Some ecological and evolutionary aspects of bear–salmon interactions in coastal British Columbia

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Abstract: I examine here quantity and characteristics of chum salmon (*Oncorhynchus keta*) captured by black bears (*Ursus americanus*) during autumn spawning migration in an old-growth watershed on Moresby Island (Haida Gwaii), western Canada. Spawning-salmon numbers ranged from 2300 to 6300 over 3 years of investigation (1992–1994) and there were a maximum of eight bears in the watershed. Following capture of a salmon, bears ate an average of 1.6 kg from each salmon carcass, including the brain, ovaries, and dorsal musculature, and generally tended to abandon viscera, testes, and bony remnants such as jaws. Complete counts of these jaws throughout the watershed in autumn 1993 demonstrated a total capture of 4281 salmon, for an average consumption rate of 13 salmon per day per bear over the 45-day spawning period. This comprised 74% of the salmon entering the stream (range among years 58–92%). Most salmon (70–80%) taken by bears were partially or completely spawned-out at the time of capture. Marginally but significantly higher predation rates occurred on males relative to their proportion in the stream, and on larger rather than smaller salmon of both sexes. Higher-quality salmon (larger, fresher) were transferred farthest from the capture site by bears, possibly to minimize competitive interference. Bear predation in this locality does not appear to seriously constrain total reproduction of the salmon, but it may have several genetic influences: (*i*) there may be selection against large body size of salmon in both males and females and (*ii*) high predation levels on partially spawned males may facilitate multiple paternity in spawning females and, therefore, increase effective genetic variance among fertilized eggs.

Résumé : J'ai déterminé le nombre et les caractéristiques des Saumons keta (*Oncorhynchus keta*) capturés par des Ours noirs (*Ursus americanus*) au cours de la migration de fraye de l'automne dans un bassin hydrographique, dans une forêt ancienne de l'île Moresby (Haida Gwaii), dans l'ouest du Canada. Le nombre de saumons en fraye au cours des 3 ans qu'ont duré notre étude (1992–1994) allait de 2300 à 6300 et il y avait au maximum huit ours dans le bassin. Après la capture, les ours mangeaient en moyenne 1,6 kg de chaque carcasse, cerveau, ovaires et musculature dorsale, et avaient généralement tendance à laisser les viscères, les testicules et les restes osseux, notamment les mâchoires. Le nombre total de ces mâchoires dans le bassin à l'automne de 1993 a été de 4281, ce qui se traduit par un taux moyen de consommation de 13 saumons par jour pendant une fraye de 45 jours, soit 74 % des saumons qui sont entrés dans le ruisseau (étendue durant les 3 années, 58 à 92 %). La plupart (70–80 %) des saumons capturés par les ours avaient déjà fini ou presque fini de frayer au moment de leur capture. La prédation exercée sur les mâles était faiblement mais significativement plus élevée proportionnellement à leur nombre dans le ruisseau et celle des gros poissons des deux sexes, plus élevée que celle des plus petits poissons. Les saumons de meilleure qualité (plus gros, plus frais) étaient emportés plus loin du site de capture que les autres saumons, probablement pour minimiser l'interférence compétitive. La prédation par les ours à cet endroit ne semble pas imposer de contrainte critique sur la reproduction des saumons, mais peut avoir des conséquences génétiques : (*i*) la sélection peut avantager une plus petite taille chez les saumons des deux sexes, (*ii*) une forte prédation sur les mâles partiellement vidés de leur semence peut favoriser la paternité multiple chez les femelles en fraye et augmenter ainsi la variance génétique effective des oeufs fécondés.

[Traduit par la Rédaction]

Introduction

Adult spawning migrations of Pacific salmon (*Oncorhynchus* spp.) are a major ecological factor in coastal watersheds of western North America, as they provide an important yearly nutrient source for a diverse assemblage of predators and scavengers (Cederholm et al. 1989; Willson and Halupka 1995). The largest and most widely distributed of the terrestrial predators on salmon are bears (*Ursus* spp.). While there has been some attention directed towards description of bear foraging behaviour (Egbert and Stokes 1976; Barnes 1990; Reimchen 1998) and numerical impacts on salmon populations (Shuman 1950; Clark 1959; Gard 1971; Frame 1974), there has been only limited attention directed towards the ecological dynamics of bear and salmon associations.

The most quantitative investigation of bear–salmon associations was undertaken at Olsen Creek estuary, Alaska, in which Frame (1974) determined that (*i*) black bears consumed about 10% of the total spawning run, (*ii*) bears targeted gravid females when these were available, (*iii*) consumption of senescent (spawned-out) carcasses represented 80% of the total consumption, and (*iv*) there appeared to be

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only a marginal effect on the total reproductive output of the salmon population. These results provide insight into this common and widely distributed predator–prey association and suggest that historical declines in salmon numbers cannot be attributed to bears (e.g., Shuman 1950).

Haida Gwaii (formerly Queen Charlotte Islands), 100 km off the midcoast of British Columbia, has old-growth watersheds with spawning salmon populations and resident black bears. In this study, I document trophic and behavioural interactions between migrating chum salmon (*Oncorhynchus keta*) and the black bear (*Ursus americanus*), the only large terrestrial predator in the archipelago. I quantify characteristics of salmon captured by bears, including major tissues consumed, numbers eaten over the spawning period, sex ratio, reproductive condition, and body size. Based on previous studies that have emphasized the caloric value of prey (Frame 1974; Gilbert and Lanner 1995), bears are predicted to favour (*i*) high-quality tissues such as eggs and brain, (*ii*) female rather than male salmon, (*iii*) prespawned rather than spawned-out salmon, and (*iv*) large-bodied rather than small-bodied salmon.

Study area

Bag Harbour watershed and its estuary are located in a remote mountainous area near the south end of Haida Gwaii (Fig. 1). The estuary has broad intertidal flats with the upper zone covered in *Fucus distichus* and the lower intertidal and subtidal regions covered with dense beds of eelgrass (*Zostera*) in which salmon frequently congregate prior to movement into the stream. Gulls (*Larus* spp.), North-western Crows (*Corvus caurinus*), Common Ravens (*Corvus corax*), Bald Eagles (*Haliaeetus leucophala*), harbour seals (*Phoca vitulina*), and from one to eight black bears are seen in the estuary during salmon spawning migration (Reimchen 1994).

The estuary is surrounded by old-growth forest and has one major salmon-spawning stream. The width of Bag Harbour stream ranges from 5 to 20 m, with depths generally less than 0.5 m. The stream often undercuts the dense root system of large conifers, resulting in subsurface stream flow; this subsurface flow can represent 10% of the channel width. Occasionally large trees have fallen across the stream under which salmon will sometimes shelter. Most of the spawning gravels occur in the lower 1400 m of the stream. Black bears are the only significant species in the watershed that capture live salmon and carry them onto gravel banks or the forest floor. Marten (*Martes americanus*), eagles, gulls, crows, ravens, and a broad diversity of insects (Diptera, Coleoptera) scavenge salmon carcasses that have been abandoned by bears (Reimchen 1994).

The Department of Fisheries and Oceans monitors the number of adult salmon in numerous coastal streams of British Columbia every 10–15 days from the middle of September to early November. The first salmon generally enter Bag Harbour estuary and stream during the last week of September and, by 10 November, all spawning is complete and only decaying carcasses remain. The total number of salmon entering the stream each year has varied over the study period (1992, $N = 2300$; 1993, $N = 5800$; 1994, $N = 3900$); the majority (>90%) were chum salmon, with the remainder being pink (*Oncorhynchus gorbuscha*) and coho (*Oncorhynchus kisutch*) salmon. These counts are marginally conservative, as they do not include salmon carcasses that were swept into the estuary, those that were eaten in their entirety, or those that were carried well into the forest by scavengers. In the 1993 field season, I obtained estimates of these additional factors and calculated that total numbers were approximately 10% greater than existing counts. The numbers of salmon returning to this river are well below maximum (35 000 observed in 1947; Reimchen 1994).

Methods

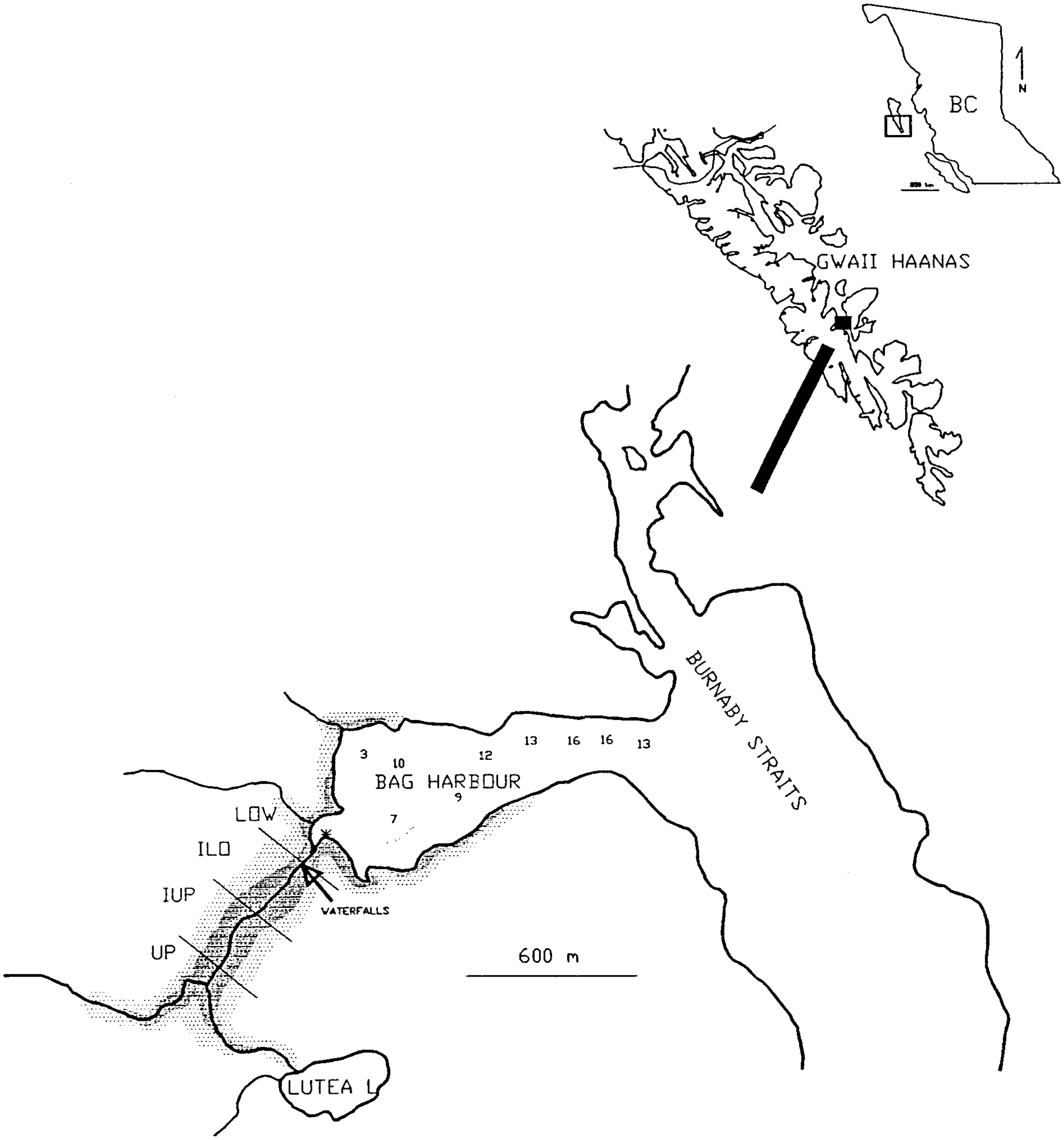
In 1992, I made field observations during 13 days (8–21 October) encompassing the second half of the spawning run. In 1993, I surveyed during most of the spawning period (28 September – 26 October, 13–14 November), while in 1994, I made surveys only near the middle and at the end of the spawning run (12–13 October, 2–3 November).

Abandoned remnants of bear-captured salmon accumulated in the watershed over the duration of the spawning migration. These remnants typically have characteristic bear signatures, including multiple tooth punctures and brain removal. I made daily searches for these remnants (hereinafter, “carcasses”) on gravel bars, stream bank, and forest floor. I took the following measurements in 1993, conditional on the completeness of the carcass: standard body length (±10 mm), lower-jaw length (±1 mm), sex, mass of carcass (±10 g), mass of intact testes (±5 g), number of ripe eggs in the body cavity, number of ripe eggs on the substrate under or adjacent to the carcass, presence or absence of brain, and distance (m) of the carcass from the stream. I also estimated general body condition at the time of capture (new, old). “New” carcasses generally had red flesh, no loss of body pigmentation, and no fin deterioration, and resembled new adults entering the stream. “Old” carcasses had pale flesh, major depigmentation of the body, and erosion of fins, and resembled the spawned-out and senescent salmon found dead in the stream channel. For male salmon, I also scored an “intermediate” category.

To estimate the total number of salmon taken by bears, I counted carcasses throughout the watershed, including gravel bars, stream banks, and forest floor. For carcasses on the forest floor, I searched multiple 10 m wide transects perpendicular from the stream into the forest and counted all carcasses within each transect. Each transect extended from 50 to 150 m into the forest, and I searched 50 m beyond the last recorded carcass within each transect (Fig. 1). These transects were positioned along the stream, including both its major branches, from the estuary to the lake and provided a total carcass count of the forest floor. I also counted senescent or spawned-out salmon (with no evidence of bear predation) that accumulated on the gravel bars and in pools. Carcass surveys were undertaken twice in 1992 (8 and 18 October), five times in 1993 (29 September; 7, 17, and 25 October; and 13 November), and twice in 1994 (3 October and 2 November). The final count during each year was made at the end of the spawning season, when there were no live salmon remaining in the estuary and stream. To avoid duplicate counting of carcasses within or among surveys, lower jaws were “marked” by cutting the symphyses. For each of the nine surveys, I made a complete carcass count on the stream banks and forest floor on the right side of the stream, while on four of the surveys, I also made complete counts on the stream banks and forest floor on the left side of stream. Bears also foraged on the estuary and carried the salmon to the edge of the forest surrounding the estuary. Of 31 successful captures observed, one-quarter of the salmon were eaten directly in the intertidal zone, while the remainder were carried to the high-tide mark and forest edge. The fresh carcass remnants did not persist in the intertidal zone, owing to tidal movement and aquatic scavengers that dispersed the remnants. The remnants above the high-tide mark tended to persist and accumulate over the study period and I counted all carcasses in this region at the end of the spawning season.

Body mass, body length, and lower-jaw length were measured on 53 intact and prespawned salmon stranded during the receding tide in the estuary. Average mass was 2.96 kg. The regression equation for jaw length (x) against body mass (y) was $y = 314.04^{0.018x}$ for males ($P < 0.001$) and $y = 194.94^{0.027x}$ for females ($P < 0.001$), and I used these exponentials to estimate original mass from the jaw length measured on the carcass remnants.

Fig. 1. The study area at Bag Harbour, Moresby Island. Dark shading indicates the distribution of carcasses and light shading indicates the zones included in the search for carcasses.



I obtained information on the reproductive condition of the carcasses. During daylight, I occasionally observed bears capturing fresh salmon, which I then examined after the bears had finished eating. In each of four cases where bears had captured a gravid female, I found mature eggs scattered on the moss substrate, as well as some remaining within the body cavity. When examined on subsequent days, the number of eggs gradually declined, owing to scavengers, but even 4 days after the initial capture, occasional eggs were still present on the substrate and in the body cavity. Therefore, the presence of eggs associated with fresh carcasses would indicate the capture of a prespawned or a partially spawned female. As a result, on fresh bear-killed salmon detected during the daily surveys, I counted mature eggs remaining in the body cavity and on the substrate. Information was also recorded for male salmon. Bears rarely consumed testes and these were commonly found within or adjacent to the carcasses. Accordingly, during the daily surveys of the watershed, masses were obtained for all complete testes on fresh carcasses and converted to relative masses of the predicted prespawned testes masses. Mass loss from drying of the testes is probably minimal, as frequent rainfall and high levels of substrate moisture and shade at Bag Harbour facilitate saturation of the tissues. To determine prespawned testes masses, I weighed testes on fresh salmon carcasses from the estuary that had become stranded during receding tides and on prespawned salmon captured by bears in the lower estuary. These testes averaged 3.1% of body mass (range 2.1–4.3, N = 22). Khorevin (1987) found the same value for relative testes mass of prespawned chum salmon from eastern Russia. He also found that relative masses decreased linearly on larger fish (regression $y = 4.547 - 0.000369 \times$ body mass (g), where y is the mass of the testes as a percentage of body mass). I have incorporated this correction in my estimates of prespawned testes masses. I also weighed testes from 17 intact senescent (spawned-out) fish found dead in pools below spawning gravels. Testes averaged 1.2% of the body mass or about 28% of the prespawned testes mass.

Results

Tissue consumption

Bears exhibited preferences for particular tissues. On capture of a salmon, bears generally bit through the top of the skull and ate the brain. When a gravid female was captured, bears applied pressure to the abdominal cavity either with their nose or foot, causing eggs to extrude onto the ground, which were then licked up. The abdominal cavity was then ripped open and additional eggs consumed. Subsequently, bears usually ate portions of the dorsal and lateral trunk musculature and generally ignored remaining tissues.

Although the brain was a preferred tissue, this depended on the size and condition of the salmon. The brain was eaten with higher frequency in larger than in smaller salmon (Fig. 2A). In addition, the brain was eaten with high frequency in fresh salmon but was rarely eaten in old salmon (Fig. 2B), even though the decaying trunk musculature of the latter group was eaten regularly.

Bears consumed approximately one-half of each carcass before they abandoned it. The mean mass of 689 carcasses on the forest floor was 1.3 kg (range 0.04–4.6 kg). Bears often returned on successive days and scavenged additional tissues.

Number of salmon taken by bears

1992

On 9 October, 2 weeks after the onset of the spawning migration, a survey of the right side of the watershed yielded a total of 475 bear-captured salmon. On 21 October, the same area produced 370 new carcasses for a total of 845 salmon. Counts on the right side of the stream on 9 October yielded 307 carcasses or 65% of the number observed on the left side for the same time period. Assuming this proportion of 65% is representative, then, on 21 October, there will be an estimated 549 carcasses in the right riparian zone. This yields a total count of 1394 carcasses over the duration of the spawning period and comprises 61% of the total run.

Although the carcass counts provide a robust estimate of total capture by bears, the counts are conservative, as they do not include salmon that were entirely consumed or scavenged prior to my survey. Of the 475 carcasses marked on 9 October, I found 334 “recaptures” on the 21 October survey. Consequently, 141 carcasses disappeared, representing a 2.5% daily loss. Extrapolation of this value over the complete spawning run leads to an estimated loss of 660 carcasses that would have gone undetected in my surveys. If this extrapolation is realistic, it would increase total salmon captures to 2054 or 89% of the spawning run.

1993

Summarized data on the abundance of carcasses recorded during 5 surveys are shown in Table 1. By the completion of the spawning run in early November, a cumulative total of 2848 carcasses had been recorded from the stream and the right side of the watershed. Approximately one-third of the carcasses were found in the stream channel. I also made total carcass counts in the left side of the watershed on 25 October and 13 November 1993 and these produced 82.8 and 58.3%, respectively, of the numbers recorded for the right side for the same dates. Using an average value (71%) to estimate carcass abundance on the left side, and combining this with the data from the right side, yields a total of 4121 carcasses.

Bears also captured salmon in the estuary. When all salmon had entered the stream, I made a complete survey of the tide line and forest edge and found 142 salmon carcasses. In combination with those eaten in the intertidal zone, I estimate that there were a total of 200 salmon taken in the estuary.

Carcasses were also lost from the substrate over the study period. Among the 210 carcasses marked on 29 September, 189 were recaptured on 7 October. This represents a daily loss of 1.1%. On 17 October, 626 marked carcasses were recovered out of a total of 737 previously marked (on 29 September and 7 October) for a daily loss of 2.5%. On 25 October, 692 marked carcasses were recovered from a total of 1053 previously marked (on 29 September and 7 and 17 October) for a daily loss of 3.4%. Of 410 carcasses marked in the stream channel (on 29 September and 7 October), 130 were lost by 17 October, yielding an average daily loss of 3.2%. Using the most conservative estimate of a 1.1% daily loss yields an estimate of 472 carcasses lost over the 45 days of the spawning run.

Summation of carcass data from the watershed indicates that bears captured and consumed 4321 salmon in 1993, representing 67.7% of the total spawning run (N = 6380). This is a conservative value, as it does not include carcasses that were fully scavenged and not detectable in my surveys. Including these data increases the estimated total capture to 4793 salmon or 75% of the spawning run.

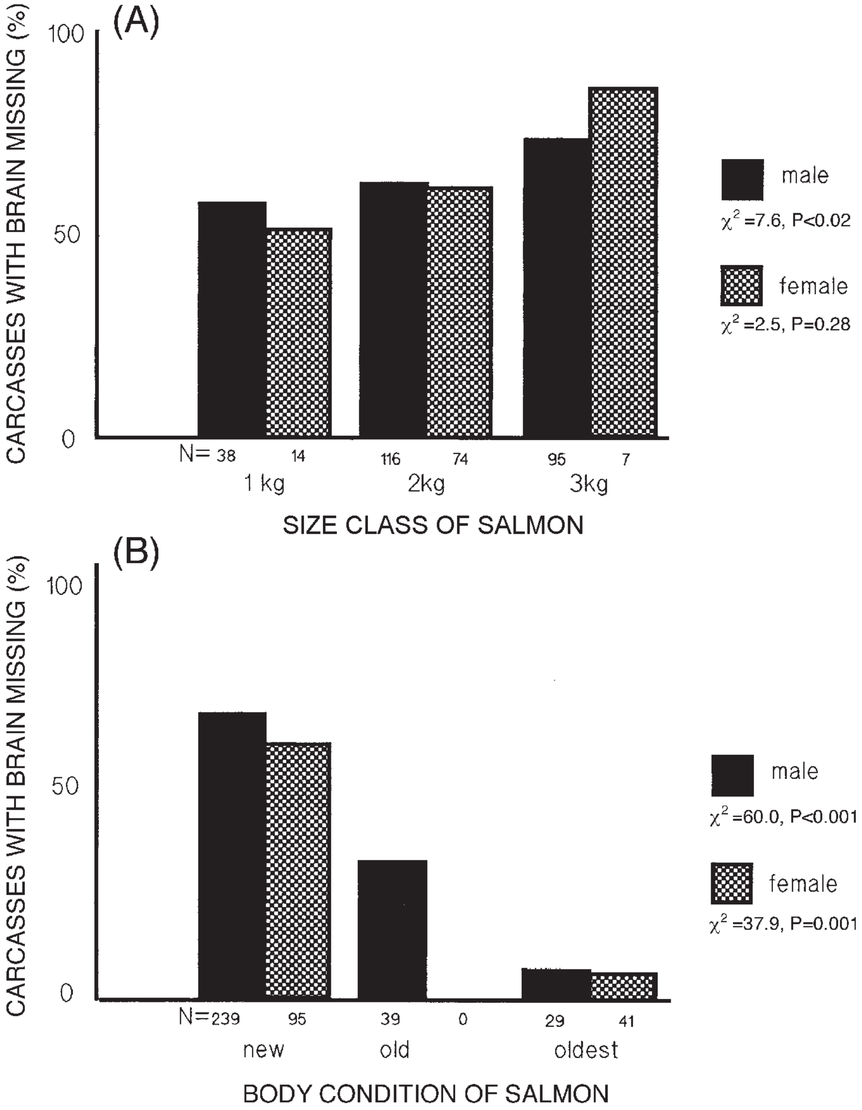
1994

Counts on 12 October, near the middle of the run, yielded 270 carcasses on the right side of the stream and 265 carcasses on the left side. A complete count on the right side of the stream on 3–4 November, after the end of the spawning season, gave 654 carcasses. Assuming equality of use of both sides of the stream yields an estimate of 1308 carcasses over the duration of the run. If daily carcass loss is 1.1%, as in 1993, this would yield an additional 288 carcasses for a total of 1596 salmon. If the proportions consumed in the estuary were comparable with those of 1993, then there would be an additional 80 captures for a total of 1676 salmon in all habitats or 43% of the spawning run.

Sex ratio of bear-captured salmon

Direct observation of bears foraging below a small waterfall where prespawned salmon congregated prior to movement upstream showed differential feeding on the sexes. During a continuous 1-h observation period, a single bear captured 16 male and 3 female salmon. However, 15 of the 16 males were released within 10 s of capture, while each of the females was eaten (Fisher’s exact test, P = 0.004). Given this bias, which is consistent with the original prediction,

Fig. 2. (A) Relationship between salmon brain consumption by black bears and size class of salmon, at Bag Harbour in 1993. Note the increased probability of brain consumption by bears of larger salmon. (B) Relationship between salmon brain consumption by black bears and carcass condition, at Bag Harbour in 1993. Note the reduction in brain consumption by bears of salmon with poorer body condition.



then, over the duration of the spawning run, the sex ratio of bear-captured salmon should be markedly skewed towards an excess of females relative to their proportion in the population.

In 1993, I recorded the sex ratio for 4472 salmon sampled over the duration of the spawning season, a number close to 80% of the entire run. These comprised strandings in the estuary, senescent individuals from the bottom of pools, and carcasses from the stream banks and forest floor. Overall "population" sex ratio was 1.8 ♂♂ : 1 ♀. The sex ratio of all salmon taken by bears was 2.0 ♂♂ : 1 ♀ and this did not differ significantly ($P = 0.08$) from the population sex ratio. Partitioning sex ratios among habitats indicates a slight excess of males relative to their proportion in the population in each. In the estuary, prior to migration into the stream, the sex ratio of bear-captured salmon was 3 ♂♂ : 1 ♀ ($N = 216$). In the stream channel, it was 1.9 ♂♂ : 1 ♀ ($N = 1030$), while in the riparian zone, it was 2.0 ♂♂ : 1 ♀ ($N = 2520$). Therefore, the prediction that female salmon would be subject to higher mortality levels than male salmon is not supported by the examination of carcasses.

There is at least one source of error that could have biased the sex ratios. If bears tended to consume the entire carcass of females, perhaps as a consequence of their smaller body size, then evidence of the capture would go undetected in the total carcass counts and this would lead to an apparent deficiency of females in carcass surveys. The possibility can be tested by examining the of sex ratio of uninjured senescent carcasses that accumulated in pools during the spawning run. There should be fewer females than males remaining in this spawned-out group compared with the population sex ratio, if females were targeted by bears. In total, I examined 932 senescent salmon and, contrary to prediction, there was an excess rather than a deficiency of females relative to the

Table 1. Surveys of bear-captured carcasses and senescent salmon (post-reproductive, non-injured) from Bag Harbour, Gwaii Haanas (29 September – 13 November 1993).

	Bear-captured salmon				Senescent salmon			
	No. of male carcasses	No. of female carcasses	Total no. of carcasses	Percent occurrence of females	No. of male carcasses	No. of female carcasses	Total no. of carcasses	Percent occurrence of females
29 September	175	74	249	29.7	9	4	13	30.8
7 October	645	274	919	29.8	3	10	13	76.9
17 October	465	230	695	33.1	153	159	312	51.0
25 October	264	144	408	35.3	337	171	508	33.7
13 November	334	243	577	42.1	30	56	86	65.1
Total no. of carcasses	1883	965	2848	33.9	532	400	932	42.9

Note: Data for bear-captured carcasses are restricted to stream and west forest.

population frequency (1.3 ♂♂ : 1 ♀; $\chi^2 = 20.1$, $P < 0.001$). Similar patterns occurred during most periods of the spawning run (Table 1). In the first 2 weeks of the run, the sex ratio of senescent carcasses was 1 ♂ : 1.2 ♀♀ compared with 2.4 ♂♂ : 1 ♀ for bear-captured salmon for the same period ($\chi^2 = 7.0$, $P < 0.008$). Near the middle of the run, the sex ratio of senescent carcasses was 1 ♂ : 1 ♀ compared with 2 ♂♂ : 1 ♀ for bear-captured salmon during the same period ($\chi^2 = 71.0$, $P < 0.001$). On 25 October, the sex ratio of senescent carcasses was 2 ♂♂ : 1 ♀ compared with 1.8 ♂♂ : 1 ♀ for bear-captured salmon ($\chi^2 = 0.3$, $P = 0.61$), while on 13 November, at the end of the run, the sex ratio of senescent carcasses was 1 ♂ : 1.9 ♀♀ compared with 1.3 ♂♂ : 1 ♀ for bear-captured salmon ($\chi^2 = 16.1$, $P < 0.001$). Therefore, the marginal deficiency of female carcasses observed among bear-captured fish in the surveys likely does not represent a difference in my detection levels, but rather, a proportional reduction in predation levels on females relative to males.

Reproductive condition of bear-captured salmon

In the 1992 surveys during the latter period of the spawning run, bears were commonly observed feeding on dead salmon rather than on active spawners. Examination of 56 male salmon captured by bears showed that all were either partially or completely spawned-out, judging by the body deterioration. Among 25 female salmon examined, three (12%) had remnants of ripe ovaries and, as a result, are assumed to have been prespawned or partially spawned at the time of capture. The remaining females (88%) had advanced body deterioration and no eggs in the body cavity and were probably spawned-out at the time of capture.

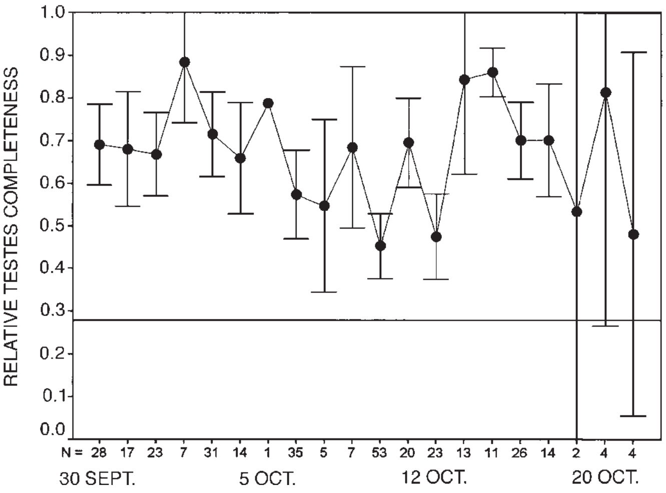
In 1993, the reproductive condition of bear-captured salmon was evaluated throughout the spawning run. During daylight, I regularly observed bears scavenging senescent and decaying carcasses adjacent to large groups of highly visible active spawners in shallow waters. Even when crossing the stream, bears seldom gave pursuit to the evading salmon. Rather, bears continued to scavenge additional senescent carcasses on the opposite banks. However, during darkness, bears foraged more commonly on active salmon (Reimchen 1998). In my daily surveys of carcasses on stream banks and the forest floor during which “condition” was estimated, 85% of the male salmon ($N = 440$) and 84% of the female salmon ($N = 199$) were classified as new, indicating capture when the salmon were still active. Of 176 fresh female carcasses examined, 71% had no eggs on the ground, suggesting that the salmon were spawned-out at the time of capture. The remaining females (29%) had eggs in the body cavity and on the ground and are presumed to have been captured before completing spawning. I also examined 19 intact (no injuries) senescent female carcasses from the bottom of pools and anticipated that there would be no eggs left in the ovaries as these salmon would presumably be spawned-out; however, three of these fish (14%) still had a substantial number of ripe eggs (100–400) present.

Males attempt to spawn with many females and lose about 5% of total testes volume during each fertilization (Salo 1991); consequently, testes masses will gradually decline with successive fertilizations. Data obtained on 338 bear-captured salmon demonstrate that the average relative testes mass was 59% (range 10–140%) of prespawned mass, indicating that the average male taken by bears could have spawned up to eight times before capture. Values were low for carcasses found on gravel bars in the stream channel ($\bar{x} = 42\%$, $N = 79$) and higher for those on the forest floor ($\bar{x} = 67\%$, $N = 187$) (ANOVA, $F_{[264]} = 57.9$, $P < 0.001$). Average relative testes masses of bear-captured salmon also varied over the duration of the spawning run (Fig. 3). Lowest masses occurred during periods of low water levels in the stream (12 and 14 October), while the three periods with marked increases in testes masses (2, 15, and 22 October) occurred when schools of new salmon entered the stream from the estuary. On the arbitrary but conservative criterion that relative testes masses of greater than 90% indicate a prespawned male, then 19% of the males captured by bears would be prespawned males.

Size of salmon captured by bears

The average size of salmon captured by bears differed from that of noncaptured fish. In the estuary, bear-captured male salmon were significantly larger (based on jaw length) than those that were stranded in the estuary (bear-captured, $\bar{x} = 122.6$ mm, SE = 1.1, $N = 149$; stranded, $\bar{x} = 112.1$ mm, SE = 3.1, $N = 27$; $F = 13.3$, $P < 0.001$). Bear-captured female salmon did not differ in average size from stranded salmon but samples of the latter were small (bear-captured, $\bar{x} = 95.5$ mm, SE = 1.4, $N = 51$; stranded, $\bar{x} = 91.2$ mm, SE = 4.1, $N = 6$; $F = 1.1$, $P = 0.31$). Comparable results

Fig. 3. Relative testis mass of bear-captured salmon over the study period. Values near unity indicate prespawned condition. Values near 0.28 indicate spawned-out condition.

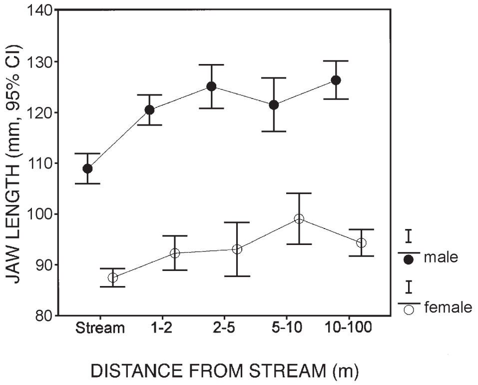


were obtained from the stream habitat. Bear-captured male salmon were significantly larger than senescent males (bear-captured, $\bar{x}$ = 118.9 mm, SE = 0.9, N = 317; senescent, $\bar{x}$ = 104.8 mm, SE = 3.2, N = 18; F = 14.7, P < 0.001), while females did not differ (bear-captured, $\bar{x}$ = 91.1 mm, SE = 0.7, N = 156; senescent, $\bar{x}$ = 88.6 mm, SE = 1.7, N = 19; F = 1.4, P = 0.24).

Carcass attributes and feeding sites

Carcasses differed in their quality depending on the habitat in which they were found. I examined carcass quality (condition, new or old) and size (jaw length), predicting that bears would more likely consume lower-quality prey (old salmon, small salmon) in the stream channel and take higher-quality prey (new, large) into the forest where there would be less competitive interference. Data were consistent with the prediction. Among old salmon consumed by bears, 76 (87%) were eaten directly in the stream channel, while only 11 (9%) were carried into the forest; among new salmon, 61 (21%) were eaten in the stream channel, while 230 (79%) were carried into the forest (χ^2 = 127.8, P < 0.001). Furthermore, for both male and female salmon, large individuals were more likely to be found on the forest floor than in the stream channel (males: stream, $\bar{x}$ = 111.2 mm, SE = 1.6, N = 103; forest, $\bar{x}$ = 122.7 mm, SE = 0.9, N = 214; F = 44.1, P < 0.001; females: stream, $\bar{x}$ = 87.2 mm, SE = 1.1, N = 57; forest, $\bar{x}$ = 93.5 mm, SE = 0.9, N = 99; F = 20.1, P < 0.001). I also examined salmon size in relation to distance carried into the forest and found a modest association (male, F = 15.4, P < 0.001; female, F = 6.9, P < 0.001) in which the largest salmon were carried furthest into the forest (Fig. 4).

Fig. 4. Average lower-jaw length of bear-captured salmon and distance (m) found from the stream at Bag Harbour, 1993.



Discussion

Salmon constitute an important source of nutrients for bears in coastal regions of western North America. Recent studies with stable nitrogen isotopes demonstrate that this short seasonal pulse of nutrients can represent the major yearly source of protein for bears (Hildebrand et al. 1996), as well as comprising a major source of nitrogen for aquatic primary producers (Kline et al. 1990) and riparian vegetation (Bilby et al. 1996; Ben-David et al. 1998). When salmon are abundant, the population density of bears can be 20 times greater than in the interior continental areas where salmon do not occur (Gilbert and Lanner 1995). Major historical fluctuations in the number of salmon returning to spawning streams will influence the carrying capacity of the habitats (Willson et al. 1998).

The yearly proportion of the prey population taken by predators is highly variable among species but, for large-bodied carnivores, including felids and canids, values range from 5 to 15%, occasionally rising to 35% in the case of wolf–caribou communities in northern ecosystems (Ricklefs 1990). Bears exhibit extensive variability in the proportion of salmon spawning run numbers consumed in watersheds. On large Alaskan rivers with high salmon numbers (>10 000), brown bears took about 2.5% of the spawning run, while on small rivers, where salmon numbers are lower, the proportion was as high as 85% (Shuman 1950; Clark 1959; Gard 1971). Frame (1974) estimated that 18 black bears took approximately 2% of the pink salmon (N = 27 600) and 17% of the chum salmon (N = 26 000) entering the estuary at Olsen Creek, Alaska, values comparable with those for felids and canids. My values for Bag Harbour, which has a small stream with relatively low numbers of salmon ($N \approx$ 5000), show that consumption levels over 3 years are from 45 to 80% of the total population, consistent with data for brown bears on smaller rivers.

The daily rate of salmon consumption by bears can be determined either from direct observations on foraging individuals or from carcass counts. Using direct observation, Frame (1974) estimated that, over 60 days, 18 black bears consumed 4820 fresh salmon (88% chum and 12% pink) and 13 200 senescent carcasses, yielding an average consumption of 14.9 salmon per bear per day. Using carcass counts, I estimated that, at Bag Harbour in 1993, eight black bears consumed 4641 salmon over 45 days, yielding a consumption of 13 salmon per bear per day, close to the value obtained by Frame (1974). My estimate of daily consumption is potentially too low, as I could not be confident that the full complement of eight bears was present daily throughout the spawning period. Bears consumed an average of 1.6 kg of tissues from each carcass, which would lead to an ingestion of 21 kg/day based on the estimate of daily capture. Over the 45-day spawning period, total consumption would be 945 kg/bear. This estimate, however, could diverge substantially for individual bears.

Black bears occasionally capture but then abandon salmon without consuming any tissues (Frame 1974). This surplus predation has been reported for other carnivores and is ascribed to behavioural compromises when prey are superabundant (Kruuk 1972; DelGiudice 1998). I also observed this behaviour at Bag Harbour and could identify two major classes of abandonment: (*i*) the release of live salmon within seconds of capture—this was observed in pools below waterfalls where bears had easy access to high densities of prespawn salmon; (*ii*) abandonment of intact carcasses on the stream bank—this occurred intermittently throughout the study period and involved both fresh and old salmon. In each case of monitoring these "abandoned" carcasses, bears returned and fed on the tissues within several days. This behaviour is more equivalent to food caching than to surplus predation, as it allows later access to a food source when the capture of new salmon may be difficult. As well as occasionally abandoning complete carcasses, bears regularly left about one-half of each carcass uneaten, tending to consume selected tissues with high lipid levels, such as the brain and the ovaries (see Gilbert and Lanner 1995), and to abandon lipid-poor tissues, such as viscera, testes, and bony parts. The brain was not invariably the preferred tissue, particularly of senescent salmon, when the brain was rarely eaten, although decaying trunk musculature was scavenged. It is possible that the accumulation of aldehydes and ketones, the breakdown products of lipids, may contribute to the apparent unpalatability of the brains of senescent salmon. Each of these instances of "surplus" predation and incomplete consumption presumably reflects foraging decisions wherein low-quality prey items can be ignored as long as high- quality prey are available (Goss-Custard 1977; Krebs 1978).

The selective retention by bears of gravid females captured in pools with high salmon density, as well as the higher caloric value of female salmon (Gilbert and Lanner 1995), leads to the prediction that over the duration of the spawning migration, females should comprise a larger proportion of a bear's diet than would be expected from their proportion in the stream. Yet, contrary to this prediction, data from carcass surveys at Bag Harbour showed that there was a significant excess of males in the diet relative to the population sex ratio throughout the spawning period. I was not able to estimate any changes in sex ratio over the duration of the run but, in Alaskan chum salmon, this is about 1.5 males to 1 female in the early part of the run, which shifts to approximately 1:1 during the latter part of the run (review in Salo 1991). At Bag Harbour, there was an excess of males among bear-captured (ca. 2:1) salmon throughout most of the spawning run. Excess male salmon consumption was also observed in the Alaskan brown bear (Burgner 1991; Gard 1971), as well as in red foxes (*Vulpes fulva*; Gard 1971). Burgner (1991) suggested that the excess capture rate of male sockeye salmon (*Oncorhynchus nerka*) by bears might be the result of their conspicuous red colouration. Although male chum salmon lack the red colouration of sockeye, they are marginally more colourful than females. However, as most predation occurs during darkness, the marginal difference in colouration in chum salmon is unlikely to account for male-biased predation. This differential predation on the sexes could be due to several factors. Male salmon are active in streams for up to 15 days, compared with females that spawn and die within several days of entering the stream (Salo 1991). The extended residence of males would therefore increase the number and duration of encounters with bears (Gard 1971). Furthermore, males are larger than females and may be easier to capture in shallow water. There are fewer consequences to total salmon reproduction of male-biased than female-biased predation. Males are numerically more abundant than females on the spawning gravels (Khorevin 1987; Salo 1991; this study) and each male is capable of spawning many times (Salo 1991).

The potential impact of bear predation on the reproductive output of salmon is primarily a function of the reproductive condition of the females at the time of capture. From analyses of carcasses, I determined that the majority of females (70%) taken by bears were spawned-out, with the remainder being prespawned or partially spawned. There are several potential biases in these data. I used the absence of eggs on the underlying substrate as a criterion for spawned-out status. However, if black bears ate the entire ovaries of a prespawned salmon (see Frame 1974), I would have classified the carcass as spawned-out and this would lead to overestimating predation levels on spawned-out fish. I cannot reject this possibility but suspect that the frequency of such instances is uncommon, as eggs were scattered around the carcass in each active capture of a gravid female ($N = 5$) that I monitored directly. The data may be biased in the opposing direction, so that consumption of spawned-out females was underestimated. Up to 20% of the senescent and uninjured carcasses that I retrieved from the bottom of pools still had ripe eggs in the body cavity. Such egg retention occurs regularly in spawned-out chum salmon (Salo 1991). Because I observed bears scavenging senescent salmon from the bottom of pools, it is probable that some of the carcass remnants on the stream bank and forest floor with scattered eggs represented these spawned-out fish with egg retention. These would have been classified as prespawned or partially spawned and would lead to overestimating the consumption of this group. Of the female salmon taken by bears, 30% were prespawned or partially spawned and I could not readily differentiate along this continuum when examining the carcasses. Females release only a small proportion of their eggs in each spawning event and require about 2 days to complete the full spawning cycle (Salo 1991). Consequently, some unknown proportion of females that are captured by bears will be unspawned, while others will have had multiple spawning events and may be largely spent. Endocrine signatures in tissues may eventually allow fine-tuned classification of spawning condition at the time of capture. My estimate of a 70% consumption of spawned-out salmon is congruent with several other studies. Among three Alaskan streams, 69–99% of the female salmon taken by brown bears were spawned-out (Clarke 1959; Gard 1971). Frame (1974) found that in Olsen Creek estuary, Alaska, 35% of the live female salmon taken by black bears were spawned-out but, when data for scavenged senescent carcasses were included, approximately 80% of all salmon consumed were post-reproductive. These observations are important, as there has been a general perception that bear predation has contributed to the decline of salmon in the coastal regions of western North America. The evidence at hand suggests that bears do not exert a substantive impact on the reproductive output of female salmon during the spawning period.

The reproductive condition of male salmon is also potentially important in assessing the impacts of bear predation. I estimated the reproductive condition of male salmon captured by bears and found that the average testes mass was 40% less than prespawn testes masses and, consequently, the average salmon taken by bears may have spawned about eight times prior to capture. If there was a skewed sex ratio with a deficiency of males on the spawning gravels, then females could be limited in their capacity to complete spawning. This did not seem to occur, as males outnumbered females about 2:1 throughout the spawning period. As a result, I infer that the consumption of partially spawned males does not have a serious impact on the reproductive output of the population.

The general consumption of senescent or spawned-out salmon observed at Bag Harbour is inconsistent with my original prediction that bears would optimize their foraging by capturing higher-quality prey. In each year, I regularly observed bears scavenging senescent and decaying carcasses adjacent to large groups of highly visible active spawners in shallow waters. Spawned-out salmon have about one-half the caloric value of prespawned salmon (Gilbert and Lanner 1995) and, therefore, bears would have to forage for longer periods to obtain equivalent levels of nutrients. The probable explanation for this inconsistency is that the costs of capturing prespawned salmon are much higher than those of capturing spawned-out fish. Prespawned or actively spawning salmon are very responsive to stream-edge disturbance and have rapid evasive responses compared with weakened post-reproductive fish. Bears rarely pursued salmon on the spawning gravels during daylight and, when this did occur, they were frequently unsuccessful at capture (Reimchen 1998). A second factor that may contribute to the elevated consumption of spawned-out salmon is the encounter rate. Prespawned female chum salmon are available for only a short period in the stream, as egg laying on the spawning gravels occurs soon after arrival (Salo 1991). Male salmon remain on or near the spawning gravels for up to several weeks and will remain near the spawning gravels during post-spawning periods. Each of these factors contributes to increasing the encounter rate with post-reproductive individuals. The consequence of this extensive scavenging by bears indirectly minimizes demographic consequences for the salmon population.

Prey-size preferences are a common feature of foragers and reflect strategies that maximize net energy gain (Krebs 1978). Measurement of chum salmon jaw length at Bag Harbour demonstrated that the average size of bear-captured salmon was significantly larger than that of noncaptured fish from both estuary and stream habitats, confirming original predictions that bears would take larger fish. That the salmon which were carried farthest into the forest also had the largest body size is further evidence that bears place greater value on larger salmon. Movement into the forest reduces the likelihood of competitive interference with other bears and reduces harassment by gull and corvid scavengers, which are primarily streamside in their activity (Reimchen 1994, 1998).

Although bears preyed primarily on post-reproductive salmon, which therefore leads to few genetic effects for the salmon population, predation on partially spawned and prespawned fish may have evolutionary consequences for the salmon. Foraging failures by bears were common during pursuit of the salmon (Reimchen 1998) and this can be expected to produce selection on various aspects of salmon behaviour such as activity periods in the stream and escape responses. It seems likely that the elevated capture rates of larger-bodied salmon in both males and females will impose some genetic selection against large size, assuming heritable influences on adult size, and this will in part counter the well-established advantage of large size from sexual selection during territorial conflicts on the redds and during female mate choice (Schroder 1982). Most of the bear predation on this salmon population occurred during darkness, when capture success appeared to be associated with tactile or auditory senses (Reimchen 1998). This can be expected to select for different defensive or evasive responses by the salmon compared with the visually mediated responses required during daylight. One of the broader evolutionary consequences resulting from bear predation on partially spawned male salmon may be to influence genetic variability in salmon. On average, individual male salmon would not be able to dominate any female or groups of females before they were removed from the spawning population. As a result, there would be increased likelihood that females would have multiple male partners over the spawning cycle and that a greater proportion of the numerically abundant males would be involved in fertilizations. This “predator-induced” polyandry would increase genetic variability in the fertilized ova. Considering the varied and diverse habitats encountered by salmon throughout their complex freshwater and marine life history, increased genetic variance may translate into increased fitness. If so, one would predict a gradual erosion of genetic variability in salmon populations from watersheds currently lacking bear populations, where presumably, a smaller number of dominant males would be responsible for most of the matings.

For much of post-glacial history in western North America, brown bears and black bears have probably been the major predators of adult salmon in rivers. The now extinct cave bear was also a major consumer (Hildebrand et al. 1996). This long-established and geographically wide-spread predator–prey association can be expected to yield as yet undescribed behavioural and morphological adaptations. The highly predictable and seasonally pulsed occurrence of salmon migration, combined with the movement of bears and other predators to rivers, is ecologically comparable with the large ungulate migrations and felid associations found in African grasslands (cf. Sinclair 1979).

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