TEN YEARS OF VARYING LAKE LEVEL AND SELECTION ON SIZE-AT-MATURITY IN SOCKEYE SALMON

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Abstract. Despite the ubiquity of studies quantifying the strength and form of selection in nature, rarely is the ecological context for contemporary selection understood. Here we report a case where lake level is a selective factor acting on sockeye salmon body size-at-maturity because low lake levels cause large salmon to strand and die rather than reach the breeding grounds. As a result of a semelparous life history, death for salmon at this stage results in a lifetime fitness of zero. We combined information on the level of Lake Aleknagik (southwestern Alaska, USA) from 1952 through 2006 with a detailed comparison of the body size of mature salmon that died at the mouth of Hansen Creek vs. individuals that successfully ascended to the spawning grounds over 10 breeding seasons (1997–2006). The percentage of salmon stranding at the mouth varied among years: 2–42% in males and <1– 26% in females. Formal selection analyses indicated that the largest individuals were most susceptible to stranding mortality, especially in years when many salmon stranded, and these were years with low lake levels. Taken together, these results suggest that lake level was a strong and consistent selective force acting on this salmon population, acting synergistically with size-selective predation by bears. Salmon breeding in Hansen Creek tend to be smaller, younger, and more streamlined than conspecifics from neighboring populations, suggesting that selection against large individuals could be driving these patterns.

Key words: body size; climate; Lake Aleknagik, Alaska, USA; life-history traits; natural selection; Oncorhynchus nerka; reproductive success; selection in sockeye salmon; survival; water level.

The biotic and abiotic environment is the context that gives rise to the relationship between phenotype and fitness (selection). The analysis of the causes of selection is in essence a problem in ecology.

—Wade and Kalisz (1990:1947)

INTRODUCTION

A plethora of research has documented the strength and form of selection in natural populations (see reviews in Endler [1986] and Kingsolver et al. [2001]), yet the ecological context for selection is rarely understood. This is unfortunate because a complete understanding of selection in nature requires knowledge of the factors driving selection (Endler 1986). Selection pressures are context-dependent and likely fluctuate in both space and time due to variation in biotic and abiotic factors. For example, spatial variation in selection due to predation resulted in different populations of guppies (*Poecilia reticulata*) evolving differences in color patterns (e.g., Endler 1978, 1980) and life-history traits (e.g., Reznick et al. 1996, 2004).

Climate variation has also been implicated as a factor driving variation in selection. Some of this research examined selection during a single, short-term climate perturbation whereas other studies focused on longer time series of selection and environmental conditions. The most well-known example of the former is Bumpus' analysis of selection on house sparrows (*Passer domesticus*) after a severe storm (Bumpus 1899), which revealed that smaller birds were more likely to survive the storm than large ones. Long-term studies have also revealed the importance of strong episodes of selection due to short-term, variable climate events. For instance, in a 30-year study, Grant and Grant (2002) demonstrated that the Medium Ground-Finch (*Geospiza fortis*) experienced multiple episodes of natural selection on beak size as a consequence of El Niño and La Niña events, which influenced the amount of rainfall and hence the kind of seeds that were available (large, hard seeds available after droughts favored birds with large beaks; small, soft seeds available after wet years favored birds with small beaks).

In aquatic systems, flow regimes and water level likely represent powerful agents of selection (Lytle and Poff 2004). In natural/pristine (non-regulated) lake systems, water level provides an integrated measure of climate variability both among and within years due to shifting balance of inputs (from tributaries, precipitation, and groundwater) and losses (to outflow, evaporation, and
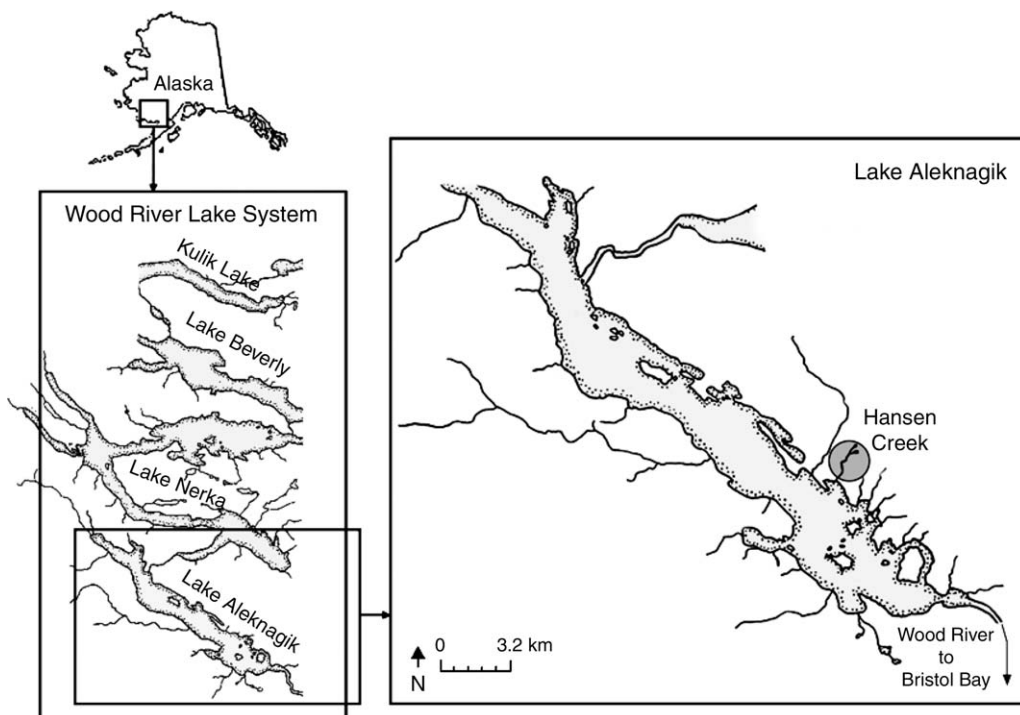
FIG. 1. Map of Hansen Creek and Lake Aleknagik relative to the Wood River Lakes, southwestern Alaska, USA.

transpiration). The edges of lakes are important breeding and foraging habitat for many organisms, and fluctuations may therefore have diverse effects. Moreover, fluctuations in lake level have been implicated as a factor driving evolutionary change (e.g., the diversification of cichlids in Lake Malawi, Owen et al. 1990). Using a long-term data set, we investigate whether climate-induced variation in lake level is a selective factor acting on body size-at-maturity in a population of sockeye salmon (*Oncorhynchus nerka*).

The system

The life history of sockeye salmon includes both anadromy and semelparity (Burgner 1991, Quinn 2005). Adults lay their eggs in the gravel of streams, rivers, or along the beaches of lakes in late summer and fall, and the free-swimming fry emerge the following spring. Juveniles typically rear in lakes for one or two years prior to migrating to the North Pacific Ocean where they spend another 1–3 years feeding and growing. Maturing adults migrate back into freshwater during early summer, complete maturation, and then make the final transition from the lake to their natal sites where they breed and die. Here we study this last critical transition—from the lake into the stream where they breed. Mortality at this stage results in a lifetime reproductive fitness equal to zero.

Herein, we ask whether the mortality at the mouth of a stream (Hansen Creek; Fig. 1) is selective on the basis of sex or body size. We measured individuals that died

as they attempted to ascend the shallow mouth of this creek and individuals that died in the creek itself (i.e., successfully ascended the mouth) over 10 breeding seasons (1997–2006). We then performed formal selection analyses to determine the intensity of size-selective mortality for each combination of year and sex. We predicted that lower lake levels during the migration period would increase the proportion of the population dying at the mouth, and that male salmon would be more likely to strand than females because males are both longer and deeper bodied than females (Quinn and Buck 2001). We also predicted that lower lake levels during the migration period would increase the strength of size-dependent stranding mortality, and that the strength of selection on male salmon would exceed that on female salmon due to the aforementioned differences in body size. Finally, we determined whether or not there was a long-term trend in lake level during the salmon migration period, and used regional environmental-data sources to develop a simple model for understanding the factors affecting this variable.

MATERIALS AND METHODS

Study area and data collection

Hansen Creek is a small, spring-fed creek that flows 2 km from a beaver pond to Lake Aleknagik in the Wood River Lakes system of southwestern Alaska (Fig. 1). The creek is both narrow (averaging 3.9 m wide) and shallow (averaging 10 cm deep) during the July–August breeding period (Marriott 1964), making it amenable for daily

TABLE 1.　Ten years of data on sockeye salmon returning to Hansen Creek from Lake Aleknagik, Alaska, as well as the proportion stranding at the mouth.

	Males					Females				
			Body length of all fish†					Body length of all fish†		
Year	Total no. salmon returning	Proportion stranding at mouth	Mean	SD	Proportion with 3 yr in ocean‡	Total no. salmon returning	Proportion stranding at mouth	Mean	SD	Proportion with 3 yr in ocean‡
1997	4192	0.11	473.04	36.74	0.22	4259	0.04	454.89	35.65	0.07
1998	6389	0.11	428.04	25.65	0.07	7257	0.07	415.44	20.68	0.07
1999	7150	0.23	438.90	29.50	0.03	12 354	0.13	421.46	22.75	0.03
2000	1556	0.11	477.25	33.30	0.84	1904	0.06	452.51	34.99	0.63
2001	1078	0.02	495.45	32.87	0.74	898	<0.01	477.93	33.32	0.80
2002	3605	0.09	449.41	38.33	0.13	4483	0.10	429.13	29.93	0.07
2003	4858	0.24	441.12	31.31	0.03	6288	0.17	425.75	25.87	0.06
2004	1298	0.42	455.66	39.06	0.22	2169	0.26	431.29	29.38	0.17
2005	1937	0.12	436.46	32.23	0.12	1991	0.12	423.75	24.80	0.12
2006	7075	0.31	410.47	24.08	0.03	13 365	0.25	402.22	17.79	0.02

† Average body length of all fish regardless of their fate.

‡ Proportion of the salmon that had spent three years growing in the ocean prior to returning to fresh waters to breed.

surveys over the entire salmon-breeding season. The flow of Hansen Creek itself is very steady, neither flooding after rain nor diminishing after dry periods. For instance, discharge was recorded on each of four occasions between 20 July and 9 August in both 2004 and 2005 and, in both years, the discharge varied little during this period when salmon were in the stream (2004 discharge = 0.07 ± 0.013 m^3/s [mean ± SD]; 2005 discharge = 0.04 ± 0.015 m^3/s; J. Moore, *unpublished data*). However, the reach where the creek drains into Lake Aleknagik is controlled by lake level rather than stream discharge. Our records indicate a virtually linear relationship between lake level and the distance across this delta because the slope of the beach is nearly constant (i.e., lake level vs. distance with water <15 cm deep: $r^2 = 0.99$; T. Quinn, *unpublished data*), thus lake level determines distance across the delta. When the lake is high, salmon can easily swim into the creek but when the lake is low they struggle over more than 30 m of water only a few centimeters deep to reach the creek. Salmon that cannot maintain forward motion and lose their equilibrium fall on their side, desiccate and die, or attacks by Glaucous-winged Gulls (*Larus glaucescens*) hasten their death.

Since 1997, daily surveys of the entire creek were conducted over the course of the salmon–breeding season. All live and dead salmon were enumerated, and records of each individual's sex, and mode and location of death (e.g., stranded at the mouth, bear-killed or senescent in the upper reaches of the creek, etc.) were taken. From these data, we determined the proportion of the total population that died at the creek mouth in each year (Table 1). Furthermore, for a subset of these fish, body length was also measured (mid-eye to hypural plate, Table 2). This measurement of body length is not biased by the extended jaws that characterize mature males, and so facilitates a comparison of size between the sexes. Each breeding season, sagittal otoliths (ear bones) were collected from 100

individuals of each sex for age determination, allowing us to estimate the proportion of the population spending 2 or 3 years in the ocean before returning to freshwater to breed (no age-1 females were observed and age-1 males make up only 1.7% of the males on average and so were excluded from this analysis, Quinn et al. 2001*b*: Table 3).

Lake level

Since 1952, Fisheries Research Institute personnel have measured the level of Lake Nerka, directly upstream of Lake Aleknagik (Fig. 1), from a fixed location throughout the summer. In general, the lake level rises in early June as snow melts, then drops from late June to late August because the snow has all melted and the weather is generally dry, and then the lake rises with fall rains before it freezes in winter. However, more than 1 m variation has been observed among years at any given period of the season. Since 1999, similar data have been collected for Lake Aleknagik. To estimate Lake Aleknagik levels that Hansen Creek salmon would have experienced during the past decades, we developed a relationship between the water levels of the two lakes. The arrival patterns of fish into Hansen Creek each year (determined from the daily surveys) revealed that the 15-day period (23 July–6 August) centered around the median date (30 July) encompassed on average 78.2% of the arrivals (mean of annual means; range: 60.6–99.1%). Regression of the average levels of the two lakes during this period revealed a very close correspondence ($r^2 = 0.96$, $P < 0.001$, $n = 8$ years), allowing us to estimate Lake Aleknagik's level from Lake Nerka data in the years for which no Lake Aleknagik data were available. However, despite the strong relationship between the two lake levels, all eight data points used to generate the Lake Aleknagik extrapolation were derived from the end of the time series and so it is conceivable that the correlation was weaker in earlier years.

TABLE 2. Total number of salmon, by sex, that died at the mouth of Hansen Creek (i.e., stranded) and that died in the stream (i.e., successfully ascended the mouth), together with the total number of fish in each category that were measured for body length, the number that were included in the selection analysis, and the total sample size for each selection analysis.

	No. fish dead		No. fish measured		No. subsampled for selection analysis		
Year	At mouth	Instream	At mouth	Instream	Mouth	Instream	Total
Male							
1997	480	3712	327	1345	174	1345	1519
1998	696	5693	434	2825	345	2825	3170
1999	1655	5495	1429	892	269	892	1161
2000	176	1380	146	962	123	962	1085
2001	18	1060	10	677	10	589	599
2002	313	3292	180	1383	131	1383	1514
2003	1174	3684	539	1238	395	1238	1633
2004	539	759	334	447	317	447	764
2005	238	1699	198	920	129	920	1049
2006	2204	4871	498	866	392	866	1258
Female							
1997	155	4104	112	1628	61	1628	1689
1998	514	6743	193	3795	193	2532	2725
1999	1612	10 742	1353	1482	222	1482	1704
2000	115	1789	90	1171	75	1171	1246
2001	1	897	0	548	n/a	n/a	n/a
2002	440	4043	193	1460	159	1460	1619
2003	1084	5204	336	1492	311	1492	1803
2004	568	1601	378	1217	378	1065	1443
2005	245	1746	198	1556	198	1411	1609
2006	3284	10 081	649	1708	556	1708	2264

Note: In 2001 all but one female ascended the mouth, so no selection analysis was possible for those data (indicated by "n/a" in the table).

Data sets for estimating selection

Not all individuals were measured for body length, and the proportions measured often differed between those stranded at the mouth and those that successfully ascended the creek. To prevent bias in the analyses, we subsampled the fish that were measured so that the proportion of fish included in the analyses that stranded at the mouth or ascended into the creek corresponded with the population-level patterns in that year. For example, in 1997, 11% of the males stranded at the mouth and the other 89% of males successfully ascended into the creek's spawning grounds (Table 1). Of the 4192 males that returned to Hansen Creek in 1997, 1672 were measured for body length (327 that stranded at the mouth + 1345 that died in the creek; Table 2). For the selection analyses, we therefore included 1345 observations on successful males but only 174 observations on unsuccessful males so that the proportion of unsuccessful to successful would correspond to the population-level pattern (i.e., $174/(174 + 1345) = 0.11$; Table 2). To generate bootstrapped confidence intervals for our selection coefficients, we randomly sampled (with replacement) 174 unsuccessful males as well as 1345 successful males, merged the two data sets, performed

TABLE 3. Selection acting on body size-at-maturity in sockeye salmon.

	Males				Females			
	Logistic selection differential, b				Logistic selection differential, b			
Year	Mean	95% CI	P	I	Mean	95% CI	P	I
1997	−1.041	≤−0.824 to ≤−0.606	<0.001	0.129	−1.178	≤−0.808 to ≤−0.443	<0.001	0.037
1998	−0.444	≤−0.338 to ≤−0.232	<0.001	0.122	−0.538	≤−0.403 to ≤−0.255	<0.001	0.076
1999	−0.661	≤−0.521 to ≤−0.378	<0.001	0.302	−0.586	≤−0.460 to ≤−0.333	<0.001	0.150
2000	−0.807	≤−0.573 to ≤−0.368	<0.001	0.128	−0.686	≤−0.418 to ≤−0.154	0.001	0.064
2001	−0.793	≤−0.145 to ≤0.437	0.478	0.017	n/a	n/a	n/a	n/a
2002	−0.657	≤−0.492 to ≤−0.321	<0.001	0.095	−0.291	≤−0.151 to ≤0.003	0.050	0.109
2003	−0.563	≤−0.448 to ≤−0.334	<0.001	0.319	−0.651	≤−0.516 to ≤−0.391	<0.001	0.209
2004	−1.014	≤−0.845 to ≤−0.678	<0.001	0.710	−0.670	≤−0.549 to ≤−0.435	<0.001	0.355
2005	−1.110	≤−0.898 to ≤−0.709	<0.001	0.140	−0.592	≤−0.457 to ≤−0.319	<0.001	0.140
2006	−0.568	≤−0.435 to ≤−0.305	<0.001	0.453	−0.368	≤−0.267 to ≤−0.177	<0.001	0.326

Notes: We report the average logistic selection differential (b) with bootstrapped 95% confidence intervals based on Efron's percentile method (Efron 1982); median P value, and the opportunity for selection (I) based on 1000 random subsamples of our data (see *Materials and methods: Data sets for estimating selection*). In 2001 all but one female ascended the mouth, so no selection analysis was possible for those data (indicated by "n/a" in the table).

the selection analysis (see below), and then repeated this procedure 1000 times. This yielded a total of 1000 selection analyses for each sex and year combination. We present the average selection coefficient with bootstrapped 95% confidence intervals based on Efron's percentile method (Efron 1982) as well as the median P value based on the 1000 random subsamples of our data.

Selection analyses

We used standard procedures (Lande and Arnold 1983, Brodie et al. 1995, Janzen and Stern 1998) to estimate the strength and form of selection acting on length-at-maturity across 10 breeding seasons varying in lake level. A fish that successfully ascended the creek mouth (i.e., survived the mouth) was assigned an absolute fitness of 1 whereas a fish that stranded at the creek mouth (i.e., died at the mouth) was assigned an absolute fitness of 0. Fish that died at the mouth did not breed at all, as all breeding sites are farther upstream. However, not all fish that ascended to the breeding grounds would have equal opportunities to breed (Quinn et al. 2001a), and the realized reproductive success would certainly have varied among even the breeders (e.g., Dickerson et al. 2005). Thus the binary code is a great oversimplification but it serves to focus on the selection associated with migration past the mouth and effect of the climate-related factor. Table 2 provides details on the numbers of fish with data for body length during each breeding season, as well as the number of those fish successfully ascending the creek mouth. An individual's relative fitness was then determined by dividing its absolute fitness by the mean absolute fitness of all individuals of that sex in that breeding season (Lande and Arnold 1983, Janzen and Stern 1998). The opportunity for selection (I) in each breeding season was calculated as the variance in relative fitness.

We estimated selection during each breeding season as the regression of relative fitness on standardized body length (standardized to a mean of 0 and a standard deviation of 1), using logistic regressions because of the dichotomous nature of the response variable (Janzen and Stern 1998). Coefficients from these regressions estimate logistic selection differentials, which represent the total strength of selection acting on body length (i.e., direct selection on the trait plus indirect selection acting through correlations with other traits).

Finally, we used univariate cubic splines (Schluter 1988) to visualize the relationship between absolute fitness and body length for each combination of year and sex. In 2001, however, few individuals died at the mouth of Hansen Creek (2% of males, <1% of females) and so no cubic splines were generated for these data. To generate year- and sex-specific cubic splines, we used only a single representative sub-sample of data (see *Data sets for estimating selection*, above). Specifically, we generated splines based on a subsample of data that closely approximated the average selection coefficient

and P value based on 1000 random samples for that year and sex combination (i.e., the values presented in Table 3). We used a binomial model in combination with a smoothing parameter (λ) to minimize prediction error (male body length, $\lambda = 6$; female body length, $\lambda = 6$).

Results

In total, 94 106 dead Hansen Creek sockeye salmon were examined, and of these 16% died at the mouth, never having reached the breeding grounds. The proportion of fish stranding at the mouth of the creek varied between the sexes and among the years (Table 1). As predicted, in a given year, a larger proportion of males stranded at the mouth of Hansen Creek than females (Wilcoxon one-sided paired-sample test, $n = 10$ years, $T_{min} = 3$, $P = 0.005$). There was a close correspondence between the proportions of males and females stranding among years (Spearman rank correlation coefficient, $r_s = 0.88$), suggesting that both sexes were susceptible to stranding when conditions for creek entry were suboptimal. For both males and females, stranding mortality was lowest in 2001 (2% of males, <1% of females; Table 1) and highest in 2004 (42% of males, 26% of females; Table 1). Moreover, the proportion of fish stranding at the mouth was positively related to lake level, although this relationship was only apparent after ignoring one outlier, 1997, when the lake was exceptionally low but the proportions stranding were moderate. Analysis of the other years indicated a strong relationship between lake level and the proportion stranding for both males (ordinary least squares [OLS] regression, $F_{1,7} = 8.774$, $r^2 = 0.56$, $P = 0.021$, Fig. 2A) and females (OLS regression, $F_{1,7} = 27.542$, $r^2 = 0.80$, $P = 0.001$, Fig. 2C).

The opportunity for selection (i.e., variance in relative fitness) also varied between the sexes, within a year, as well as among years for a given sex (Table 3). With few exceptions, the opportunity for selection in males exceeded that in females (Table 3). For both sexes, the opportunity for selection was strongest in 2004. For males, the opportunity for selection was weakest in 2001, and in that year all but one female successfully ascended the mouth and so no selection analysis was performed on these data. Considering only the subset of years included in the selection analysis, the opportunity for selection was weakest in 1997 for females (Table 3). Averages and variances for body length differed between the sexes, within a year, as well as among years, within a sex (Table 1). Coefficients of variation for body length were large enough that selection should have substantial substrate to act on (range: 5.9–8.6% and 4.4–7.8% for males and females, respectively).

The strength of directional selection varied among years within a sex (Table 3) but several general patterns emerged. First, for both males and females, selection always favored shorter individuals as differentials were always negative (i.e., large fish were more prone to strand, Table 3). This conclusion was supported by
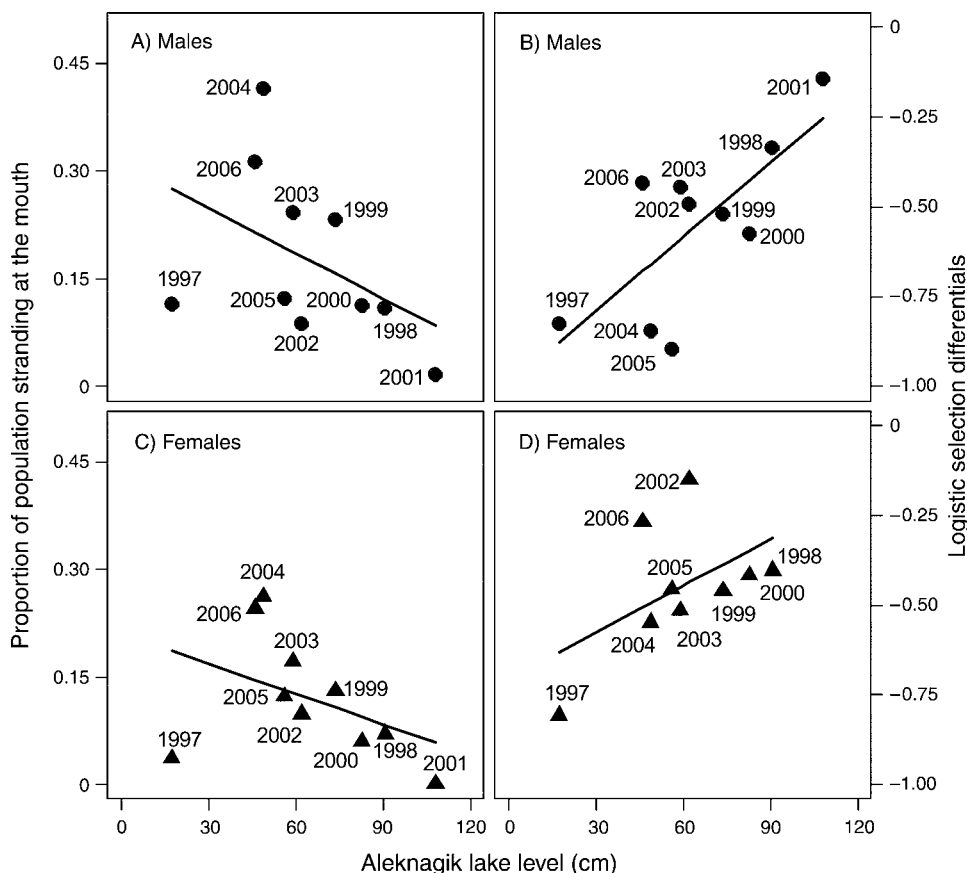
FIG. 2. Year-specific proportion of salmon stranding at the mouth (A and C; Table 1) and logistic selection differentials (B and D; Table 3) plotted against the year-specific lake level. Numbers associated with points are years.

cubic splines, which revealed that the smallest individuals had the highest fitness (males, Fig. 3A; females, Fig. 3B). Second, in all but one case, selection was strong (i.e., significant). The one exception occurred in 2001 when the lake was so high that <2% of the males and only a single female stranded at the mouth of Hansen Creek. Third, the strengths of selection on males and females within a year were positively related (OLS regression, $F_{1,7} = 3.365$, $r^2 = 0.33$, $P = 0.109$). Fourth, for both sexes, the strength of directional selection was related to lake level (OLS regression: males, $F_{1,8} = 9.302$, $r^2 = 0.54$, $P = 0.016$; females, $F_{1,7} = 2.585$, $r^2 = 0.27$, $P = 0.152$). That is, in years when the lake was especially low, the mortality was especially size selective (Fig. 2B, D). Finally, in each year our sample sizes were large compared to most studies of selection in nature (e.g., see review by Kingsolver et al. [2001]; range in the present study: 503–3194 and 1215–2571 for males and females, respectively), suggesting that our results represent a robust analysis of selection.

Our final objective was to link the variation in lake level to simple climate-related factors using the complete data set (1952–2006). The level of Lake Aleknagik fluctuated by >1 m during the period when ~80% of the

salmon enter Hansen Creek to breed (Fig. 4A). First, we tested for evidence of a temporal trend in lake level. To do this, we first performed an autoregressive time-series analysis to determine whether there was evidence of autocorrelation in the data (i.e., whether the autoregression coefficient differed from zero), which there was not ($P = 0.89$). This allowed us to test for a temporal trend in lake level using OLS regression, which revealed no trend over the 55-year period of record ($F_{1,53} = 0.455$, $r^2 = 0.01$, $P = 0.503$). Second, we developed a simple model to relate variation in lake level to variation in regional environmental factors. This revealed that nearly half of the interannual variation in lake level could be explained by interannual variation in May air temperature (warm spring air rapidly melts the accumulated snow, leaving creeks as base flow early in the summer, Fig. 4B) and July precipitation (rain near the time of creek entry by salmon raises the lake because the creeks are short, Fig. 4C; OLS regression, $F_{2,32} = 14.975$, $r^2 = 0.48$, $P < 0.001$).

DISCUSSION

Several noteworthy results emerged from this study. First, from 1997 through 2006, the level of Lake
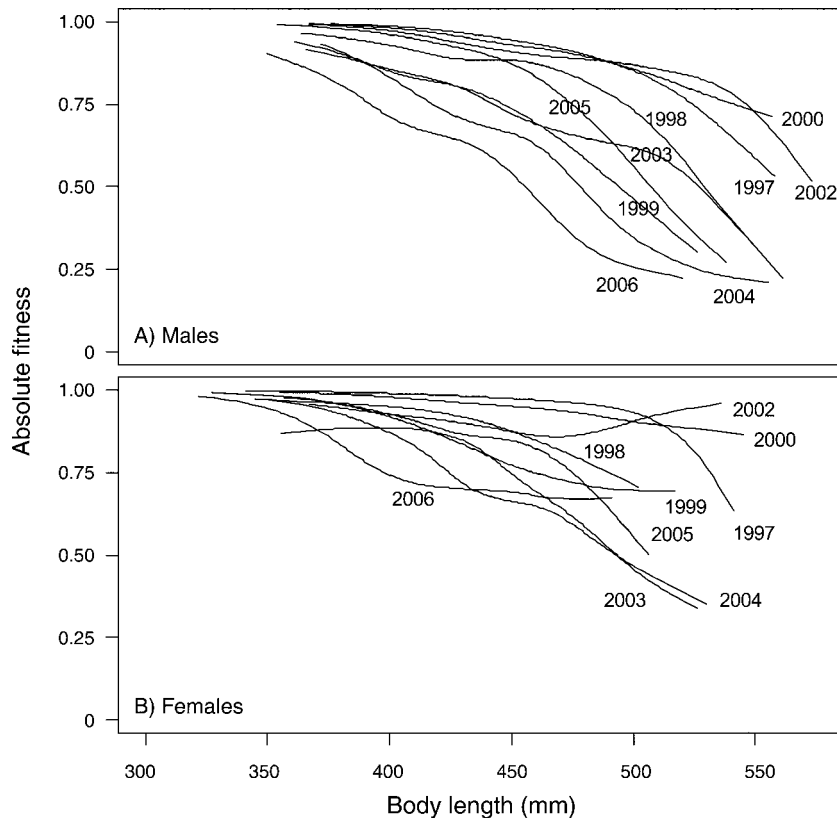
FIG. 3. Relationship between body length and an individual's fitness for each year (noted for each line) and sex. The lines are univariate cubic splines (Schluter 1988; λ = 6, see *Materials and methods: Selection analyses*). No results are presented for 2001 as so few individuals stranded at the creek mouth (Table 1).

Aleknagik during the period when salmon enter Hansen Creek to breed varied by 91 cm. Second, the proportion of the population stranding at the mouth varied dramatically among years: 2–42% in males and <1– 26% in females. Third, males were more susceptible to stranding at the mouth than females (i.e., a larger proportion of the males returning to Hansen Creek stranded than females in nearly all years, Table 1). Fourth, despite the difference in the absolute proportion stranding, there was a high degree of correspondence between the proportion of males and females stranding within a year, suggesting that entry conditions affected both sexes. Fifth, in each year, large individuals of both sexes were more prone to strand as the logistic selection differentials were always negative (Table 3). Cubic splines supported this result because the smallest individuals had the highest fitness (Fig. 3). Sixth, this size-selective mortality was strong (i.e., significant) in all but one year (Table 3), when the lake level was so high that almost no fish stranded (Table 1). Taken together, these latter two results suggest that unless stranding is negligible, it is highly size selective and favors smaller individuals. Finally, the proportion of fish stranding and the strength of size-selective stranding in a given year were both related to lake level. In years when the lake

level was low, a larger proportion of males and females stranded (males, Fig. 2A; females, Fig. 2C) and, for both males and females, larger individuals were disproportionately affected (males, Fig. 2B; females, Fig. 2D).

Gender differences in selection

The strength of selection acting on male body size consistently exceeded the strength of selection acting on female body size (Table 3). Male sockeye salmon are both longer and deeper bodied for their length than females (Quinn et al. 2001b). Their higher center of gravity and greater lateral compression make the males less maneuverable and more prone to lose equilibrium in shallow water, and this greater vulnerability drives the observed gender differences in selection. Despite this strong and consistent selection against large-bodied males in Hansen Creek, males are still generally larger than females in this population. Why might this be? A likely possibility is that sexual selection, favoring large males, is working in the opposite direction to maintain some larger fish in this population (Hamon and Foote 2005). Indeed, behavioral studies have suggested that females prefer to mate with males that are both long and deep bodied for their length (Quinn and Foote 1994). However, the extent of sexual dimorphism in Hansen
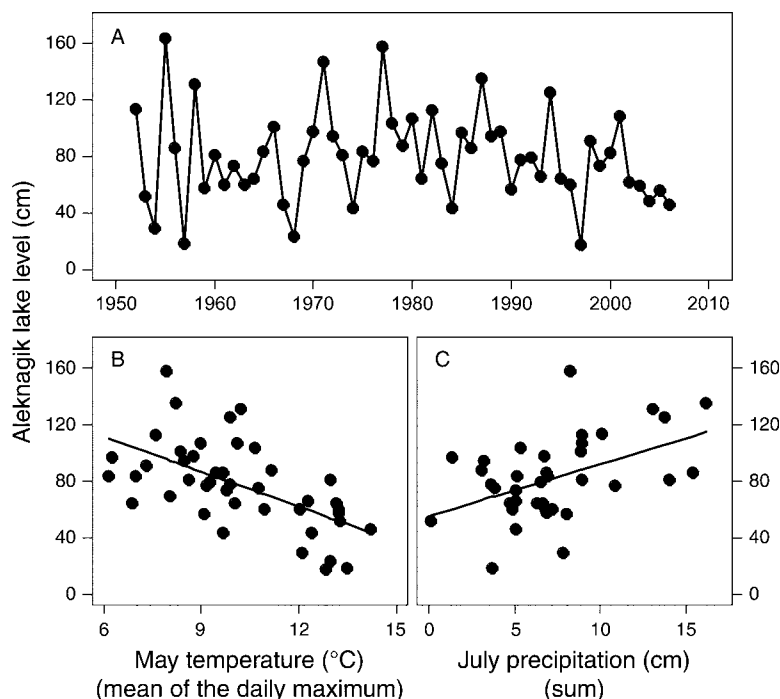
FIG. 4. Water level of Lake Aleknagik, (A) 1952–2006, during the period when sockeye salmon enter Hansen Creek, as well as the relationship between Aleknagik water level during the focal period and both (B) May air temperature and (C) July precipitation. Note that the lake level from 1952 to 1998 is estimated from the water level of Lake Nerka, directly upstream of Lake Aleknagik (see *Materials and methods: Lake level*; Fig. 1), measured from a fixed location.

Creek is less than in nearby populations (Quinn et al. 2001*b*), which suggests that this strong selection against large-bodied males in Hansen Creek has resulted in a meaningful change in body size and shape.

Multiple episodes of selection

The Hansen Creek population is also subject to intense predation from brown bears (*Ursus arctos*) that selectively kill the largest salmon (Ruggerone et al. 2000, Quinn et al. 2001*a*). Thus, both selection at the mouth and selection due to bear predation act in the same direction (against large individuals). Because these two episodes of selection are sequential (mortality due to stranding at the mouth is followed by mortality due to predation in the creek), this sets up the potential for variation in lake level to moderate the strength of selection due to bear predation. That is, the strength of selection due to predation is only fully realized when selection at the mouth is weak, which is rare (Table 3). Nevertheless, predation pressure tends to be higher in Hansen Creek relative to populations breeding in nearby creeks (Quinn et al. 2001*b*). What are the implications of this consistent and strong selection against large individuals at the mouth (due to stranding) and in the creek (due to bears)? Relative to salmon returning to nearby streams, the Hansen Creek population has fewer old (large) adults, smaller body size-at-maturity, more streamlined bodies, and a higher proportion of very young males, smaller than the smallest females in the

population (Quinn et al. 2001*b*). These results indicate that variation in selection against large individuals could be driving and maintaining these patterns.

Also, we note that the individuals sampled were only those that escaped the commercial fisheries in Bristol Bay (southwest Alaska, Fig. 1), and the gillnets used in these fisheries are size-selective to some extent (Burgner 1964, Bue 1986; Alaska Department of Fish and Game, *unpublished data*; N. Kendall, *unpublished data*,). Therefore, the disproportionate capture of larger fish in the nets probably altered the natural size distribution of the population. Nevertheless, the overall patterns of size-selective stranding mortality and variation among years as a function of lake level would undoubtedly be observed, and may even be stronger, in the absence of fishing as well.

Climate variation and change

Hansen Creek provides a dramatic example of a climate-driven pattern of selection. The stranding that occurs there is not characteristic of salmon streams in general, but many salmon populations experience stressful conditions during their homing migration that are related to climate. High temperatures have been linked to elevated mortality rates of sockeye salmon migrating up the Fraser (Gilhousen 1990) and Columbia (Naughton et al. 2005) rivers. Low water levels combined with high temperatures in the Klamath River during the summer of 2002 set the stage for a disease

outbreak that resulted in the death of ~30 000 adult Chinook salmon (*Oncorhynchus tshawytscha*; e.g., Guillen 2003). Short-term climate perturbations such as those mentioned above can drive large mortality events, which should increase the opportunity for selection up to a point. In support of this, the stranding mortality was highest overall in 2004 (Table 1) as was the opportunity for selection (i.e., variance in relative fitness, Table 3) and, moreover, 2004 was characterized by very strong selection against large-bodied individuals (Table 3, Figs. 2B, D and 3).

In addition to short-term climate perturbations driving strong selection, longer-term (directional) changes in climate have the potential to drive strong and consistent selection. For instance, Réale et al. (2003) demonstrated that the timing of breeding in a red squirrel (*Tamiasciurus hudsonicus*) population advanced by 18 days over a 10-year period because warmer spring temperatures increased food supply. To the extent that climate is changing in north-temperate ecosystems, lake levels might also be changing. While there has been extensive consideration of warming trends (e.g., Magnuson et al. 2000), patterns of precipitation and the balance between rainfall and snowfall may also be changing (e.g., Hamlet et al. 2005, Mote et al. 2005, 2006, Stewart et al. 2005). Because these factors affect lake level (Fig. 4B, C), it is plausible that lake level during the period when salmon enter the creeks may also be changing (although this is not yet apparent in Lake Aleknagik, Fig. 4A).

In summary, future climate changes are likely to affect Pacific salmon and other migratory fishes in complex ways. Some research indicates positive effects for juvenile salmon experiencing longer growing seasons (e.g., Schindler et al. 2005). However, to date, research on migrating adults suggests that changes will likely have detrimental effects (e.g., Cooke et al. 2004, 2006a, b, Wagner et al. 2005, Young et al. 2006). If the trends toward earlier spring run-off (e.g., Stewart et al. 2005) and earlier date of ice melting (Magnuson et al. 2000) continue, there may be profound hydrological as well as thermal changes in many areas. It is unknown whether salmon populations will be able to adapt to changing conditions quickly enough to avoid extirpation.

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