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Size-selective and sex-selective predation by brown bears on sockeye salmon

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Abstract Breeding activity increases the vulnerability of many animals to predation, and such predation can affect the subset of animals successfully reproducing. To study the ways in which predation might affect the evolution of Pacific salmon, we measured the intensity and selectivity of predation by bears (primarily brown bears, *Ursus arctos*) on mature sockeye salmon (*Oncorhynchus nerka*) breeding in a series of small, spring-fed ponds and creeks near Pedro Bay, Alaska, from 1994 to 1998. Bears killed male salmon more often than females; males constituted 60% of the kills but only 35% of the salmon that died of senescence. The bears also killed fish that were larger, on average, than those dying of senescence (males: 462 vs 452 mm; females: 453 vs 443 mm). The level of predation varied greatly, from 4% (females) and 10% (males) in 1994 to 100% of both sexes in 1996 and 1997. The rate of predation also varied among habitats, being lower in larger ponds than in smaller, shallower ponds and the very small interconnecting creeks. Despite the intense and size-selective predation, the salmon in safer habitats (large ponds) were not larger than those in riskier habitats, and salmon densities were only slightly higher in the safer areas. Compared to a nearby population that experiences no bear predation (Woody Island), the male sockeye salmon from the Pedro Pond system had shallower bodies (i.e., less exposure in shallow water) for a given length, consistent with the hypothesis that selective predation can affect the extent of sexual dimorphism among populations. However, the average length at age for both males and females was greater in the Pedro Pond fish, indicating that selective factors besides predation affect length. Overall, the results indicate that bears can be an agent of natural selection within (and perhaps between) sockeye salmon populations, and predation can greatly affect reproductive success among individuals and years for the population as a whole.

Key words *Oncorhynchus nerka* · *Ursus arctos* · Predation · Selection · Sexual dimorphism

Introduction

Most animals risk predation during at least part of their lives, and life history, morphology, and behavior can be influenced by predation pressure. Many animals display patterns of morphology, resource use, and behavior that reflect trade-offs between risk of predation and other activities such as feeding (Godin 1990) and reproduction (Magnhagen 1991). For example, predation risk may decrease male advertisement (Ryan et al. 1982), choosiness of mates (Forsgren 1992; Berglund 1993; Godin and Briggs 1996), mating frequency (Sih 1988; Berglund 1993), movement patterns and habitat use (Sih 1988), choice of breeding habitat (Candolin and Voigt 1998), and may play a role in the evolution of communal sexual displays (Ryan et al. 1981). The nature of the breeding system or the sizes of the males and females often result in markedly sex-biased predation (e.g., Gwynne 1987; reviewed by Magnhagen 1991). When predation is also size biased (e.g., Trexler et al. 1994; Sparkes 1996), it can affect the breeding system and life history traits of the species or population. The patterns of coloration, behavior, and life history traits displayed among and within populations of guppies illustrate the evolutionary pressure that can be exerted by predation. In populations exposed to high rates of predation, males are less colorful, more wary, and court less often, while females breed early in life and produce many small offspring relative to populations with lower predation rates (reviewed by Endler 1995; Houde 1997).

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It may be difficult to study the interactions between predator avoidance and reproduction because of additional interactions with feeding behavior (Sih et al. 1990; Abrahams 1993; Endler 1995), especially in natural settings. However, many populations of Pacific salmon (*Oncorhynchus* spp.) spawn in small streams that expose them to predation by brown (*Ursus arctos*) and black bears (*U. americanus*). These situations present an excellent opportunity to study the interplay between reproduction and predation risk because the salmon do not feed on the spawning grounds and will inevitably die of senescence if they are not killed. Bears can kill many live salmon, often before they have completed spawning (Shuman 1950; but see Merrell 1964). The magnitude of predation seems to vary; estimates of predation on sockeye salmon (*Oncorhynchus nerka*) in streams on Kodiak Island, Alaska, ranged from 31 to 79% (Shuman 1950; Gard 1971). The extent to which bear predation is sex biased is also unclear. Frame (1974) reported that ripe (unspawned) females were more likely to be retained and consumed, but other authors (Gard 1971; Konovalov and Shevlyakov 1979; Hanson 1992; G.T. Ruggerone, R. Hanson, D.E. Rogers, unpublished data) reported heavier predation on males. Without knowing the patterns and magnitude of predation and its consistency from year to year it is difficult to assess how important bears might be in the population dynamics and evolution of salmon.

Despite the risk of predation, salmon must move onto the spawning grounds or die without reproducing (Groot and Margolis 1991), and body size influences reproductive success in females and males. Larger females lay larger and more eggs than smaller females (Beacham and Murray 1993). Large size and prior access are favored in female intrasexual competition for nest sites (Van den Berghe and Gross 1989; Foote 1990; Quinn and Foote 1994). Larger females tend to dig deeper nests than smaller females (Steen and Quinn, in press), affording greater protection against nest disturbance by other females (McNeil 1964) or streambed scour. Size also influences the reproductive success of males, as large males tend to dominate smaller males in competition for females (Hanson and Smith 1967; Fleming and Gross 1994). Not only is body length related to status among males but the depth of the body (the dorsoventral distance that increases at maturation), independent of length, is correlated with status and access to females (Quinn and Foote 1994). However, small males may successfully gain access to spawning females by sneaking (Gross 1985; Foote 1990). Males commonly vary more in size and age than females, reflecting these alternative reproductive patterns (Groot and Margolis 1991).

Size and shape are thus important to the reproductive success of individual salmon but these traits vary among populations (e.g., Blair et al. 1993; Wetzel 1993). The variations in average age, size, and shape of sockeye salmon populations in western Alaska were hypothesized to reflect, in part, a balance between sexual selection, favoring large, deep-bodied fish, and predation, selecting against such individuals (Rogers 1987; Blair et al. 1993; Quinn and Foote 1994). Consistent with this hypothesis, Hanson (1992) and G.T. Ruggerone, R. Hanson and D.E. Rogers (unpublished data) reported that the sockeye salmon killed by bears were larger than those dying of senescence in two small tributaries of Lake Aleknagik, Alaska. An understanding of the role played by bear predation in the ecology and evolution of salmon populations depends on accurate assessment of the magnitude of predation, the selectivity of the predation, and the factors influencing predation rate.

The overall goal of this 5-year study was to examine the patterns of predation by bears on sockeye salmon in a complex of small creeks and ponds near Pedro Bay, Alaska. Our specific objectives were to test the predictions that the level of predation is (1) similar among years, (2) higher on males than females, and higher on larger fish than smaller ones, and (3) more intense in narrower, shallower habitats than in wider and deeper ones. We also tested the predictions that (4) the high-risk habitats have smaller-bodied salmon and lower salmon densities than low-risk habitats, and (5) the body depth of male salmon and the length of both males and females in the population subject to predation is smaller than in a nearby predation-free population.

Materials and methods

Site description and habitat surveys

The study site was a series of small spring-fed ponds connected by shallow creeks flowing into Pedro Bay in the northeastern region of Iliamna Lake, Alaska (Fig. 1). This site was selected because preliminary observations in 1992 and 1993 detected evidence of predation by bears and because the ponds and creeks present diverse spawning habitats for salmon. We initially chose a series of five ponds and the reaches of creek connecting them for our study (designated Pedro Pond, creek 1A, pond 1A, creek 1, pond 2, creek 2, pond 3, creek 3, pond 4, and creek 4). For convenience we will refer to these habitats as the Pedro pond-creek system. We also sampled another nearby pond (designated Grass Pond) which flows into the Pedro pond-creek system below the surveyed section of creek 4. Physical habitat measurements (depth, width, velocity, and substrate type) were collected on 23–24 August 1995. We recorded depth, width, and velocity at mid-channel at five equidistant points along each creek and estimated its area as the length (measured with tape) times average width. Water velocity was measured at the thalweg of the creeks but was negligible in the ponds. These measurements were generally representative of the habitats, though the methods tended to undersample the edges. We estimated the area of each pond from a series of tape measurements and digitized aerial photographs, and measured depth at equidistant points throughout the ponds. Substrate was visually estimated for all habitats as the percent of material that was silt (<1 mm diameter organic material), fine sand (1–2 mm), coarse sand (2–5 mm), gravel (5–20 mm) and cobble (>20 mm). Observations indicated that the conditions were very similar on all sampling dates in the other years, probably as a consequence of the spring water source, producing stable flow and temperature regimes and uniformly clear water. In addition to the measurements of the Pedro pond-creek system and Grass Pond, we also measured depth and area in two other ponds, designated Bear and Trail ponds.

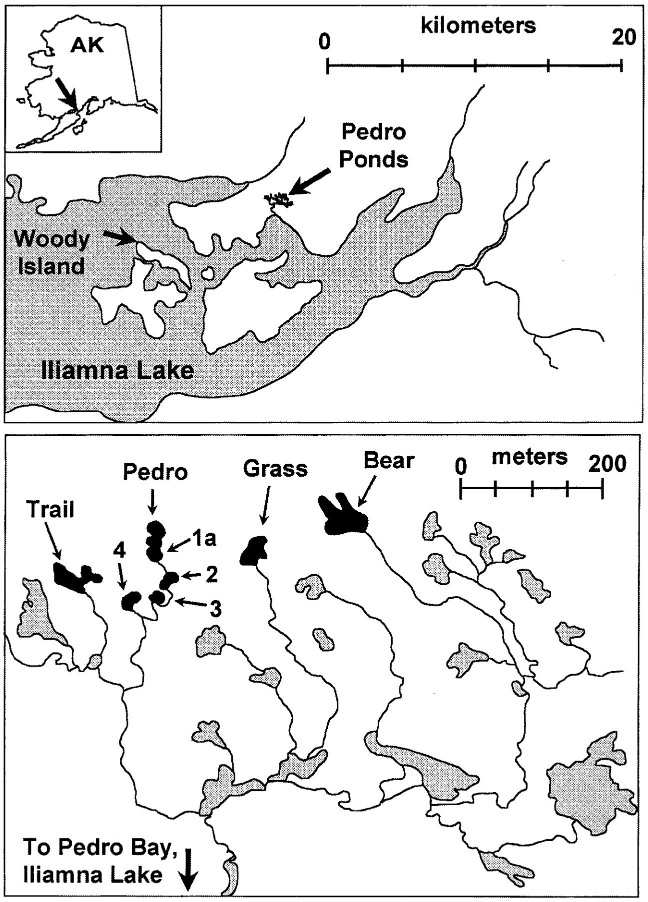

Fig. 1 Map of the Pedro pond-creek system in Iliamna Lake, Alaska, showing the ponds surveyed for salmon and bear predation. The creeks surveyed were below the corresponding ponds (e.g., creek 4 flows out of pond 4)

Surveys of salmon

Surveys and sampling of live and dead salmon were conducted in mid–late August from 1993 to 1998 but their frequency and scope varied from year to year. Based on aerial surveys conducted by the Alaska Department of Fish and Game, the Pedro Bay ponds support several thousand spawning sockeye salmon per year (Regnart 1996) but the abundance of salmon and rate of predation varied so greatly among years that the data collected had to vary as well. In 1993, we sampled 100 males and 100 females, measuring their body length and removing otoliths for age analysis. We did not collect data on predation but qualitative observations motivated the sampling in subsequent years. Length was measured from the middle of the orbit of the eye to the hypural plate (effectively the end of the spinal column). This measurement estimates the extent of somatic growth and is not biased by the greater lengthening of the jaws in male salmon and the fraying of the tail commonly observed in females.

In 1994, we surveyed Pedro Pond by foot every other day from 16 to 24 August, and the rest of the pond-creek system and Grass Pond on 24 August. These habitats were selected on the basis of high salmon densities seen in 1993. On each day, all dead salmon were sexed and counted. All salmon killed by bears were measured (body or snout length, depending on condition) and a random subsample (every fifth fish encountered) of those dead of senescence was also measured. In addition to body length, we measured the lengths of the snouts (mid-eye to tip of upper jaw) of a subsample of dead males and females. The relationships between head length and body length (males: r^2 = 0.64, n = 59, females: r^2 = 0.62, n = 60) enabled us to estimate the body length of many bear-killed salmon whose bodies had been consumed. The average observed and estimated body lengths of fish for whom head and body were both measured differed by <0.01 mm, indicating that the estimates were not biased. We also tallied salmon whose jaws were too mangled for even a snout measurement. After being counted and measured, all carcasses were removed from the immediate vicinity of the stream or pond to prevent repeat counting. These surveys provided data to address the hypotheses concerning the size distributions of bear-killed and naturally dead salmon, predation rates on males and females, and the spatial distribution of salmon in the system.

In 1995, we repeated the surveys for dead fish and head length-body length regressions were again established for males and females to estimate the length of fish whose bodies had been eaten. Measurements were made as in 1994 except that the entire Pedro pond-creek system and Grass Pond were surveyed on every other day from 15 to 29 August. In addition, live male and female salmon were counted in each creek and pond in the Pedro pond-creek system and Grass Pond. These live counts were made by two observers, walking slowly on either side of the creeks, a few meters back from the edge. In the ponds, counts were made from the banks and by wading slowly through the pond. Counts in the creeks and small ponds were considered highly accurate, as were the counts in large ponds when few fish were present. When there were many fish in the large ponds, the accuracy was about ±10%. In 1996, we surveyed the Pedro pond-creek system and Grass Pond, as well as two other ponds (Trail and Bear) every day from 20 to 24 August but very few live or dead salmon were found. Not a single senescent dead fish was found and all the salmon killed by bears were too completely consumed to enable us to measure anything but the head length in a few cases. Accordingly, we used regression relationships combining data from 1993, 1994, and 1995 (r^2 = 0.53 and n = 123 for males; r^2 = 0.62 and n = 173 for females) to estimate body length from head length. In addition, we often found scraps of tissue, especially pyloric cecae and liver, but no other body parts. When these were in sufficiently discrete locations, they were tallied as they had presumably come from sockeye salmon because no other large fish were ever seen in these ponds. In some sites we did not see live fish but we collected and removed fresh scraps of tissue each day, indicating that salmon were being killed before we could count them. We also counted redds as an index of the number of live females (redds are usually dug within 1–2 days of arrival on the spawning grounds; McPhee and Quinn 1998). Comparable data were not collected in other years because there were so many redds and salmon, so the redd counts were not added to the formal counts of live or dead fish.

In 1997, the entire system was visited on 15 and 25 August but no live salmon were seen and only a few scraps of tissue were collected. In 1998, the entire system was surveyed once over a 2-day period (24–25 August) and counts were made of live and dead salmon. As with 1996, there were very few whole carcasses, so regression relationships from 1993, 1994, and 1995 were combined to estimate body length from head length. Because of the variation in effort among years, some analysis (e.g., size-biased predation) used all the data but other analyses examined the data collected through 24 or 25 August because samples were taken on one of those dates each year. The live counts on that date and the cumulative counts of dead salmon provided a basis for comparison among years. Based on data from 1995, when we sampled both before and after that time (Fig. 2), 24–25 August is well past the peak of spawning and many salmon would be dead of senescence but others would still be alive in the absence of predation and a few salmon would be arriving. Sockeye salmon populations in the area show very little interannual variation in spawning date so surveys on a fixed date sample fish at about the same point in the breeding season.

The mutual wariness of the bears and humans towards each other and the demands of sampling the salmon prevented us from quantifying the number of bears using the pond system, and observing their fishing techniques or other behavior. The region has both brown and black bears but the former seem to be much more abundant and we only saw brown bears. The highest density was

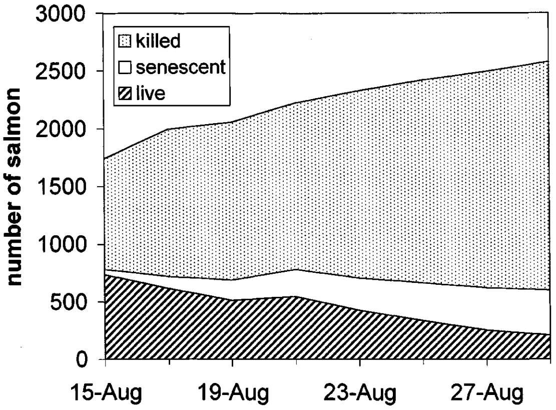

Fig. 2 Number of sockeye salmon observed alive and cumulative counts of senescent dead salmon and salmon killed by bears in the Pedro pond-creek system in 1995

Table 1 Physical characteristics of ponds and creeks in the Pedro Bay study site. Depths and velocities of creeks and ponds were measured at equidistant points over the areas used by salmon on 23 and 24 August 1995. Velocities were negligible in the ponds

Site	Number of samples	Area (m^2)	Depth in cm (SD)	Velocity (cm/s)
Pedro Pond	25	695	26.0 (6.5)	–
Creek 1A	5	60	10.3 (1.2)	24.2
Pond 1A	9	165	13.5 (3.9)	–
Creek 1	5	115	11.2 (2.0)	32.4
Pond 2	9	355	16.5 (3.7)	–
Creek 2	5	188	17.8 (6.1)	24.2
Pond 3	9	265	26.7 (12.3)	–
Creek 3	5	93	14.9 (4.0)	47.8
Pond 4	10	340	32.9 (6.6)	–
Creek 4	5	91	23.0 (6.7)	24.4
Grass Pond	27	1070	19.9 (6.6)	–
Trail Pond	26	1135	38.5 (8.6)	–
Bear Pond	17	1820	41.6 (7.6)	–

observed in 1996, when three female brown bears (with one, two and three cubs, respectively) were seen by us or others in the immediate area, in addition to at least two other brown bears and a black bear.

Size, age, and morphology

Adult sockeye salmon have been sampled on several of the major spawning grounds in the Iliamna Lake system since the 1960s, and Blair et al. (1993) reported differences in age composition, length at age, and morphology (notably the body depth of males, measured from the anterior insertion of the dorsal fin to the belly, perpendicular to the body axis). These traits were not reported for the Pedro Bay populations so we collected otoliths from dead salmon (about 100 males and 100 females in each of four years: 1993, 1994, 1995, and 1998) that were measured for body length. The otoliths were examined by an experienced reader and the age of each fish was estimated from annuli representing the number of years spent in freshwater prior to seaward migration and the number of years spent at sea prior to return. We were specifically interested in comparing the Pedro Bay fish with a nearby population that spawns on beaches of the lake at Woody Island. These sockeye salmon experience no predation from bears and their access to the spawning grounds is not limited by shallow water as they spawn in water from 0.5 to >4 m deep, and have very deep bodies (Blair et al. 1993; Quinn and Foote 1994). We collected comparable length and age data from Woody Island sockeye salmon but only used data from 1993 to 1995 and 1998 in the comparison with Pedro Bay fish to avoid the confounding influence of interannual variation (Blair et al. 1993).

Body length can be measured accurately from dead salmon but the body depth of sockeye salmon shrinks as they approach death (Quinn and Blair 1992) so we took measurements from 85 male sockeye salmon in peak development (judged by body color, absence of scars and marks) captured in 1993, 1994, and 1995, primarily in Pedro Pond. The slope and elevation of the body length-body depth relationship were compared to comparable data collected for 525 Woody Island sockeye salmon between 1988 and 1995. We used ANCOVA to first determine if the populations had similar allometric slopes for their length-depth relationships (after log transformation). We then compared the elevations of the slopes and estimated the mean body depth for each population, adjusted to a common length for ease of comparison.

Results

Habitat features

The creeks were very small, averaging 2.1 m wide and 64 m long, with an average mid-channel depth of 15 cm and velocity of 0.31 cm/s (Table 1). The substrate was a mix of fine and coarse sand and gravel. The ponds averaged 731 m^2 and ranged from 1820 m^2 (Bear) to 165 m^2 (pond 1A). Their average depth was 27.0 cm and the substrate was primarily fine and coarse sand with the exception of pond 3, which had more silt.

Magnitude and selectivity of predation

During the five seasons of the study, we counted 4968 dead salmon whose sex could be determined and another 68 of undetermined sex. Of these, 1460 (29%) had died of senescence and 3576 (71%) had apparently been killed by bears. It was not possible to determine the sex ratio of the entire population precisely, but over all years combined, surveys on 24 or 25 August revealed 54.1% males among the dead (killed and senescent) and 47.8% males among all the fish (live and dead combined; Table 2). These approximate a 50:50 ratio, so this was used as a baseline against which the sex ratio of selected samples could be compared. Females were over-represented among the senescent dead as of August 25 (63%) and in the entire sample, including data from subsequent dates when available (65%, $\chi^2 = 130.2$, 1 *df*, $P < 0.001$), whereas males were over-represented among the bear kills as of August 25 (61%) and in the entire sample (60%, $\chi^2 = 139.7$, 1 df, $P < 0.001$). Surveys on 24 or 25 August revealed a total of 1570 live salmon over all the sites surveyed on all years, of which 71% were females. Thus females were more likely to be alive at a given point than males, were more likely to reach the end of their natural lives, and were less likely to be killed by bears than males. Predation was not only selective with respect to sex but also size (ANOVA, $P < 0.001$). From 1994 to 1998, the mean lengths of salmon killed were about 10 mm longer than those that died of senescence (males: 462.3 mm, SD = 27.3, $n = 386$ vs 451.6 mm, SD = 27.5, $n = 226$; females: 452.8 mm, SD = 27.0, $n = 619$ vs 443.0 mm, SD = 26.9, $n = 555$).

Table 2 Live counts and cumulative dead counts of adult sockeye salmon in a series of ponds and creeks near Pedro Bay, Alaska, on 24 or 25 August 1994–1998. The total number of bear-killed salmon includes some whose sex could not be determined

Year	Site	Live		Senescent dead		Bear-killed		
		Males	Females	Males	Females	Males	Females	Total
1994	Pedro			380	407	53	21	74
	Small ponds			89	128	2	0	2
	Creeks			10	22	1	2	3
	Total			479	557	56	23	79
1995	Pedro	49	153	26	236	392	367	759
	Small ponds	3	17	0	1	263	184	447
	Creeks	0	0	1	3	103	89	192
	Grass	19	95	3	58	177	180	357
	Total	71	265	30	298	935	820	1755
1996	Pedro	0	1	0	0	0	0	5
	Small ponds	0	0	0	0	4	0	10
	Creeks	0	0	0	0	0	6	10
	Grass	0	1	0	0	4	0	4
	Trail	0	1	0	0	4	6	47
	Bear	6	69	0	0	11	3	30
	Total	6	72	0	0	23	15	106
1997	Pedro	1	1	0	0	4	1	5
	Small ponds	0	0	0	0	1	1	2
	Creeks	0	0	0	0	0	0	0
	Grass	0	0	0	0	8	4	12
	Total	1	1	0	0	13	6	19
1998	Pedro	17	66	0	11	254	143	397
	Small ponds	0	1	0	0	127	37	164
	Creeks	9	12	0	0	141	29	170
	Grass	50	170	0	8	255	133	388
	Trail	184	225	1	1	142	28	170
	Bear	120	300	1	10	75	29	104
	Total	380	774	2	30	994	399	1393
Grand total		458	1112	511	885	2021	1263	3352

The level of predation and abundance of salmon varied greatly among years (Table 2). In 1994, there was a relatively large number of salmon (1115 dead by 24 August), of which only 7% had been killed, mostly males. In 1995 and 1998, there were relatively large numbers of salmon (about 300 live fish in the Pedro pond-creek system and Grass Pond, and over 2000 live and dead fish in each year). Although the total abundance was similar to that in 1994, the rates of predation were much higher, as very few senescent dead were found, especially in 1998 (Table 2).

In 1996 and 1997, very few salmon entered the study section and 100% were killed. Not only were no senescent dead fish found but salmon were clearly getting killed within days or hours of entering the system. For example, we observed 1 live salmon in Trail Pond on 21 August, 26 live fish there on 22 August, and all were killed by 23 August. In several ponds, we continued to find and remove jaws and other bits of salmon tissue but did not see live fish, or saw redds but no females guarding them. In Grass Pond, no salmon were seen in mid-afternoon of 23 August, but in the evening there were five males and a female. By the next morning all five males had been killed and the female was alone. Bear Pond, the largest pond, had 69 live females and only 6 males on 25 August and 133 distinct redds. The other ponds and creeks combined had no males, only 3 live females and 124 redds, indicating that salmon were being killed very soon after entering the system. In 1996 and 1997, not only had all dead salmon been killed but none were sufficiently intact for us to measure body length directly. In contrast, in 1994 (the year with lowest overall predation), we were able to directly measure length on 59.5% of the kills, indicating lower levels of consumption as well as.

The predation level not only differed between males and females and among years but it also differed among habitats. Specifically, the proportion of salmon killed in the creeks was higher than in the ponds. Of the 4592 dead salmon recovered from ponds over the 5 years, 69.0% had been killed whereas 91.9% of the 444 dead fish in the creeks had been killed ($\chi^2 = 103.16$, 1 *df*, $P < 0.001$). The level of predation (i.e., percentage of fish killed among all the live and dead) was negatively related to habitat volume, estimated as the mean depth times the surface area ($r^2 = 0.92$). Specifically, the fish were most vulnerable in the creeks and small ponds (ponds 1A, 2, 3, and 4) and less so in the large ponds (Pedro, Trail, Grass, and especially Bear, the largest pond). However, closer examination of the data, separating ponds from creeks, revealed that area, not depth was the important factor in ponds ($r^2 = 0.97$, compared to $r^2 = 0.49$ for depth), whereas depth was the more important factor for creeks ($r^2 = 0.83$, compared to $r^2 = 0.003$ for area; Fig. 3).

Salmon density was estimated by the number of live salmon observed on 24 or 25 August plus the cumulative count of dead fish to date (averaged over 1994, 1995, 1996, and 1998) and divided by the area. The density in the large ponds was 1.06 fish/m^2, compared to 0.77 in the small ponds and 0.79 in the creeks.

Patterns of salmon age, size, and shape

Analysis of the relationships between body depth and length (log transformed) of male sockeye salmon from Pedro Pond ($n = 85$) and Woody Island ($n = 525$) indicated that there was a common, allometric slope for the populations (1.358) but that Woody Island males were significantly deeper-bodied than Pedro Pond males (ANCOVA, $P < 0.001$; Fig. 4). At a common length of 450 mm, the mean body depths of the populations were 178 mm (Woody Island) and 166 mm (Pedro Pond). However, the Woody Island males were shorter on average than Pedro Pond fish (448 vs 460 mm), so the average observed body depths of the Woody Island and Pedro Pond males (177 vs 171 mm) were more similar than the adjusted means.

Analysis of 1300 adult sockeye salmon collected for otolith analysis from Pedro Pond and Woody Island confirmed the pattern seen in the morphology sample; Pedro Pond sockeye salmon were longer than Woody Island fish. A three-way ANOVA indicated no significant interactions, and significant ($P < 0.001$) effects of population, sex, and age. Pond fish were longer than island fish, males were longer than females, and fish that spent 3 years at sea were longer than those that spent 2 years (Table 3). In addition to differences in mean size between sexes and populations, there were also differences in variance. Males varied more in length than females (considering fish of all ages) in the Pedro Bay population ($F = 1.34$, $P = 0.001$) but were slightly less variable than females in the Woody Island population ($F = 1.21$, $P = 0.07$). Pedro Bay males varied much more than Woody Island males ($F = 1.73$, $P < 0.001$) but females from the populations had similar variances ($F = 0.93$, $P = 0.28$).

Because predation was clearly size related and the habitats varied in physical features that seemed to affect predation rate (depth and area), we tested the hypothesis that salmon in the high-risk habitats (creeks and small ponds: 1A, 2, 3, and 4) would be smaller than those in the lower-risk large ponds (Pedro, Grass, Trail, and Bear). All data on body length (senescent dead and bear kills) were combined to give the best estimate of the size distributions of salmon in the habitats ($n = 1786$ overall). Although males were larger than females, there was no consistent pattern of fish size among habitats. Males

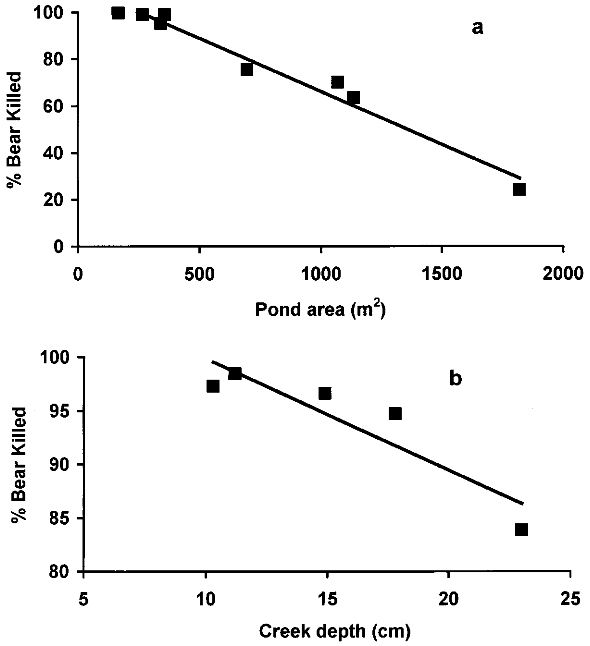

Fig. 3 Intensity of predation on adult sockeye salmon in a series of ponds and creeks in Pedro Bay, Alaska, as a function of the mean surface area of the ponds (**a**) and depth of the creeks (**b**). Predation intensity was estimated as the percentage of fish killed by bears out of the total number of live fish observed on 24 or 25 August, and cumulative number of dead fish as of that date, averaged over 1995, 1996, and 1998

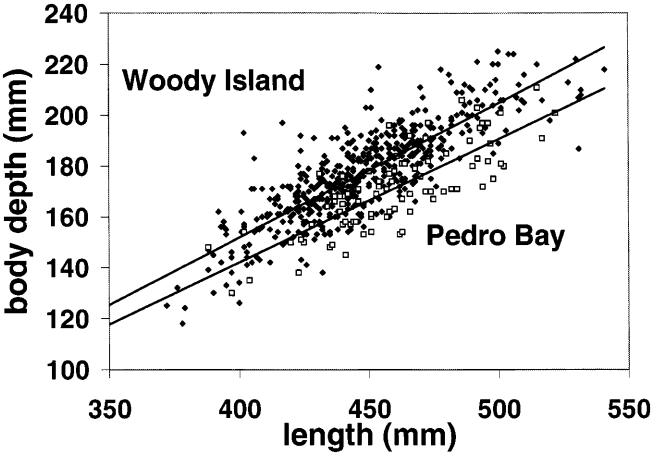

Fig. 4 Relationship between body length and body depth (anterior insertion of dorsal fin to belly) of ripe male sockeye salmon from Woody Island (*closed diamonds*) and Pedro Pond (*open squares*), Alaska

Table 3 Mean lengths (mid-eye to hypural plate; mm) of adult sockeye salmon from Woody Island and Pedro Ponds, sampled in 1993, 1994, 1995, and 1998. Samples are separated by number of years spent at sea ("marine age") based on otolith examination

		Marine age 2		Marine age 3	
		Woody	Pedro	Woody	Pedro
Males	Mean	438.2	454.1	491.9	519.0
	SD	21.9	24.1	20.7	32.0
	n	229	383	10	33
Females	Mean	413.2	437.3	473.1	493.1
	SD	22.7	21.6	25.9	25.5
	n	219	345	22	59

in large ponds (mean = 456.8 mm, SD = 27.7) were smaller than those in creeks (467.0 mm, SD = 23.0) or small ponds (473.9 mm, SD = 27.7) but smaller females were found in small ponds (443.6 mm, SD = 28.5) than in large ponds (448.1 mm, SD = 27.4) and creeks (454.2 mm, SD = 25.0).

Comparisons among habitats are confounded by the fact that some habitats can only be accessed by migrating through others. Trail, Bear, and Grass ponds are separate from each other but the rest of the sites are almost entirely lined up (the only exception being that pond 4 can be bypassed by upstream migrants; Fig. 1). Thus it is possible that some of the fish killed in the lower habitats were migrating upstream when killed whereas others might have been spawning there. If there were a "culling" effect of size-selective predation, then the smaller fish (more likely to escape predation) should be found in the upper units. To examine this, we separated the data for males and females from the Pedro Pond, creek 1A, pond 1A, and creek 1 (designated the upper region) and compared the mean lengths to those from the lower region (ponds 2, 3, and 4, and creeks 2, 3, and 4). The mean lengths for the females did not differ (upper: 450.2 mm vs 451.8 from the lower section; $t = 0.44$, $P = 0.33$) but the males from the lower region were larger than those from the upper region (471.7 vs 458.7 mm; $t = 2.99$, one-tailed $P = 0.001$).

Discussion

The results revealed intense, selective predation on sockeye salmon by bears. Although the uncontrolled (i.e., non-experimental) nature of the study inevitably involved some confounding factors, the results were very consistent in general pattern between sexes and among habitats and years; it was primarily the magnitude of the predation that differed, not the selectivity. Male salmon were killed much more often than females. This might be a consequence of either direct selection (i.e., preference) by bears, greater vulnerability of male salmon related to their greater length (increasing visibility to bears), greater body depth (making them less maneuverable in shallow water and easier for the bears to catch), or differences in arrival pattern (males typically enter before females) or behavior between the sexes. Most studies have reported higher rates of predation on males than females (Gard 1971; Konovalov and Shevlyakov 1979; Hanson 1992; G.T. Ruggerone, R. Hanson, D.E. Rogers, unpublished data) but Frame (1974) reported that ripe (unspawned) females were more likely to be retained and consumed than males. Surveys of 10 creeks in 1997 and 13 in 1998 in the Wood River system of Bristol Bay, Alaska, revealed that the sex ratio of live fish was nearly even (48% males, $n = 42{,}063$), whereas 61% of the 16,560 senescent dead were females and 56% of the 19,001 bear-killed fish were males (T.P. Quinn, unpublished data). However, more females were killed than males in two of the creeks surveyed in 1997 and three of those surveyed in 1998. Thus higher predation on males seems to be the overall pattern but exceptions exist. The ovaries in unspawned females are a particularly rich food resource for bears and some interaction between the foraging of individual bears, habitat-specific features (see below), and the relative benefits of killing male and female salmon or using other available food may explain the variation in sex-biased predation.

In addition, for each sex, the larger fish were more likely to be killed than the smaller individuals. As with the sex bias in predation, this might result from either preference by the bears or greater visibility or vulnerability of larger fish. It might seem unlikely that bears could distinguish salmon that differ in length by only a few centimeters. However, male salmon whose length differs by only 1 and 5 cm (i.e., about 2% and 10% of their length, respectively) would differ in area (as seen from the side) by about 5% and 25%, respectively. Because they are not only shorter on average but less deep-bodied, females present a much smaller visual area than males. Regardless of the mechanism, the consequence is natural selection against large size at age and higher marine age. The effect of the selective predation on succeeding generations depends on the differential reproductive success of phenotypes. Ironically, in years such as 1996 and 1997 when the predation level was highest, there may have been negligible selection for size because all salmon, small and large, were killed.

The males from Pedro Bay were also less deep-bodied than those spawning at a nearby habitat without predation (Woody Island), consistent with the prediction (Blair et al. 1993; Quinn and Foote 1994) that predation might affect the extent of sexual dimorphism. We acknowledge that the habitats differ in other attributes besides predation. Notably, the fish spawning in the beach are not constrained by depth whereas those in the ponds and creeks must migrate through (and some spawn in) very shallow water. To illustrate this one need only compare the distribution of body depths of male salmon from the two populations (Fig. 4) to the average depths of the habitats (Table 1). Even in the absence of predation, there would probably be selection against very deep bodied males in the pond system from the standpoint of physical access and maneuverability. The deep-bodied shape of Woody Island males is consistent with the morphology of sockeye salmon spawning on lake beaches elsewhere in Bristol Bay, Alaska, and sockeye salmon spawning in creeks have a consistently lower dorsoventral distance (Wetzel 1993; T.P. Quinn, unpublished data), thus some pattern of selection, whether bears or physical access, seems to be operating.

Selection against large size must be counterbalanced by benefits of large size. Larger males dominate access to females (e.g., Fleming and Gross 1994; Quinn and Foote 1994), though the alternative mating tactic of sneaking rather than fighting favors small fish. Such sneaking tactics are not practised in the Woody Island population (Quinn and Foote 1994; Quinn et al. 1996), perhaps because there is no cover for small males. Pedro Bay males were much more variable in length than Woody Island males, reflecting a larger number of Pedro Bay males that were very small, having only spent 1 year at sea, and also more large fish that had spent 3 years at sea. It is unclear why the Woody Island fish are rather small for their age; presumably some factor other than predation on adults in freshwater is operating. However, the structurally simple, predator-free beach environment does not seem to favor the variation in size and age of males that we observed in the pond system. Thus habitat features and patterns of predation on spawning grounds seem to have broad effects on life history patterns, including growth rate (i.e., size at age) and age structure, particularly in males. Selection against large size in females is counterbalanced by the positive relationships between length and both egg size and fecundity (Quinn et al. 1995), egg burial depth (Steen and Quinn, in press), and competition (Van den Berghe and Gross 1989).

The selective effect of the predation on phenotypes in the population depends not only on the difference in mean size between fish killed and those coming to the natural end of their lives but also their reproductive success. The distinctly different reproductive roles of males and females will result in different relationships between predation and reproductive success (i.e., opportunity for selection). Males are able to spawn until they are too weak to compete, so predation reduces their breeding opportunities in proportion to the number of days of their lives that are cut short, their declining ability to compete, and the operational sex ratio. On the other hand, females spend all but the first few days on the breeding grounds guarding their nest, so the effect of predation on reproductive success would be a step function. Predation prior to egg deposition would have severe effects on reproductive success but predation after breeding (i.e., egg deposition) would only be important if other females arrived and disturbed the first female's nest.

In addition to the effects on individual reproductive success, the effects of predation on population size also depend on whether females are killed before or after spawning, and whether the carrying capacity of the spawning grounds has been exceeded. In years prior to commercial fishing (i.e., prior to the late 1800s), the abundance of salmon would have exceeded the capacity of the spawning grounds in some years so predation would have reduced the magnitude of density-dependent processes such as nest disturbance by females. Males are surplus in most populations and do not limit reproduction (Mathisen 1962), so even heavily male-biased predation would not affect population abundance. The timing of predation with respect to spawning was not determined directly in this study but the level of predation was very low in 1994, especially on females, and most seemed to have spawned all of their eggs. In 1996 and 1997, the predation rate was 100% and many fish were almost certainly killed before they could spawn. Bear Pond (the largest) was the only habitat that sustained more than a few live fish and there were about ten times more females than males there each day. In 1995 and 1998, the vast majority of fish were killed but there were still many live fish in the large ponds and many of the females had obviously spawned their eggs. We plan to follow the salmon population in the ponds in the future to see if the heavy predation in 1996 and 1997 results in a cyclic pattern of salmon abundance.

Predation levels varied among habitat units and the very high patterns of covariation suggest the ways in which fish may find refuge (albeit limited) from bears. In ponds, area was correlated with safety because there was no deep water so the only escape was lateral (and perhaps the bears fished from the edges). In the creeks, depth was correlated with safety, perhaps because salmon have limited mobility in shallow water, and their splashing might attract bears. The creeks and ponds both lacked structural elements such as trees that might give cover in other systems. Despite the predation risk, the fish in the creeks and small ponds were not smaller than those in the large ponds, as would be predicted if the fish were expressing habitat choice based on condition-dependent predation risk or if they had adapted genetically to these specific habitats. This analysis is confounded by the fact that the habitats in the Pedro pond-creek system were arranged almost linearly. That is, in order to reach the largest pond, the salmon had to swim up all the creeks and enter all the small ponds except pond 4. Some of the fish killed in creeks may have been migrating rather than spawning there, and size-selective predation in the lower region would reduce the number of large fish available to occupy the upper region. Females did not differ in length between lower and upper regions but the males in the lower region were significantly larger than those farther up, consistent with some such "culling" effect on the population as they move up. Although the fish in safer habitats were not larger than those in riskier habitats, the safer habitats (i.e., large ponds) had higher densities than the small ponds and creeks. This may reflect predator avoidance but habitat selection based on physical features presumably also operates.

Our estimates of predation have two main sources of error: scavenging of dead salmon and removal of carcasses from the survey area. Based on a tagging study elsewhere in Alaska, both factors can operate (T.P. Quinn and G. Buck, unpublished data). Counting as killed salmon that were actually scavenged after death would inflate the estimated predation rate. This might have occurred in some cases, especially in 1995 when some of the fish classified as killed were in an advanced state of senescence. On the other hand, salmon killed and eaten entirely or removed from the survey area would not have been recorded at all and this would have deflated the predation rate estimate. Carcass removal probably occurred, though the carcasses seemed to be concentrated in the creeks and ponds themselves, or in distinct "bear dining rooms" or paths very close to the water. Complete consumption of carcasses might have resulted in some undercounting, especially in 1996 and 1997, when many fish were only represented by scraps of tissue found in or adjacent to the ponds. Despite these sources of error (offsetting, for the most part), it is clear that there was great variation in predation pressure among the 5 years, ranging from very light to extraordinarily intense. This variation in predation intensity means that estimates of predation must be based on many years of data. Single-year estimates could be entirely unrepresentative of the predation pressure under which the populations evolved, or that they are presently experiencing.

Variation in predation intensity likely results from the depensatory effect of large numbers of salmon in some years and from variation in abundance and behavior of bears. Salmon in this and many other stream systems in Alaska are often very abundant and readily available during predictable, albeit brief, periods of time. Most sockeye salmon enter Iliamna Lake in July and are present on spawning grounds primarily from mid-August until mid-September (Demory et al. 1964). The Iliamna Lake system as a whole has seen variation in adult sockeye salmon abundance, ranging from as few as several hundred thousand to over 20 million since 1956 on a 4- to 5-year cycle (Eggers and Rogers 1987). Thus there are years with few salmon overall, and some habitats have few fish despite the abundance elsewhere in a given year. Brown bears are omnivorous (e.g., Mealey 1977) and some do not eat salmon, even in regions where salmon are plentiful (Hilderbrand et al. 1996). However, bear populations with a large proportion of dietary meat in general, and salmon in particular, tend to have higher densities, larger bears, and larger litters than populations whose diet is dominated by vegetation (Hilderbrand et al., in press), and the movements of bears reflect the seasonal availability of salmon (Berns et al. 1977; Barnes 1989). Given the importance of salmon to bears, one might expect many salmon to be killed each year. Distances between streams may constrain bears to forage at one stream during a season, so if the salmon are scarce the bears may kill most of them and eat what they kill (e.g., 1996 and 1997). However, the density of bears and the presence of alternative food resources may also affect predation intensity. Finally, studies of bear predation are further complicated by interactions among bears (Egbert and Stokes 1974; Mattson and Reinhart 1995) and individual variation in fishing and other foraging patterns (Luque and Stokes 1974; Fagen and Fagen 1996).

The evolutionary and ecological interactions between bears and salmon are less amenable to experimental manipulation than those of the smaller animals that have been such useful model systems for predator-prey research. Controlled breeding studies on salmon take years and bears pose special challenges for researchers. Despite these difficulties, the breeding system of salmon lends itself to detailed studies of reproductive success and salmon populations show a remarkable capacity for genetic adaptation to local selection pressures. Following Sih's (1994) call for integration of predation studies into behavioral, population, and community ecology, future research may better define the links between the dynamics and evolution of salmon and bear populations. These animals have coevolved over long periods of time and each species is probably very important to the other.

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