Balancing natural and sexual selection in sockeye salmon: interactions between body size, reproductive opportunity and vulnerability to predation by bears

Thomas P. Quinn,* Andrew P. Hendry[‡] and Gregory B. Buck

Fisheries Research Institute, School of Aquatic and Fishery Sciences, Box 355020, University of Washington, Seattle, WA 98195, USA

ABSTRACT

Traits that increase reproductive success, such as body size and sexual dimorphism, may compromise survival, leading to opposing pressures of natural and sexual selection. Discrete populations exposed to different balances between selective forces should differ in phenotypic traits associated with natural and sexual selection. We used two proximate populations of sockeye salmon (*Oncorhynchus nerka*) that differ in body size as a model for studying this kind of balancing selection. We hypothesized that large body size would enhance potential reproductive success through relationships with duration of nest guarding in females, and dominance and duration of reproductive life in males, but that it would be opposed by probability of premature death, chiefly from predation by bears. Longevity on the breeding grounds was primarily controlled by predation, which varied between creeks and years. Pick Creek salmon experienced less predation than those in Hansen Creek and also tended to live longer before being killed, giving Pick Creek females a higher probability of completing egg deposition and males a greater opportunity to breed than those in Hansen Creek. In addition, Hansen Creek salmon were subjected to strong, size-selective predation and also selective mortality from stranding as they ascended the mouth of the creek, whereas we found no evidence of size-selective mortality among Pick Creek salmon. Male dominance in courtship for access to females favoured large salmon, except when predation was very intense. These patterns of balancing selection were consistent with the larger body size of sockeye salmon in Pick Creek. We also found that premature mortality, especially predation by bears, can significantly truncate the reproductive opportunities of salmon, raising a cautionary note regarding controlled studies in which predation cannot occur.

Keywords: bears, evolution, Pacific salmon, predation, reproductive success.

INTRODUCTION

Natural and sexual selection often oppose each other in nature. Sexual selection frequently leads to the evolution of exaggerated traits, usually in males, because these traits often

increase mating success (Darwin, 1871; Andersson, 1994). Sexually selected traits include morphology, colour, body size, mating calls and display behaviour (Clutton-Brock, 1988; Andersson, 1994). Although these traits can increase mating success, they often comprise the survival of individuals that express them (Ryan *et al.*, 1982; Magnhagen, 1991; Sih, 1994; but see Jennions *et al.*, 2001). Natural selection can thus oppose the exaggeration of mating signals that are otherwise favoured by sexual selection. Such traits, therefore, should vary among populations and species in proportion to the relative intensities of natural and sexual selection. A classic example is the coloration of male guppies (*Poecilia reticulata*) in the streams of Trinidad (Endler, 1995). Brightly coloured males are favoured as mates by females (Houde, 1987, 1997) but are more conspicuous to predators (Endler, 1978). As a result, guppies in environments with low predation are more brightly coloured than guppies in environments with high predation (Endler, 1980). Here, we describe another system in which natural and sexual selection oppose each other during reproduction, causing some traits to vary among populations.

The breeding season for sockeye salmon (*Oncorhynchus nerka*) is characterized by intense natural and sexual selection, as in other members of the family Salmonidae (Fleming, 1998). On the breeding grounds, females compete with each other for high-quality nesting sites (Foote, 1990) and males compete with each other for access to breeding females (Quinn *et al.*, 1996). Male mating success is determined primarily by competition and female choice (longer and deeper-bodied males obtain more mates; Quinn and Foote, 1994) and the availability of ripe females (Quinn *et al.*, 1996). Female reproductive success is less variable (nearly all females obtain mates) but is influenced by body size through positive correlations with the number and size of eggs (Quinn *et al.*, 1995), competition for breeding sites (Foote, 1990; Quinn and Foote, 1994) and egg burial depth (Steen and Quinn, 1999). These factors all select for larger body size in adults (but see Holtby and Healey, 1986). Large body size also seems to be favoured at earlier life-history stages because larger juveniles are more likely to survive in fresh water (West and Larkin, 1987) and at sea (Henderson and Cass, 1991).

Several factors appear to select against large body size. First, rapid growth requires aggressive foraging, which may increase susceptibility to predators (Holtby and Healey, 1990). Second, achieving a large size at maturity often requires spending more years at sea, thus incurring a higher probability of mortality (Healey, 1987). Third, predation by bears and the possibility of stranding may select against large adults in shallow streams (Quinn and Kinnison, 1999; Ruggerone *et al.*, 2000; Quinn and Buck, 2001). When factors favouring or opposing body size vary spatially, discrete populations should evolve different body sizes to suit local selective regimes.

In the present study, we investigated the selective forces shaping body size in sockeye salmon populations by quantifying natural selection (primarily bear predation) and sexual selection (dominance status and breeding lifespan of males, and duration of nest defence by females) in two streams in the Wood River Lake system, southwestern Alaska. This comparison allowed us to examine the effects of stream size and predation because the two populations otherwise experience similar conditions (e.g. foraging opportunities at sea, migration distance, timing of breeding, climate). The sockeye salmon in Pick Creek are both longer and deeper-bodied than those in Hansen Creek (Quinn and Buck, 2001; Quinn *et al.*, in press). We hypothesized that this difference can be attributed to more intense natural selection against large size in Hansen Creek. We individually tagged a large number of fish of known size and monitored their reproductive life span (termed 'longevity' for our

purposes) and cause of death. Unlike previous studies that estimated selection by examining carcasses (e.g. Quinn and Kinnison, 1999; Quinn and Buck, 2001), the tagging approach allowed us to (1) measure the morphology of salmon near the peak of their development (Hendry and Berg, 1999), (2) determine the entry date of each fish into the stream, (3) estimate if females deposited their eggs before they died, (4) observe the social status of males and (5) determine longevity in the creek.

Our overall aim was to evaluate the extent to which variation in the intensity and size-bias of premature mortality influence the evolution of body size in salmon. To do so, we quantified the interactions of body size with sex, date of entry into the stream (arrival date) and cause of mortality (especially predation), as they affected sockeye salmon longevity and probability of reproduction. First, we predicted that Hansen Creek salmon (the smaller-bodied population) would experience a higher probability of premature mortality and that these mortality agents (stranding and predation) would have a greater effect on probability of successful reproduction than they would on Pick Creek salmon. Second, we predicted that premature mortality would select against larger fish within a given creek. As a result, the relationship between body size and longevity should vary between creeks and years, depending on the intensity of predation. Third, we predicted that large males would be more often in the dominant position when courting females, reflecting sexual selection for larger body size. Failure to support these predictions would indicate that the differences in body size between the populations could not be attributed to the balance between natural and sexual selection. To test the predictions, we also considered arrival date because it may be correlated with longevity and size (McPhee and Quinn, 1998; Hendry *et al.*, 1999, 2001). Early arrivals tend to live longer than late arrivals if they die of senescence but they may also have a higher probability of predation.

METHODS

Site descriptions

Our study was conducted on Hansen and Pick creeks, two small, stable streams in the Wood River system of lakes, flowing into Bristol Bay in southwestern Alaska. Hansen Creek flows 2 km from a beaver pond into the lower end of Lake Aleknagik. It is a single meandering channel throughout its length, with little additional inflow except a small spring-fed pond that feeds it 0.5 km downstream from the beaver pond. The creek is very small, averaging 10 cm deep and 3.9 m wide (Marriott, 1964; Quinn *et al.*, in press), with little variation in water depth and width throughout its length. It has very stable flows, responding only slightly to rainfall. The creek flows into the lake across a very shallow delta where the average depth of the water is 4 cm (Quinn *et al.*, in press). The length of the delta depends on lake level but can be as long as 30 m. Many salmon die trying to cross the delta and enter the creek in some years. Despite the delta, the creek has high densities of salmon. Since 1990, annual mid-season surveys have averaged 7478 salmon or approximately one salmon per square metre (T.P. Quinn, unpublished data).

Pick Creek originates in a series of spring-fed ponds (Marriott, 1964) and then meanders for 2 km, with some small side channels, before entering Lake Nerka. Pick Creek is larger than Hansen Creek, averaging 33 cm deep and 7.8 m wide but, like Hansen Creek, Pick Creek has stable flows and temperatures (Hendry *et al.*, 1999, 2001), owing to the low gradient topography and influence of ground water. Spawning occurs at high densities

throughout much of the creek (Hendry *et al.*, 2001); the average mid-season number of salmon since 1990 is 5633 or about 0.36 salmon per square metre.

Tagging and survey methods

Sockeye salmon were tagged and observed in 1995 and 1996 at Pick Creek and in 1999 and 2000 at Hansen Creek. Our methods were similar at both sites, with only minor differences. The fish were caught with beach seine nets at the mouths of the creeks, anaesthetized and measured. At both creeks we used callipers to measure body length from the middle of the orbit of the eye to the end of the hypural plate (essentially the end of the spinal column). This measurement represents somatic length and is not biased by the greater elongation of the jaws in male salmon. We also measured body depth from the anterior insertion of the dorsal fin to the bottom of the abdomen, perpendicular to the long axis of the fish. In sockeye salmon, this measurement is equivalent to the maximum dorso-ventral extent of the fish (Blair *et al.*, 1993). These body depth measurements were made using callipers at Hansen Creek and digitized photographs at Pick Creek (for details, see Hendry *et al.*, 2001). To assess body depth independent of its correlation with body length, we calculated the relationship between body length and body depth for each sex at each creek (Pick females, $r^2 = 0.83$; Pick males, $r^2 = 0.75$; Hansen females, $r^2 = 0.58$; Hansen males, $r^2 = 0.74$). From these relationships we calculated the expected body depth for each fish and subtracted the expected from the observed measurement to yield 'residual body depth' (see Quinn and Foote, 1994). This measure indicated whether a fish had a deeper or shallower body than average for its body length.

After being measured, the salmon were marked with a pair of uniquely lettered plastic disk tags, attached to the fish's sides below the dorsal fin with a pin (see Quinn and Foote, 1994; Hendry *et al.*, 1999). In Pick Creek the salmon were tagged over a range of dates (19 July to 1 August 1995 and 18 July to 9 August 1996), whereas in Hansen Creek they were all tagged on a single day each year (21 July 1999 and 22 July 2000). Salmon entered the creeks over a range of dates, which we expressed relative to the date when the first salmon (tagged or otherwise) entered that creek in that year. Some tagged fish never entered the creeks at all; we believe that they were probably fish from other creeks that were shoaling off the mouths of Pick and Hansen creeks as part of their homing process. There are many other spawning sites in the Wood River system and surveys of Happy and Eagle creeks, about 1 km on either side of Hansen Creek, revealed some tagged fish. Fish tagged but never sighted again in Hansen Creek or Pick Creek were excluded from all analyses.

On each day of the spawning season (about 4 weeks in Hansen Creek and 6 weeks in Pick Creek), we walked the entire length of each creek looking for tagged live and dead fish in the creek and adjacent riparian zone. Carcasses were categorized by the apparent cause of death. The most common categories were a 'senescent' death (emaciated body, tattered fins, scarred skin and fungus on the body) and 'bear-killed'. Bear-killed fish typically had obvious bites in the cranial region, dorsal hump, belly or a combination of these areas (Gende *et al.*, 2001). In addition to these two categories, many salmon were seen repeatedly in the creek but then disappeared. We categorized these fish as 'missing'. Given the clear, shallow water and generally good viewing conditions, we consider it highly unlikely that these fish continued to live in the creeks unnoticed. We have observed bears killing salmon and removing them from both creeks, and scavenged salmon are often removed from the creeks and consumed in the woods (Quinn and Buck, 2000). In the interests of time and

safety, we did not thoroughly survey the terrestrial environment for such carcasses but we have occasionally found tags some distance from the stream. We are convinced that most of the missing salmon were eaten entirely or were carried from the stream by bears. Data on missing and bear-killed fish were compared and pooled when they were similar.

Two other categories of death were observed. Hansen Creek has a very shallow (<4 cm) delta where the creek flows into Lake Aleknagik, downstream of all spawning areas. Some salmon were found dead at this delta, having become stranded in the shallow water. There were also salmon that had been pecked through the body cavity by glaucous-winged gulls (Mossman, 1958). We do not know if the gulls killed the salmon or (more likely) scavenged them after death (Quinn and Buck, 2000), so salmon were recorded as either 'stranded' or 'gull-pecked'. Pick Creek does not have a shallow area where salmon strand but some fish were found with gull-wounds. Collectively, the bear-killed, missing, stranded and gull-pecked fish were referred to as 'premature' mortalities.

We examined longevity and cause of death as functions of sex, body length, body depth and date of arrival (i.e. first observation) in the creek. Longevity was calculated as the number of days from the arrival date (not tagging) until death (for details, see Hendry *et al.*, 1999). If a fish was first seen alive in the creek on one day and was found dead the next day, its longevity would be 2 days because we assumed it lived for some portion of the day on which it was killed. Thus a fish that was dead the first time it was seen in the creek had a longevity of 1 day. Missing fish were assumed to have died on the day after they were last seen alive.

We were able to make some additional observations of tagged salmon during our daily surveys at Hansen Creek. Fish of both sexes actively moving upstream were categorized as 'migrating'. Females on nests were categorized as 'ripe', 'partially spawned' or 'completely spawned', based on observations of belly distension and body condition. Males were categorized as 'dominant' (the only male courting a ripe female or the male clearly excluding other males from proximity to the female), 'competitor' (battling for access to a ripe female but not obviously dominant or submissive), 'satellite' (males associated with a ripe female but clearly excluded from proximity to her by a dominant male) or 'alone' (not associated with any ripe female). Determination of status was sometimes impossible, either because we disturbed the fish or they were too dense for accurate determination (especially in 1999). Because the categories were qualitative and the numbers of observations varied among fish, we adopted a conservative approach to estimating male reproductive opportunities. In addition to number of days alive, we summed the number of daily observations when the male was either a dominant or a competitor (indications of high status or opportunity) and subtracted the number of observations when he was either a satellite or alone. This index of status, while not quantitatively equivalent to reproductive success, did indicate the relative status of the males.

Estimating the strength of natural selection

We estimated the strength of directional selection acting on body length, residual body depth and arrival date in Hansen Creek for males and females separately (years pooled to increase sample sizes). We did not perform similar analyses for Pick Creek fish because the data were less precise; for example, we did not know the day when individual females deposited their eggs. We estimated the absolute fitness of Hansen Creek females based on whether they survived to reproduce (i.e. were observed after completion of spawning:

fitness = 1) or died before they could reproduce (fitness = 0). This approach was analogous to scoring fitness based on whether or not individuals survive during a given episode of selection (Brodie and Janzen, 1996). We estimated the absolute fitness of Hansen Creek males as a positive linear function of the number of days they survived in the creek, which provides a rough surrogate for reproductive opportunity. A male that died on its first day in the creek was assigned an absolute fitness of zero, one who died on the second day an absolute fitness of 1, and so on. We then calculated relative fitness by dividing the absolute fitness of each fish by the average fitness of all fish of that sex (Lande and Arnold, 1983). We next standardized each trait value (body length, arrival date and residual body depth) for each individual by subtracting the mean trait value and dividing by the standard deviation of trait values for that sex.

We used simple linear regressions of each trait versus relative fitness to estimate the total strength of selection (direct and indirect) acting on each trait for each sex separately. We then used a multiple linear regression to estimate the strength of direct selection acting on each trait for each sex (Lande and Arnold, 1983). We also preformed these analyses using simple and multiple logistic regressions for females because their fitness values were dichotomous (Janzen and Stern, 1998). The shape of the selection function acting on body length and arrival date (the two important terms) was visualized for each sex using cubic splines (Schluter, 1988). See Brodie *et al.* (1995) for a review of techniques for visualizing and quantifying selection.

RESULTS

Factors affecting longevity

We obtained data for 305 tagged sockeye salmon at Hansen Creek and 556 at Pick Creek (Table 1). Our initial approach was to consider all measured factors that were hypothesized to affect longevity (creek, year, cause of death, sex, body length, body depth, residual body depth, arrival date). Principal components analysis detected three factors (components) indicating underlying common effects. Consistent with our predictions, most (43.6%) of the explained variation in longevity was associated with a factor that included creek, year and cause of death (rotated factor loading values: 0.924, 0.920 and 0.656 respectively). The second component explained 1.9% of the variation and included arrival date and residual body depth (rotated factor loadings: 0.911 and 0.480 respectively). The third component explained 0.4% of the variation and included body depth, body length and sex (rotated factor loadings: 0.916, 0.813 and 0.679 respectively). Forward stepwise regression indicated that all three components contributed to longevity, with the first component (creek, year, cause of death) being the most important (partial $t = 26.14$, $P < 0.001$), followed by the second (associated with arrival date; partial $t = 5.44$, $P < 0.001$) and the third (sex, body length and body depth; partial $t = 2.58$, $P = 0.01$).

Longevity was strongly influenced by cause of death, and the patterns of mortality differed between creeks and years, hence the importance of the first component. Pick Creek fish lived longer than Hansen Creek fish whether they died of senescence (19 *vs* 11 days; Mann-Whitney rank sum test, $T = 7047.0$, $P < 0.001$) or prematurely (11.5 *vs* 2 days; $T = 31136.5$, $P < 0.001$; Fig. 1). The proportion of fish dying of senescence in Hansen Creek was also much lower than in Pick Creek (27 *vs* 50%; pooling years and sexes, $\chi^2_1 = 43.26$, $P < 0.001$; Table 1), so the overall comparison of longevity was even more skewed. In

Table 1. Percentage of tagged female and male sockeye salmon in two creeks, sampled in two different years, that were killed by bears, stranded, pecked by gulls, missing or dying a natural (senescent) death, and the median number of days in the stream for each of those groups

Year	Sex		Bear-killed	Missing	Stranded	Gull-pecked	Premature	Senescent
					Cause of death			
Hansen Creek								
1999	Female	% ($n = 38$)	7.9	39.5	2.6	2.6	52.6	47.4
		median	3	2	1	1	2	12
	Male	% ($n = 93$)	9.7	29.0	5.4	3.2	47.3	52.7
		median	2	2	1	1	2	13
2000	Female	% ($n = 57$)	66.7	17.5	5.3	0.0	89.5	10.5
		median	2	2	2	—	2	3.5
	Male	% ($n = 117$)	54.7	26.5	11.1	0.0	92.3	7.7
		median	3	2	1	—	2	5
	Total	% ($n = 305$)	37.4	27.2	7.2	1.3	73.1	26.9
		median	2	2	1	1	2	11
Pick Creek								
1995	Female	% ($n = 114$)	5.3	34.2	0.0	0.0	39.5	60.5
		median	10	17	—	—	14	22
	Male	% ($n = 119$)	21.0	68.1	0.0	0.0	89.1	10.9
		median	13	8	—	—	9	17
1996	Female	% ($n = 167$)	1.8	18.6	0.0	7.2	27.5	72.5
		median	6	12	—	9.5	10	18
	Male	% ($n = 156$)	6.4	45.5	0.0	0.0	51.9	48.1
		median	14.5	12	—	—	13	18
	Total	% ($n = 556$)	7.9	39.9	0.0	2.2	50.0	50.0
		median	13	11	—	9.5	11.5	19

Note: The category 'Premature' combines bear-killed, missing, stranded and gull-pecked fish.

Pick Creek, the median longevity was 16 days and the 25th–75th percentiles were 10–20 days, whereas in Hansen Creek it was only 3 days and the 25th–75th percentiles were 2–8 days.

There were important differences in the causes of death between the creeks and sexes that affected longevity. Four times more salmon were stranded or pecked by gulls at Hansen Creek than at Pick Creek (8.5 *vs* 2.2%; $\chi_1^2 = 18.93$, $P < 0.001$). At Hansen Creek, these fish were primarily males and almost all died while entering the creek (median longevity = 1 day; Table 1), whereas at Pick Creek no fish became stranded and those pecked by gulls (exclusively females) were already in the creek, with a median longevity of 9.5 days.

Most of the fish at Hansen Creek were bear-killed (37.4%) or missing (27.2%); as the longevity distributions of these two groups were similar, we combined them for further analyses. Both males and females tended to be killed soon after they entered the creek but the reduction in longevity of killed fish was greater in females (median = 2 days in females
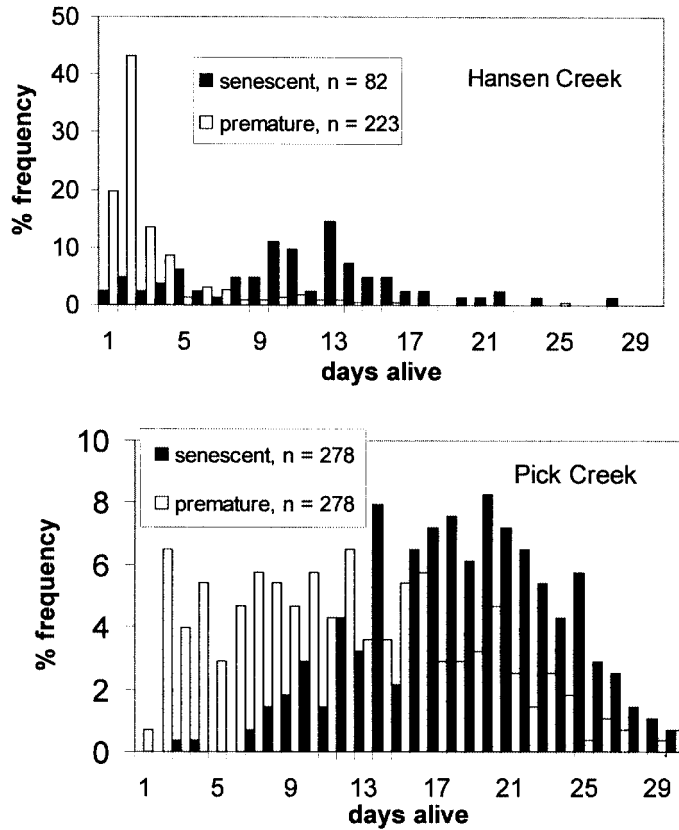
Fig. 1. Longevity of sockeye salmon from Hansen and Pick creeks whose deaths were senescent or premature (primarily from predation). Note the much greater reduction in longevity from premature death in Hansen Creek than Pick Creek and the generally greater longevity in Pick Creek.

and 3 days in males; Mann-Whitney rank sum test, $T = 13081$, $P = 0.042$). Salmon dying of senescence lived much longer in 1999 (12–13 days) than in 2000 (4–5 days; $T = 24576$, $P < 0.001$), apparently because of variation in predation (82.2% of the fish were killed or missing in 2000 *vs* 41.2% in 1999). In 2000, only the fish with the shortest intrinsic life spans could die of senescence before being killed by bears.

At Pick Creek, as at Hansen Creek, the senescent fish lived significantly longer than all other groups (Kruskal-Wallis ANOVA on ranks; females: $H = 48.851$, $P < 0.001$; males: $H = 73.84$, $P < 0.001$). Likewise, missing fish had similar longevity to bear-killed fish among females (Mann-Whitney rank sum test, $T = 251.5$, $P = 0.10$) and even shorter lives than the confirmed bear-kills among males (10.5 *vs* 14 days; $T = 4120.5$, $P = 0.004$), supporting our assumption that the missing fish had been killed rather than died of senescence and going unnoticed. However, median longevity (all causes of death) was greater for Pick Creek females than males (18 *vs* 14 days; $T = 64801.5$, $P < 0.001$), apparently because more females than males died of senescence (67.6 *vs* 32.0%; $\chi_1^2 = 70.52$, $P < 0.001$). In contrast, the proportion of senescent fish at Hansen Creek was similar between males (27.6%) and females (25.3%; $\chi_1^2 = 0.18$).

The probability of being killed (including missing) varied with arrival date but the pattern was not consistent between years or creeks. Salmon that arrived in the beginning (days 1–7 of the run) and middle (days 8–14) of the run tended to have a higher probability of predation than those that arrived at the end of the run (after day 14) in Hansen Creek in 2000 (83 and 85 *vs* 71%) and Pick Creek in 1995 (68 and 69 *vs* 47%). However, the opposite pattern was observed in Hansen Creek in 1999 (early 38%, middle 42%, end 54%) and Pick Creek in 1996 (early 30%, middle 34%, end 46%).

Multiple linear regression combining all causes of death indicated that longevity at Hansen Creek in 1999 was positively correlated with early arrival in both sexes combined ($t = 4.37$, $P < 0.001$) and negatively correlated with body length ($t = 2.92$, $P < 0.004$; combined $r^2 = 0.15$). In 2000, neither variable explained longevity ($r^2 = 0.01$). Female body length was not correlated with longevity in either year (1999: $r^2 = 0.04$, $P = 0.20$; 2000: $r^2 < 0.01$, $P = 0.99$). In 1999, male longevity decreased with body length ($r^2 = 0.08$, $P = 0.004$; Fig. 2), whereas in 2000 no relationship was detected ($r^2 = 0.01$, $P > 0.20$). Longevity of Pick Creek females was associated with early arrival (partial $t = 9.66$, $P < 0.001$, partial $r^2 = 0.31$) and large size (partial $t = 3.31$, $P = 0.001$, partial $r^2 = 0.34$). Among males, longevity was also correlated with early arrival (partial $t = 4.01$, $P < 0.001$, partial $r^2 = 0.05$), but the correlation with body length was weakly negative (partial $t = 1.77$, $P < 0.08$, partial $r^2 = 0.01$).

Size-selective mortality

At Hansen Creek, the salmon that were killed, missing and stranded tended to be large, whereas those dying of senescence tended to be small, as were the few gull-pecked fish (Table 2). Two-way analysis of variance (ANOVA) revealed that males and females did not differ in average body length ($F = 1.3$, $P = 0.26$), but premature mortalities were larger than salmon dying due to senescence ($F = 32.47$, $P < 0.001$; Table 2, Fig. 3). The lack of an interaction between these factors ($F = 0.39$, $P = 0.53$) indicated similar relationships between premature death and body length for males and females. The largest and smallest fish showed dramatic differences in proportions dying prematurely in both sexes (Fig. 3), consistent with size-biased mortality patterns. Residual body depths tended to be greater among fish that died prematurely but the difference was not significant for either sex ($F = 0.29$, $P = 0.59$). Unlike Hansen Creek, there was no evidence of size-selective premature mortality at Pick Creek ($F = 0.44$, $P = 0.51$), nor was there any evidence of selection on residual body depth (Table 2).

Body size and probability of reproduction

Taken together, the above results indicate an underlying pattern of greater intrinsic longevity for earlier arriving salmon in both creeks. Imposed on this was a loss of some Hansen Creek salmon to stranding as they ascended the creek (highly size-biased and greatly reducing longevity). In addition, bear predation on Hansen Creek salmon was equally intense for both sexes, was size-biased and greatly reduced longevity. At Pick Creek, predation was not only less intense than at Hansen Creek (48.9 *vs.* 70.6% of the salmon not stranded or gull pecked; $\chi^2_1 = 35.33$, $P < 0.001$), but it took place later in the lives of the fish and was not size-biased.
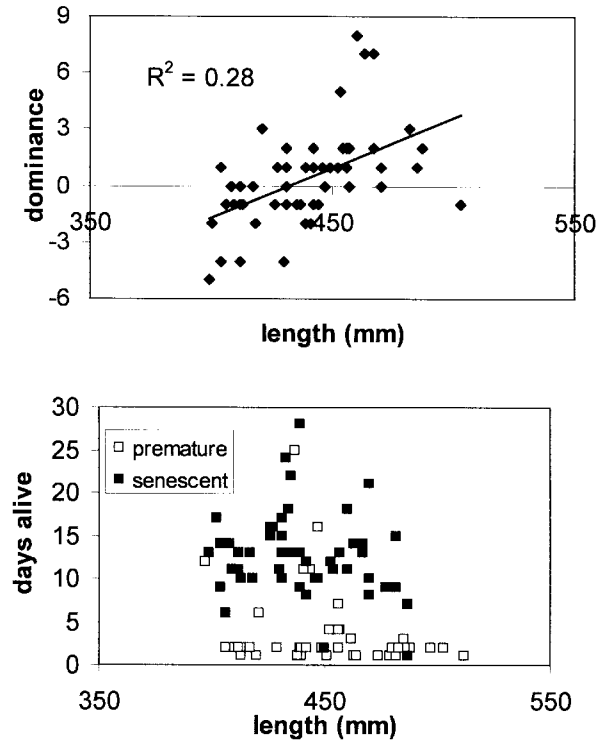
Fig. 2. Relationships between body length and longevity in the stream and dominance for Hansen Creek male sockeye salmon in 1999. Longevity data are separated according to whether the salmon's death was senescent or premature.

Body length affected the probability of reproduction in both males and females at Hansen Creek. A substantial fraction of the females died before they completed spawning (44.7% in 1999 and 78.9% in 2000); these females were longer than those that completed spawning (466.0 *vs* 453.4 mm; two-sample *t*-test, $t_{93} = 1.962$, $P = 0.053$). Male body length was positively correlated with the index of dominance in 1999 ($r^2 = 0.28$, $P < 0.001$; Fig. 2) but not in 2000 ($r^2 < 0.01$, $P = 0.93$), perhaps because in the latter year the males had such short life spans that there was little opportunity for data collection. In neither year was residual body depth correlated with the index of dominance (1999: $r^2 = 0.01$, $P = 0.51$; 2000: $r^2 < 0.01$, $P = 0.87$).

Natural selection (acting on spawning success) favoured females in Hansen Creek that were smaller and that entered later in the season, but did not act on residual body depth (Table 3). The strength of direct selection acting on body length and arrival date (gradients, from multiple linear regression) was less than the combined strength of direct and indirect selection acting on either trait (differentials, from simple linear regression). This result arose because larger females tended to arrive earlier in the season (Pearson's $r = -0.227$, $P = 0.027$). Thus, selection acting against body length was due to the direct effect of differential mortality and an indirect effect acting through arrival date (selection favoured later females and later females were smaller). Cubic splines did not reveal any evidence of

Table 2. Average length and residual body depth (i.e. observed body depth − expected depth based on sex- and site-specific relationships between length and body depth) of sockeye salmon (in millimetres) categorized by cause of death in Hansen and Pick creeks

Sex	Year	Data	Cause of death					
			Bear-killed	Missing	Stranded	Gull-pecked	Premature	Senescent
Hansen Creek								
Female	1999	Length	465.3	437.1	446	409	440.4	436.8
		Depth	−5.5	1.1	−5	3.3	−0.1	0.3
	2000	Length	474.6	488.9	487		478.2	466.7
		Depth	0.8	−1.3	−2.2		0.2	−2
	Total	Length	474	457.8	476.8	409	467.5	444.3
		Depth	0.3	0.1	−2.9	3.3	0.1	−0.3
Male	1999	Length	455.3	446.8	472.4	432.3	450.5	439.3
		Depth	1.4	0.6	−0.3	−5.1	0.3	−0.7
	2000	Length	486.7	481.8	491.4		485.9	486.6
		Depth	−0.5	1	1.8		0.2	0.1
	Total	Length	482.8	465.5	486.1	432.3	475.6	446.6
		Depth	−0.3	0.8	1.2	−5.1	0.2	−0.5
Pick Creek								
Female	1995	Length	482.5	495.5			493.8	493.8
		Depth	2.7	0			0.4	−1
	1996	Length	433	447.1		427.6	441.1	454.3
		Depth	1.8	−0.5		−1.3	−0.6	0.6
	Total	Length	466	474.1		427.6	467.2	468.6
		Depth	2.4	−0.2		−1.3	−0.1	0.1
Male	1995	Length	500.9	504.7			503.8	503.7
		Depth	−3.1	−0.3			−0.9	−2.5
	1996	Length	468.9	472.8			472.4	480.9
		Depth	1.8	−1.3			−0.9	2.8
	Total	Length	491.8	489.8			490.2	484.3
		Depth	−1.7	−0.8			−0.9	2

Note: The category 'Premature' combines bear-killed, missing, stranded and gull-pecked fish.

disruptive or stabilizing selection on body length or on arrival date (Fig. 4) or residual body depth (not shown).

Natural selection (acting on longevity) favoured males in Hansen Creek that were smaller and that entered earlier in the season, but did not act on residual body depth (Table 3). The strength of direct selection acting on body length and day of entry (gradients) was roughly equivalent to the combined strength of direct and indirect selection acting on each trait (differentials), indicating that body length and arrival date were roughly independent from the perspective of selection. Cubic splines did not reveal any evidence of disruptive or stabilizing selection on body length or day of entry (Fig. 5) or on residual body depth (not shown).

Table 3. The strength of selection (*P*-value in parentheses) acting on body length, residual body depth and day of entry for Hansen Creek female and male sockeye salmon

	Body length	Residual body depth	Day of entry
Females			
Linear differential	−0.275 (0.053)	−0.014 (0.925)	0.280 (0.046)
Logistic differential	−0.427 (0.052)	−0.021 (0.924)	0.422 (0.048)
Linear gradient	−0.221 (0.127)	−0.040 (0.779)	0.024 (0.103)
Logistic gradient	−0.348 (0.127)	−0.070 (0.758)	0.360 (0.109)
Males			
Linear differential	−0.403 (< 0.001)	−0.010 (0.880)	−0.178 (0.010)
Linear gradient	−0.404 (< 0.001)	0.014 (0.827)	−0.182 (0.004)

Note: All data were standardized to a mean of zero and a standard deviation of one. Linear differentials and gradients were calculated using the methods of Lande and Arnold (1983). Logistic differentials and gradients were calculated using the methods of Janzen and Stern (1998).
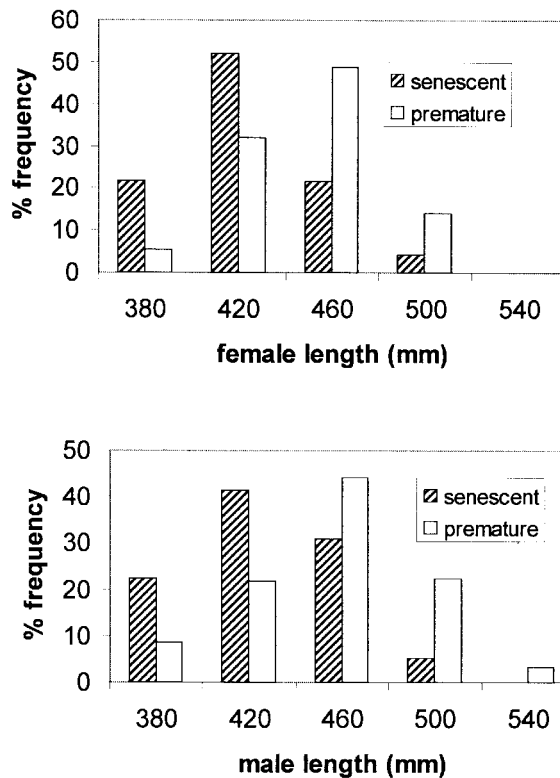

Fig. 3. Length frequency histograms of Hansen Creek sockeye salmon whose deaths were senescent and premature (primarily from predation) in 1999 and 2000.
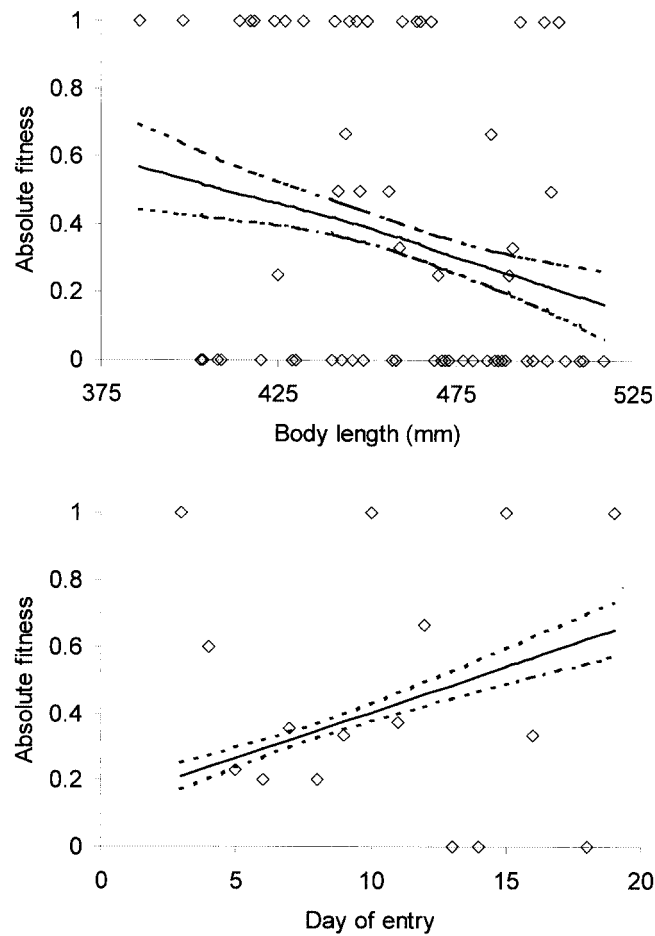
Fig. 4. Cubic spline (Schluter, 1988) visualizations of selection acting on female body length and day of entry. Absolute fitness took values of 0 (died before reproduction) or 1 (survived long enough to reproduce). Intermediate values represent mean fitness when more than one individual had the same trait value. Dashed lines represent bootstrapped standard errors around the spline.

DISCUSSION

Natural and sexual selection may often operate against each other, but demonstrating these opposing effects in natural populations can be difficult. For example, a recent meta-analysis found that 'males with larger ornaments or weapons, greater body size, or higher rates of courtship showed greater survivorship or longevity' (Jennions *et al.*, 2001). In sharp contrast to this finding, our present and previous work on sockeye salmon has shown that: (1) sexual selection favours large males (they obtain more matings) and large females (they obtain better nest sites and are more successful at defending them); (2) salmon that die prematurely, primarily from predation but also stranding, are larger than those that die of senescence, and this natural selection against large body size can be quite strong; (3) in
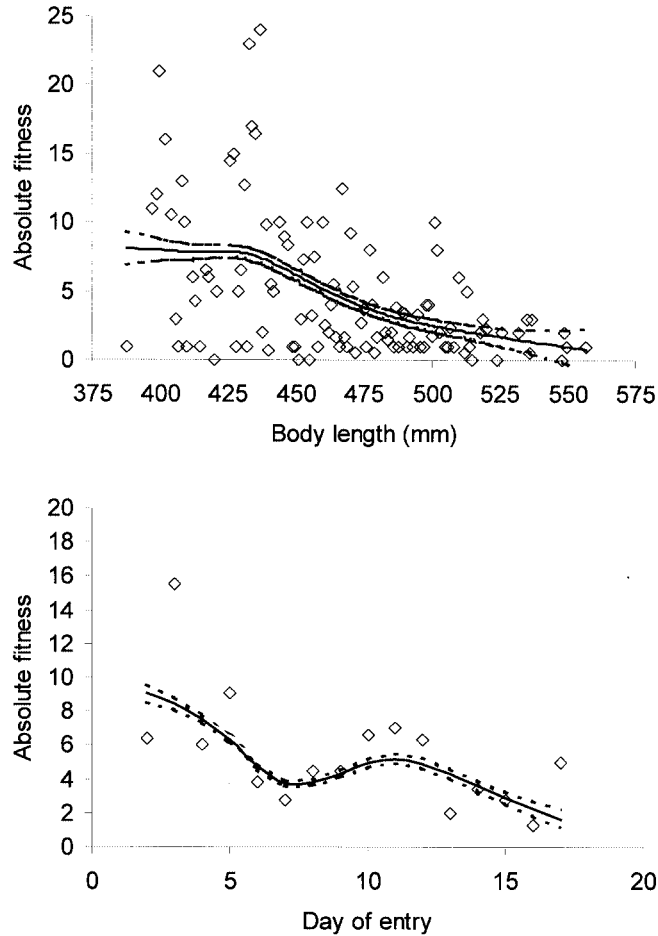
Fig. 5. Cubic spline (Schluter, 1988) visualizations of selection acting on male body length and day of entry. Absolute fitness took values directly related to the number of days in the stream (averaged for males with the same body length or day of entry). Dashed lines represent bootstrapped standard errors around the spline.

the absence of predation, salmon that begin breeding early in the season live longer than salmon breeding late in the season; and (4) populations subject to higher predation have evolved smaller body size (Blair *et al.*, 1993; Quinn and Foote, 1994; McPhee and Quinn, 1998; Hendry *et al.*, 1999, 2001; Quinn and Kinnison, 1999; Ruggerone *et al.*, 2000; Quinn and Buck, 2001). We summarize these relationships in Fig. 6, which depicts the interactive influences of arrival date and predation on longevity, and the influences of longevity and body size on reproductive success. The interaction between sockeye salmon and bears presents a clear case of natural and sexual selection opposing each other in the evolution of body size. The fitness benefits of large size (here owing to sexual selection) have frequently been documented in nature (Andersson, 1994). The fitness costs of large
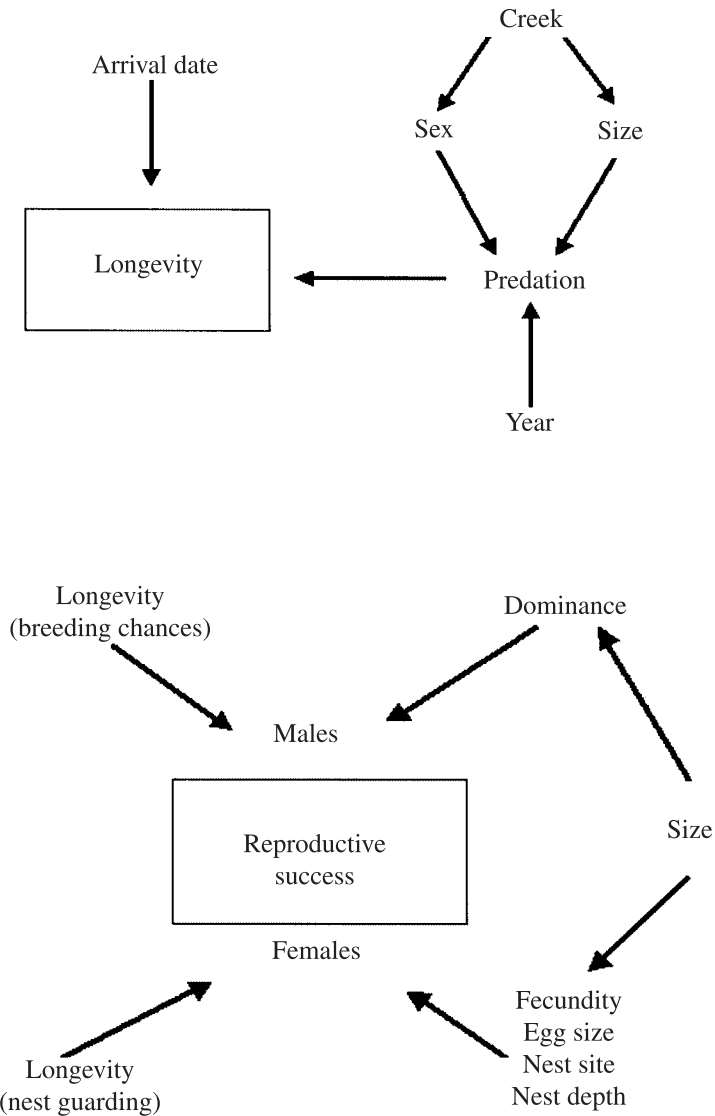
Fig. 6. Diagrammatic representation of the primary factors affecting reproductive success in salmon. The upper panel shows the factors affecting longevity, including predation (which varies among years and creeks, and can vary with the size and sex of the salmon) and arrival date. The lower panel integrates longevity with size-related factors affecting reproductive success: egg production, nest construction and defence in females and social dominance in males.

body size (here owing to predation), however, have often proved difficult to demonstrate (Blanckenhorn, 2000).

Our success in detecting opposing natural and sexual selection may have resulted from the fact that the salmon were subjected to intense predation but only over a brief period. Indeed, earlier stages in the salmon's life cycle are characterized by positive correlations

between size and survival (West and Larkin, 1987; Henderson and Cass, 1991), although there may be survival costs associated with fast growth (Holtby and Healey, 1990). In addition, the comparison of populations with different intensities of natural selection is a powerful tool for uncovering opposing selection. The work on guppies provides a particularly elegant example of the benefits of this approach (Endler, 1995).

A large fraction of the fish (sometimes the majority) died prematurely in both creeks and years, long before they would have died of senescence. Many females failed to complete spawning or had reduced periods of nest guarding, and males lost a large fraction of their potential breeding opportunities. Cause of death (chiefly predation) was the dominant factor affecting longevity, and the creek and year effects were linked to variation in predation. In addition to these extrinsic factors, the most important intrinsic factor was arrival date (early arrivals lived longer), with lesser influences of sex (when they differed, females lived longer) and body length (when it was significant, smaller fish lived longer).

Natural selection for successful egg deposition at Hansen Creek favoured smaller females and females that entered later in the season (Table 3). Most of these effects are attributable to selection acting directly on each trait, which was strong relative to other values observed in nature. The linear differentials for body length and arrival date were in the 74th and 75th percentiles, respectively, of all values reported in Kingsolver and co-workers' (2001) review (raw data obtained from J.G. Kingsolver). This selection against large size in Hansen Creek females is presumably countered by their greater number and size of eggs (Quinn *et al.*, 1995), their ability to obtain and defend better nest sites (Foote, 1990) and their ability to dig deeper and hence safer nests (Steen and Quinn, 1999).

Hansen Creek is shallower and narrower than Pick Creek and the sockeye salmon, especially females, experienced heavier bear predation in Hansen Creek. The salmon killed by bears in Pick Creek tended to live much longer than those in Hansen Creek; this is at least as important from an evolutionary standpoint as is the proportion of salmon killed. We did not specifically record when the Pick Creek females completed spawning but, if they all did so within 3 days in the creek (based on McPhee and Quinn, 1998, and our Hansen Creek data), only 3.6% of the tagged females would have failed to spawn (compared with 69.5% based on this criterion and 65.3% based on our direct observations at Hansen Creek). Even assuming 4 days were required to spawn, all but 6.4% of the females would have completed spawning in Pick Creek. Thus natural selection from predation would be weaker in Pick Creek than in Hansen Creek.

The fish killed by bears had much shorter reproductive lives in Hansen Creek than in Pick Creek. Bears can catch salmon so easily in Hansen Creek that they probably prefer large, newly arrived fish because they are more energetically rewarding (somatic energy stores decreased from the start of spawning to death by 40.8% in females and 28.6% in males; Hendry and Berg, 1999). Pick Creek is deeper and wider than Hansen Creek, affording more escape opportunities for the salmon, so the bears may be less selective and typically catch salmon that have been in the creek for some time, perhaps because such fish are less vigorous as they deplete their energy stores and approach death. By way of comparison, a person can easily catch salmon by hand in Hansen Creek, whereas this is almost impossible in Pick Creek unless the fish are near death. In 2000, the salmon that died of senescence in Hansen Creek did so sooner than in 1999. We believe this merely reflects the fact that predation was so intense in 2000 that the only fish dying before being killed by bears were those with extremely short intrinsic life spans. If predation had been the same in both

years, senescent longevity would probably also have been similar. However, the difference in senescent longevity between Pick Creek (19 days) and Hansen Creek (11 days) may reflect an intrinsic difference between the two populations. Predation may have had the evolutionary effect of reducing the senescent longevity of sockeye salmon in the more vulnerable population, as expected from life-history theory (Stearns, 1992).

In addition to variation in the proportion of salmon killed between creeks, there was also variation in predation intensity between years. The much lower predation at Hansen Creek in 1999 than in 2000 was probably a consequence of the much higher salmon density in 1999 (19,504 *vs* 3460 in 2000; T.P. Quinn, unpublished data). At Pick Creek, predation was slightly more intense in 1995 (Table 1) when salmon abundance was lower (4418 in 1995 *vs* 6189 in 1996; T.P. Quinn, unpublished data). Although predation intensity varies among years, Hansen Creek appears to have generally higher levels than Pick Creek. Examination of untagged carcasses revealed 45.6% killed at Hansen Creek (13 years of data) compared with 37.1% at Pick Creek (12 years of data; Quinn *et al.*, in press).

We predicted that large males would be more often in the dominant position when courting females but that this sexual selection would be countered by a higher probability that predators would kill larger fish. In 1999, larger males were more often dominant or actively engaged in courtship (as opposed to 'satellites' or those alone) than were smaller males, consistent with previous work on sockeye salmon (Quinn and Foote, 1994) and other salmonids (Fleming, 1998). Dominant males do not fertilize all the eggs deposited by females but, on average, they fertilize more eggs than less dominant males (Schroder, 1982; Chebanov *et al.*, 1983). We did not observe a positive effect of size on dominance in 2000, but so many of the salmon were killed within a few days of entry into the creek that our ability to detect trends was weak.

Countering the sexual selection for larger males, bear predation was size-selective in Hansen Creek, consistent with other work there (Ruggerone *et al.*, 2000; Quinn and Buck, 2001) and elsewhere (Konovalov and Shevlyakov, 1978; Quinn and Kinnison, 1999). The selection was very strong; the linear differential for body length was in the 87th percentile of values from Kingsolver and co-workers' (2001) review. Such intense, size-selective predation may have contributed to the generally smaller size of Hansen Creek sockeye, relative to those in Pick Creek and other sites within the Wood River Lake system (Rogers, 1987). The lack of evidence for size-selective predation in Pick Creek supported the hypothesis that variation in predation intensity among streams affects traits that increase mating success (assuming the intensity of sexual selection is similar). Where natural selection acts most strongly against traits favoured by sexual selection, those traits showed the least exaggeration. However, measurement of a large number of untagged carcasses at Pick Creek indicated size-selection, so this pattern is probably prevalent but less strong than at Hansen Creek (Quinn and Buck, 2001).

In addition to bear predation, the mouth of Hansen Creek is exceedingly shallow and some salmon became stranded or were attacked by gulls before even reaching the spawning grounds. Although a smaller fraction of the population than the bear-kills, such fish died before reaching the breeding grounds and so their direct reproductive fitness was zero. The stranding mortality, especially among the males, was even more size-selective than predation by bears (Table 2; Quinn and Buck, 2001). In contrast, no Pick Creek fish became stranded and the few fished pecked by gulls had been in the creek for about a week and so almost certainly would have spawned.

We did not detect an effect of residual body depth on male dominance or premature

mortality in either sex. Selection (e.g. stranding and predation) probably acts primarily on body depth *per se*, not residual body depth. Had we used unadjusted body depth rather than body length we would have found significant selection, but much of the selection on body depth was removed by our calculation of residual body depth. Quinn and Foote (1994) reported that access to females was correlated with residual body depth; however, their study was conducted in a population without bear predation where body depth is exaggerated. In neither our study nor that of Quinn and Foote (1994) did length explain most of the observed variation in access to females. Most males, even those with high intrinsic qualities, may not be able to gain access to ripe females because the operational sex ratio is highly male-biased in salmon populations during much of the breeding period (Quinn *et al.*, 1996). Thus correlations between size, shape and reproductive opportunity in natural systems will typically be weak. Hansen Creek males and females tend to be both shorter and less deep-bodied than those in Pick Creek and other nearby populations (Quinn *et al.*, in press). The present life history and morphology may reflect 'the ghost of selection past' to such an extent that very large and deep-bodied individuals have been eliminated from populations in the smallest creeks.

The relationships between body size and longevity were consistent with the patterns of mortality between creeks. At Hansen Creek, body size did not influence longevity except for a negative relationship for males in 1999. In Pick Creek, with less intense predation, there was no relationship for males and a positive one for females. In general, there appears to be little or no relationship between body size and intrinsic longevity in sockeye salmon but, if larger fish arrive earlier, as happened in Pick Creek, then large fish may appear to live longer simply because early arrivals live longer (Perrin and Irvine, 1990; McPhee and Quinn, 1998; Hendry *et al.*, 1999, 2001). However, intense size-selective predation can cause an overall reduction in longevity associated with large size. In the case of females at Hansen Creek, large size was also associated with a lower probability of spawning.

Early arriving salmon may also be more vulnerable to bears, assuming that the bears kill a fixed number of salmon and so take a larger fraction of the early fish. Daily surveys of Hansen Creek during the 1990–2000 spawning seasons indicated that the percentage of fish in the creek killed per day was highest at the beginning of the breeding season, decreased rapidly as salmon abundance increased, and then increased again at the end of the season (T.P. Quinn, unpublished data). However, this effect was only seen in one of two years in the present data set. The patterns of predation may depend on the abundance of alternative food resources for the bears and their abundance and social interactions. Consequently, early arriving fish may not always experience very high levels of predation.

In conclusion, we note the prevalence of premature mortality in these creeks (largely from bears) and in many other streams in Alaska and British Columbia (Quinn and Buck, 2001; Gende *et al.*, 2001, and references therein). Of the dozens of studies published on salmon reproductive behaviour, most have been carried out in experimental pens or arenas (e.g. Schroder, 1982; Foote, 1990; Fleming and Gross, 1994; de Gaudemar and Beall, 1999), in natural sites with no predation (e.g. Quinn and Foote, 1994; Quinn *et al.*, 1996) or natural sites with so little predation that it was not mentioned (e.g. van den Berghe and Gross, 1989). We do not doubt the patterns observed in these studies, but firmly believe that bears subject many Pacific salmon populations to substantial predation. Such predation may have been an important factor shaping the life history, morphology, breeding phenology and behaviour of salmon, and controlled studies should explicitly consider the effects that predation would have had on the results.

ACKNOWLEDGEMENTS

REFERENCES

Andersson, M. 1994. *Sexual Selection*. Princeton, NJ: Princeton University Press.

Blair, G.R., Rogers, D.E. and Quinn, T.P. 1993. Variation in life history characteristics and morphology of sockeye salmon (*Oncorhynchus nerka*) in the Kvichak River system, Bristol Bay, Alaska. *Trans. Am. Fish. Soc.*, **122**: 550–559.

Blanckenhorn, W.U. 2000. The evolution of body size: what keeps organisms small? *Quart. Rev. Biol.*, **75**: 385–407.

Brodie, E.D., III and Janzen, F.J. 1996. On the assignment of fitness values in statistical analyses of selection. *Evolution*, **50**: 437–442.

Brodie, E.D., III, Moore, A.J. and Janzen, F.J. 1995. Visualizing and quantifying natural selection. *Trends Ecol. Evol.*, **10**: 313–318.

Chebanov, N.A., Varnavskaya, N.V. and Varnavskiy, V.S. 1983. Effectiveness of spawning of male sockeye salmon, *Oncorhynchus nerka* (Salmonidae), of differing hierarchical rank by means of genetic-biochemical markers. *J. Ichthyol.*, **23**: 51–55.

Clutton-Brock, T.H., ed. 1988. *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems*. Chicago, IL: University of Chicago Press.

Darwin, C. 1871. *The Descent of Man and Selection in Relation to Sex*. London: John Murray.

de Gaudemar, B. and Beall, E. 1999. Reproductive behavioural sequences of single pairs of Atlantic salmon in an experimental stream. *Anim. Behav.*, **57**: 1207–1217.

Endler, J.A. 1978. A predator's view of animal color patterns. *Evol. Biol.*, **11**: 319–364.

Endler, J.A. 1980. Natural selection on color patterns in *Poecilia reticulata*. *Evolution*, **34**: 76–91.

Endler, J.A. 1995. Multiple-trait coevolution and environmental gradients in guppies. *Trends Ecol. Evol.*, **10**: 22–29.

Fleming, I.A. 1998. Pattern and variability in the breeding system of Atlantic salmon (*Salmo salar*), with comparisons to other salmonids. *Can. J. Fish. Aquat. Sci.*, **55**(suppl. 1): 59–76.

Fleming, I.A. and Gross, M.R. 1994. Breeding competition in a Pacific salmon (coho: *Oncorhynchus kisutch*): measures of natural and sexual selection. *Evolution*, **48**: 637–657.

Foote, C.J. 1990. An experimental comparison of male and female spawning territoriality in a Pacific salmon. *Behaviour*, **115**: 283–313.

Gende, S.M., Quinn, T.P. and Willson, M.F. 2001. Consumption choice by bears feeding on salmon. *Oecologia*, **127**: 372–382.

Healey, M.C. 1987. The adaptive significance of age and size at maturity in female sockeye salmon (*Oncorhynchus nerka*). *Can. Spec. Publ. Fish. Aquat. Sci.*, **96**: 110–117.

Henderson, M.A. and Cass, A.J. 1991. Effect of smolt size on smolt-to-adult survival for Chilko Lake sockeye salmon (*Oncorhynchus nerka*). *Can. J. Fish. Aquat. Sci.*, **48**: 988–994.

Hendry, A.P. and Berg, O.K. 1999. Secondary sexual characters, energy use, senescence, and the cost of reproduction in sockeye salmon. *Can. J. Zool.*, **77**: 1663–1675.

Hendry, A.P., Berg, O.K. and Quinn, T.P. 1999. Condition dependence and adaptation-by-time: breeding date, life history, and energy allocation within a population of salmon. *Oikos*, **85**: 499–514.

Hendry, A.P., Berg, O.K. and Quinn, T.P. 2001. Breeding location choice in salmon: causes (habitat, competition, body size, energy stores) and consequences (life span, energy stores). *Oikos*, **93**: 407–418.

Holtby, L.B. and Healey, M.C. 1986. Selection for adult size in female coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.*, **43**: 1946–1959.

Holtby, L.B. and Healey, M.C. 1990. Sex-specific life history tactics and risk-taking in coho salmon. *Ecology*, **71**: 678–690.

Houde, A.E. 1987. Mate choice based on naturally occurring color pattern variation in a guppy population. *Evolution*, **41**: 1–10.

Houde, A.E. 1997. *Sex, Color, and Mate Choice in Guppies*. Princeton, NJ: Princeton University Press.

Janzen, F.J. and Stern, H.S. 1998. Logistic regression for empirical studies of multivariate selection. *Evolution*, **52**: 1564–1571.

Jennions, M.D., Møller, A.P. and Petrie, M. 2001. Sexually selected traits and adult survival: a meta-analysis. *Quart. Rev. Biol.*, **76**: 3–36.

Kingsolver, J.G., Hoekstra, H.E., Hoekstra, J.M., Berrigan, D., Vignieri, S.N., Hill, C.E., Hoang, A., Gilbert, P. and Beerli, P. 2001. The strength of phenotypic selection in natural populations. *Am. Nat.*, **157**: 245–261.

Konovalov, S.M. and Shevlyakov, A.G. 1978. Natural selection in Pacific salmon (*Oncorhynchus nerka* Walb.). *Zh. Obsch. Biol.*, **39**: 194–206.

Lande, R. and Arnold, S.J. 1983. The measurement of selection on correlated characters. *Evolution*, **37**: 1210–1226.

Magnhagen, C. 1991. Predation risk as a cost of reproduction. *Trends Ecol. Evol.*, **6**: 183–186.

Marriott, R.A. 1964. Stream catalog of the Wood River lake system, Bristol Bay, Alaska. *US Fish Wildlife Service, Spec. Sci. Rept., Fish.*, **494**: 210 pp.

McPhee, M.V. and Quinn, T.P. 1998. Factors affecting the duration of nest defense and reproductive lifespan of female sockeye salmon, *Oncorhynchus nerka*. *Environ. Biol. Fish.*, **51**: 369–375.

Mossman, A.S. 1958. Selective predation of glaucous-winged gulls upon adult red salmon. *Ecology*, **39**: 482–486.

Perrin, C.J. and Irvine, J.R. 1990. A review of survey life estimates as they apply to the area-under-the-curve method for estimating the spawning escapement of Pacific salmon. *Can. Tech. Rept. Fish. Aquat. Sci.*, **1733**: 1–49.

Quinn, T.P. and Buck, G.B. 2000. Scavenging by brown bears, *Ursus arctos*, and glaucous-winged gulls, *Larus glaucescens*, on adult sockeye salmon, *Oncorhynchus nerka*. *Can. Field-Nat.*, **114**: 217–223.

Quinn, T.P. and Buck, G.B. 2001. Size and sex selective mortality of adult sockeye salmon: bears, gulls, and fish out of water. *Trans. Am. Fish. Soc.*, **130**: 995–1005.

Quinn, T.P. and Foote, C.J. 1994. The effects of body size and sexual dimorphism on the reproductive behaviour of sockeye salmon, *Oncorhynchus nerka*. *Anim. Behav.*, **48**: 751–761.

Quinn, T.P. and Kinnison, M.T. 1999. Size-selective and sex-selective predation by brown bears on sockeye salmon. *Oecologia*, **121**: 273–282.

Quinn, T.P., Hendry, A.P. and Wetzel, L.A. 1995. The influence of life history trade-offs and the size of incubation gravels on egg size variation in sockeye salmon (*Oncorhynchus nerka*). *Oikos*, **74**: 425–438.

Quinn, T.P., Adkison, M.D. and Ward, M.B. 1996. Behavioral tactics of male sockeye salmon (*Oncorhynchus nerka*) under varying operational sex ratios. *Ethology*, **102**: 304–322.

Quinn, T.P., Wetzel, L., Bishop, S., Overberg, K. and Rogers, D.E. in press. Influence of breeding habitat on bear predation, and age at maturity and sexual dimorphism of sockeye salmon populations. *Can. J. Zool.*

Rogers, D.E. 1987. The regulation of age at maturity in Wood River sockeye salmon (*Oncorhynchus nerka*). *Can. Spec. Publ. Fish. Aquat. Sci.*, **96**: 78–89.

Ruggerone, G.T., Hanson, R. and Rogers, D.E. 2000. Selective predation by brown bears (*Ursus arctos*) foraging on spawning sockeye salmon (*Oncorhynchus nerka*). *Can. J. Zool.*, **78**: 974–981.

Ryan, M.J., Tuttle, M.D. and Rand, A.S. 1982. Bat predation and sexual advertisement in a neotropical anuran. *Am. Nat.*, **119**: 136–139.

Schluter, D. 1988. Estimating the form of natural selection on a quantitative trait. *Evolution*, **42**: 849–861.

Schroder, S.L. 1982. The influence of intrasexual competition on the distribution of chum salmon in an experimental stream. In *Salmon and Trout Migratory Behavior Symposium* (E.L. Brannon and E.O. Salo, eds), pp. 275–285. Seattle, WA: School of Fisheries, University of Washington.

Sih, A. 1994. Predation risk and the evolutionary ecology of reproductive behaviour. *J. Fish Biol.*, **45**(suppl. A): 111–130.

Stearns, S.C. 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.

Steen, R.P. and Quinn, T.P. 1999. Egg burial depth by sockeye salmon (*Oncorhynchus nerka*): implications for survival of embryos and natural selection on female body size. *Can. J. Zool.*, **77**: 836–841.

van den Berghe, E.P. and Gross, M.R. 1989. Natural selection resulting from female breeding competition in a Pacific salmon (coho: *Oncorhynchus kisutch*). *Evolution*, **43**: 125–140.

West, C.J. and Larkin, P.A. 1987. Evidence for size-selective mortality of juvenile sockeye salmon (*Oncorhynchus nerka*) in Babine Lake, British Columbia. *Can. J. Fish. Aquat. Sci.*, **44**: 712–721.

Wetzel, L.A. 1993. Genetic, morphometric and life history characteristics of sockeye salmon (*Oncorhynchus nerka*) in the Wood River Lake system, Bristol Bay, Alaska. Master's thesis, University of Washington, Seattle, WA.