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[Article]

Contrasting Ecology Shapes Juvenile Lake-Type and Riverine Sockeye Salmon

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Abstract.—Here we compare the body shape of juvenile (age-0) sockeye salmon *Oncorhynchus nerka* that rear in lakes (lake type) with that of those that rear in rivers (riverine) and relate rearing habitat to morphology and ecology. The two habitats present different swimming challenges with respect to water flow, foraging strategy, habitat complexity, and predation level. We present morphological data from three riverine and three lake-type populations in southwest Alaska. Using multivariate analyses conducted via geometric morphometrics, we determine population- and habitat-specific body shape. As predicted, riverine sockeye salmon have a more robust body shape, whereas lake-type sockeye salmon have a more streamlined body shape. In particular, we found differences in caudal peduncle depth (riverine deeper), eye size (riverine larger), and overall body depth (riverine deeper). One lake-type population did not follow the predicted pattern, exhibiting an overall exaggerated riverine body shape. Differences between the habitats in terms of predation, complexity, and foraging ecology are probably drivers of these differences. Allometry differed between life history types, suggesting that there are habitat-specific developmental differences.

Sockeye salmon *Oncorhynchus nerka* exhibit a high degree of morphological diversity and are locally adapted to their spawning habitats at a fine spatial scale (Blair et al. 1993; Hendry and Quinn 1997; Taylor et al. 1997; Pon et al. 2007). Flow conditions, predation, migration difficulty, incubation temperature, and substrate size are some of the environmental factors that correlate with morphological or behavioral differences of sockeye salmon. Pon et al. (2007) found that juveniles emerging in lake outlets have body morphology and swimming ability that facilitates their migration against river currents to arrive at their nursery lake. This is just one example demonstrating how morphology and behavior can vary at a fine spatial scale.

However, nearly all work documenting morphological divergence in sockeye salmon has focused on the adult stage and exclusively on a single life history type in which fry and parr rear in lakes (lake type). Sea-type (Semko 1960) and river-type sockeye salmon (Gilbert 1918) rear in riverine habitat, and we refer to both as "riverine" (Beacham et al. 2004). In these life histories, migration to the ocean occurs before the first winter (sea type), or after one or more winters in freshwater (river type). These populations rear in a variety of riverine habitats including slack water side channels, sloughs, or riffles (Murphy et al. 1989; Wood et al. 1994; Pavey et al. 2007; Wood et al. 2008). Though

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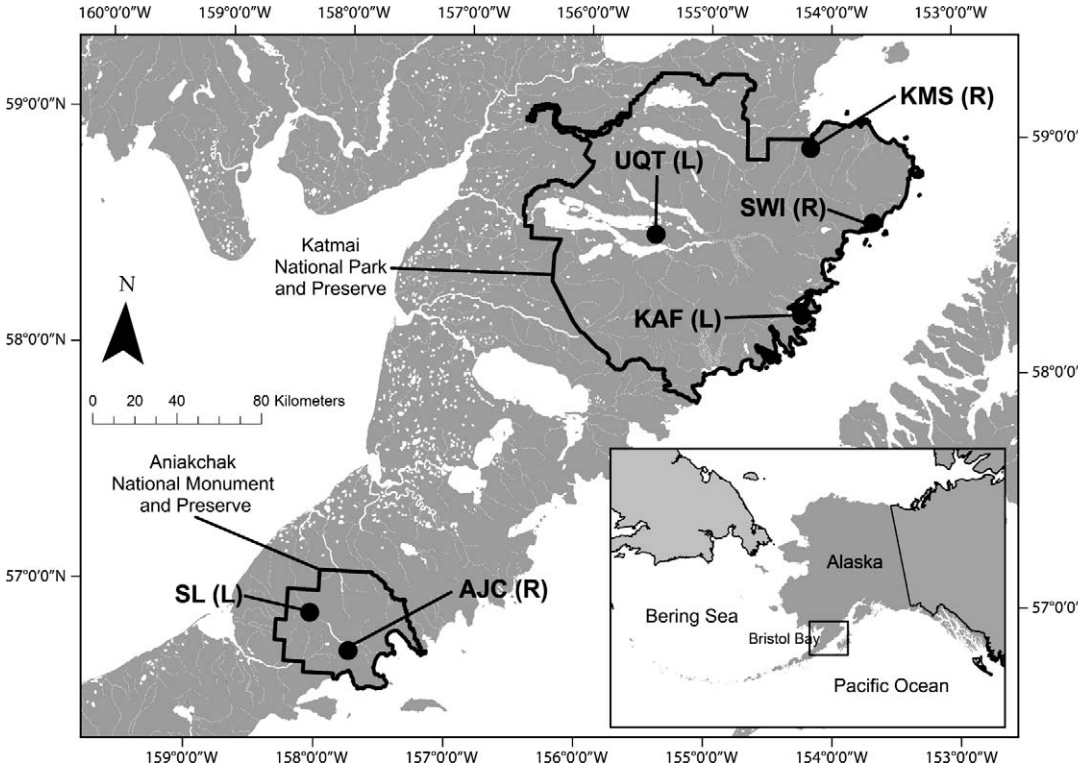

FIGURE 1.—Map of the study area in the Alaska Peninsula where the body shapes of age-0 sockeye salmon were compared among six sampling locations. Three of the locations were riverine (R)—the Kamishak River (KMS), Swikshak River (SWI), and Albert Johnson Creek (AJC)—and three were lake locations (L)—Upper Q-tip Lake (UQT), Lower Kaflia Lake (KAF), and Surprise Lake (SL).

present riverine populations tend to be of lesser abundance than lake-type populations, during previous glaciations, they were probably widespread and abundant and appear to have played an important role in recolonizing new watersheds as glaciers receded (Wood et al. 2008). Recent emphasis on population genetics of sockeye salmon with these alternative life histories has helped to clarify their relationship to lake-type sockeye salmon (Wood 1995; Beacham et al. 2004; Beacham et al. 2006a; Beacham et al. 2006b; Wood et al. 2008; McPhee et al. 2009). The recurrent and rapid evolution of sockeye salmon ecotypes in riverine and lake habitats, which differ in flow regime and available food items, presents an ideal opportunity to analyze correlates of body shape with ecology.

In this study, we compared body shape between age-0 lake-type and riverine sockeye salmon populations. We expected lake types to have a streamlined body to facilitate continuous swimming and riverine fish to have a deep, robust body for burst swimming. We explore the ecological factors of water current, foraging, habitat complexity, and predator avoidance in shaping sockeye salmon morphology.

Methods

Study area.—Katmai National Park and Preserve and Aniakchak National Monument and Preserve (Figure 1) in southwest Alaska provide a unique system to study the interactions of lake-type and riverine sockeye salmon life history forms, where populations rear in both lake and river environments. In the Aniakchak River both forms coexist in the same drainage (Pavey et al. 2007). Our lake-type locations included Surprise Lake (SL), Upper Q-tip Lake (UQT), and Lower Kaflia Lake (KAF). Our riverine locations included Albert Johnson Creek (AJC), Swikshak River (SWI), and Kamishak River (KMS). These riverine habitats appear to differ from those described in other studies (Wood et al. 1987; Murphy et al. 1989; Wood et al. 1994), being characterized by clear water, substantial current, and little or no glacial influence. All of our sample locations drain into the Gulf of

TABLE 1.—Sockeye salmon sampling locations, dates sampled, sample size (*N*), fork length (population means with SDs in parentheses), rearing habitat, and drainage.

Population	Date sampled	*N*	Fork length (mm)	Habitat	Drainage
Albert Johnson Creek (AJC)	7 Jun 2003	296	36.1 (4.9)	Riverine	Pacific Ocean
Kamishak River (KMS)	1–6 Jun 2007	133	37.0 (2.8)	Riverine	Pacific Ocean
Swikshak River (SWI)	16–20 Jun 2006	91	30.0 (3.1)	Riverine	Pacific Ocean
Lower Kaflia Lake (KAF)	6 Jun 2006	97	39.0 (4.4)	Lake	Pacific Ocean
Surprise Lake (SL)	3–4 Jun 2003	74	28.2 (1.5)	Lake	Pacific Ocean
Upper Q-Tip Lake (UQT)	8–11 Jul 2006	108	36.3 (4.9)	Lake	Bering Sea

Alaska in the northern Pacific Ocean, except UQT, which drains into Bristol Bay of the Bering Sea.

Fish collections and measurements.—We sampled a total of 1,000 age-0 sockeye salmon from the six locations in the summers of 2003, 2006, and 2007 (Table 1). We euthanatized each fish with MS-222 (tricaine methanesulfonate) and then photographed it in a standard position with a 35-mm manual camera, a macro lens, and a table stand. Slides were scanned with a Nikon Super Coolscan 5000 ED. We digitized 12 landmarks on each image using TpsDig (Figure 2; Rohlf 2006). These landmarks represent homologous points that could be identified on every fish and were selected to appropriately capture the profile of each fish. Landmark 1 is the most anterior point on the dentary bone. Landmarks representing the width of the orbit were taken at the anterior (landmark 2) and posterior (landmark 3) extremes of the orbit. Landmarks 4 and 5 together were included to capture the body depth in the region of the fish directly posterior to the head. Landmark 4 indicates the point along the body directly below the pectoral fin insertion point. Landmark 5 is the point on the dorsal side of the body directly above the most posterior point of the gill operculum. Landmark 6 is the most anterior point of the dorsal fin along the body. Landmarks along the ventral side of the body include points directly below the pelvic (landmark 7) and anal (landmark 8) fin insertion points. Landmarks representing the caudal peduncle were defined as the most anterior attachment points of the caudal fin onto the dorsal (landmark 9) and ventral (landmark 10) sides of the body. Landmark 11 lies at the hypural plate, and landmark 12 represents the center of the fork in the caudal fin.

Using the digitized landmarks, we analyzed shape variation using geometric morphometrics (Rohlf and Marcus 1993; Zelditch et al. 2004; Langerhans et al. 2007). We used TpsRelw (Rohlf 2007) to perform generalized Procrustes analysis, which translates, scales and rotates landmark configurations to remove information unrelated to shape and generates shape variables for each fish (partial warps and uniform components). Although this method does effectively remove all isometric effects of size on shape, allometric relationships remain. We calculated centroid size, which is the square root of the sum of the squared distances from each landmark to the arithmetic center. This is a more complete proxy of size than fish length. We visualized shape differences between pairs of populations that had similar distributions of centroid size with TpsRegr, which accepts centroid size as a covariate. This enables shape that differs only by habitat to be visualized independent of size differences. We then performed a multivariate nested analysis of covariance (MANCOVA) to test for the significance of differences in profile of the body shape among populations and habitats (Langerhans et al. 2007). The partial warp scores, including the uniform components, are the dependent variables, and centroid size, habitat (lake type versus riverine), and population nested in habitat are the independent variables. The inclusion of the centroid size variable captures allometric aspects of shape. The habitat variable captures shape differences due to habitat, and the inclusion of population nested within habitat captures shape differences among populations within habitats. We ran this analysis with and without the interaction term centroid size $\times$ habitat to determine whether allometry differs among habitats. We also ran the analysis with and without the inclusion of the UQT population, which was substantially different in body shape than the other lake-type populations. We then correlated each specimen's habitat canonical score with the superimposed landmarks (Langerhans et al. 2007). This illustrates the extent to which each landmark differs between habitats. We performed the MANCOVA and canonical analysis in JMP 7.0.2 (SAS institute). We correlated the canonical score for each specimen with the superimposed landmark coordinates in SYSTAT 10.

We used a discriminant function analysis to examine whether the morphological information contained in the partial warp scores could be used to distinguish riverine and lake-type populations. The analysis was conducted seven times, once with all populations, and once after removal of the individuals from each population in turn. The percent of successful classifications of individuals to their originating habitat under

jackknife procedures is reported for all populations, as well as for the five populations remaining after removal of UQT. In addition, the percentage of classification of each population into the appropriate habitat types is reported without jackknifing. We also plotted the results of the discriminant function analysis against centroid size, including all six populations and excluding UQT. The discriminant function analysis was performed in SYSTAT 10.

Results

We sampled a total of 1,000 sockeye salmon juveniles (ages 0 and 1), ranging from 74 to 296 per population, at the six locations (Table 1). In lakes, fish were captured in shallow beach habitat with a varied substrate. Riverine habitats sampled were clear, shallow, and flowing. We excluded two outliers and also all age-1 fish by creating fork length frequency distributions and eliminating individuals from the larger node if present. We used the resulting 799 age-0 individuals in subsequent analyses.

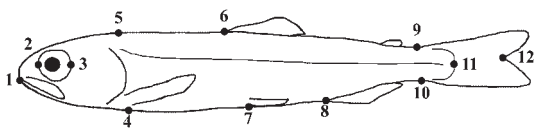

FIGURE 2.—The 12 landmarks used for morphometric analysis of age-0 sockeye salmon. These landmarks were placed on the digital image of each fish examined.

Five of six sockeye salmon populations followed the general pattern found among salmon species, lake-type populations exhibiting a shallow body and riverine populations a deep body (Figure 3). The striking exception was the lake-type UQT population, which was characterized by the deepest bodies of all populations. We found significant differences in body shape among populations and between habitats, both including and excluding UQT, as indicated by the significant habitat term ($P < 0.001$; Table 2). Body shape was also different within habitats among populations, as indicated by the significant population (habitat) term ($P < 0.001$). The interaction term habitat $\times$ centroid size was significant ($P < 0.001$), so we retained this term in the models. However, retaining or excluding the interaction term yielded highly correlated canonical scores ($P < 0.001$, $r^2 = 0.97$). This was also true excluding UQT ($P < 0.001$, $r^2 = 0.99$). This means that shape did vary with size differently among habitats, but the overall effect was very small.

The correlations between canonical scores of the habitat effect and the superimposed landmarks changed substantially depending on the inclusion or exclusion of UQT (Table 3). These results depict which part of the fish shape changed based solely on habitat and how including and excluding UQT affected the life history type shape. Pearson's product-moment correlation

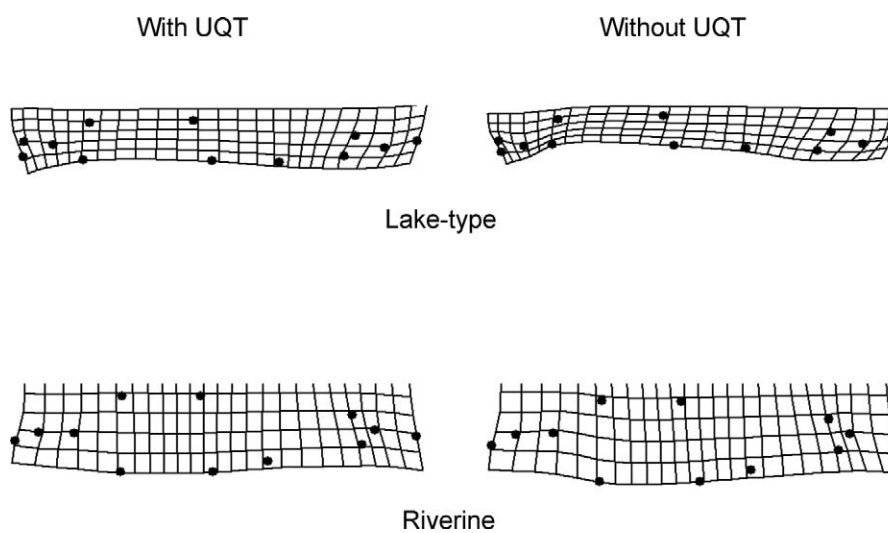

FIGURE 3.—Deformation grid based on the habitat variable of lake-type and riverine sockeye salmon with and without the inclusion of Upper Q-Tip Lake (UQT). Results were generated with tspRegr and are exaggerated 3$\times$ the range of the sample to allow visual comparison of the differences in body shape between lake-type and riverine sockeye salmon. Riverine sockeye have a deeper body, deeper caudal peduncle, and larger orbit. The differences are more pronounced when the UQT population is removed because lake-type UQT had some riverine morphological features, including a deep body.

TABLE 2.—Results of the nested multivariate analysis of covariance for all six populations of sockeye salmon and the same populations excluding that of Upper Q-Tip Lake (UQT). The dependent variables were the multivariate partial warp scores. We included all covariates, including the interaction term and habitats nested in populations. Variables in the model are centroid size (csize), habitat, populations nested within habitat (pop [habitat]), and the interaction term csize × habitat. Body shape changed in relation to all covariates, and the significant interaction term means that shape changed with size differently between habitats. Factor degrees of freedom are given before the commas and error degrees of freedom after them.

Variable(s)		Including UQT	Excluding UQT
Csize	df	19, 773	19, 666
	F	166.61	100.49
	P	<0.001	<0.001
Habitat	df	19, 773	19, 666
	F	15.80	28.96
	P	<0.001	<0.001
Pop (habitat)	df	76, 3,047.3	57, 1,986.6
	F	40.78	33.11
	P	<0.001	<0.001
Csize × habitat	df	19, 773	19, 666
	F	9.27	6.70
	P	<0.001	<0.001

TABLE 3.—Pearson's product-moment correlation coefficients between superimposed sockeye salmon landmark coordinates (see Figure 2) and the canonical axis; larger numbers indicate important landmark axes in the morphological comparison of riverine and lake-type fish. Values in bold italics are significant after Bonferroni correction. Results are for the six Alaska sample sites (see Figure 1), including and excluding Upper Q-Tip Lake (UQT).

Landmark	Including UQT	Excluding UQT
X1	***0.2918***	***0.1296***
Y1	***0.2468***	***0.5813***
X2	0.0053	***0.1746***
Y2	***−0.4094***	−0.0958
X3	−0.0559	−0.0349
Y3	***−0.4290***	***−0.2059***
X4	***−0.5177***	***−0.5111***
Y4	***0.2293***	***−0.4198***
X5	***−0.1883***	−0.0217
Y5	0.0686	***0.5135***
X6	0.0671	***0.1272***
Y6	0.0133	***0.5085***
X7	***0.1285***	***0.2104***
Y7	***0.2089***	***−0.3364***
X8	***0.2385***	***0.3374***
Y8	***0.2300***	***−0.2336***
X9	−0.0154	−0.0951
Y9	0.0252	***0.4362***
X10	***−0.1778***	−0.0693
Y10	***−0.2101***	***−0.1150***
X11	0.1095	−0.0677
Y11	***−0.1460***	***0.1894***
X12	−0.0214	***−0.3132***
Y12	***−0.1636***	0.0048

coefficients that relate to overall body depth, caudal peduncle depth, and orbital size were statistically significant (bold numbers in Table 3). The lake-type body shape is more fusiform than the riverine in both cases, though this difference is more pronounced when UQT is excluded, and the caudal peduncle also differs between habitats: shallow and long for lake-type fish and deep and short for riverine fish (Table 3; Figure 3). Orbital size differed between life histories, riverine fish having a larger orbital region. We graphically compared the lake-type UQT population with the other populations that had individuals most closely matching in size, which included riverine KMS and AJC and lake-type KAF (Table 1). Upper Q-tip Lake sockeye salmon did not fit with the lake-type trend. This population appears to have exaggerated riverine body depth and orbital size differences, but the caudal peduncle differences are more complex. Upper Q-tip Lake sockeye salmon retain the caudal peduncle geometric shearing feature of the other lake-type populations but have similar caudal peduncle length and depth of riverine populations. Shearing is "translating landmarks along one axis by a distance proportional to their location along the other axis" (Zelditch et al. 2004). The shearing feature of the caudal peduncle is illustrated by comparing the lake-type and riverine deformation grids in Figure 3. This shearing is more extreme with the removal of UQT (Figure 3). In summary, riverine fry generally have deeper bodies, shorter and deeper caudal peduncles and larger orbits than lake-type sockeye salmon. However some of the characteristics of lake-type UQT fish appear to be exaggerated riverine.

In the discriminant function analysis, individuals were assigned to the proper habitat type with an accuracy of 70% for lake-type fish and 77% for riverine fish under jackknifing procedures (Table 4; Figure 4). Removal of UQT resulted in jackknifed classifications of 80% for lake-type and 89% for riverine fish. Of all the analyses run with single populations removed, UQT was the only removal that improved assignment accuracy in all remaining populations and provided the best overall assignment accuracy. Assignment of individuals from the SL population was least accurately assigned in both data sets, but removal of UQT improved the classification accuracy of this population from 58% to 72% (Table 4; Figure 4). The DFA makes use of the information that best allows separation of populations into habitats, which makes for the similarities in the two sets of panels. Excluding UQT results in the addition of three of the body depth landmarks (and the loss of one) as significant contributors to the differentiation among habitats (Figure 3). This change is largely responsible

TABLE 4.—Results of the discriminant function analysis with numbers of sockeye salmon from six locations (Figure 1) correctly (bold italics) and incorrectly classified to habitat based on morphology. Results are presented both including and excluding fish from Upper Q-Tip Lake (UQT).

Type and % correct	Riverine			Lake type		
	AJC	KMS	SWI	SL	KAF	UQT
Including UQT						
Lake type	53	24	32	***43***	***83***	***76***
Riverine	***243***	***109***	***59***	31	14	32
% Correct	82	82	65	58	86	70
Excluding UQT						
Lake type	25	19	7	***53***	***86***	
Riverine	***271***	***114***	***84***	21	11	
% Correct	92	86	92	72	89	
Difference (%)	***9***	***4***	***27***	***14***	***3***	

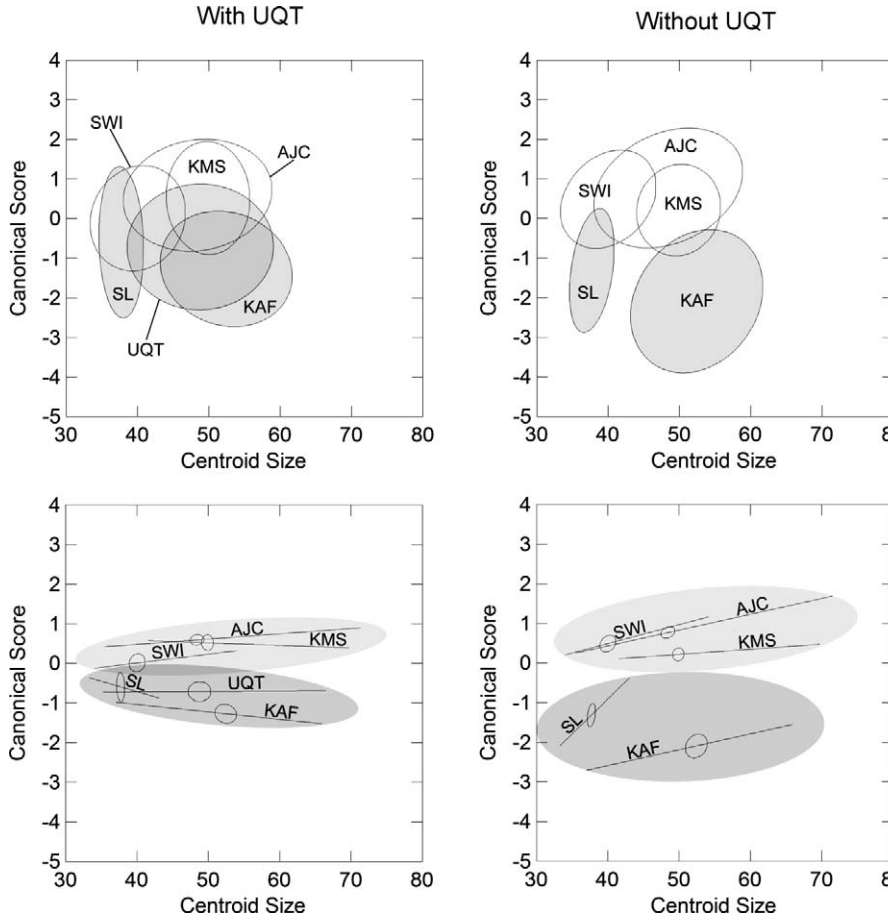

FIGURE 4.—Habitat canonical scores plotted against centroid size. Panels on the left include all six populations of sockeye salmon (see Figure 1); panels on the right present the same analysis excluding Upper Q-tip Lake (UQT) samples. The top panels depict 67% sample ovals, where clear ovals are for riverine populations and gray ovals for lake-type populations. The lower panels show the regression line and centroid circle for each population, where light gray ovals are for riverine populations and dark gray ovals for lake-type populations. Habitat separation is greater when the UQT population is removed because lake-type UQT fish had some riverine morphological features, including a deep body.

for the improved ability of the DFA to separate by habitat in the second set of panels with UQT excluded.

Discussion

We found that age-0 riverine sockeye salmon were deeper bodied and had a deeper but shorter caudal peduncle and larger orbit, whereas age-0 lake-type fish were shallower bodied with a shallow, yet longer caudal peduncle and smaller orbit. This is an important initial step in understanding how morphology relates to the ecology of these life history types. These results are similar to other studies of freshwater-rearing salmon within and among species (Hoar 1958; Scott and Crossman 1973; Swain and Holtby 1989). However this pattern was not consistent between all population pairs; in particular, UQT did not follow this pattern. To address these findings, we explore water current, foraging strategies, predator interactions, and habitat complexity as ecological factors influencing trends in body shape at three taxonomic levels: all fishes, among salmon species, and the sockeye populations reported here.

Ecology and Fish Shape: All Fishes

Fish body shape often represents a compromise between steady (continuous or sustained) and unsteady (burst and maneuverability) swimming. Langerhans (2008) developed a model relating morphology and swimming performance to flow regime and found that flowing water was correlated with a streamlined body shape in 42 of 58 intraspecific comparisons and 13 of 17 interspecific comparisons. The premise of the model is that fish in flowing water must swim continuously to maintain their position and this necessitates morphological and physiological adaptations for continuous swimming.

In addition to flow regime, predation and habitat complexity may also be important ecological aspects that affect morphology. Langerhans and Reznick (2010) found that in four divergent fish species, populations subject to high predation had larger caudal regions and superior burst swimming than populations with less predation. They also found variation in body shape across 32 species relating to habitat complexity, where species in open environments had higher endurance but lower ability for turning radius and acceleration than species in complex habitats (Domenici 2003; Langerhans and Reznick 2010).

Ecology and Fish Shape: Pacific Salmon

In a simplistic assessment of the hydrodynamic differences and in the absence of other ecological and behavioral factors, we may expect riverine rearing species of Pacific salmon (genus *Oncorhynchus*) to have a more fusiform body shape than lake rearing salmon species (Langerhans 2008). However, the general observation is the opposite morphological pattern in freshwater-rearing Pacific salmon (Hoar 1958; Scott and Crossman 1973; Swain and Holtby 1989). Habitat specific foraging strategies may result in riverine species avoiding strong currents by holding positions behind rocks, close to the bottom or in side vegetation (Bisson et al. 1988). Foraging strategy, habitat complexity, and predation regimes may influence body shape more than current (Swain and Holtby 1989).

For freshwater-rearing Pacific salmon, foraging behavior may be a more important factor in body shape than water velocity. Salmon species with extensive river residence tend to have a deep robust shape and exhibit agonistic behavior, whereas species inhabiting lakes tend to be more shallow-bodied and streamlined and less agonistic (Hoar 1951; Hoar 1954; Hoar 1958; Scott and Crossman 1973; Taylor and McPhail 1985a; Taylor and Larkin 1986). In salmon, a deep robust shape is thought to favor burst swimming (Pon et al. 2007; Langerhans 2008). Riverine populations hold and defend territories, and this robust shape may also increase the effectiveness of aggressive displays. A shallower, more streamlined body is better suited for lacustrine habitats, where the strategy is cruising in schools and feeding on zooplankton in the open water instead of territoriality with associated burst swimming. This dichotomy has also been observed intraspecifically among populations of coho salmon *O. kisutch* and Chinook salmon *O. tshawytscha* in different rearing environments (Taylor and McPhail 1985a; Taylor and Larkin 1986). Swain and Holtby (1989) found that riverine-foraging coho salmon juveniles were more agonistic and had deeper, more robust bodies than those of an adjacent lake-rearing population.

Other ecological factors, such as predation and habitat complexity, may also influence body shape in salmon (Swain and Holtby 1989; Langerhans and Reznick 2010). Rivers present greater structural complexity than the open water column of lakes, and this is expected to favor a deeper and more maneuverable body shape (Langerhans and Reznick 2010). Common garden rearing experiments have confirmed that these morphological and behavioral differences have both genetic and environmental components (Taylor and McPhail 1985a; Taylor and McPhail 1985b; Rosenau and McPhail 1987; Pakkasmaa and Piironen 2001; Pon et al. 2007). In this study, we do not know the relative roles of genetics and the environment on body shape. Future research should

focus on clarifying these roles through common garden and quantitative genetics experiments.

Ecology and Fish Shape: Sockeye Salmon

Like other lake-rearing Pacific salmon, age-0 lake-type sockeye salmon feed on plankton in schools and are nonaggressive toward each other (Hoar 1954; Swain and Holtby 1989). This foraging strategy favors continuous swimming ability over burst swimming in salmon (Foerster 1968; Hartman and Burgner 1972; Eggers 1982; Burgner 1991). The general shape differences between lake-type and riverine life history forms of sockeye salmon found in this study are similar to the differences among species of Pacific salmon. Superficially, riverine sockeye salmon rear in flowing water and lake-type sockeye salmon rear in still water. However, previous studies of riverine sockeye salmon habitat were in very low flow and turbid riverine habitats (Wood et al. 1987; Murphy et al. 1989). The riverine habitats where we captured sockeye in this study are neither low current (slack water) areas nor turbid, although we did not measure either variable. If riverine sockeye salmon have a similar foraging strategy as other river-rearing Pacific salmon, including aggressively defending territories near the substrate, this may have resulted in plastic or adaptive responses favoring burst swimming capability (Swain and Holtby 1989).

Predator interactions are probably an important element in age-0 sockeye salmon body shape. Sockeye salmon rearing in Alaskan lakes have a largely nonoverlapping distribution with potential predator species and therefore have low levels of predation (Roos 1959; Foerster 1968; Burgner 1991). Predation on lake-type sockeye salmon occurs mainly during the migration to the nursery lake and the seaward migration in lake outlets and in rivers (Burgner 1991). On the other hand, riverine sockeye salmon spend this rearing time in close proximity with predators including Dolly Varden *Salvelinus malma*, lake trout *Salvelinus namaycush*, and coho salmon. The presence of these predator species should favor burst swimming and a deep caudal region (Domenici et al. 2008; Langerhans and Reznick 2010). Gape-limited predation could also favor deeper body morphology (Nilsson and Bronmark 2000). In studies of riverine sockeye salmon in British Columbia (Wood et al. 1987; Murphy et al. 1989), turbid water may limit the effects of predation, whereas our riverine study sites were less glacially influenced and visually quite clear. In both foraging and predation, the riverine ecology favors burst swimming and a deep body shape.

Habitats of higher structural complexity like riverine rearing habitat are also expected to favor unsteady swimming and a deeper morphology to enable maneuvering, breaking, and accelerating around structures (Langerhans and Reznick 2010). Because this attribute occurs also in the presence of higher predation and territorial foraging strategy, we cannot asses the relative contributions of these ecological aspects on age-0 sockeye salmon morphology.

Sockeye salmon from UQT were shaped differently than the other two lake-type populations. They have deeper bodies and larger orbits than any other population, including the riverine populations. Their caudal peduncle included shape aspects of both life histories. The basis for these differences is undetermined, and there are many nonexclusive potential explanations. It is possible that there are multiple ecotypes within this lake such as benthic–limnetic pairs found in other lake-dwelling salmonids (Chouinard and Bernatchez 1998; Gislason et al. 1999). It is possible that sampling by beach seine preferentially sampled a deep bodied benthic ecotype at this location. This is the only population that was sampled in July; all others were sampled in the month of June. Although the individuals in UQT were of similar length as populations collected in June (Table 1), fish condition that changes as the summer progresses could explain some body depth differences.

The UQT population is geographically separated from the others; it is the only sampling location that drains into the Bering Sea. There may be unique foraging strategies or predation regimes that may differ among lake-type populations. Northern pike *Esox lucius* are present in lakes in the Bering Sea drainages but are not present in the north Pacific drainages. Dietary differences and alternative predatory regimes may force unique ecotypic response in these freshwater-rearing sockeye salmon. It is also possible that there is no general pattern in lake-type sockeye salmon, and the variability within lake type individuals exceeds the variability between lake-type and riverine life histories. However, even with UQT included in the discriminant function analysis, the life history groups separate although the separation is more distinct when UQT is removed (Figure 4). Also, removing UQT from the discriminant function analysis was the only removal that resulted in improvements in assignment for all other populations. Larger studies and more populations and geographic areas will clarify the generality of our findings.

In sockeye salmon, lake-type spawning adults have deeper bodies in still-water habitats (lakes) than inflowing habitats (lake outlets and inlets; Quinn et al. 2001b; Pavey et al. 2010). These studies only involve lake-type life history, and there are currently no studies comparing riverine to lake-type spawning adults. Spawning adults are large compared with fry

and probably cannot hide as effectively from water current, so the hydrodynamic advantage of a shallow body may be more important in adults (Pavey et al. 2010). Breeding adult salmon stop feeding upon entry into freshwater, so foraging energetics should not be a factor in adult body shape. However, selection in breeding populations has been shown to include effects of access limitation (Quinn and Buck 2001), sexual selection (Quinn and Foote 1994; Hamon and Foote 2005), and predation (Quinn and Foote 1994; Quinn and Buck 2001; Quinn et al. 2001a; Quinn et al. 2001b; Hamon and Foote 2005). The difference in absolute size of individuals in relation to the depth of the water environment, as well as the changed focus from feeding to reproduction, appears to favor different patterns of phenotypic differentiation in adults and fry.

The interaction term (csize × habitat) in the MANCOVA was significant, and this indicates habitat-specific allometric differences (Table 2; Figure 4). Though the results of the other model covariates including and excluding this term were highly correlated, this suggests possible developmental differences among habitats and populations. The significant population nested within habitat term suggests population-specific body shape characteristics (Table 2; Figure 4). In fact, with UQT excluded, the population nested within habitat term has an equivalent effect on morphology as the habitat term (Table 2). Differing development within habitats, as well as population-specific ecological factors, may contribute to fine-tuning body shape for each population.

Our results indicate that age-0 sockeye salmon differ in body shape among populations rearing in different habitats. The specific differences may be affected by predation, plasticity, or other factors, but in our samples these differences seem to favor deep bodies in moving-water rearing environments, probably as a result of the foraging environment. The generality of this pattern, or the frequency of aberrant populations like UQT, will only become know with the examination of more populations in different areas and ecological contexts. We do not know to what extent genetic and environmental factors are influencing body shape in freshwater-rearing sockeye salmon. In many cases, phenotypic plasticity itself is adaptive; however this could also result in apparent phenotypic mismatches in individual populations. In addition, we cannot exclude nonadaptive genetic process, such as drift or mutation resulting in morphological differences (Lande 1976). The difference in phenotypic pattern between adult and freshwater-rearing sockeye salmon using flowing and still water environments probably relates to the shift in emphasis from foraging in fry to breeding activity in adults, as well as the difference in size of the animal in relation to its immediate environment.

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