PCA of morphological data from fry used in the burst-swimming performance experiment. PC1 represents a gradient of increasing body size and PC2 represents a gradient of increasing body depth and decreasing caudal fin size. See Table 1 for specific details. Axis descriptions include the amount of variation (%) accounted for by each principle component. *Black dots* represent Adams fish, *open dots* represent Weaver fish

although less variation was explained than that from $PC1_{burst}$, probably because of the more restrictive size range used for Weaver fish in the prolonged swimming experiment. $PC2_{prolonged}$ accounted for 9% of the variation in the morphological dataset, and primarily explained variation among fish in body depth and pectoral fin length (Table 1). Populations differed along $PC1_{prolonged}$ (t_{30}=–2.127, P=0.042), despite the use of selectively smaller Weaver fish; populations also differed along $PC2_{prolonged}$ (t_{30}=3.139, $P < 0.004$) with Weaver fry being deeper-bodied than Adams fry.

Most of the MANOVAs identified differences between populations in terms of the specific morphometric swimming-performance variable combinations (Table 2). The vector coefficients from the canonical variates analyses always indicated that the dominant factor differentiating populations was morphometric variability, however. Variability in swimming performance was a relatively minor contributor. We found

Table 1 Pearson correlations (r) and associated probabilities (P) between the original variables and the retained PC axes, for analysis of fish used in burst (n=59) and prolonged (n=32) swimming trials, are presented to assign descriptions to PC axes

Body measure	Burst				Prolonged			
	PC1		PC2		PC1		PC2	
r	*P*	*r*	*P*	*r*	*P*	*r*	*P*	
FL	0.97	**< 0.001**	0.09	0.496	0.84	**< 0.001**	0.15	0.407
DORPEL	0.96	**< 0.001**	–0.27	**0.036**	0.90	**< 0.001**	–0.35	**0.048**
ADAN	0.98	**< 0.001**	–0.10	0.432	0.87	**< 0.001**	–0.13	0.473
PEC	0.93	**< 0.001**	0.21	0.104	0.86	**< 0.001**	0.37	**0.035**
CAUD1	0.93	**< 0.001**	0.30	**0.022**	0.80	**< 0.001**	0.28	0.115
CAUD2	0.94	**< 0.001**	0.28	**0.035**	0.91	**< 0.001**	0.20	0.261
% Variation explained	90.89		5.15		76.62		8.73	

FL represents fork length, DORPEL and ADAN are measures of body depth, and PEC, CAUD1, and CAUD2 are measures of fin lengths. See Fig. 2 for details. Variation explained by each PC axis is presented and correlations significant at $P \leq 0.05$ are given in bold

Table 2 Levels of significance, associated *F* values, and degrees of freedom (*df*) for four MANOVAs examining specific contrasts of swim performance (burst or prolonged swimming) and morphometric descriptor variables ($PC1_{burst}$, $PC2_{burst}$, $PC1_{prolonged}$, $PC2_{prolonged}$) between Weaver and Adams fish

Variables used in MANOVA	*df*	*F*	*P*	CV coefficients
Burst and $PC1_{burst}$	2,56	16.3	<0.001	Burst (0.009), $PC1_{burst}$ (0.652)
Burst and $PC2_{burst}$	2,56	14	<0.001	Burst (–0.012), $PC2_{burst}$ (2.604)
Prolonged and $PC1_{prolonged}$	2,29	2.19	0.13	NA
Prolonged and $PC2_{prolonged}$	2,29	4.79	0.016	Prolonged (<0.001), $PC2_{prolonged}$ (4.053)

Also presented are the coefficients of the canonical variates (CV) axis, which describes the relative contribution of each variable to inter-population differences. NA, not appropriate

no general correlations between swimming performance measures and PC axes: burst swimming versus $PC1_{burst}$ (r=0.093, P=0.485, n=59), burst swimming versus $PC2_{burst}$ (r=0.028, P=0.834, n=59), prolonged swimming versus $PC1_{prolonged}$ (r=0.054, P=0.771, n=32), prolonged swimming versus $PC2_{prolonged}$ (r=–0.069, P=0.707, n=32).

Discussion

Our results supported one of our main predictions—that fry from the outlet population (Weaver) would have better burst-swimming performance than those from the inlet population (Adams), and the former would develop a larger and more robust morphology. Although the differences we identified in body size and shape between populations were consistent with our prediction, the roles that size and shape play in causing the observed differences in burst performance were not clear. During the burst experiment, Weaver fry were 6.7% longer (approx. 5 mm on average) and their burst performance (in cm s^{-1}) was 31% better than that of Adams fish. When we looked more generally for direct relationships between size or shape variables and burst-swimming performance, we could not find any, however. It is possible that the size and shape of outlet fry did not affect their swimming performance—outlet fry may simply be metabolically better provisioned for burst swimming. A biochemical assessment of muscle enzyme activity in emergent outlet fry found they had greater anaerobic capacity than emergent inlet fry (Patterson et al. 2004). We cannot exclude the possibility that although we could not find a direct morphology–swim performance relationship, the larger and more robust bodies of Weaver fry may facilitate burst swimming in a way that we were unable to measure. It is also possible that population-specific differences in fry body morphology that we uncovered may be related to a subsequent life-stage when these morphological characteristics may be adaptive traits that just happened to be expressed at fry emergence. This issue will be addressed below.

Patterson et al. (2004) found elevated levels of whole-body enzymatic activity of citrate synthase (CS) and cytochrome *c* oxidase (CCO) in emergent fry from an inlet population compared with an outlet population, indicating greater aerobic capacity in the former. This had led us to predict we may find better prolonged-swimming performance in Weaver fry; we did not obtain such a result, however. It is possible that inlet fry had better swimming stamina than outlet fry but we were unable to detect a difference. We used somewhat smaller Weaver individuals in the prolonged swimming experiments, whose average length was the same as that of the Adams fry; we may, therefore, have inadvertently eliminated a small segment of the population with the best stamina. The 75% of the Weaver population we did use did not differ in prolonged performance from the Adams population, however, and, when we ''re-created'' the average size difference between populations by contrasting the largest Weaver fish with the smallest Adams fish, we could find no differences in prolonged performance. Power analysis indicated that even with much larger sample sizes, we would probably not have been able to identify population-specific

differences. It is quite possible that our original prediction may have been incorrect and the lack of difference between populations in prolonged-swimming performance is a real phenomenon. Burst-swimming ability rather than prolonged-swimming ability, may be the most important behaviour enabling inlet fry to reach lakes during high spring flows, so bursting ability may be under relatively strong selection compared with stamina-swimming ability. Interestingly, the differences between the aerobic capacity of inlet and outlet populations reported by Patterson et al. (2004) were, in fact, relatively weak compared with their findings for anaerobic capacity (i.e. LDH). It is possible that greater aerobic capacity identified by Patterson et al. for their inlet population may generate benefits for other life stages, which we did not study.

We swim-tested our fish a few months after their ''lakeward'' migrations would normally have occurred, so one assumption we must acknowledge is that the differences we observed between the relative swimming abilities of our populations reflect differences that would have existed at the time of their ''lakeward'' migrations. This is not an unrealistic assumption, because other swim-performance studies with juvenile fishes in which repeated assessments were made over a several-month period, found consistency in individual swim performance (e.g. Kolok 1992; Gregory and Wood 1998, 1999; McCarthy 2000). For example, standard metabolic rate in juvenile Atlantic salmon, *Salmo salar*, was consistent over a period of several months of growth under laboratory conditions (McCarthy 2000). In terms of active metabolism, individual repeatability of stamina-swimming performance has been observed in rainbow trout, *O. mykiss* (Gregory and Wood 1999). Therefore, although our study does not specifically measure swim performance at the exact time of migration it probably enabled reasonable approximation of such measurements. The relative differences we found between stocks should not, therefore, be affected by the timing of our observations.

To help with the interpretation of our results, they must be discussed in a more complete life-history context, and in terms of what is known about morphological and bioenergetic relationships for the specific populations used in our study. Although we did not examine egg sizes in this study, it has been shown that Weaver adults produce much larger eggs (~20% heavier per egg) than Adams adults (Crossin et al. 2004). The enzymatic physiology of a young sockeye salmon is primarily determined by the amount of energy the mother invested in it when it was an egg (Patterson et al. 2004). Thus, these larger eggs are probably one reason Weaver fry grow faster than Adams fry and, as suggested by Patterson et al. (2004), may be a reason why Weaver fry are metabolically better provisioned than Adams fry for superior swimming performance. Despite being the same size at maturity, Weaver adult females have much larger energy reserves available to allocate to eggs than Adams females, because Adams adults travel four times the distance up-river during spawning migrations and expend much more of their limited energy reserve on transport costs than do Weaver adults (Crossin et al. 2004).

As we found with fry, Weaver adults have deeper bodies than Adams adults (Crossin et al. 2004). Although we were unable to directly link fry morphological variation with their swimming performance, studies on adults, including studies on our populations, have been more successful at doing this. There is good evidence that adult Pacific salmon, which migrate long distances upriver, have smaller, more fusiform bodies (Hendry and Berg 1999; Kinnison et al. 2001, 2003; Crossin et al. 2003, 2004), and swim-performance experiments have revealed that these morphologies enable adults to utilize energy reserves more efficiently (Lee et al. 2003a). Without such energy-conserving morphologies and behaviour, the ability of long-distance migrating adults to complete upriver migration and have enough energy reserves for gonad maturation and spawning would be severely affected (Hinch et al. 2005). Thus, the relatively smaller and more fusiform shape of Adam's fry may reflect an adaptation that benefits adult migrations—an hypothesis previously suggested by Taylor and McPhail (1985a, b) to explain the more fusiform shapes of interior, relative to coastal, populations of juvenile coho salmon.

We found that Weaver fry had better burst-swimming capabilities than Adams fry; this pattern seems to be opposite to that for their adults, however. Long-distance adult-migrating Fraser

sockeye have better burst-swimming ability than Weaver and other short-distance adult migrants (Lee et al. 2003b). Long-distance migrating adult sockeye in the Fraser must not only be adept at saving energy, to be able to spawn successfully, they must also ascend several sections of rapids (Hinch et al. 2005); good burst-swimming ability would therefore be needed by those adults if theyare to reach spawning areas successfully. Weaver adults have a relatively short and easy upstream migration, never encountering rapids or similar obstructions (Crossin et al. 2004).

In conclusion, we provide evidence that juvenile migratory demands may be a factor affecting among-population differences between the burst-swimming performance of outlet and inlet juvenile sockeye salmon. Interpreting differences among populations in swimming performance and morphological traits of juveniles in terms of specific adaptations requires thorough understanding of selection pressures during all stages of their life history. Our study examined one discrete component of a very complex life-history, in two populations only, and our interpretations must be viewed in this context. Although no single study can be expected to assess the underlying causes of morphological and behavioural adaptations in sockeye salmon fry, our results and those of Patterson et al. (2004) are first steps. Future studies should examine inlet/outlet fry populations in watersheds both near and distant from the ocean, to enable better elucidation of the relative roles of adult and juvenile migratory conditions on morphology and swim performance at different stages of their life history.

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