Size- and Sex-Selective Mortality of Adult Sockeye Salmon: Bears, Gulls, and Fish Out of Water

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Abstract.—Pacific salmon *Oncorhynchus* spp. exist as reproductively isolated breeding populations and display marked variation in size and age at maturity within and among populations. We conducted a detailed study of mortality on adult sockeye salmon *O. nerka* in Hansen Creek, a small stream in southwestern Alaska, to test the prediction that predation by brown bears *Ursus arctos* and death by stranding during upstream migration would selectively remove males and large (old) individuals. During the 3 years of this study, 13.7% of the mature salmon died in shallow water at the creek's mouth before reaching the spawning grounds. Males had proportionally higher mortality at the mouth than females (17.6% versus 10.8%), and the fish of both sexes that died at the mouth were larger and older than those that survived to ascend the creek. Of the fish that died at the mouth, females were more often attacked (chiefly scavenged) by glaucous-winged gulls *Larus glaucescens* than males, and the gulls tended to attack fish that were smaller than average. Of the fish that reached the spawning habitats in Hansen Creek, those killed by bears were larger and older than those that died of senescence. Thus, there was highly size-selective mortality in this population. Data from four other nearby sockeye salmon populations confirmed the tendency for bears to kill predominately large salmon and males. Data from 14 other populations revealed that the predation intensity was generally, but not always, higher on males than females. Overall, the results indicated that there can be substantial selective mortality in salmon populations in small streams, which may influence their life history evolution.

The life history traits of many animals reflect a balance between different selective pressures, including conflicts between traits associated with reproductive success and predator avoidance (Magnhagen 1991; Sih 1994). Large males or those with conspicuous colors or features may have an advantage in intrasexual competition or female choice (Clutton-Brock 1988; Andersson 1994), but predators may selectively capture such individuals, leading to inverse relationships between sexual dimorphism and predation pressure (Endler 1995). In females, the need to grow large to produce or guard offspring may also conflict with predator avoidance. However, it can be difficult to quantify the magnitude and selectivity of mortality associated with body size (see review by Blanckenhorn 2000) or the differential mortality between males and females. Such data are essential for critically testing models of selection.

Semelparous Pacific salmon *Oncorhynchus* spp. present a tractable system for studying selective mortality on sexually mature individuals once they return to their natal stream to spawn. On the spawning grounds, the adults spawn and quickly run out of energy or succumb to disease and die within a few weeks (Hendry and Berg 1999). During this time salmon that spawn in small streams may be subjected to selective mortality, notably from bears and sometimes gulls. Bears tend to attack males and larger salmon (Quinn and Kinnison 1999; Reimchen 2000; Ruggerone et al. 2000), whereas gulls attack primarily females (Mossman 1958). Such selective mortality may play a role in the evolution of population-specific life history and morphology (Blair et al. 1993), countering the reproductive advantages of size. Large males tend to win contests for access to spawning females (Fleming and Gross 1994; Quinn and Foote 1994), and larger females have higher fecundity and larger eggs (Beacham and Murray 1993; Quinn et al. 1995) and can bury their eggs deeper than smaller females (Steen and Quinn 1999).

The frequency with which salmon are attacked by bears or gulls may depend on stream depth and width (Quinn et al., in press [a]). Some streams are small enough that many salmon are killed before they die of senescence. In particular, Hansen Creek, in Bristol Bay, southwestern Alaska, has been the site of several salmon mortality studies. Mossman (1958) and Mathisen (1962) reported selective attacks by glaucous-winged gulls *Larus glaucescens* on female sockeye salmon *O. nerka* ascending the creek to spawn, but they did not

report predation by brown bears *Ursus arctos.* More recently, Ruggerone et al. (2000) documented high levels of predation by brown bears on Hansen Creek sockeye salmon, but they did not document attacks by gulls. Our observations have indicated a more complex pattern of mortality. Some salmon strand at the very shallow mouth of the stream and die before reaching the spawning grounds upstream; others are attacked by gulls or bears at the mouth of the stream (before or after stranding); and others strand, are killed, or die of senescence in the creek. Salmon dying at the mouth of the creek, regardless of the cause, would have failed to spawn, whereas fish killed upstream would have had a chance to spawn. Consequently, the location of the mortality affects the strength of the resulting selection.

The objective of this study was to quantify the extent of size- and sex-selective mortality of sockeye salmon. Specifically, we recorded the length and sex of Hansen Creek sockeye salmon, categorized by mode of death, from 1997 to 1999 to test the hypotheses that bear predation would be most intense on large fish and males, that gulls would attack primarily smaller females, and that large fish (especially males) would be stranded. We also collected data from less intensive surveys of four other, larger streams in the Bristol Bay region to test the generality of the Hansen Creek findings with respect to size-selective predation by bears. Finally, we collected data on 14 streams besides Hansen Creek to test the generality of the patterns of sex-selective predation by bears.

Methods

Site description.—Hansen Creek meanders 2 km from a beaver pond to Lake Aleknagik in the Wood River system of southwestern Alaska (Figure 1). It is also fed by spring ponds that enter about 1.5 km from the mouth. The stream is very shallow, averaging 10 cm deep and 4 m wide during the July–August spawning period (Marriott 1964). Additional measurements of stream depth, taken adjacent to sockeye salmon redds in 1997, averaged 7.7 cm ($N = 45$, SD = 1.5; Ryan Steen and Thomas Quinn, Fisheries Research Institute, University of Washington, unpublished data). The water is very clear and flow fluctuations are negligible, even after rainfall, because of the moderating influences of the ponds, springs, and topography. These features greatly facilitate surveys for live and dead salmon because flooding does not wash carcasses into the lake or the riparian zone, and live salmon can be easily counted. In addition,

they result in very similar flow conditions among years in the creek.

There is an especially shallow section where Hansen Creek enters Lake Aleknagik. The topography of the delta depends on lake level, which generally declines during the period when sockeye salmon enter Hansen Creek (late July to mid-August). However, the lake can rise in response to prolonged heavy rainfall. Areas at the delta that are very shallow but passable at one water level may be impassable or dry a week later. It is thus difficult to calculate the area and average depth of this region but during typical migration periods the delta is composed of one or more useable channels that average 4–5 cm at their deepest points and range from 10 to 30 m long, depending on lake level (T. Q., unpublished records). The delta ends at a discrete bend in the creek where depth is no longer affected by lake level, and it is sufficient for spawning. The delta was never used for spawning, and we distinguished it from the rest of the creek because, unlike salmon that died upstream, those that died on the delta would have had no chance to spawn. The other discrete habitat that we sampled was the spring-fed pond that flowed into the creek about 1.5 km from the lake. This pond averaged 18.7 cm deep ($N = 30$, SD = 6.4) and its area was estimated to be 510 m^2.

Hansen Creek surveys.—During the 1997–1999 spawning seasons we walked the entire length of the creek daily from the first day when salmon were seen entering until the run was nearly finished in mid-late August. All dead salmon were examined and categorized by sex, location (mouth, creek, and pond), and mode of death. In 1997 we recorded death as senescent, bear killed, or stranded. Stranded fish were found dead at the stream's mouth without signs of bites by bears. Some were unmarked but others showed distinct signs of pecking through the body wall by gulls. During the 1997 season, we noted that although males were more often stranded than females, more of the females seemed to have been pecked by gulls. In 1998 and 1999 we distinguished stranded fish that had been pecked by gulls from those that had not. All fish dead at the mouth were probably affected to some extent by the shallowness of the water and many of those apparently killed by bears or gulls undoubtedly stranded and were scavenged. We often observed fish trying to ascend channels that got progressively shallower until the fish could no longer swim, and they died. Nevertheless, we noted cases where the fish's body wall had been penetrated by gulls. The wounds associated with
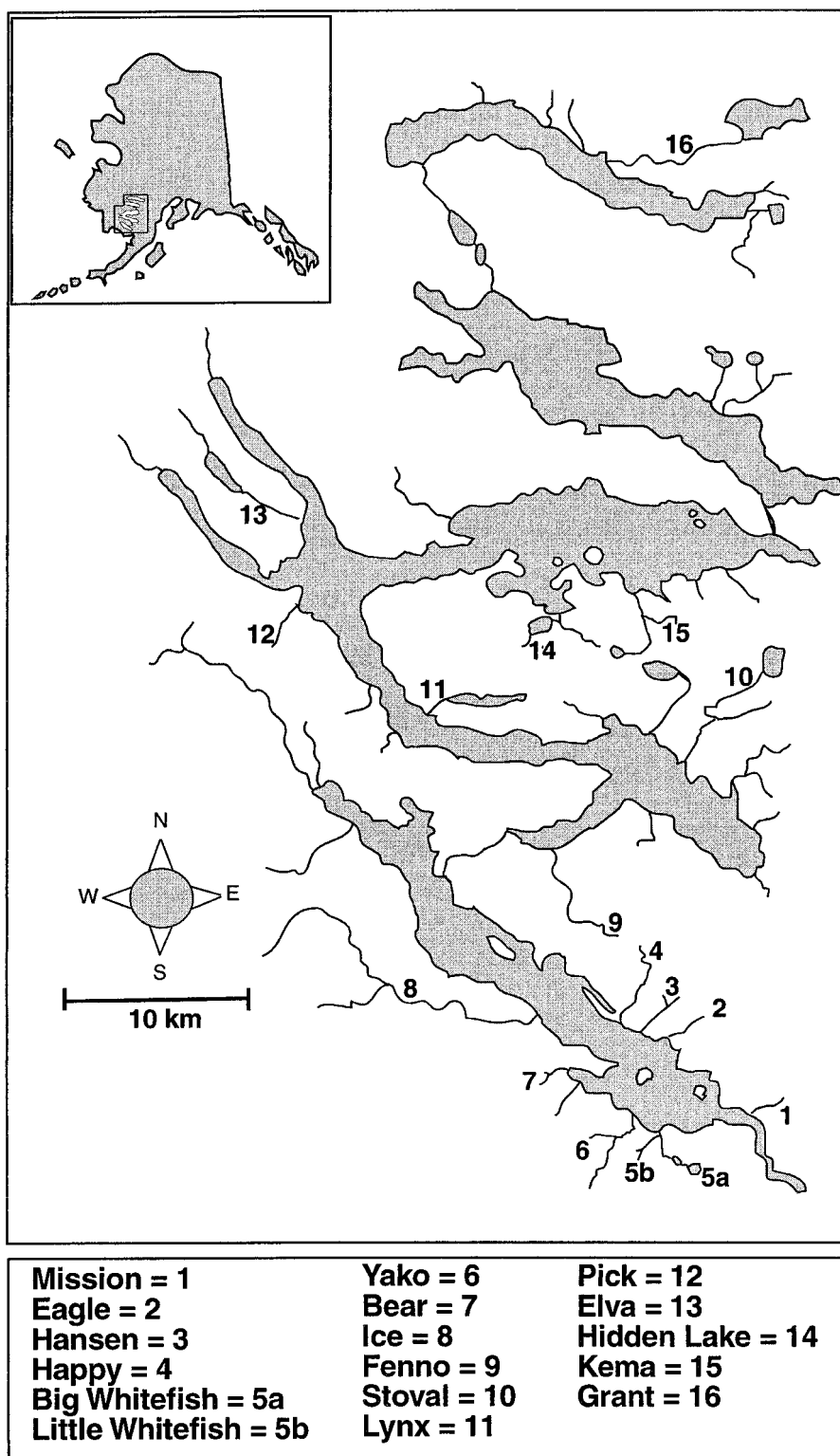
FIGURE 1.—Map of the Wood River system of lakes and the creeks sampled to examine bear predation and gull attacks on sockeye salmon.

bears and gulls were very different. The action of bears was characterized by holes from the canine teeth or large chunks of the body bitten off (typically the bellies of females, the dorsal humps of males, and the upper part of the skull). Gull wounds were characterized by radial chiseling marks around a break in the skin, most often in the anal region, around the dorsal fin, or behind the gills and pectoral fin. So many dead salmon had their eyes (or at least the one on the upper, exposed side) pecked out that this wound pattern was ignored. The birds at the delta were almost all glaucous-winged gulls. There were a few Bonaparte's *L. philadelphia* and mew *L. canus* gulls, but they were not observed attacking salmon. Eagles, ravens and other large birds were rarely seen so we attributed the attacks to glaucous-winged gulls, but a small fraction might have been caused by other species.

In 1998 and 1999, fish in all areas (mouth, stream, pond) were categorized as stranded, gull-pecked, or bear-killed. Additionally, fish that appeared to have died of senescence were counted in spawning areas (creek and pond). Stranded fish were in shallow water or on gravel bars in relatively fresh condition, apparently trapped during migration, reproductive competition or trying to escape bears. Senescent fish had reached the end of their natural lives and were distinguished from stranded fish by frayed fins, gaunt bellies, scars from fights, and fungus on the body. The categorization of fish by mode of death was generally unequivocal, but there were some ambiguous cases. We attempted to be as consistent as possible but some salmon are scavenged after death and left in the stream (about 25–30% were scavenged one day after they died in Hansen Creek; Quinn and Buck 2000) and others are removed from the stream to the woods and so would not be found (about 30%; Quinn et al., in press [b]). Nevertheless, hundreds of dead salmon were found in or immediately adjacent to the creek every day, and only a few were found more than 5 m from the stream. We feel that the rigorous, daily surveys allowed us to find and correctly categorize most carcasses, and the categorization of salmon mortality from the surveys was consistent with the results of tagging studies on Hansen Creek (Quinn et al., in press [b]).

Carcass lengths were measured from the middle of the eye to the hypural plate. This measurement approximates the somatic growth of the fish and is not biased by the elongated snout of males. It also enables fish (especially females) with very frayed tails to be accurately measured. Many of the bear-killed salmon were partially consumed and the body length could not be measured. We estimated their body length from regression relationships developed from a large number of measurements of body length and head length (mid-eye to tip of snout) from intact carcasses of each sex in each year. The relationships for all years combined were body length = head length $\times$ 3.61 + 262.42 for females (N = 147, r^2 = 0.56, $P <$ 0.001) and body length = head length $\times$ 3.10 + 206.87 for males (N = 309, r^2 = 0.80, $P <$ 0.001). We attempted to measure body or head length of every salmon, but at some point in each season this became impossible because there were so many dead salmon. Subsequently, we measured fish in the order that they were encountered (to avoid bias in selecting fish to measure) until a set number (usually 20) in each sex and category were measured in each of three sections of the creek each day; the rest were counted and categorized. After measurement, carcasses were thrown as far as possible into the forest on one side of the creek to prevent repeated measurements.

The combination of counts and measurements allowed us to estimate the probability that fish of each sex in a given size category would die at the mouth of the stream (i.e., unspawned) or be killed in the creek. To determine the likelihood of prespawning mortality and predation as functions of fish age, we collected otoliths and measured about 100 carcasses of each sex from Hansen Creek and Bear Creek (see below) in 1998 and 1999.

Surveys of other creeks and ponds.—In addition to the data from Hansen Creek, we counted and measured fish from two other larger creeks in the Wood River system: Bear Creek (5.1 m wide, 19.3 cm deep) and Pick Creek (7.6 m, 37.9 cm; Marriott 1964; Quinn, unpublished data; Figure 1). We also sampled salmon at two sites in the Iliamna Lake system, which is about 270 km east of the Wood River lakes: Chinkelyes Creek (larger than either Pick or Bear creek at 15.2 m wide and 35.6 cm deep) and the Pedro Bay Pond system (a series of ponds and interconnecting creeks). These ponds range from about 20 to about 40 cm deep and from about 300 to about 1800 m^2 in area; the creeks are very small (1–3 m wide, 10–20 cm deep; Demory et al. 1964; Quinn and Kinnison 1999).

The extent of sampling varied among sites and years owing to the abundance of fish and logistic constraints (e.g., travel difficulties and other activities), but in all cases we visited the creeks on one or more days during the season (late July and

August), measured senescent dead and bear-killed sockeye salmon, and made complete or partial carcass counts. Data were collected at Bear Creek on 25 d from 1995 to 1999, at Pick Creek on 10 d from 1995 to 1998, at Chinkelyes Creek on one day each in 1994, 1995 and 1999, and at the Pedro Bay ponds on 6 d in 1999. Sex- and site-specific regression relationships between head length and body length were used to estimate the length of fish whose bodies were partially consumed. For Pick Creek, body length was 2.77 × head length + 212.98 for males ($r^2 = 0.75$) and 4.08 × head length + 215.98 for females ($r^2 = 0.66$). For Bear Creek, body length was 2.36 × head length + 270.41 for males ($r^2 = 0.61$) and 4.03 × head length + 231.67 for females ($r^2 = 0.61$). For the Pedro Bay Ponds, body length was 2.55 × head length + 249.34 for males ($r^2 = 0.59$) and 4.01 × head length + 230.98 for females ($r^2 = 0.60$; $P < 0.001$ in all cases). At Chinkelyes Creek, only fish measured for body length were used in the analysis. Length data were analyzed using a separate two-way analysis of variance (ANOVA) with creek and mode of death as factors for males and females because the size difference between sexes is so well-established (e.g., Blair et al. 1993; Quinn and Kinnison 1999) and because combining the sexes into 3-way analyses resulted in unbalanced sample sizes. Carcasses too deteriorated for measurement were counted to estimate the sex ratios of senescent and bear-killed fish. As with Hansen Creek, we combined the data on the size distributions of bear-killed salmon from Bear Creek with the relative abundance of killed and senescent fish to produce estimates of the probability of predation on males and females of different size-classes. The data were combined over the years of sampling, and we then used the data on size at age to estimate predation as a function of fish age.

Excluding Hansen, Pick, and Bear creeks, 14 other creeks (Figure 1) were sampled on one day during the 1997–1999 spawning seasons in the Wood River Lake system. Six creeks were surveyed every year (Eagle, Happy, Hidden Lake, Ice, Lynx, and Yako creeks), six in 2 of the 3 years (Big Whitefish, Little Whitefish, Elva, Kema, Mission, and Stovall creeks), and 2 were sampled in only 1 year (Fenno and Grant creeks). On these surveys, the crew counted the total number of live, senescent dead and bear-killed sockeye salmon by sex over the entire creek or over an established reference reach if the creek was too large for a comprehensive survey. Methods were similar among years and provided an index of predation.

To compare with the more intensive data from Hansen, Bear and Pick creeks and the Pedro Bay ponds, we initially calculated the sex ratio of live, bear-killed, and senescent dead salmon from these 32 surveys. For subsequent analyses we included the data from the comprehensive annual surveys on Pick (in 1998) and Bear Creek (1997–1999) and the results from the total counts on Hansen Creek (1997–1999) to provide the best characterization of the range of sex-biased predation among all sites in the Wood River system. For Hansen Creek, the fish classified as stranded or gull-pecked in the detailed analysis (above) were classified as senescent deaths for comparison with other creeks.

The sites we sampled include most of streams in the Wood River Lake system that produce sockeye salmon. These ranged from creeks smaller than Hansen Creek (Mission Creek) to ones considerably larger than Bear and Pick creeks (Ice Creek and Grant River) and included sites with simple stream channels lacking pools and structural complexity (Big Whitefish, Little Whitefish and Mission creeks), sites with more complex stream channels and deeper pools (Happy and Yako creeks), creeks where many salmon spawn in spring-fed ponds (e.g., Hidden Lake Creek), and creeks ranging in gradient from steep (Elva and Hidden Lake creeks) to low gradient (Eagle Creek). We could not obtain representative samples from large rivers, but our observations indicate that predation is negligible in such habitats. We used a chi-square contingency test to examine the null hypothesis that the sex ratio would not depend on status (live, senescent dead, or bear-killed). We first pooled the entire data set to determine the overall pattern, then examined the data for each creek and year separately, and finally included the comparable data from Bear, Hansen, and Pick creeks (i.e., a single comprehensive survey on 1 d each year) in these analyses.

Results

Hansen Creek Surveys

On average, 13.7% of the salmon died at the mouth of Hansen Creek below the spawning grounds (7.9% in 1997, 9.3% in 1998, and 20.2% in 1999; Table 1). A disproportionate number of the dead salmon at the mouth were males (55.4% males versus 41.4% males upstream; $P < 0.001$, all 3 years combined). Location of mortality, year, and gender were not independent, based on a two × two × three contingency test; males were more likely to die at the mouth, but the proportion dead

TABLE 1.—Numbers of male and female sockeye salmon that died in Hansen Creek, Alaska, and the percentages that died at the mouth before reaching the spawning grounds, 1997–1999.

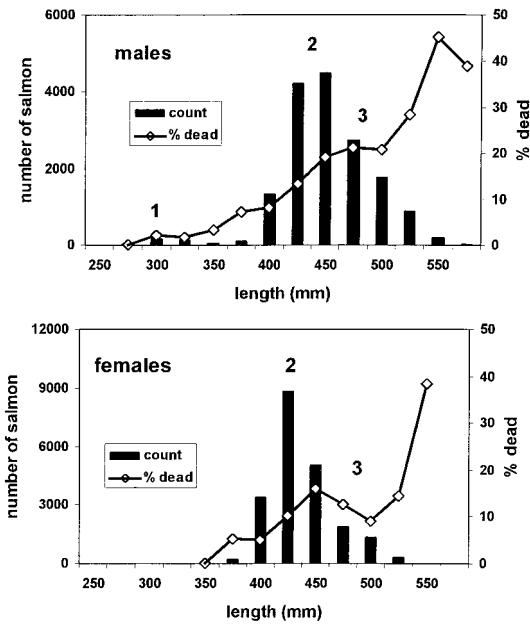| Year	Sex	Total dead	Percent dead at mouth
1997	Female	4,037	3.8
	Male	3,956	12.1
	Both	7,993	7.9
1998	Female	6,904	7.4
	Male	6,128	11.4
	Both	13,032	9.3
1999	Female	10,154	15.9
	Male	6,024	27.5
	Both	16,178	20.2
Combined		37,203	13.7

FIGURE 2.—Length-frequency histograms of male and female sockeye salmon that arrived at Hansen Creek from 1997 to 1999 and the percentages of each size category that died at the mouth of the creek. The average lengths of fish that spent 1 (males only), 2, and 3 years at sea are indicated by bold numerals.

at the mouth varied among years ($P < 0.001$, Table 1). In total, 17.6% of the male salmon that reached Hansen Creek died at the mouth, and 10.9% of the females died there.

The fish of both sexes that died at the mouth of Hansen Creek tended to be larger than those that ascended the creek (ANOVA, $P < 0.001$ in both cases; Table 2), and the probability that a fish would die at the mouth increased with size for both males and females (Figure 2). However, there was a much higher probability of mortality at the mouth in 1999, when only 6 of the 52 largest fish were able to ascend the creek. In the other 2 years, about 40% of the salmon in the largest size categories died at the mouth. Of the fish that died at the mouth, females were more often bitten by bears than were males (strongly so in 1997, weakly so in 1998, and not so in 1999) and were much more likely to be pecked by gulls (Table 3). In contrast, males were more often dead but not scavenged or attacked. There was also significant variation in length among fish in different categories of mortality at the mouth (ANOVA, $P < 0.001$ in both sexes). The largest fish were stranded but not gull-pecked, the next largest were bear-bitten, and the smallest were gull-pecked (males were 460, 450,

and 436 mm, respectively; females were 445, 431, and 427 mm).

Upstream of the mouth, the fish of both sexes killed by bears were larger on average than those dying of senescence. Fewer salmon were killed by gulls and stranded upriver than at the mouth, but for both sexes larger fish were generally either bear-killed or stranded and smaller fish died of senescence or were gull-pecked (Table 4). In 1998, many males were very small (about 290–300 mm), having only spent 1 year at sea; these fish were least likely to be stranded but were frequently gull-pecked (Table 4). The probability of a fish being

TABLE 2.—Average (SD) lengths and sample size (N) of sampled male and female sockeye salmon that died at the mouth of Hansen Creek versus those that survived to ascend the creek, 1997–1999.

Year	Sex	Mouth		Upriver	
		Length (mm)	N	Length (mm)	N
1997	Females	476 (33.5)	115	454 (34.8)	1,737
	Males	499 (33.2)	333	465 (44.2)	1,590
1998	Females	427 (23.9)	500	418 (20.6)	4,827
	Males	441 (35.1)	641	424 (39.0)	3,670
1999	Females	428 (21.7)	1,607	418 (21.9)	1,664
	Males	445 (29.0)	1,639	432 (27.1)	1,037

TABLE 3.—Sources of mortality of sockeye salmon found dead at the mouth of Hansen Creek, expressed as percentages of the total that were bear-killed, stranded, and gull-pecked, 1997–1999.

Year	Sex	Bear-killed	Stranded	Gull-pecked	Total number
			Percentage		
1997	Female	11.6	88.4[a]		155
	Male	5.6	94.4[a]		480
1998	Female	38.3	3.5	58.2	514
	Male	34.8	26.1	39.1	696
1999	Female	10.8	13.3	75.9	1,612
	Male	11.4	48.9	39.7	1,655

[a] In 1997, stranded and gull-pecked fish were not distinguished and so are combined here.

killed by a bear increased greatly with size for males and females (Figure 3) and males were larger (though more variable) than females. The spring-fed pond offered some safety from predation, relative to the rest of the creek, in all 3 years. Overall, 9.0% of the 1,068 sockeye salmon found dead in the pond had been killed, whereas 41.7% of the 31,023 dead salmon in the rest of the creek above the mouth had been killed.

Based on length-at-age data collected in 1998 and 1999, the average Hansen Creek male salmon spending 1, 2, or 3 years at sea was 291, 423, and 462 mm long and the average female spending 2 or 3 years at sea was 414 and 469 mm long. Bear Creek fish were larger for a given marine age: males age 2 = 443 mm, age 3 = 495 mm; females age 2 = 419, age 3 = 472 mm. No fish of marine age 1 were sampled from Bear Creek. These data were used to estimate the probability of mortality from various causes as a function of age (Figures 2, 3, 4).

Surveys of Other Creeks and Ponds

Males were overrepresented among the bear-killed salmon at all four creeks relative to the dead salmon that had not been killed (χ^2 values with 1
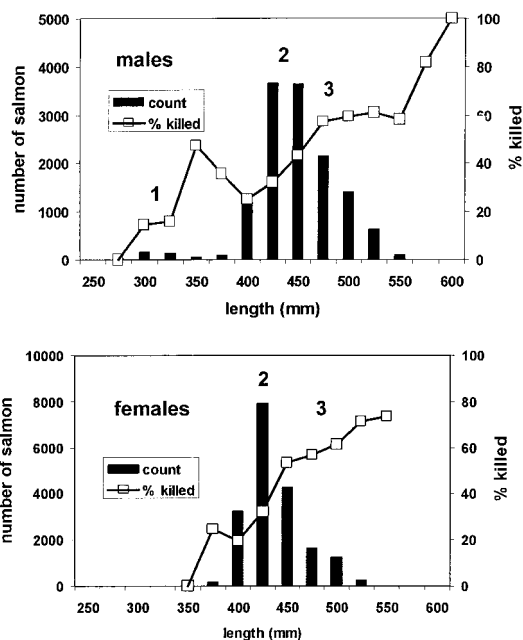

FIGURE 3.—Length-frequency histograms of male and female sockeye salmon that ascended Hansen Creek (i.e., excluding those dead at the mouth) from 1997 to 1999 and the percentages of each size category killed by bears. Bold numerals indicate the average lengths of fish that spent 1 (males only), 2, and 3 years at sea.

df) at Bear Creek (44.87), Chinkelyes Creek (102.07), Pedro Bay ponds (28.32), and Pick Creek (564.94; $P < 0.001$ in all cases) and among the sites pooled together ($\chi^2 = 736.82$, $P < 0.001$; Table 5). The lengths of females varied among those four sites ($P = 0.002$), but there was no overall difference between the lengths of bear-killed and senescent dead females ($P = 0.159$; Table 6). However, at three of the four sites the bear-killed females were larger than the senescent dead females, and the difference was significant at Bear Creek (two-tailed test, $t = 2.57$, $P = 0.01$) and Pick Creek ($t = 3.17$, $P = 0.001$). Among males,

TABLE 4.—Average lengths (sample sizes in parentheses) of sockeye salmon that ascended Hansen Creek, categorized by mode of death: bear-killed, stranded, gull-pecked, and senescent, 1997–1999.

Year	Sex	Bear-killed	Stranded	Gull-pecked	Senescent
			Length (mm)		
1997	Female	456 (1,187)	454 (71)[a]		450 (479)
	Male	469 (890)	477 (162)[a]		454 (538)
1998	Female	424 (2,406)	427 (41)	416 (340)	411 (2,040)
	Male	434 (1,695)	444 (244)	359 (100)	415 (1,631)
1999	Female	426 (625)	421 (57)	417 (156)	413 (843)
	Male	440 (413)	438 (75)	424 (15)	425 (545)

[a] In 1997, stranded and gull-pecked fish were not distinguished and so are combined here.
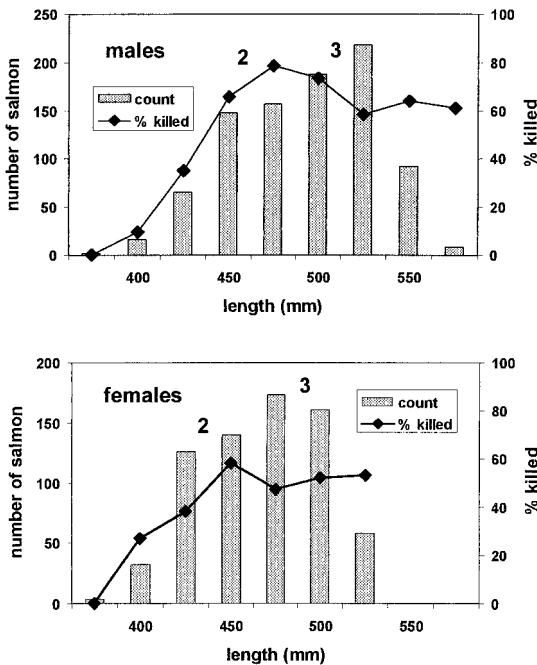
FIGURE 4.—Length-frequency histograms of male and female sockeye salmon that ascended Bear Creek from 1995 to 1998 and the percentages of each size category killed by bears. Bold numerals indicate the average lengths of fish that spent 1 (males only), 2, and 3 years at sea.

TABLE 5.—Percentages of the dead male and female sockeye salmon that were killed by bears at four spawning sites in the Wood River system, Alaska, 1997–1999.

	Females		Males	
Site	Bear-killed (%)	Total number	Bear-killed (%)	Total number
Bear Creek	65.9	1,507	76.2	1,941
Chinkelyes Creek	20.5	268	59.2	458
Pedro Bay ponds	78.7	409	90.2	721
Pick Creek	36.4	3,167	66.9	2,930
Total	47.2	5,351	72.1	6,050

ANOVA revealed significant variation among sites ($P < 0.001$) and a strong tendency for bear-killed fish to be larger than those dying of senescence ($P < 0.001$; Table 6). Although the average lengths of bear-killed and senescent fish differed by only a few millimeters, the probability of being killed increased greatly with size (e.g., see Bear Creek in Figure 4).

On the 32 different surveys of 14 different creeks, 111,126 salmon were counted, of which 67.0% were live and 33.0% were dead. Of the 36,634 dead salmon, 44.5% had been killed (54.1% of the males and 36.5% of the females) and 55.5% had died of senescence. Males were overrepresented among the bear-killed fish (55.5%) and underrepresented among the senescent dead fish (37.8%) and relative to the overall sex ratio (46% males; $\chi^2 = 12{,}135.04$, 2 df, $P < 0.001$). Examination of the data from individual surveys revealed, however, that male-biased predation was not always the case. Including the data from three surveys each on Bear and Hansen creeks and one from Pick Creek, the average of the 39 surveys was 44.38% males among all the fish; the mode was 50% males, but there was a skew towards female-biased counts. In contrast, the distribution of percent males among the bear-killed fish showed modes at 40% and 65% males; fewer surveys reported nearly even sex ratios. In 25 surveys there was a significant overrepresentation of males among the kills, in 5 surveys females were significantly overrepresented, and in 9 there was no deviation from the sex ratios of the live and senescent dead fish (chi-square test with 2 df and $P < 0.001$ to correct for multiple comparisons: $0.05/39 = 0.0013$). There was no ap-

TABLE 6.—Average lengths (mm) and sample size (*N*) of adult sockeye salmon from four Wood River, Alaska, spawning sites that were killed by bears or died from senescence, 1997–1999.

Site		Females		Males	
		Bear-killed	Senescent	Bear-killed	Senescent
Bear Creek	Length	459.4	452.7	482.2	477.3
	N	257	437	487	408
Chinkelyes Creek	Length	441.3	450.0	483.1	462.4
	N	12	291	76	266
Pedro Bay ponds	Length	450.8	446.5	460.2	452.3
	N	177	86	283	66
Pick Creek	Length	465.2	450.9	486.0	469.1
	N	114	269	335	340
Total	Length	457.5	451.0	478.1	469.5
	N	560	1,083	1,181	1,080

parent pattern in the sex-biased predation with re-spect to creek. That is, individual creeks did not consistently have male-biased or female-biased re-sults among years.

Discussion

Our results indicated that predation by bears was selective with respect to size and sex in a range of salmon habitats, though the patterns were not always the same. Without directly observing bears, it is not possible to know the mechanism under-lying the selective predation. Large fish may be easier to see and catch than smaller ones, and be-cause males tend to be larger than females, this may contribute to the pattern of sex-biased pre-dation. Male sockeye salmon are also deeper-bod-ied for their length than females (Blair et al. 1993; Quinn et al., in press [a]), so they might be more conspicuous or less maneuverable in shallow water than females. The tendency for bears to kill male salmon was evident in the large, overall data set but was less clear when annual surveys in the creeks were considered separately. In some creeks and years females were more often killed than males, so direct selection by bears may also take place, albeit in some years there was no pattern. We are unable to explain this variation, but it might arise from differences in foraging choices among bears. The patterns of partial carcass consumption by bears differed markedly with the sex and size of the salmon (Quinn and Buck 2000; Gende et al. 2001), and this is consistent with some amount of active selection by the bears.

Sex-selective predation might be expected to disrupt the breeding system (Clutton-Brock and Parker 1992; Kvarnemo and Ahnesjö 1996) and perhaps lower overall productivity. However, salmon typically have male-biased operating sex ratios (i.e., more ripe males than ripe females) be-cause males remain reproductively active through-out their lives on the spawning grounds; females quickly deposit their eggs and then guard them, so are not available for courting (Quinn et al. 1996; Hendry et al. 1999). Thus, even severe selection against males is unlikely to affect the productivity of the population (Mathisen 1962).

In addition to the selective predation by bears, the shallow mouth of Hansen Creek presented strong selection against males and especially large ones. The frequency of mortality there varied among years, but in 1999 very few large fish (>500 mm) were able to ascend to the breeding grounds. Although overall bears killed more fish upstream than died at the mouth of the creek, all mortality at the mouth occurred before spawning, whereas fish killed upriver had a chance to spawn. Combining the length-at-age data with the patterns of mortality, we estimated that the average male returning after just 1 year at sea had about a 2% probability of dying at the mouth and a 12% chance of being killed by bears upriver. In contrast, average males of marine ages 2 and 3 had roughly 25% and 32% chances, respectively, of dying at the mouth and 38% and 56% chances of being killed by bears if they ascended the creek. Older females also experienced higher mortality rates than younger ones at the mouth and upriver. Not surprisingly, Hansen Creek has a smaller percent-age of sockeye salmon spending 3 years at sea than most other creeks and rivers in the Wood River system (Rogers 1987; Quinn et al., in press [a]).

Bear Creek sockeye salmon were older, on av-erage, than Hansen Creek fish (Rogers 1987) and larger for a given age (our results), indicating low-er selection against large salmon in Bear Creek. Unlike Hansen Creek, the mouth of Bear Creek is sufficiently deep that sockeye salmon do not strand there (personal observations). Bear Creek also has had a lower average annual predation rate than Hansen Creek (30% versus 46%; Quinn et al., in press [a]). Moreover, the estimated predation rates in Bear Creek differed little between salmon of marine ages 2 and 3. Predation seemed to level off at about 60% among the largest Bear Creek fish, whereas in Hansen Creek the estimated rate dif-fered more with age and approached 80–100% for the very largest fish (compare Figures 3 and 4).

The extent of stranding at the mouth of Hansen Creek is the most extreme that we have observed in the Wood River and Iliamna Lake systems but several other streams in Lake Aleknagik (e.g., Mis-sion Creek and a small, unnamed creek near Bear Creek) also have very shallow mouths where some fish strand. The fish from shallow creeks tend to be less deep-bodied than those from rivers and beaches in the lakes, consistent with the selective effects of predation and stranding (Quinn et al., in press [a]). In addition to selection effects on life history and morphology, the mouths of these creeks may also be important in selecting for spawning date. The level of the lakes is generally high in spring due to snow melt and declines dur-ing July and August, when sockeye salmon enter most of the small creeks. The mouth of Hansen and the other creeks is easiest to ascend early in the season and gets progressively more difficult later. The early spawning in Hansen Creek (relative

to other creeks in the Wood River system) may be related, in part, to access.

The sockeye salmon that die at the mouth of Hansen Creek are unable to reproduce, regardless of the apparent cause of death (i.e., stranding, bear bites or gull attacks). However, the gulls pecked predominately females, and much of the pecking was directed at the belly region, consistent with data on scavenging by gulls (Quinn and Buck 2000). Mossman (1958) characterized the gulls at Hansen Creek as predators, but we are reluctant to do so without further, quantified observations. Many salmon struggle to ascend the mouth and simply flop over from exhaustion or ascend a part of the delta that gets progressively shallower and does not lead to the main channel. Such fish die even in the absence of gulls, and we have seldom observed gulls actually attacking vigorous fish migrating upstream. However, in 1998 there were many jacks (males that only spent 1 year at sea) and quite a few were pecked by gulls in Hansen Creek proper (note the small average size of gull-pecked males; Table 4). These fish, so small (about 300 mm) that they were unlikely to have stranded, may have been the object of direct predation by gulls rather than postmortem attacks.

Predation seems to exert selection against large salmon in general, but there is variation in vulnerability within stream systems. The Hansen Creek pond was a refuge from predation, compared with the rest of the creek, which is consistent with findings in the Pedro Bay Pond system (Quinn and Kinnison 1999). Habitat heterogeneity within streams may present salmon with a conflict between habitat quality and predation. We do not know whether salmon home to specific habitat units, such as the pond, but if so, this might present the opportunity for selection to favor divergent phenotypes in the different habitats. In any case, physical habitat seems to exert direct selection on body size, in the extreme case of stranding, and indirect selection by facilitating bear predation. Such clear evidence of selective mortality of large individuals has proven difficult to obtain in many cases (Blanckenhorn 2000). Some salmon populations spawn in large rivers where bears are probably unable to catch significant numbers. However, many salmon spawn in small streams where bears would have greater access to them, and selective predation may have played a role in the evolution of body size and age at maturity in salmon, along with patterns of mortality and growth at sea (e.g., Healey 1987).

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