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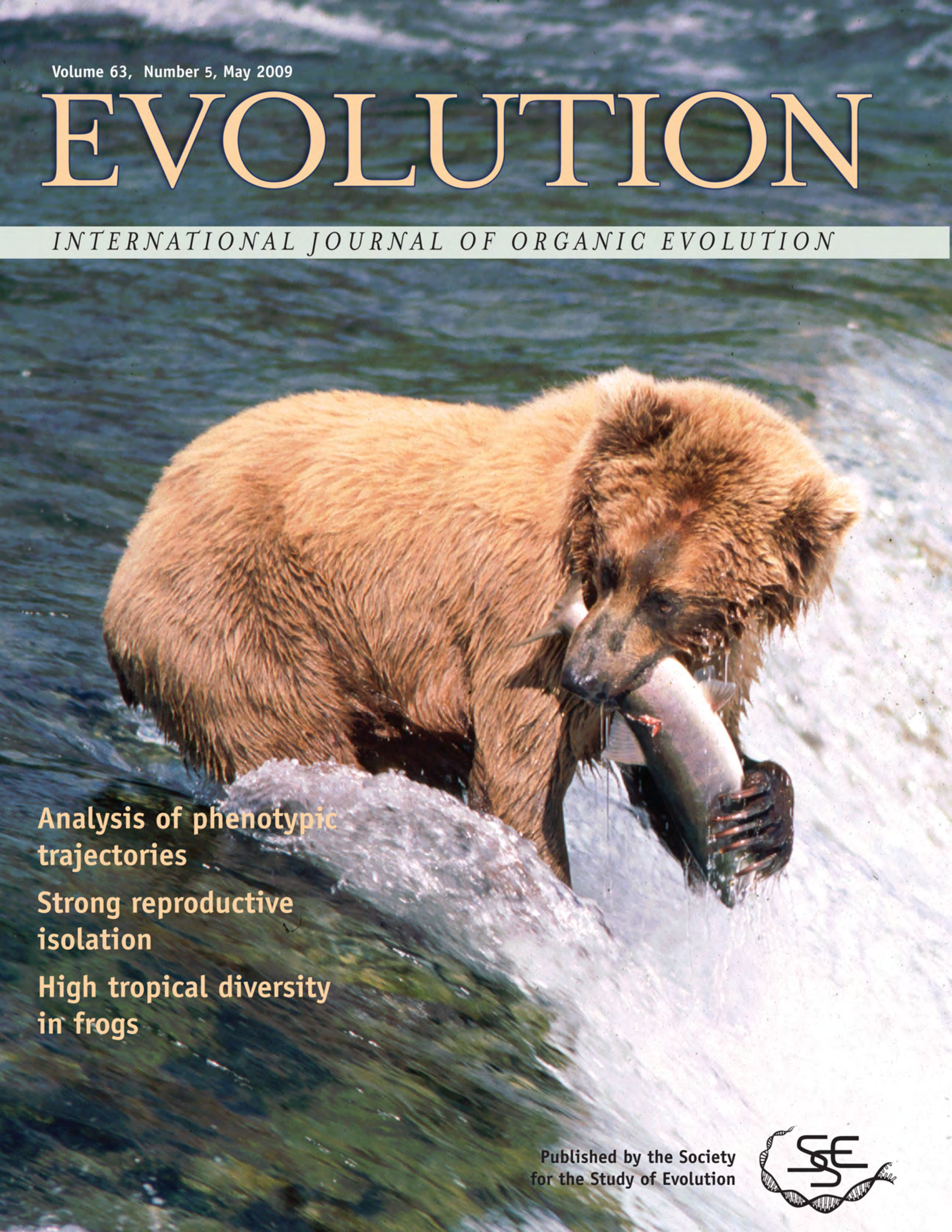

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DOES VARIATION IN SELECTION IMPOSED BY BEARS DRIVE DIVERGENCE AMONG POPULATIONS IN THE SIZE AND SHAPE OF SOCKEYE SALMON?

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Few studies have determined whether formal estimates of selection explain patterns of trait divergence among populations, yet this is one approach for evaluating whether the populations are in equilibria. If adaptive divergence is complete, directional selection should be absent and stabilizing selection should prevail. We estimated natural selection, due to bear predation, acting on the body size and shape of male salmon in three breeding populations that experience differing predation regimes. Our approach was to (1) estimate selection acting within each population on each trait based on an empirical estimate of reproductive activity, (2) test for trait divergence among populations, and (3) test whether selection coefficients were correlated with trait divergence among populations. Stabilizing selection was never significant, indicating that these populations have yet to attain equilibria. Directional selection varied among populations in a manner consistent with trait divergence, indicating ongoing population differentiation. Specifically, the rank order of the creeks in terms of patterns of selection paralleled the rank order in terms of size and shape. The shortest and least deep-bodied males had the highest reproductive activity in the creek with the most intense predation and longer and deeper-bodied males were favored in the creeks with lower predation risk.

KEY WORDS: **Brown bears, divergent selection, local adaptation, morphology, natural selection, *Oncorhynchus nerka*, Pacific salmon, predation, *Ursus arctos*.**

The importance of divergent selection in driving phenotypic differentiation among conspecific animal populations and among species has long been recognized (e.g., Darwin 1859; Simpson 1953; Fairbairn and Preziosi 1996; Schluter 2000); yet, the mechanisms of divergent selection are rarely identified (Schluter 2000). Most research has focused on the role of resource competition in driving divergence (e.g., Schluter and Grant 1984; Schluter 2000; Benkman 2003). Recent work has also linked sexual selection and/or predation (Nosil and Crespi 2006; Svensson et al. 2006; Meyer and Kassen 2007; Svensson and Friberg 2007) to adaptive population divergence by demonstrating a correlation between the strength of divergent selection and trait divergence. Schluter (2000) suggested that studies designed to test the hypothesis of divergent natural selection should attempt to both demonstrate that selection is truly divergent, and identify the mechanism of selection. This latter goal has been particularly difficult to meet in natural systems and the mechanisms identified typically "represent an educated guess" (Schluter 2000, p. 106).

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Qualitative differences in predation have repeatedly been shown to influence trait divergence (reviewed in Vamosi 2005). For instance, life-history traits (e.g., Reznick 1982; Reznick and Endler 1982; Reznick et al. 1996, 2004), locomotor performance (e.g., O'Steen et al. 2002; Ghalambor et al. 2004), and color patterns (e.g., Endler 1978, 1980; Houde 1987, 1997) of guppies, *Poecilia reticulata*, vary among sites with different levels of predation. Threespine stickleback, *Gasterosteus aculeatus*, populations vary in body size (Reimchen 1991, 1994), body shape (Walker 1997), and the degree of defensive armor (Vamosi and Schluter 2004) as a function of predation intensity. However, no study has determined whether formal estimates of selection due to predation explain the observed patterns of trait divergence among conspecific populations (for within population examples, see Brodie 1992; Young et al. 2004). The additional value of this latter approach is that it provides a greater ability to evaluate the possibility of evolutionary equilibrium. Populations in equilibrium should experience stabilizing selection around mean trait values but if equilibrium has not been attained, each population should experience directional selection to move its mean toward the adaptive peak (Schluter 2000).

Numerous studies have quantified selection in wild, unmanipulated populations (reviewed by Endler 1986; Hoekstra et al. 2001; Kingsolver et al. 2001; Hereford et al. 2004) but most have focused on a single population (median number of spatial replicates = 1 among studies included in the review by Kingsolver et al. 2001). Moreover, when investigators have attempted to determine how differences in selection drive phenotypic divergence, selection has often not actually been quantified. We here address these two issues in a natural system by quantifying natural selection due in part to predation from brown bears (*Ursus arctos*) acting within multiple populations of sockeye salmon (*Oncorhynchus nerka*), allowing us to determine whether selection coefficients were correlated with interpopulation trait divergence. Our work complements the recent work of Svensson et al. (2006, 2007) and Nosil and Crespi (2006) by linking variation in predation intensity and selectivity to phenotypic differentiation among populations that is consistent with the strength of directional selection on each population.

PACIFIC SALMON

Pacific salmon (*Oncorhynchus* spp.) present an excellent opportunity to study the importance of selection in driving phenotypic divergence because their homing behavior promotes reproductive isolation and the formation of numerous discrete breeding populations that experience different selective pressures (e.g., Quinn 2005). These populations have differentiated in many phenotypic traits (Taylor 1991), including body size, age, and shape at maturity (Roni and Quinn 1995; Quinn et al. 2001b), and rates of senescence (Carlson et al. 2007), all of which can influence individual fitness. Body size has many important influences on fitness of both females and males. Female size affects reproductive potential through positive correlations with fecundity and egg size (Beacham and Murray 1993; Quinn et al. 1995; Hendry et al. 2001), egg burial depth (Steen and Quinn 1999), and competition for nest sites (e.g., Foote 1990; Quinn and Foote 1994). Male size correlates positively with mating success, at least in the absence of alternative mating tactics by small males (Gross 1985; Foote and Larkin 1988; Foote 1990; Fleming and Gross 1994; Quinn and Foote 1994; Quinn et al. 2001a; Hamon and Foote 2005). In addition to the importance of overall body size in males, the extent of sexual dimorphism (e.g., elongation of jaws and dorsoventral compression) has also been linked to breeding success (Fleming and Gross 1994; Quinn and Foote 1994). Specifically, males with more exaggerated features for their length were more often dominant in competition for females.

Previous research has revealed the importance of bears as an agent of selection acting on salmon populations (Quinn and Kinnison 1999; Ruggerone et al. 2000). Bears tend to kill larger than average salmon, and salmon populations experiencing high rates of bear predation tend to be smaller-bodied than those experiencing lower predation rates (Quinn et al. 2001b). However, the death of the salmon at the end of their first breeding season is inevitable, regardless of the bears, so the evolutionary effect of the bears depends on the extent to which reproductive opportunities are curtailed. The ability of bears to kill newly arrived salmon varies among streams (Gende et al. 2004a; Carlson et al. 2007), and the extent of prereproductive mortality probably varies as well.

OBJECTIVES

To determine the evolutionary effect of bears on salmon size and shape, we studied three proximate breeding populations that vary in the intensity of bear predation, and in the age at maturity, size at age, and shape of adult salmon (Quinn et al. 2001b). To do this, we first quantified the intensity of predation from bears by estimating both the percent of salmon killed in each population and the tendency of bears to kill fish early in their stream life (i.e., early stage breeders). Second, we estimated the strength and form of selection acting on male body size and shape within these populations. Third, we quantified trait divergence among the populations. Fourth, we tested whether estimates of divergent selection corresponded with the observed trait variation among populations. We predicted that the population most susceptible to bear predation would have the smallest body sizes (because bears are more likely to kill large than small salmon). Finally, we evaluated whether these populations are in evolutionary equilibria by comparing the strength and form of selection acting on each trait in each population with theoretical predictions (i.e., directional selection should be absent if adaptive divergence is complete).

Table 1. Narrow-sense heritability (h^2) estimates for four life-history traits in salmonine fish. These data represent the median heritability estimate (95% confidence intervals around the median estimate presented in parentheses) across all available estimates for each trait included in a recent review by Carlson and Seamons (2008).

Trait	Number of estimates	h^2
Age-at-maturity	25	0.21 (0.13–0.38)
Length-at-maturity	12	0.21 (0.10–0.35)
Mass-at-maturity	14	0.22 (0.14–0.29)
Shape-at-maturity	8	0.11 (−0.12–0.29)

We suspect that differences among the populations in these traits are the result of local adaptation because (1) gene flow is limited among populations in this lake system (pairwise F_{ST}s based on microsatellites for populations breeding in four creeks that flow into Lake Aleknagik vary from -0.0004 to 0.0085, with significant differences between two of our study populations [Hansen and Yako, $F_{\mathrm{ST}} = 0.0085$, $P < 0.05$ after Bonferroni correction] Lin et al. 2008; J. Lin, unpubl. data) and (2) these traits are heritable in salmonine fishes (Table 1, reviewed in Carlson and Seamons 2008). Specifically, controlled breeding experiments revealed a heritable basis for body depth and jaw length in male Chinook salmon (Kinnison et al. 2003), and many studies have shown a genetic control over size at age and age at maturity in salmon (reviewed in Carlson and Seamons 2008).

Materials and Methods

STUDY ORGANISM AND SITES

Sockeye salmon lay their eggs in the gravel of streams, rivers, and lake beaches in late summer and fall. Embryos incubate for several months prior to hatching, complete yolk-absorption, emerge from the gravel in spring, and migrate to a lake where they feed for 1 or 2 years before migrating to sea (Burgner 1991). After feeding for 1–3 years in the North Pacific Ocean, individuals migrate back to their natal lake system, often remaining in a lake for several weeks until they have fully matured, at which point they enter their natal site (stream, river, or beach), attempt to reproduce, and die.

The Wood River system in southwestern Alaska (Fig. 1) has many populations of sockeye salmon breeding in streams and rivers, where they are subject to predation from bears. Stream width explains over 50% of the variation among populations in

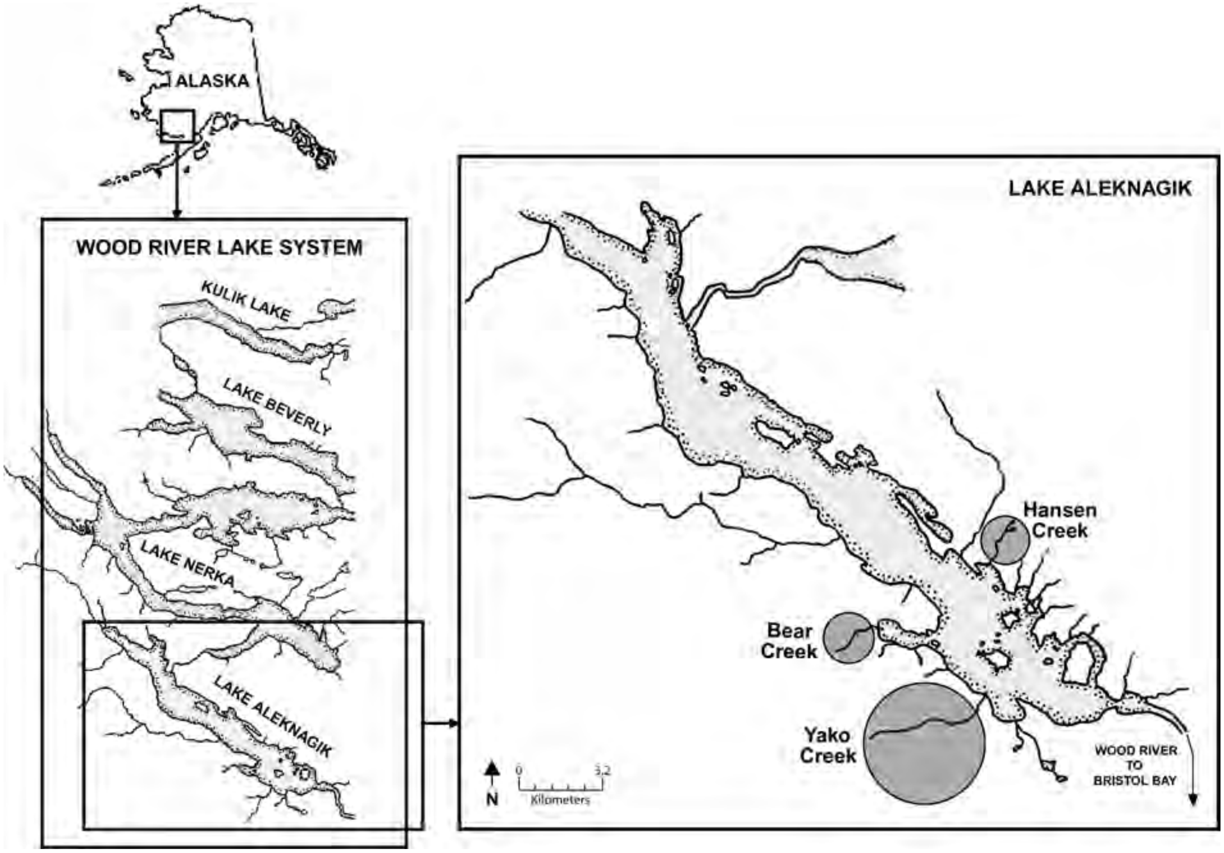

Figure 1. Map of Lake Aleknagik and the three study sites (Hansen Creek, Yako Creek, and Bear Creek) relative to the Wood River Lakes, southwestern Alaska.

Table 2. **Average annual abundance and density of sockeye salmon (mean±SE, total number of years indicated in parentheses), physical habitat attributes including average stream width and depth, as well as the distance and elevation gained during the breeding migration for three sockeye salmon populations.**

Population	Abundance mean±SE (years)	Density fish/m^2 (years)	Width (m)	Depth (cm)	Migration distance (km)	Migration elevation gain (m)
Hansen	3699±499	0.45±0.06	3.9	9.8	42	10
	(50)	(50)				
Yako	2563±309	0.11±0.01	4.2	22.6	39	10
	(51)	(51)				
Bear	3796±277	0.24±0.02	5.1	19.3	44	10
	(59)	(59)				

the average annual percent of salmon killed within a population (henceforth "overall predation rate"; Quinn et al. 2001a); the wider the stream the lower the predation rate. The three study sites (Hansen, Yako, and Bear creeks) are all tributaries of Lake Aleknagik, the southern-most lake in the Wood River Lakes system (Fig. 1). Adult sockeye salmon in these populations return from the ocean at the same time of the year (Hodgson and Quinn 2002) and have similarly short migrations to their natal sites without substantial elevation gain (Table 2), allowing us to study the patterns of selection acting on these populations in the absence of these potentially confounding factors.

OVERALL PREDATION RATE AND PREDATOR SELECTIVITY

Carlson et al. (2007) recently quantified two aspects of bear predation for six populations within the Wood River Lakes system, based on estimation methods described in two earlier papers (Quinn et al. 2001b; Gende et al. 2004b). We here focus on three of those populations and present the pertinent data from Carlson et al. (2007) in Table 3. In short, we used the method of Quinn et al. (2001b) to estimate overall predation rate (average annual percent of salmon killed, based on counts of live, bear-killed, and senescent dead salmon [$n = 16$–18 years among populations]) and the method of Gende et al. (2004a) to estimate the per day probability of predation on fish in each of the three focal creeks, based on daily observations of tagged fish. The average of daily predation rates during the first three days in stream was used as an estimate of selectivity of bears for newly arrived, energy rich salmon. We refer readers to these earlier papers for a thorough description of these estimation methods.

PHENOTYPIC TRAITS, FITNESS, AND SELECTION

The reproductive success of male salmon was estimated as the difference between the expected prereproductive gonad mass for a given body size (referred to as "reproductive potential") and the observed gonad mass at death (Schroder 1973; Semenchenko 1986, 1987; Fleming and Gross 1992). This difference accurately reflects the number of spawning events in which a male salmon participated (Fleming and Gross 1993). Moreover, this method is more integrative over the entire breeding period than the average of point estimates of social dominance (e.g., Quinn and Foote 1994), although the male's success in actually fertilizing eggs is not known in either case.

To use this approach, we first determined expected reproductive potential as a function of body length in each of the three study populations (Fig. 2) by sacrificing males of varying lengths from each population prior to breeding and measuring their gonads via

Table 3. **Overall predation rate and predator selectivity for newly arrived salmon breeding in Hansen, Yako, and Bear creeks, southwestern Alaska. The overall predation rate represents the average of the yearly percent of salmon killed by bears and the SD represents the among year variation in that percentage. Predator selectivity represents the average ±SD of the predicted daily predation rate on newly arrived (first three days in-stream), energy rich salmon. See Carlson et al. (2007) for further details on the calculation of these two indices of predation.**

Population	Overall predation rate (%) (mean±SD (years))	Predator selectivity for newly arrived fish (mean±SD)
Hansen	48.56^{A,1}±20.00	0.175^{C}±0.006
	(18)	
Yako	29.58^{B}±12.38	0.091^{D}±0.010
	(15)	
Bear	29.80^{B}±12.35	0.067^{D}±0.008
	(16)	

[A,B] Indicate the results of a nonparametric multiple comparison (Dunn) test. Groups sharing a common superscript do not differ from one another at α=0.05.

[C,D] Superscripts indicate the results of a comparison of 95% confidence intervals. Groups sharing a common superscript do not differ in mean predator selectivity for newly arrived fish at α=0.05.

[1] Note that some salmon strand and die at the mouth of Hansen Creek. If we instead calculate the percent of salmon killed by bears as a function of only those fish that successfully ascended the mouth (as opposed to the total number of fish returning to Hansen Creek), overall predation rate increases to 64%.

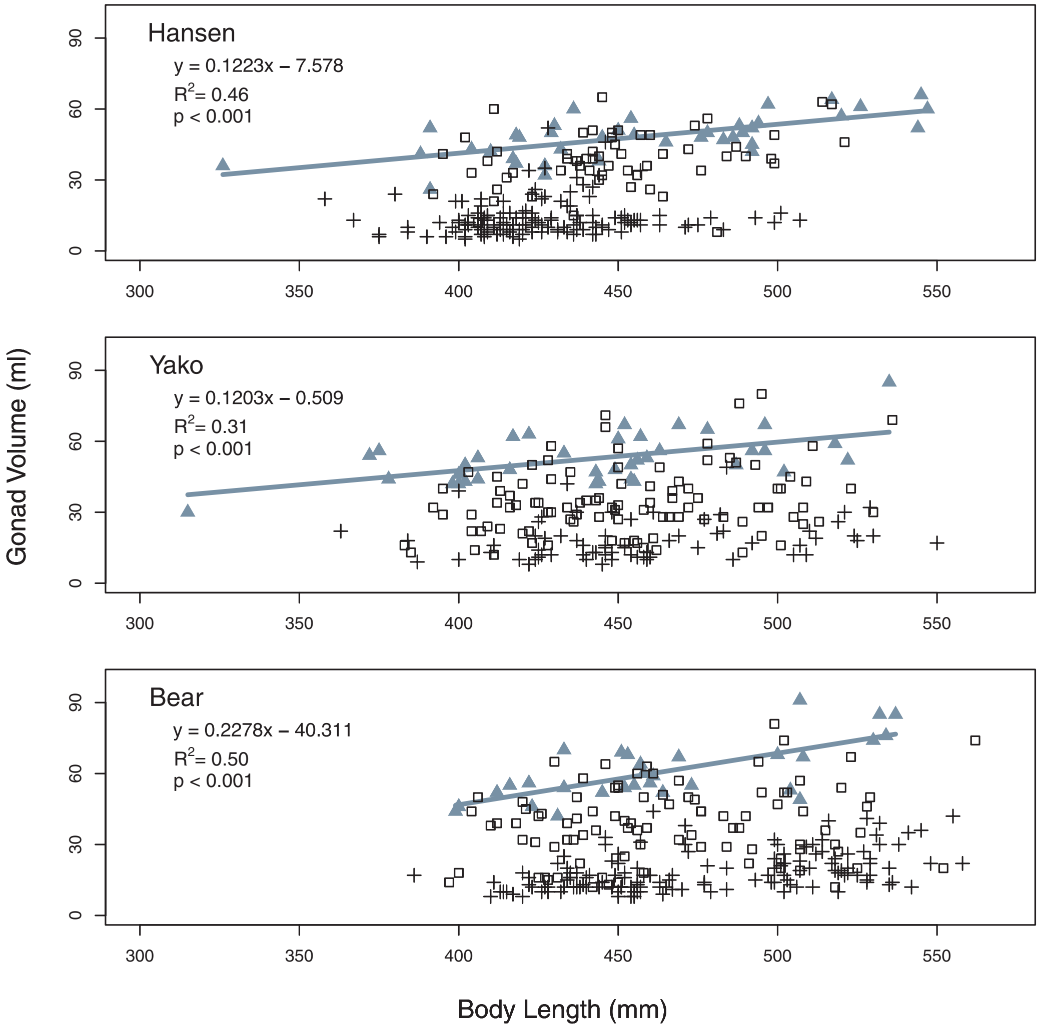

Figure 2. Gonad volume (y-axis) plotted against body length (x-axis) for male salmon from Hansen Creek (top), Yako Creek (middle), and Bear Creek (bottom). The results are grouped by status (sold gray triangles and regression line, prereproductive; open black squares, bear-killed; crosses, Senescent).

volume displacement ("prereproductive" males). We then sampled dead males on the spawning grounds, determined their gonad volume and mode of death, and estimated their reproductive activity as the difference between their gonad volume at death and their expected prereproductive gonad volume, given their length. We measured the male's body length (mid-eye to hypural plate), body depth (from the anterior insertion of the dorsal fin to the ventral surface of the fish), and jaw length (mid-eye to the tip of the upper jaw), as previous work has related these sexually dimorphic traits to male breeding opportunities (e.g., Fleming and Gross 1994; Quinn and Foote 1994). Data were collected in at least 2 years from each population (Bear and Yako: 2003–2004; Hansen 2003–2005) but were pooled to ensure adequate sample sizes for a robust analysis of selection (sample sizes presented in Table 4).

We analyzed selection on body length, body depth, and jaw length (trait means and standard errors provided in Table 4). Due to significant positive correlations between the traits (Table 5), relative jaw length and relative body depth were used in selection analyses instead of raw trait values. Relative trait values for these traits were estimated as residuals from their relationship with body

Table 4. Means±1 SE for the traits body length, body depth, and jaw length based on raw trait values. Numbers of individuals are indicated in parentheses.

Population	Trait		
	Body length	Body depth	Jaw length
Hansen	436.7±1.7	129.9±0.9	81.2±0.7
	(*n*=387)	(*n*=228)	(*n*=240)
Yako	451.8±2.7	142.5±1.5	87.3±0.8
	(*n*=205)	(*n*=146)	(*n*=202)
Bear	471.1±2.4	153.3±1.5	92.0±0.7
	(*n*=262)	(*n*=170)	(*n*=262)

Table 5. Bivariate (Pearson) correlations between all pairwise combinations of body length, body depth, and jaw length based on raw trait values. Sample sizes (*n*) are based on the subset of individuals for which both focal traits were measured. *$P < 0.001$.

Population	Trait–trait correlations		
	Body length–body depth	Body length–jaw length	Body depth–jaw length
Hansen	0.83*	0.80*	0.74*
	(n=228)	(n=240)	(n=221)
Yako	0.87*	0.82*	0.85*
	(n=146)	(n=202)	(n=145)
Bear	0.86*	0.80*	0.83*
	(n=170)	(n=262)	(n=170)

***P<0.001.

length (jaw length: Bear: $r^2 = 0.68$, $P < 0.001$, $n = 232$; Hansen: $r^2 = 0.53$, $P < 0.001$, $n = 201$; Yako: $r^2 = 0.66$, $P < 0.001$, $n = 164$; body depth: Bear: $r^2 = 0.74$, $P < 0.001$, $n = 140$; Hansen: $r^2 = 0.60$, $P < 0.001$, $n = 189$; Yako: $r^2 = 0.79$, $P < 0.001$, $n = 108$). As evident from variation in the above sample sizes, not all measurements could be obtained from all fish (e.g., owing to wounds from bear predation). We therefore performed two sets of selection analyses, one in which we estimated selection acting on length and relative jaw length and a second analysis in which we estimated selection acting on length and relative body depth. Sample sizes for the length/jaw length dataset were larger than for the length/depth dataset and the former dataset was therefore used in all analyses in which only data on length were required (e.g., regressions for generating the linear and quadratic length differentials, see below).

DATASETS FOR ESTIMATING SELECTION

Selection on the entire population depends, in part, on the relative frequencies of bear-killed and senescent salmon. The fish included in our selection analyses were a small proportion of the entire population (at least 2500 fish in each creek in each year, 2003–2004 data presented in Rich et al. 2006; 2005 data, Fisheries Research Institute, unpubl. data), and so may yield unrepresentative proportions of the two mortality categories. We therefore subsampled the fish in the selection analysis to more accurately represent the population as a whole. For instance, in the length and residual depth analysis for Bear Creek, we sampled 56 bear-killed males and 85 senescent males. The average annual percent of bear-killed fish in Bear Creek was 30% ($n = 16$ years, Table 3). For the selection analysis, we included 36 observations on bear-killed individuals and 85 observations on senescent individuals so that the proportion of bear-killed to senescent in the sample would match the population pattern (i.e., $36/(36 + 85) = 0.3$). This yielded 121 individuals to be included in the selection analysis, 30% of which had been killed by bears (i.e., 36 / 121) with the remaining 70% representing senescent individuals (i.e., 85/121). Details on the number of bear-killed and senescent individuals included in each selection analysis can be found in Table 6. To generate bootstrapped confidence intervals for these selection coefficients, we randomly sampled (with replacement) the 56 bear-killed individuals as well as 85 senescent individuals, merged the two datasets, performed the selection analyses (described below), and then repeated this procedure 10,000 times. This yielded a total of 60,000 selection analyses (10,000 each for the residual depth and residual jaw datasets for each of the three populations). We present the average selection coefficient and bootstrapped 95% confidence intervals based on Efron's percentile method (Efron 1982) as well as the median P-value based on the 10,000 random subsamples of each dataset.

Table 6. Sample sizes for selection analyses reported by the trait(s) included in the focal analysis. We report both the total number of bear-killed or senescent individuals sampled for gonad depletion and morphology ("Total") as well as the number of individuals from each mode of death category included in selection analyses ("Subsample"). The percentage of bear-killed and senescent individuals in the subsample reflects the long-term average annual percentage of bear-killed and senescent individuals at the population level. Note that the sample sizes for the residual depth analyses are subsets of the sample sizes for the body length and residual jaw analyses.

Traits Population	Total		Subsample	
	Bear-killed	Senescent	Bear-killed	Senescent
Body length × Residual jaw length				
Hansen	51	150	51	29
Yako	99	65	28	65
Bear	92	140	60	140
Body length × Residual body depth				
Hansen	46	143	46	26
Yako	53	55	24	55
Bear	55	85	36	85

ESTIMATING SELECTION

We used standard procedures for estimating the strength and form of selection (Lande and Arnold 1983; Brodie et al. 1995). Relative fitness was calculated as the absolute fitness (i.e., reproductive activity) of the individual divided by the mean absolute fitness of all individuals from that population and dataset. We present the average opportunity for selection based on the 10,000 selection analyses performed on each dataset (see above). All traits, as well as squared and cross-product terms, were standardized to a mean of zero and a standard deviation of unity within each population. Because larger males have larger gonads (Fig. 2), the maximum "reproductive activity" of large males exceeded that of small males. Examination of residual plots confirmed that the variance in residuals ($Y - \hat{Y}$) increased with increasing X values and we therefore $\log_e$-transformed relative fitness to meet assumptions of ordinary least squares regression (transformed $Y =$ natural $\log_e(Y + 1)$, Zar 1999). However, selection coefficients generated using transformed fitness measures are no longer unbiased point estimates (Lande and Arnold 1983). We therefore present the selection coefficients from the untransformed model but the P-value from the transformed model (Mitchell-Olds and Shaw 1987). The opportunity for selection (I) was estimated as the variance in relative fitness (Brodie et al. 1995).

Selection coefficients were estimated using four sets of linear regressions of relative fitness on trait values in each population. The first set used simple linear regressions of relative fitness on the traits independently (length, relative jaw length, relative body depth). The resulting regression coefficients represent "linear selection differentials," which estimate the total strength of selection (i.e., direct selection on a trait plus indirect selection through correlations with other traits). The second set used a multiple linear regression with both traits included (length and relative jaw length or length and relative body depth). These regression coefficients estimate "linear selection gradients," representing the strength of directional selection acting directly on each trait (i.e., independent of correlations with the other trait in the analysis). The third set used multiple linear regressions for each trait independently, together with its corresponding squared term. Twice the coefficients for the squared terms represent "quadratic (nonlinear) selection differentials" (Stinchcombe et al. 2008), which are often interpreted as representing the total strength of disruptive (when positive) or stabilizing (when negative) selection. The fourth set used a multiple linear regression including both traits, squared terms for each trait, and the cross-product term between the two traits. This final regression provided estimates of "univariate nonlinear selection gradients" (twice the squared terms) and "bivariate non-linear selection gradients" (cross-product terms), the latter representing correlational selection favoring combinations of traits that are similar (when positive) or dissimilar (when negative).

Coefficients derived from this selection analysis were compared to results from other studies of selection in nature (i.e., the 749 estimates compiled by Kingsolver et al. 2001). Univariate cubic splines (nonparametric regressions, Schluter 1988) were then used to visualize the form of selection acting on each trait in each population. For each trait and population combination, we used a normal model combined with a smoothing parameter (λ) to minimize the prediction error (body length: $\lambda = 6$ (all populations); relative jaw length: $\lambda = 4$ (all populations); relative depth: $\lambda = 2$ (Hansen), $\lambda = 4$ (Yako, Bear). We also used bivariate cubic splines (Schluter and Nychka 1994) to visualize correlational selection acting on combinations of: (1) body length and relative jaw length ($\lambda = -10$ for all populations) and (2) body length and relative depth ($\lambda = -10$ for all populations).

TRAIT DIVERGENCE AMONG POPULATIONS

We employed analysis of variance (ANOVA) to test for differences in mean body length among populations, followed by a post-hoc Tukey's test to determine which means differed from each other. We used analysis of covariance (ANCOVA) to test for differences among populations in length-standardized jaw length and body depth because these traits are strongly correlated with body length (Table 5).

To determine whether estimates of divergent selection corresponded with the observed trait variation among populations, we used ordered-heterogeneity (OH) tests (Rice and Gaines 1994a,b,c). OH tests generate a composite test statistic, which incorporates two sources of information: (1) the rank order of the parameter estimates and (2) the magnitude of the variation among the parameter estimates. The composite test statistic is calculated as

$$\text{OH test statistic} = r_s * P_c, \tag{1}$$

where r_s is the Spearman's rank correlation between the observed and expected rankings (here, observed rankings of size/shape means and the expected rankings are based on the rankings of the selection coefficients for size/shape). P_c is determined as

$$P_c = 1 - P_{ANOVA} \text{ (or } P_c = 1 - P_{ANCOVA}\text{)}, \tag{2}$$

where P_{ANOVA} represents the P-value from the nondirectional heterogeneity test. Critical values are provided in Rice and Gaines (1994c).

Results

The average annual percent of salmon killed by bears differed significantly among the three focal streams (Kruskal–Wallis statistic $= 11.57$, $P = 0.003$)—a result that was driven by the significantly higher predation rate in Hansen Creek (~50% killed) relative to both Bear (Dunn multiple comparison test, $P < 0.01$) and Yako creeks ($P < 0.05$), where roughly 30% of adult salmon were killed on average. The probability of being killed early in stream life also varied among populations and was significantly higher in Hansen Creek (95% C.I.: 0.16–0.19) than in either Bear (95% C.I.: 0.05–0.09), or Yako (95% C.I.: 0.07–0.12) creeks, which did not differ from one another based on nonoverlapping confidence intervals. Taken together, these two indices indicated that the intensity of predation was highest in Hansen Creek and lower in Yako and Bear creeks, which experienced similar levels (Table 3).

In all populations, gonad mass increased significantly with body size in prereproductive males (slope = 0.12 [Hansen], 0.12

[Yako], 0.23 [Bear]; $P < 0.001$ in all cases; Fig. 2). Predation by bears tended to reduce male breeding opportunities, as evidenced by the larger gonad volumes at death of bear-killed males relative to similar-sized senescent dead males (Fig. 2). Bear-killed males were estimated to have had less reproductive activity than senescent males, calculated as the difference between a male's gonad volume at death and his predicted prereproductive gonad volume. This result was consistent among creeks (one-sided *t*-test, $P < 0.001$ in all cases), indicating that bears were killing males before they had completed breeding and significantly reducing their potential reproductive success.

SELECTION ANALYSES

The average opportunity for selection (I) differed among populations and was consistently higher in Hansen Creek than in either Bear or Yako creeks (Tables 7–9). The strength and sign of directional selection also varied among populations (linear differentials and linear gradients, Table 7). Of the 18 coefficients (differentials and gradients), eight were positive and 10 were negative. Of these, three were significant ($\alpha = 0.05$), and five others were marginally significant ($P < 0.10$). Differentials and gradients were similar in sign and magnitude, suggesting that the use of residuals had effectively removed any correlation between body length and residual jaw length or residual body depth. In Hansen Creek, directional selection favored shorter males (differential $= -0.143$, $P = 0.078$ [52nd percentile from the Kingsolver et al. 2001 database]; gradient $= -0.140$, $P = 0.085$; Table 7). In contrast, directional selection favored longer individuals in both Bear Creek (differential $= 0.160$, $P < 0.001$ [55th percentile from the Kingsolver et al. 2001 database]; gradient $= 0.161$, $P < 0.001$; Table 7) and in Yako Creek (differential $= 0.077$, $P = 0.052$ [36th percentile from the Kingsolver et al. 2001 database]; gradient $= 0.080$, $P = 0.043$; Table 7).

Differences among populations in selection on jaw length and body depth, after accounting for the effects of body length, were suggestive but weak. Males with long jaws were favored in Hansen Creek (differential $= 0.055$ [29th percentile], gradient $= 0.052$) whereas males with short jaws were favored in both Bear (differential $= -0.031$ [18th percentile]; gradient $= -0.034$) and Yako (differential $= -0.069$, $P = 0.087$ [34th percentile]; gradient $= -0.072$, $P = 0.071$) creeks, but none of these coefficients were significant at the $\alpha = 0.05$ level (Table 7). Males with small dorsal humps were favored in both Hansen (differential $= -0.041$ [23rd percentile], gradient $= -0.085$) and Yako (differential $= -0.055$ [29th percentile], gradient $= -0.055$) creeks, whereas males with large dorsal humps were favored in Bear Creek (differential $= 0.021$ [14th percentile], gradient $= 0.025$), but again, none of these coefficients were significant (Table 7).

There was little evidence of stabilizing or disruptive selection on size and shape in the populations (univariate quadratic coefficients, Table 8). Of the 18 coefficients (differentials and gradients), eight were positive (suggestive of stabilizing selection), 10 were negative (suggestive of disruptive selection), and none was significant (all *P*-values > 0.25; Table 8).

Cubic spline plots confirmed the general interpretation of the body length and relative jaw length results (Figs. 3A, B, respectively) but suggested more complicated relationships between fitness and relative body depth (Fig. 3C). For instance, in Hansen Creek, cubic spline plots revealed a fitness peak near a relative depth of 0 mm, suggesting some evidence of stabilizing selection. In Bear Creek, on the other hand, cubic spline plots revealed a fitness valley suggesting disruptive selection.

Correlational coefficients, which reflect selection on combinations of traits, were always nonsignificant (Table 9) but some interesting patterns emerged. Positive correlational coefficients are interpreted as evidence that selection favors individuals with similar trait combinations (e.g., long fish with long jaws) whereas negative correlational coefficients are interpreted as selection favoring individuals with dissimilar trait combinations (e.g., long fish with short jaws). With only one exception (Yako Creek, body length × residual jaw length coefficient) the sign of the correlational coefficients agreed with the sign of the product of the two focal directional coefficients. For example, the negative correlational coefficients for body length × residual jaw length in Hansen Creek (Table 9), combined with a negative directional coefficient for body length but a positive coefficient for residual jaw length (Table 7) suggested that short individuals with long jaws were favored. Similarly, the positive correlational coefficients for body length × residual body depth in Hansen Creek (Table 9), combined with negative directional coefficients for both body length and residual body depth (Table 7) suggested that short individuals with shallow bodies were favored.

Bivariate cubic spline plots revealed complex relationships between combinations of trait values (Fig. 4). For example, in Hansen Creek, short individuals—particularly those with shallow bodies—had much higher fitness than individuals displaying other trait combinations (Fig. 4A,B). In Yako Creek, large body size conferred a fitness advantage (Fig. 4C,D) but increases in jaw length for a given body size were associated with a reduction in fitness (Fig. 4C). In Bear Creek, the longest individuals generally had the highest fitness; jaw length and body depth were apparently less important than length in determining overall fitness (Fig. 4E, F).

PREDICTED DIVERGENCE AND OBSERVED TRAIT VARIATION AMONG POPULATIONS

The populations differed significantly in average body length (ANOVA, $F_{0.05(1),2,851} = 70.313$, $P < 0.001$; Fig. 5). A Tukey's post-hoc test revealed differences among all three populations

Table 7. Directional selection acting on body length, residual jaw length, and residual body depth in Hansen Creek, Yako Creek, and Bear Creek salmon. We present bootstrapped confidence intervals (in parentheses) around the average selection coefficient (*b*) as well as the median *P*-value and opportunity for selection (*I*) based on 10,000 random subsamples of our data (see Methods).

Population		Linear selection differentials			Linear selection gradients		
		Body length	Residual jaw length	Residual body depth	Body length	Residual jaw length	Residual body depth[1]
Hansen	*b*	−0.143 (−0.298 to −0.015)	0.055 (−0.101 to 0.217)	−0.041 (−0.226 to 0.144)	−0.140 (−0.296 to 0.020)	0.052 (−0.101 to 0.206)	−0.085 (−0.276 to 0.108)
	P	0.078	0.415	0.46	0.085	0.432	0.309
	I	0.534	0.534	0.618	0.534	0.534	0.618
Yako	*b*	0.077 (−0.0004 to 0.153)	−0.069 (−0.151 to 0.013)	−0.055 (−0.139 to 0.026)	0.080 (0.002 to 0.155)	−0.072 (−0.154 to 0.009)	−0.055 (−0.139 to 0.026)
	P	0.052	0.087	0.18	0.043	0.071	0.183
	I	0.15	0.15	0.13	0.15	0.15	0.13
Bear	*b*	0.160 (0.108 to 0.210)	−0.031 (−0.086 to 0.025)	0.021 (−0.053 to 0.096)	0.161 (0.108 to 0.211)	−0.034 (−0.084 to 0.015)	0.025 (−0.047 to 0.095)
	P	<0.001	0.25	0.39	<0.001	0.183	0.351
	I	0.16	0.16	0.143	0.16	0.16	0.143

[1] Regressions included the subset of fish for which length and residual depth data were available. Only the residual depth coefficients are reported as the length coefficients closely corresponded to those generated from the regressions that instead included body length and residual jaw length.

Table 8. Univariate selection acting on body length (length × length), residual jaw length (residual jaw × residual jaw), and residual body depth (residual depth × residual depth); and bivariate selection acting on trait combinations (length × residual jaw; length × residual depth) in Hansen Creek, Yako Creek, and Bear Creek salmon. We present bootstrapped confidence intervals (in parentheses) around the average selection coefficient (*b*) as well as the median *P*-value and opportunity for selection (*I*) based on 10,000 random subsamples of our data (see Methods).

Population		Quadratic selection differentials			Quadratic selection gradients		
		Body length	Residual jaw length	Residual body depth	Body length	Residual jaw length	Residual body depth[1]
Hansen	*b*	0.217 (−6.323 to 7.394)	−0.105 (−0.434 to 0.234)	−0.031 (−0.401 to 0.333)	0.559 (−7.107 to 8.634)	−0.037 (−0.401 to 0.330)	0.066 (−0.315 to 0.420)
	P	0.551	0.405	0.521	0.537	0.479	0.493
	I	0.534	0.534	0.618	0.534	0.534	0.618
Yako	*b*	−0.875 (−3.819 to 1.853)	−0.075 (−0.235 to 0.072)	0.018 (−0.151 to 0.171)	−0.848 (−3.614 to 2.004)	−0.067 (−0.238 to 0.085)	0.018 (−0.160 to 0.178)
	P	0.5	0.348	0.473	0.503	0.448	0.48
	I	0.15	0.15	0.13	0.15	0.15	0.13
Bear	*b*	0.262 (−2.737 to 3.006)	0.035 (−0.092 to 0.148)	−0.020 (−0.204 to 0.171)	0.050 (−2.918 to 2.810)	−0.002 (−0.107 to 0.090)	−0.080 (−0.278 to 0.102)
	P	0.446	0.382	0.358	0.462	0.530	0.251
	I	0.16	0.16	0.143	0.16	0.16	0.143

[1] Regressions included the subset of fish for which length and residual depth data were available. Only the residual depth coefficients are reported as the length coefficients closely corresponded to those generated from the regressions that instead included body length and residual jaw length.

Table 9. Correlational selection acting on combinations of traits in Hansen Creek, Yako Creek, and Bear Creek. We present bootstrapped confidence intervals (in parentheses) around the average selection coefficient (*b*) as well as the median *P*-value and opportunity for selection (*I*) based on 10,000 random subsamples of our data (see Methods).

Population		Body length × residual jaw length	Body length × residual body depth
Hansen	*b*	−0.168 (−2.767 to 2.131)	1.699 (−1.978 to 4.949)
	P	0.526	0.227
	I	0.534	0.618
Yako	*b*	0.150 (−1.005 to 1.201)	−0.327 (−1.450 to 0.811)
	P	0.448	0.484
	I	0.15	0.13
Bear	*b*	0.391 (−0.304 to 1.094)	−0.010 (−0.766 to 0.780)
	P	0.224	0.527
	I	0.16	0.143

(95% C.I. around mean length [mm]: Hansen: 433–440; Yako: 447–457; Bear: 467–475). Because of the strong positive correlations between body length and both jaw length and body depth (Table 5), we tested whether the populations differed in size-standardized jaw and depth means using ANCOVA (Fig. 6). The interaction between jaw length and body length was not significant ($P = 0.391$, common slope = 0.240), facilitating a comparison of length-standardized means, which revealed that Hansen Creek males had shorter jaws than individuals from both Bear and Yako creeks ($P < 0.001$), which did not differ from each other ($P = 0.911$). When evaluated at the grand mean length of 453.37 mm, the trait means (mm) ± 1 SE were as follows: Hansen: 85.47 ± 0.44; Bear: 87.79 ± 0.42; Yako: 87.72 ± 0.47 (Fig. 6A). The interaction between body depth and body length was significant ($P = 0.005$) precluding a comparison of length-standardized body depths. However, over the range of lengths common to all three populations, the rank order of body depths at any given body length did not differ—Bear Creek fish had deeper bodies at each length, followed by fish from Yako Creek, and then fish from Hansen Creek (Fig. 6B).

Thus, Bear Creek fish were longer, deeper bodied, and had similar-sized jaws compared to fish from Yako Creek, which were longer, deeper bodied, and had longer jaws than Hansen Creek fish (Figs. 5 and 6). OH tests revealed that body length and length-standardized depth differed among populations in a manner consistent with interpopulation variation in selection differentials (body length: $r_sP_c = 1.0$, $k = 3$, $P < 0.001$; length-standardized body depth: $r_sP_c = 1.0$, $k = 3$, $P < 0.025$). Among-population variation in length-standardized jaw length, however, did not follow variation in the jaw length selection differentials ($r_sP_c = -0.5$, $k = 3$, $P > 0.90$) but instead followed interpopulation differences in body size.

Discussion

The overall goal of this study was to predict population divergence based on quantitative estimates of natural selection in the form of predation. Our analyses yielded several general conclusions. First, the intensity of bear predation was highest in Hansen Creek and similarly low in Bear and Yako creeks (Table 3). Second, the opportunity for selection, determined as variance in relative fitness for each population, was consistently higher in Hansen Creek than the other two creeks (Tables 7–9). Third, the patterns of linear selection differed markedly among the populations. Short, shallow-bodied males with relatively long jaws were favored in Hansen

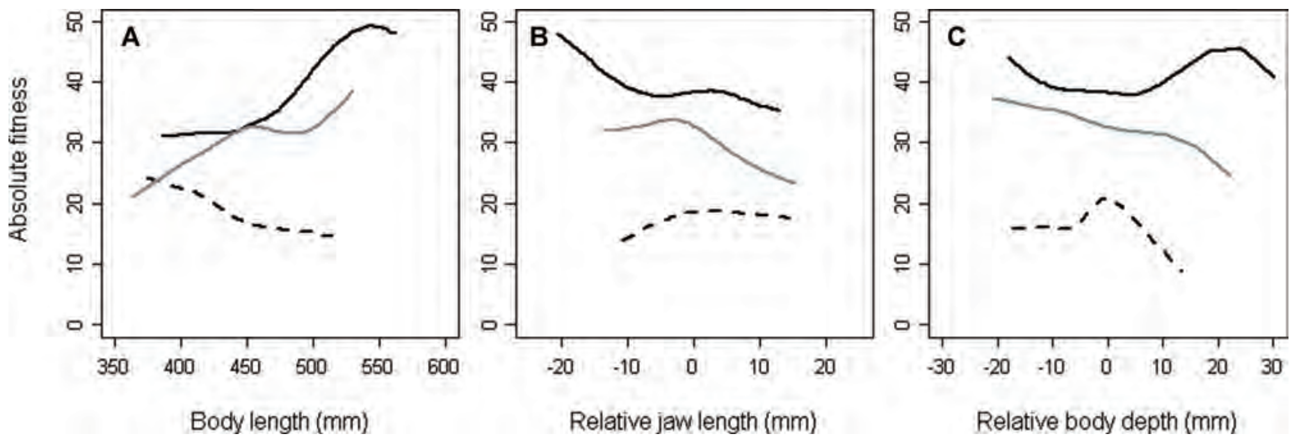

Figure 3. Relationship between an individual's absolute fitness and (A) body length, (B) relative jaw length, and (C) relative body depth of male sockeye salmon breeding in Hansen (dashed line), Yako (gray line), and Bear (black line) creeks. The lines represent univariate cubic splines (Schluter 1988).

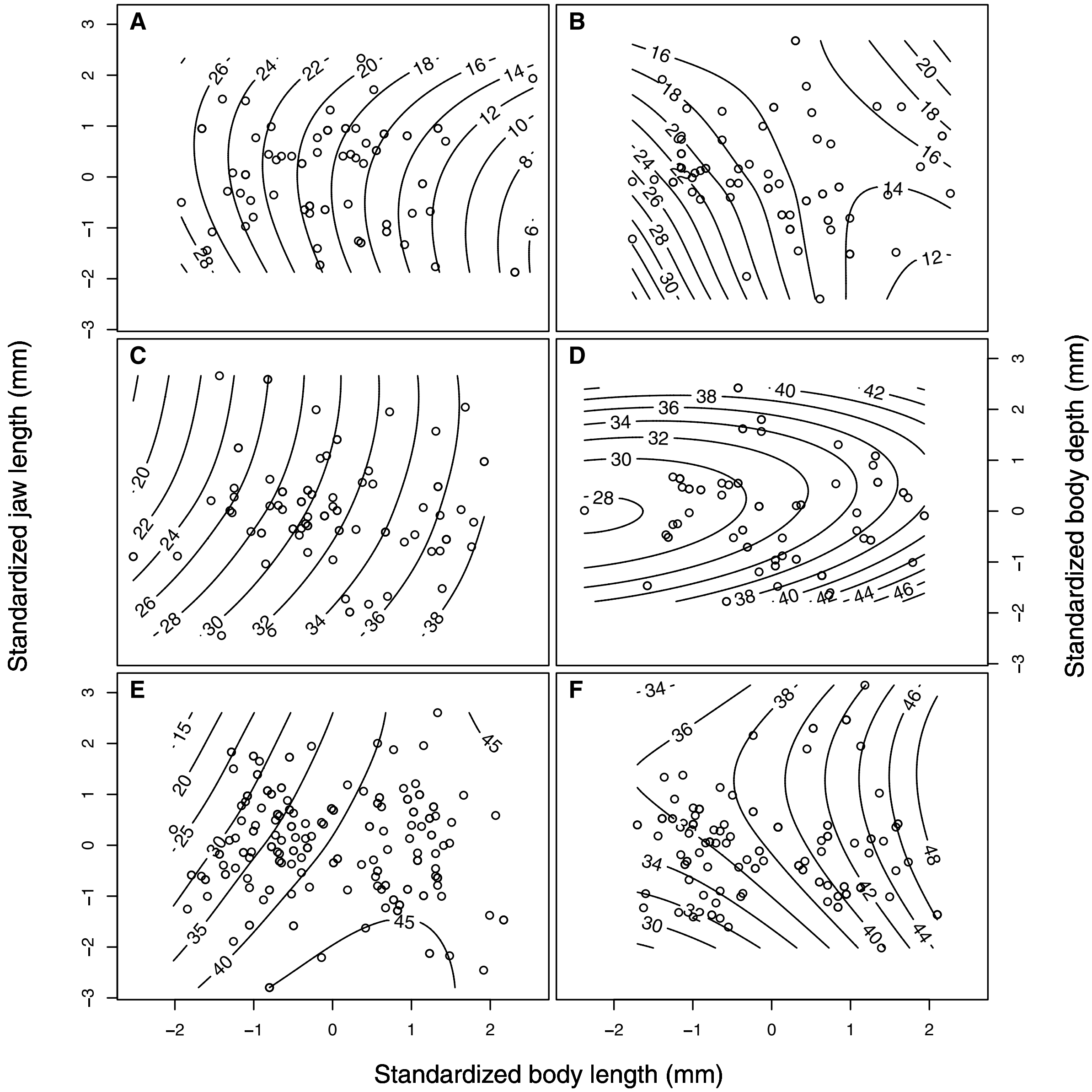

Figure 4. Bivariate spline estimation of the fitness surface relating standardized body length and either standardized jaw length (left column) or standardized body depth (right column) to an individual's absolute fitness in Hansen (A, B), Yako (C, D), and Bear (E, F) creeks. The contour lines represent an interpolated fitness surface, which was fit to the predicted fitness values generated using surface.exe (Schluter and Nychka 1994).

Creek whereas long males with short jaws were favored in Bear (together with deep-bodied fish) and Yako (together with shallow-bodied fish). Thus the combination of length and body depth, which would affect visibility to a predator and maneuverability in shallow water, were opposite in Bear and Hansen creeks, and intermediate in Yako Creek (Table 7). Third, quadratic selection (whether stabilizing or disruptive) varied in direction among traits and was never significant (Table 8). Fourth, correlational selection was nonsignificant (Table 9) but cubic splines revealed that correlational selection favored individuals that were both short and relatively shallow-bodied in Hansen Creek (Fig. 4)—a result that is consistent with the results of the directional selection analyses (Table 7). Finally, the strength of directional selection varied in a manner consistent with body length and depth variation among these populations (Bear > Yako > Hansen; for both body length and length-standardized depth, $P < 0.001$). Differences in size-standardized jaw lengths among populations instead paralleled differences in overall body size and not the variation in selection (relative jaw length: Hansen > Bear > Yako). These results demonstrate that variation in natural selection owing to bear predation may contribute to divergence among populations in the size and shape of sockeye salmon.

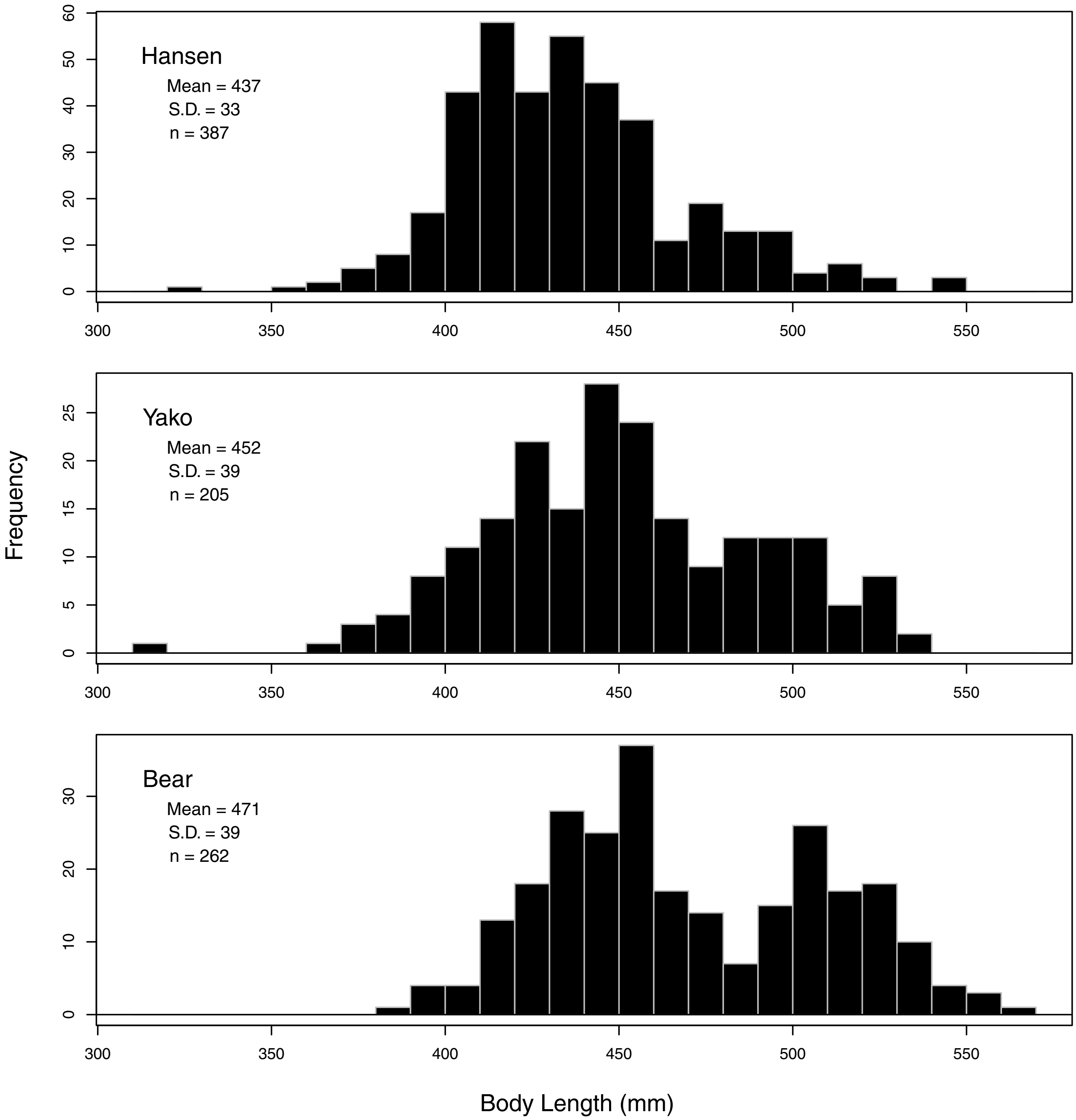

Figure 5. Population-specific length-frequency distributions for male salmon included in the selection analysis from Hansen Creek (top), Yako Creek (middle), and Bear Creek (bottom). For each population, we also report the mean and SD of length as well as the number of individuals represented.

STRENGTH OF SELECTION

Despite the evidence that selection due to bear predation was correlated with divergence in this system, the strength of selection was generally weak in comparison to other studies (i.e., compared to the studies included in Kingsolver et al. 2001). For instance, our median body length differential (0.143), relative jaw length differential (0.055), and relative body depth differential (0.041) corresponded with the 52nd, 29th, and 23rd percentiles from Kingsolver's review (Kingsolver et al. 2001). Moreover, our quadratic coefficients were never significant but sometimes strong in comparison to other studies (median length differential = 0.262, 82nd percentile; median relative jaw length differential = 0.075, 49th percentile; median relative depth differential = 0.020, 24th percentile). This latter result should be interpreted with caution because several studies included in the Kingsolver et al. (2001) review may have failed to double their quadratic coefficients

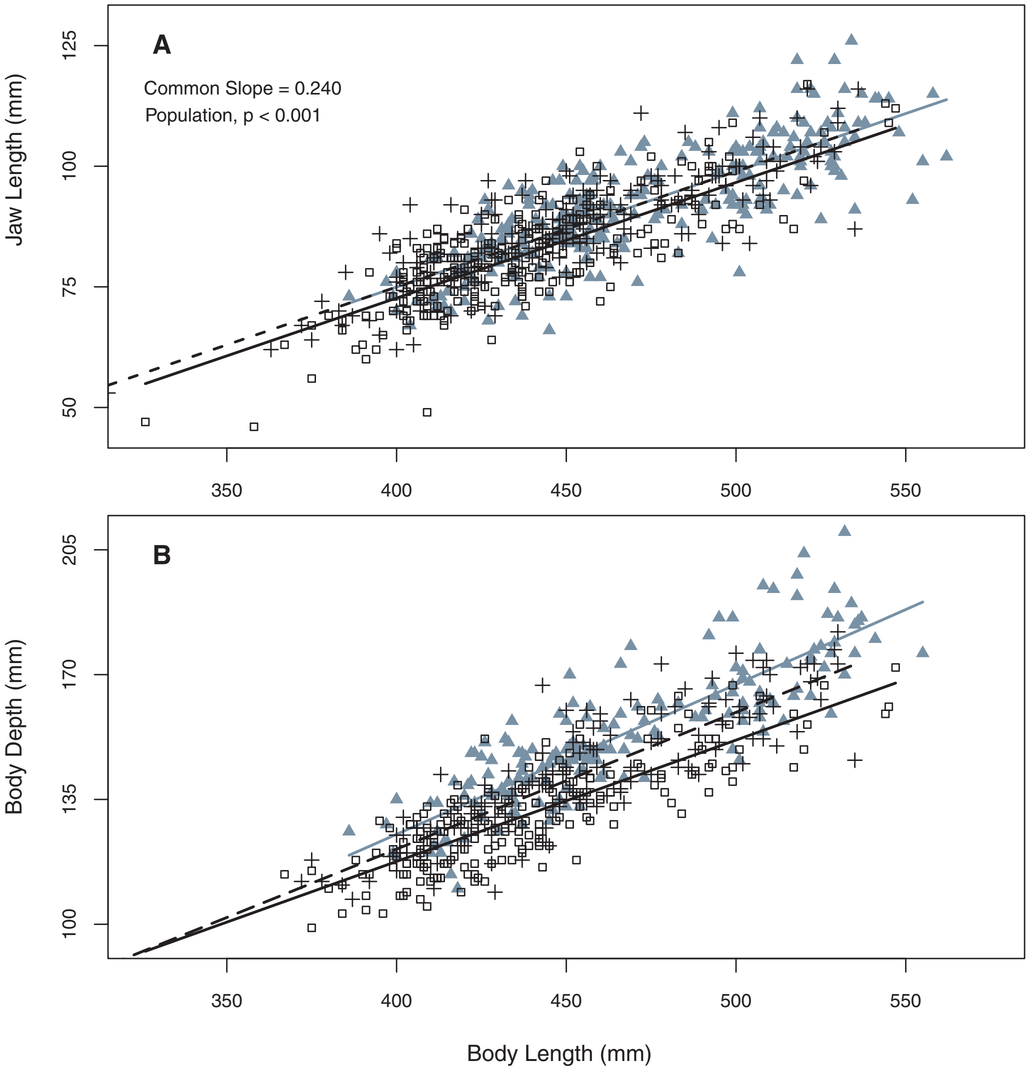

Figure 6. **Jaw length (A) and body depth (B) relative to body length for male salmon included in the selection analysis. Results presented by population: Hansen Creek (open squares, solid black line), Yako Creek (crosses, dashed black line), Bear Creek (gray triangles, gray solid line).**

and so may have reported quadratic regression coefficients as opposed to quadratic differentials/gradients (Stinchcombe et al. 2008).

Thus, on the one hand, we found that natural selection due to predation can drive divergence among populations. On the other hand, selection tended to be weak in our study populations relative to other studies of selection (Kingsolver et al. 2001), a result that might be due to low power to detect selection due to small sample sizes in some analyses (Table 6; Hersch and Phillips 2007). We interpret this as evidence that even weak selection (if temporally consistent) can drive evolution. Indeed, this same point was made by Hoekstra et al. (2001), who concluded that persistent weak directional selection (median $|\beta| = 0.15$), could shift the mean trait value in a population by one standard deviation in as few as 16 generations assuming a trait heritability = 0.5. Moreover, stronger selection in other studies (i.e., Kingsolver's database) suggests that those populations were even further out of equilibrium. Indeed, Kingsolver et al. (2001) reported that quadratic selection tended to be weaker than linear selection in natural populations and that stabilizing selection was no more common than disruptive selection.

EVOLUTIONARY EQUILIBRIA

If evolutionary equilibria among populations have been reached, each population should experience stabilizing selection around its mean. Alternatively, if equilibria have yet to be reached, each population should experience directional selection pushing the mean toward its adaptive peak (e.g., Schluter 2000). We found no evidence of stabilizing selection on any trait in any population. Rather, we found contrasting patterns of directional selection acting among populations. Results of the Kingsolver et al. (2001) review suggested that this result is generally true of natural populations—stabilizing selection tends to be quite weak in self-sustaining, natural populations. And yet self-sustaining populations are presumably well-adapted to their environments, so why might they be out of equilibria? There are several nonmutually exclusive explanations for the apparent lack of equilibria among wild, unmanipulated populations. Below we detail several explanations that are relevant to our focal salmon populations.

One possibility for the apparent lack of equilibria is that selection may be absent in these populations but we inadvertently sampled reproductively unsuccessful immigrants from other populations. This seems highly unlikely, given the strong natal homing in salmonids (Quinn et al. 1987, 1999), and the consistent differences in size, shape, and age among the populations (Quinn and Buck 2001; Quinn et al. 2001b). Precise estimates of straying rates are not available for these populations but are probably on the order of 1% of less. Such low rates of straying, combined with the numbers of spawning adults in the three focal populations (Table 2) make it unlikely that we measured a substantial number of immigrants.

A second possibility is migration with gene flow (i.e., reproductively successful strays). This would result in the production of offspring with maladapted phenotypes for the new environment and could thus be keeping the recipient population from attaining equilibrium. But, as stated above, straying rates are low and population sizes are large (Table 2), so this possibility also seems implausible. Lin et al. (2008) reported phenotypic but no genetic differentiation among three geographically proximate populations of sockeye salmon spawning in Lake Aleknagik, and concluded that divergent natural selection was overriding the homogenizing effects of gene flow. The three populations studied by Lin et al. (2008) are all clustered spatially on the east side of the lake and include one of our study populations (Hansen Creek). Bear and Yako creeks are located on the west side of the lake (Fig. 1) and further work by J. Lin (unpubl. data) revealed significant differences between populations occurring on opposite sides of the lake (Hansen and Yako, $F_{\mathrm{ST}} = 0.0085$, $P < 0.05$ after Bonferroni correction). Together these two results suggest that genetic differences are, at least in part, driven by geographic proximity (i.e., isolation-by-space). Thus, migration between these populations is probably not solely or primarily responsible for the lack of equilibria, although the process may contribute to the lack of equilibria for geographically proximate populations.

A third possibility is opposing selection at some other life stage. The observed contemporary selection acting in these populations may be maintained in part by earlier episodes of selection favoring different values of size and shape (e.g., Schluter et al. 1991). One selective agent that can influence the evolution of fish populations is commercial fishing. Sockeye salmon returning to the Wood River Lakes system are subjected to an intense commercial fishery using gillnets that are size-selective to some extent (Burgner 1964; Bue 1986; Hamon et al. 2000; Kendall and Quinn 2009; N. W. Kendall, J. J. Hard, and T. P. Quinn, unpubl. ms.). The individuals we sampled in each population, therefore, represent only the subset of individuals that "escaped" the fishery. The evolutionary effect of the fishery on these populations is currently unknown, but fishery selection is a plausible explanation for why these populations are not in equilibria or at least may be a contributing factor.

Selection from fishing will act on all populations, but to varying extents depending on their size and shape. There are, however, other forms of size-selective mortality that affect the populations unequally. In Hansen Creek, many salmon strand at the shallow creek mouth and die prior to reaching the breeding grounds, and this stranding mortality is heavily selective against large males (Quinn and Buck 2001; Carlson and Quinn 2007). Differences in the interface between the creek and the lake make this mortality especially severe at Hansen Creek, much less so at Yako Creek, and nonexistent at Bear Creek. We did not incorporate stranded fish in our analysis but had we done so the strength of selection against large males would have been greatly magnified in Hansen Creek, as the two sequential episodes of selection both favor short, shallow-bodied individuals, suggesting that this population is even further out of equilibrium than our selection differentials indicated. Although we focused our analyses on males, large females are also selectively killed by bears (Quinn and Buck 2001), and selection against large size in males is presumably correlated with selection against large size in females. Indeed, this is evident in the selection due to stranding (Carlson and Quinn 2007).

A fourth possibility is fluctuating selection among years due to shifting adaptive landscapes. Work on Darwin's finches demonstrated that adaptive landscapes may not be static but rather can shift temporally as the abundance of seeds of varying sizes fluctuates. For example, large individuals of the medium ground-finch (*Geospiza fortis*) were favored in some years (following droughts when large seeds were abundant) whereas smaller birds were favored following wet years when small seeds were abundant (Grant and Grant 2002). Fluctuating selection is exceedingly common in natural populations (A. M. Siepielski, S. M. Carlson, and J. D. DiBattista, unpubl. ms.) and has been documented in several salmonid populations (e.g., Hendry et al. 2003; Carlson and Quinn 2007; Seamons et al. 2007; Carlson et al. 2008). In our system, the intensity and strength of selection may differ among years due to, for instance, the density of salmon and/or bears. No study has yet related year-specific quantitative estimates of selection within a system to the intensity of predation in that year, but this would certainly be a profitable area for future research. The density of breeding salmon varies greatly among years in each creek (Table 2) and the proportion of salmon killed decreases with density

(Quinn et al. 2003). The strength of selection might covary positively with salmon density, if high salmon availability causes bears to preferentially remove large, energetically rewarding, individuals. Such nonstatic adaptive landscapes could certainly be contributing to the lack of equilibria in these populations.

We believe that the potential for adaptive landscapes to shift is particularly germane to the temporal trajectory of the strength and form of selection. If adaptive landscapes shift regularly (e.g., in response to local environmental conditions), selection acting to push a population toward the current adaptive peak may be acting in the wrong direction based on the adaptive landscape that will be encountered by future generations. We might therefore expect that natural populations will rarely be in evolutionary equilibrium and that directional selection should be common. Based on this view, the strength of directional selection would depend on the location on the adaptive landscape in the current generation, which is itself based on the response to selection acting on the previous generation, as well as the steepness of the adaptive peak, which can be estimated as the opportunity for selection. Long-term studies estimating the temporal stability of fitness surfaces are needed to test the above ideas.

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