

# Transportation of Pacific salmon carcasses from streams to riparian forests by bears

Thomas P. Quinn, Stephanie M. Carlson, Scott M. Gende, and Harry B. Rich, Jr.

**Abstract:** Predation on Pacific salmon by bears (genus *Ursus* L., 1758) can be an important ecosystem process because the spatial distribution of carcasses largely determines whether marine-derived nutrients cycle through aquatic or terrestrial pathways. Direct observations on three streams in southeastern Alaska indicated that 49% of the pink (*Oncorhynchus gorbuscha* (Walbaum, 1792)) and chum (*Oncorhynchus keta* (Walbaum in Artedi, 1792)) salmon killed by bears were carried into the forest. The tendency of bears to transport carcasses was independent of the sex and species of salmon, but unspawned fish were more often transported than fish that had completed spawning. Data on tagged sockeye salmon (*Oncorhynchus nerka* (Walbaum in Artedi, 1792)) in one southwestern Alaska stream indicated that 42.6% of the killed salmon were transported, and that higher percentages were transported in years when salmon densities were greater. At six other streams, on average, 68.1% of the sockeye salmon killed were apparently transported away from the stream into the forest. Combining the data from all sites, the proportion of carcasses transported increased with water depth at the site. These results emphasize the role that bears play in mediating the interactions between nutrients from salmon and the terrestrial and aquatic ecosystems, and the variation in carcass distribution among streams and among years.

**Résumé :** La prédation des ours (le genre *Ursus* L., 1758) sur les carcasses de saumons du Pacifique peut être un processus écosystémique important parce que la répartition spatiale des carcasses détermine en grande partie si les nutriments d'origine marine sont recyclés par la voie aquatique ou la voie terrestre. Des observations directes sur trois cours d'eau du sud-est de l'Alaska indiquent que 49 % des saumons roses (*Oncorhynchus gorbuscha* (Walbaum, 1792)) et kéta (*Oncorhynchus keta* (Walbaum in Artedi, 1792)) tués par les ours sont transportés dans la forêt. La tendance qu'ont les ours à transporter les carcasses est indépendante du sexe et de l'espèce de saumon, mais les poissons qui n'ont pas frayé sont transportés plus fréquemment que les poissons qui ont terminé leur reproduction. Des données de marquage de saumons rouges (*Oncorhynchus nerka* (Walbaum in Artedi, 1792)) dans un cours d'eau du sud-ouest de l'Alaska indiquent que 42,6 % des saumons tués ont été transportés et que des pourcentages plus élevés sont transportés les années de plus forte densité de saumons. Dans six autres cours d'eau, en moyenne 68,1 % des saumons rouges tués ont apparemment été transportés du cours d'eau vers la forêt. Si les données sont combinées pour tous les sites, il appert que le pourcentage de carcasses transportées augmente en fonction de la profondeur de l'eau au site. Ces résultats soulignent le rôle joué par les ours comme médiateurs des interactions entre les nutriments des saumons et les écosystèmes terrestres et aquatiques et responsables de la variation de la répartition des carcasses d'un cours d'eau à un autre et d'une année à l'autre.

[Traduit par la Rédaction]

## Introduction

In recent years the complex role that Pacific salmon (genus *Oncorhynchus* Suckley, 1861) play in freshwater and riparian ecosystems has been investigated and reviewed (Willson and Halupka 1995; Willson et al. 1998; Gende et al. 2002; Naiman et al. 2002; Schindler et al. 2003; Helfield and Naiman 2006). Marine-derived nutrients (i.e., those im-

ported into freshwater by salmon that fed and grew at sea) have been traced through various pathways leading directly and indirectly back to salmon, to trees in the riparian zone, birds, and indeed throughout the biota (Naiman et al. 2009). Many species of animals will scavenge or occasionally kill salmon, and their movement and subsequent defecation transfers nutrients to the forest, but most are too scarce, too small, or otherwise incapable of killing large numbers of salmon or transporting the fish themselves long distances. However, several studies have shown that brown bears (*Ursus arctos* L., 1758) and black bears (*Ursus americanus* Pallas, 1780) can kill at least half the salmon in small streams (Ruggerone et al. 2000; Quinn et al. 2003) and are capable of transporting carcasses from the riparian zone into the forest (Reimchen 2000).

Early research tended to consider whether or not the salmon populations were adversely affected by bear predation (Shuman 1950; Merrell 1964; Gard 1971; Frame 1974), but it is now clear that bears play an important role in the ecosystem. In addition to excretion of waste products after consumption of salmon (Hilderbrand et al. 1999), many of the salmon killed by bears are only partially consumed; often at

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least half of the tissue remains uneaten (Reimchen 2000; Gende et al. 2001). The biomass of these undigested carcasses can be so high (Gende et al. 2004b) that the location of feeding by bears affects the pathway and recipient food web of the remaining salmon tissue. For example, if a bear leaves a carcass in the stream itself or a nearby gravel bar, the remaining biomass may be scavenged by aquatic invertebrates (Winder et al. 2005) or decompose and leach through the gravel into the hyporheic zone (O'Keefe and Edwards 2002). Alternatively, if a bear carries the carcass into the forest to avoid antagonistic interactions with other bears (Gende and Quinn 2004), the biomass and nutrients are available to riparian forest consumers including other vertebrates (Cederholm et al. 1989; Ben-David et al. 1997), terrestrial insects (Meehan et al. 2005; Hocking and Reimchen 2006), and soil microbes and flora (Helfield and Naiman 2002; Wilkinson et al. 2005; Gende et al. 2007). Thus the recipient food web, aquatic or terrestrial, through which the marine-derived nutrients flow is affected by whether bears leave the carcass in the water or transport it above the stream banks and into the forest.

Despite the recognition that bears play a central role in distribution of salmon nutrients, very little is known about this behavior. We used two approaches to quantify the fate of salmon carcasses and to assess how transportation varied under different salmon densities within a stream, among streams of different sizes, and with characteristics of the carcass: (1) intensive, direct observations of brown bears feeding on pink (*Oncorhynchus gorbuscha* (Walbaum, 1792)) and chum (*Oncorhynchus keta* (Walbaum in Artedi, 1792)) salmon at three streams in southeastern Alaska during three seasons, and (2) surveys of tagged sockeye salmon (*Oncorhynchus nerka* (Walbaum in Artedi, 1792)) in seven streams (number of seasons per site ranged from 2 to 10) where brown bears prey on them. These data revealed that the fraction of the bear-killed salmon removed to the forest was (i) substantial, (ii) varied among years as a function of salmon density, and (iii) varied among creeks as a function of stream depth. The spawning status of the fish appeared to influence carcass movement at some sites but not at others.

## Materials and methods

### Observations of predation and transportation by bears

First, we used direct, observational data collected in 1998–2000 at three small streams (~6 m wide and <1 km long) on Chichagof Island, southeastern Alaska (Bear, Himmel, and Lake creeks; Table 1). Observers with binoculars watched brown bears (the only bear species present) preying on pink and chum salmon from small stands in large stream-side trees at a sufficient height (>20 m) to avoid affecting the bears' behavior (for further details on field techniques see Gende and Quinn 2004). Observations were made during 6–10 h periods, beginning in early morning or late afternoon throughout the July–August spawning season. Tree stands were located in areas that allowed observers to see the reaches of the stream where most of the spawning occurred. When bears captured a fish, the location where the bear consumed it was mapped. We examined the carcass after the 6–10 h observation period, recording the species, sex, distance from the stream bank, and the spawning status of the car-

carcass. About 5% of the carcasses could not be relocated precisely because they settled in deep pools or were carried by bears so far from the stream that they were never found. Because of varying flows and the complex riffle–pool nature of these streams, the distance from the water to streamside vegetation varied among days and stream reaches. We therefore classified the location of a carcass as “forest” if it was carried above the high water bank among streamside shrubs and trees (above-bank flooding never occurred during the three seasons of observations) or “stream” if it was consumed in the stream or on an adjacent gravel bar. These data allowed us to calculate how many of the salmon killed by bears were made available to the riparian ecosystem and associated terrestrial biota as opposed to being consumed or left within the banks of the stream. For carcasses carried above the bank (forest), we recorded distance (m) as the shortest linear distance from the bank.

We categorized females as “ripe” if eggs could be seen extruding from the body cavity when bears captured or consumed the fish or if eggs were seen scattered about the carcass when it was found, and “spawned out” if the skein had few eggs remaining. For males, who may have a significant fraction of their milt remaining even at senescent death, we were conservative in labeling fish as “ripe” if they extruded milt when gentle pressure was applied to the belly. All others were considered “spawned”.

Observations from tree stands provided direct information on the proportion of salmon transported into the forest and factors influencing whether bears carried the fish into the forest or consumed it at the stream. They also demonstrated that bears were the only species which transported fish. Of the >650 salmon observed being killed during 3 years, only 1 was killed by a predator other than a bear (a river otter, *Lontra canadensis* (Schreber, 1777)). Although bald eagles (*Haliaeetus leucocephalus* (L., 1766)) were present on the tide flats, they were never seen killing salmon along the forested section of the streams. However, tree stands limited the range of the stream that could be seen and provided no information from times of the day when no observers are present, and bear predation occurs at night as well as during the day (Klinka and Reimchen 2002). Consequently, we examined an extensive set of data on tagged sockeye salmon collected elsewhere in Alaska, initially for purposes of studying salmon behavior and in-stream longevity. These data provided strong, indirect evidence of carcass transportation and allowed us to consider the phenomenon in seven streams and as many as 10 years of data in one stream.

### Observations of tagged salmon

Tagging studies were conducted on streams tributary to lakes Aleknagik ( $n = 3$ ), Little Togiak ( $n = 2$ ), and Nerka ( $n = 1$ ) in the Wood River Lakes system, as well as a series of spring-fed ponds in Iliamna Lake ( $n = 1$ ); all are within the Bristol Bay region of southwestern Alaska. The primary tagging study site was Hansen Creek, a small tributary (mean depth 9.8 cm, mean width 3.9 m) of Lake Aleknagik flowing 2 km from a beaver dam to the lake. The shallow, clear water and absence of pools and woody debris make it ideal for visual surveys of salmon. In addition, the combination of the beaver pond and overall topography result in an exceptionally stable flow regime, so flooding that might oth-

**Table 1.** Locations and physical features of the streams where bear (*Ursus* spp.) predation on Pacific salmon (*Oncorhynchus* spp.) was studied.

| Creek             | Latitude (N) | Longitude (W) | Width (m) | Depth (cm) | Length (km) |
|-------------------|--------------|---------------|-----------|------------|-------------|
| A Creek           | 59°34'42"    | 159°08'00"    | 1.4       | 10.0       | 0.3         |
| C Creek           | 59°03'30"    | 159°09'36"    | 2.1       | 10.0       | 0.2         |
| Hansen Creek      | 59°19'42"    | 158°41'48"    | 3.9       | 9.8        | 2.0         |
| Yako Creek        | 59°16'48"    | 158°41'42"    | 4.2       | 22.6       | 2.8         |
| Bear Creek        | 59°18'12"    | 158°46'18"    | 5.1       | 19.3       | 1.4         |
| Pick Creek        | 59°33'00"    | 159°04'18"    | 7.6       | 37.9       | 2.0         |
| Pedro Bay ponds   | 59°47'00"    | 154°07'12"    | 24.3      | 38.5       | NA          |
| Lake Creek (SE)   | 57°58'33"    | 135°41'49"    | 5.7       | 14.6       | 0.9         |
| Bear Creek (SE)   | 57°59'09"    | 135°37'35"    | 5.7       | 14.9       | 0.7         |
| Himmel Creek (SE) | 57°59'34"    | 135°47'50"    | 6.4       | 30.3       | 0.3         |

**Note:** Streams are ordered approximately by size. Lengths refer to the section of stream routinely used by spawning salmon, and widths and depths are mean values. Streams designated SE are located in southeastern Alaska, whereas the others are in Bristol Bay (southwestern Alaska). The ponds in Pedro Bay vary in size and shape, but we used Trail Pond as being representative.

erwise displace carcasses (Ben-David et al. 1998) does not occur. Despite its small size the stream supports a dense population of sockeye salmon (the only Pacific salmon species that spawns in the creek), with annual escapements of ca. 2000 – 20000 over the past two decades. Hansen Creek has been used for many studies of bear predation on salmon, documenting size selectivity (Ruggerone et al. 2000; Quinn and Buck 2001), linkage between predation and senescence (Carlson et al. 2007), density-dependence (Quinn et al. 2003), selection by spawning status (Gende et al. 2004a), and selective consumption of body parts (Gende et al. 2001). Only brown bears have been seen during our surveys and this species is numerically and socially dominant over black bears in this region, so we assume that the predation was by brown bears; however, it is possible that black bears were involved in some cases.

Each year from 1999 to 2008, ~200 sockeye salmon were captured as they schooled at the mouth of the Hansen Creek, tagged, and released. At the time of tagging the salmon were measured (mid-eye to hypural plate, in mm), the sex was recorded, and a pair of plastic disk tags (3 cm in diameter) was attached to the fish by a pin through the musculature below the dorsal fin. The individually lettered tags could be read through the water and easily seen on carcasses. The salmon ascended the creek within the next few days or weeks. Each day during the spawning season, a crew of at least three people walked the entire creek and searched the stream, gravel bars, and immediate vicinity on land (~5 m from the wetted edge), noting the location of all live tagged fish and removing the tags from dead ones after recording the cause of death. About 20% of the tagged salmon were never seen in Hansen Creek and were disregarded for purposes of the analysis. These fish may have spawned in other streams, died in the lake prior to entering a stream, or entered Hansen Creek and been killed by bears and transported to the forest on the day they entered, prior to being seen. Salmon found dead had either died by stranding at the mouth or in the stream itself, were killed by gulls (Quinn and Buck 2001; Carlson and Quinn 2007), died of senescence after about 1–3 weeks in the stream (Carlson et al. 2007), or were killed by bears, as evidenced by the prominent bite marks and characteristic patterns of consumption:

brain area, belly (especially in females), and dorsal hump (especially in males), or more massive tissue loss. Each day, all live untagged fish were counted, and all dead fish were removed from the stream channel to avoid being re-counted on subsequent surveys. In all the years of surveys we have never seen a mammalian predator other than a brown bear, and other animals that might move carcasses (e.g., bald eagle) are seldom seen and never in the stream itself.

Many tagged salmon were seen in the stream, often for a number of days, but not recovered as carcasses. Several lines of evidence indicated that these fish were killed and transported by bears into the forest. Bears are the only major predator to frequent this stream, and killed, on average, 49% of the dead adult salmon found dead in the stream during the surveys (Quinn et al. 2003), based on the traumatic wounds in the carcasses. Salmon that die of stranding, of senescence, or are pecked by gulls are not found above the stream's edge, and so these sources of mortality cannot account for missing salmon. Bears commonly carry salmon from streams prior to consumption (Reimchen 2000), often as a result of interactions with other bears (Gende and Quinn 2004), and we have seen them do so at Hansen Creek. Indeed, surveys of the forest reveal salmon carcasses, though the search is time-consuming (Hanson 1992).

It is implausible that so many tagged salmon carcasses would be overlooked in a stream with such clear and shallow water, low and stable flows, and absence of deep pools and woody debris. Most tagged live fish are seen day after day in the same place, until they die or disappear. The probability of detecting a live salmon, given that it was present (inferred from its detection on previous and subsequent days), was 73% for each day. Live tagged salmon are more easily missed than dead ones, and dead salmon missed on 1 day would be seen on a subsequent day. Our conclusion that missing tagged fish were taken from the stream by bears is supported by the fact that the size distribution and number of days alive for these "missing" salmon matched the values for confirmed bear kills, and differed significantly from salmon dying of senescence (Quinn et al. 2001). Thus it is most likely that they were killed and transported, though some may have been scavenged and transported. Re-

ardless, the carcasses were moved from the vicinity of the stream into the forest.

All other tributaries of the lake were surveyed at least once each year and movement between streams was much too rare to explain the large number of missing fish. Of 2196 fish that were tagged at Hansen Creek over all the years, only 4 fish ascended Hansen Creek but were later resighted in another stream. Loss of these disk tags is also exceedingly rare; in all the years we observed only two instances of tags becoming loose and eventually coming free from the fish. Neither of these cases was classified as "transported" because we could see the tags becoming loose over several days and the fish displayed a conspicuous circular scar where the tags had been. To further exclude the possibility that tag loss accounted for the missing fish, in 2008 we double-tagged 102 salmon in Hansen Creek and 100 at the Pedro Bay ponds with disk tags and a metal band on the lower jaw. We examined all 4133 carcasses at Hansen Creek and did not find a single fish with a jaw tag and no disk tags. Of the 95 salmon with disk and jaw tags seen in the creek, both sets of tags were recovered from 94 fish. A single set of disk tags was found along the stream's margin, where they were likely deposited by a bear that consumed the rest of the carcass or deposited it, along with the jaws and jaw tags, elsewhere. At the Pedro Bay ponds we examined 2121 carcasses and found three fish with only jaw tags: one whose disk tags had broken or come off, and two whose bodies had been consumed including the dorsal area where the tags would have been, leaving only the jaws. Thus some loss of disk tags occurs, but it is far too rare to account for the large proportion of missing tagged fish. We are therefore confident that virtually all tagged salmon seen in the stream but not recovered were transported into the forest by bears, and we analyzed the data on those fish as such.

In addition to the intensive tagging efforts at Hansen Creek, we also tagged salmon at two other creeks flowing into Lake Aleknagik in 2003 and 2004: Bear Creek (only male salmon) and Yako Creek (only males in 2003), and in two creeks flowing into Little Togiak Lake (A Creek and C Creek in 2001, 2004, and 2005), farther upstream in the Wood River system. Data from Pick Creek, flowing into Lake Nerka and also in the Wood River system, collected in 1995 and 1996 (Hendry et al. 1999; Quinn et al. 2001) were re-examined and included. In 2007 and 2008, we tagged male and female sockeye salmon at a series of small, spring-fed ponds that flow into Pedro Bay, Iliamna Lake, described in Quinn and Kinnison (1999). In all cases, the tagging materials and methods were similar, and many of the same people were involved in the tagging and resighting work, assuring comparability of the data. Pick, Bear, and Yako creeks are wider and deeper than Hansen Creek but still easy to survey, and A and C creeks are even smaller than Hansen Creek (Table 1). The Pedro Bay ponds vary in size, but all are sufficiently shallow and clear to facilitate detection of tagged fish. For purposes of analysis we used the depth of Trail Pond, where sockeye salmon were most dense. Collectively, these sites represent many streams that support sockeye salmon, though spawning also takes place in larger rivers and on beaches of the lakes themselves (Marriott 1964). Data were collected from too few years at

these streams to enable comparisons of interannual variation, so they were only used to describe mean patterns of transportation. As with the Hansen Creek data, we examined only records of fish seen in the creeks. However, the estimates of salmon density on these creeks were not total counts as they were in Hansen Creek. Rather, on a date corresponding to the historical peak of abundance, each creek was surveyed and the total number of live and dead salmon was recorded. These estimates are lower than the total count would be because some salmon may enter after the survey and some have been removed by scavengers that would have been seen on daily surveys. Nevertheless, they provide a robust index of relative abundance in these creeks (Quinn et al. 2003).

## Results

### Observations of predation and transportation by bears

The records from three streams in southeastern Alaska included 99 observations of salmon killed by bears on Himmel Creek, 400 on Bear Creek, and 176 on Lake Creek. Pooled among years and streams, 49% of the salmon killed by bears were taken into the forest. Of these 675 observed bear kills, 505 were of known species (337 chum, 168 pink) and sex (325 male, 180 female). We were able to assign spawning status to 413 carcasses (301 ripe, 112 spawned). Chi-square contingency tests indicated that after pooling the data with respect to sex and spawning status, pink and chum salmon were equally likely to be consumed within the stream versus carried into the forest ( $\chi^2 = 0.04$ ,  $p = 0.82$ ). Likewise, bears were equally likely to carry males and females into the forest, after fish of different species and spawning status were pooled ( $\chi^2 = 0.15$ ,  $p = 0.69$ ). However, ripe fish were more often carried into the forest than spawned fish. Of 301 ripe fish, 180 (59.8%) were carried into the forest and 121 were consumed on the stream, but of 112 salmon that had already spawned, only 49 (43.8%) were carried into the forest and 63 were consumed at or near the stream ( $\chi^2 = 8.51$ ,  $p = 0.004$ ).

### Observations of tagged salmon

Over 10 years, 1943 sockeye salmon tagged at the mouth of Hansen Creek were seen in the creek and yielded unambiguous records. Of those, 688 were found dead and classified as bear kills (confirmed kills), 440 were missing and presumed killed (Table 2); the rest were found dead of senescence (531), stranded (203), or attacked by gulls (81). Thus, averaging the annual estimates over 10 years, 42.6% of all salmon apparently killed by bears (confirmed kills plus missing) were transported from the stream to the forest. This percentage was closely related to the total number of salmon present in that year; when salmon were more numerous, a higher percentage of the estimated total number killed was missing ( $r^2 = 0.83$ ,  $p = 0.0002$ ; Fig. 1). The overall percentage of tagged salmon killed (confirmed kills plus missing fish as a percentage of those killed and dying of senescence) decreased with the total number of salmon in the creek ( $r^2 = 0.76$ ,  $p = 0.001$ ; Fig. 2).

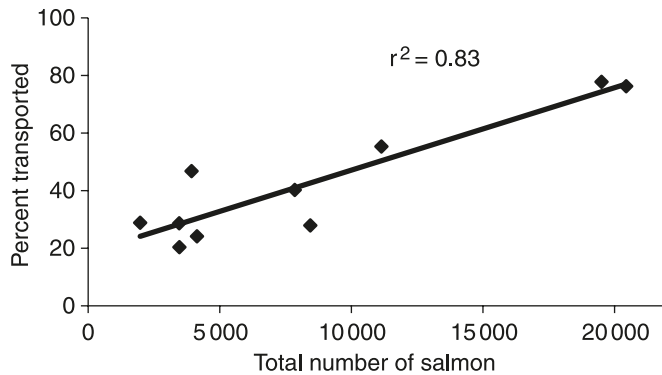
Records were complete for 544 sockeye salmon tagged in Pick Creek. Of these, 51.1% died of senescence (35.2% in 1995 and 63.0% in 1996) and the rest were found killed or

**Table 2.** Total numbers of adult sockeye salmon (*Oncorhynchus nerka*) in Hansen Creek, numbers of tagged fish seen in the creek but then not recovered (missing), and numbers found killed by bears annually from 1999 to 2008.

| Year | Total   | Missing | Killed | Missing (% of total killed) |         |       |
|------|---------|---------|--------|-----------------------------|---------|-------|
|      |         |         |        | Sexes combined              | Females | Males |
| 1999 | 19 504  | 42      | 12     | 77.8                        | 83.3    | 75.0  |
| 2000 | 3 460   | 41      | 102    | 28.7                        | 20.8    | 32.6  |
| 2001 | 1 976   | 43      | 106    | 28.9                        | 22.0    | 33.3  |
| 2002 | 8 439   | 31      | 80     | 27.9                        | 24.1    | 32.1  |
| 2003 | 11 142  | 52      | 42     | 55.3                        | 50.9    | 61.0  |
| 2004 | 3 467   | 22      | 86     | 20.4                        | 11.1    | 27.0  |
| 2005 | 3 928   | 51      | 58     | 46.8                        | 40.0    | 53.7  |
| 2006 | 20 440  | 61      | 19     | 76.3                        | 76.3    | 75.0  |
| 2007 | 7 850   | 64      | 95     | 40.3                        | 35.6    | 44.2  |
| 2008 | 4 134   | 28      | 88     | 24.1                        | 25.6    | 23.4  |
| Mean | 8 434.0 | 43.5    | 68.8   | 42.6                        | 39.0    | 45.7  |

**Note:** The percentages represent the missing fish out of the estimated total number killed (missing plus confirmed killed), calculated for all the salmon, and then calculated separately for females and males.

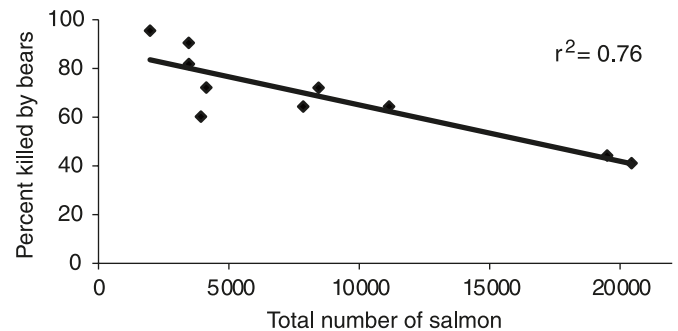
**Fig. 1.** Relationship between the total number of sockeye salmon (*Oncorhynchus nerka*) in Hansen Creek in a given year (1999–2008) and the percentage of salmon apparently taken by bears from the vicinity of the stream (percent transported), expressed as a percentage of total number killed (confirmed kills plus missing).



seen in the stream and then were missing and presumed to have been transported. Of the estimated total number killed, over 80% were missing (Table 3). Similar results were found for all the other streams. In all but two of the combinations of years and creeks, the missing were more than half of the estimated total number of salmon killed. Over all the surveys, 68.1% of the tagged salmon killed were missing (mean of annual values; Table 3).

To evaluate the relationship between probability of being transported from the stream and the condition of the fish, we first used the tagging data from Hansen Creek to test the null hypothesis that the lengths of time the salmon had spent in the creek before they were killed did not differ between confirmed kills and transported fish. Among the confirmed kills, the largest number was killed on their first day in the stream (189), followed by 173, 110, 55, and 35 for fish on their second, third, fourth, and fifth days in the stream, and progressively fewer were killed later in their lives. Direct comparison with transported fish is complicated because salmon taken from the stream on their first day in the stream prior to the survey would not have been seen at all, and so

**Fig. 2.** Relationship between the total number of sockeye salmon (*Oncorhynchus nerka*) in Hansen Creek in a given year (1999–2008) and the level of predation on tagged salmon, expressed as the percent killed by bears (confirmed kills plus missing) out of the sum of those killed and those dying of senescence.



the earliest records were for fish presumed killed on their second day in the stream. After removing the records of confirmed kills on their first day, we compared the distributions using a two-sample Kolmogorov–Smirnov test and detected no difference in the distributions of stream life between confirmed kills and the missing fish ( $Z = 0.59, p = 0.88$ ).

We then analyzed the data from the other six creeks in southwestern Alaska for evidence of condition-biased tendency to transport the carcasses. Kolmogorov–Smirnov tests indicated that the number of days that fish were alive in the stream before they were killed differed between confirmed kills and transported fish in Bear ( $p = 0.029$ ), Yako ( $p = 0.008$ ), and Pick ( $p < 0.001$ ) creeks but not in the other three sites ( $p > 0.20$  for A and C creeks and the Pedro Bay ponds). Overall, the differences in number of days alive before being killed were much larger among streams but of lesser magnitude, and inconsistent (i.e., which was greater) between confirmed kills and transported fish in a given stream (Pedro Ponds: 16 vs. 10 days; Pick Creek: 13 vs. 11 days; Bear Creek: 8 vs. 8 days; Yako Creek: 8 vs. 7 days; C Creek: 5 vs. 8 days; A Creek: 2 vs. 3 days).

**Table 3.** Numbers of tagged sockeye salmon (*Oncorhynchus nerka*) from discrete populations identified as having been killed by bears, those seen but not recovered at death (missing), and the number found dead of senescence, as well as the estimated total runs.

| Site  | Year | Total no. of runs | Missing | Killed | Senescence | Total no. killed | Missing (% of total killed) |         |       |
|-------|------|-------------------|---------|--------|------------|------------------|-----------------------------|---------|-------|
|       |      |                   |         |        |            |                  | Sexes pooled                | Females | Males |
| A     | 2001 | ND                | 136     | 56     | 8          | 192              | 70.8                        | 64.1    | 78.7  |
| A     | 2004 | 457               | 99      | 348    | 3          | 447              | 22.1                        | 19.9    | 26.4  |
| A     | 2005 | 322               | 116     | 18     | 237        | 134              | 86.6                        | 80.9    | 92.4  |
| Bear  | 2003 | 3 424             | 212     | 103    | 51         | 315              | ND                          | ND      | 67.3  |
| Bear  | 2004 | 3 454             | 269     | 133    | 112        | 402              | ND                          | ND      | 66.9  |
| C     | 2001 | ND                | 208     | 122    | 37         | 330              | 63.0                        | 67.8    | 58.8  |
| C     | 2004 | 356               | 148     | 190    | 81         | 338              | 43.8                        | 39.2    | 51.4  |
| C     | 2005 | 209               | 91      | 24     | 143        | 115              | 79.1                        | 78.9    | 80.7  |
| Pedro | 2007 | 5 079             | 105     | 53     | 53         | 158              | 66.5                        | 58.5    | 72.0  |
| Pedro | 2008 | 5 916             | 32      | 12     | 79         | 44               | 72.7                        | 75.0    | 72.2  |
| Pick  | 1995 | 4 418             | 120     | 28     | 81         | 148              | 81.1                        | 86.7    | 78.6  |
| Pick  | 1996 | 6 189             | 102     | 13     | 195        | 115              | 88.7                        | 91.2    | 87.7  |
| Yako  | 2003 | 10 276            | 233     | 59     | 55         | 292              | 79.8                        | 66.4    | 75.3  |
| Yako  | 2004 | 5 642             | 260     | 142    | 63         | 402              | ND                          | ND      | 64.7  |

Note: ND, no data available.

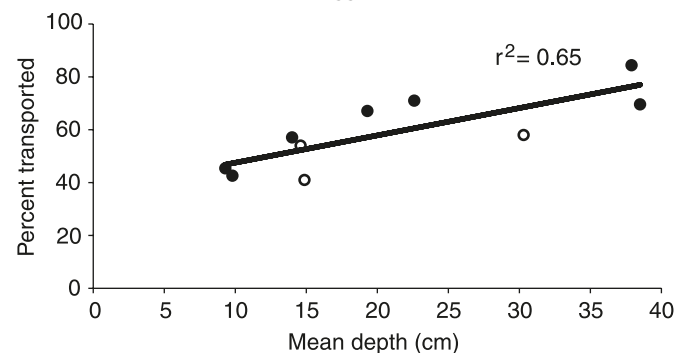
We next tested for a differential tendency for male and female salmon to be transported. To do so we compared the annual percentages of tagged salmon missing of all the kills for males and females from Hansen Creek ( $n = 10$  years) and found that males were more often transported than females (two-tailed paired  $t$  test on proportions that were arcsine and square root transformed,  $t_{[9]} = 2.51$ ,  $p = 0.033$ ). However, the differences between sexes were slight compared with the variation among years (Table 2). We then conducted similar analyses on the data from the other streams and found that the percentages of males and females missing at a given site and year were not significantly different (two-tailed paired  $t$  test on proportions that were arcsine and square root transformed,  $t_{[10]} = 1.47$ ,  $p = 0.17$ ; Table 3).

Finally, given that the geomorphology of the stream influences not only the proportion of salmon killed by bears (Quinn et al. 2001) but also patterns of salmon carcass consumption (Gende et al. 2004a), we considered the relationship between the percentage of carcasses carried from the stream and the stream's size. Combining the data from Bristol Bay and southeastern Alaska, stream depth showed a strong positive relationship with the mean percentage of carcasses carried from the stream by bears (mean of annual values for each stream,  $r^2 = 0.65$ ,  $p < 0.01$ , Fig. 3).

## Discussion

Direct observation on three streams in southeastern Alaska revealed that 49% of the pink and chum salmon killed by bears were transported into the forest rather than consumed in the stream itself or its immediate vicinity. Consistent with these observations, we estimated that 45% of sockeye salmon apparently killed by bears at Hansen Creek were taken into the forest, and even higher percentages were estimated for the other six streams in Bristol Bay. There are several implications from these findings. First, counts of bear-killed salmon in the stream and immediate riparian

**Fig. 3.** Relationship between mean stream depth and mean percentage of Pacific salmon (*Oncorhynchus* spp.) killed and transported into the forest, out of all the salmon killed by bears. ○, estimates from southeastern Alaska (Himmel, Lake, and Bear creeks are based on direct observations); ●, estimates from the streams in southwestern Alaska based on tagged salmon.



zone may substantially underestimate the overall level of predation unless a systematic survey of the forest is made. We observed bears in southeastern Alaska carrying fish >100 m from the stream, and over 33% of the fish carried into the forest were consumed 5 m or more from the stream banks. In 1989, surveys for bear-killed carcasses revealed 26% (at Hansen Creek) and 18% (at Bear Creek) of the bear-killed fish in the forest and the rest in or near the streams (Hanson 1992). These estimates are lower than those in the present study, probably because of the lower probability of detecting a carcass in the forest than one in or near the creek, especially after scavenging (Quinn and Buck 2000) and carcass decomposition (e.g., Meehan et al. 2005). Hanson's (1992) data also revealed a decreasing proportion of salmon carcasses with distance from the stream, similar to our results and others in southeastern Alaska (Willson et al. 2004) and British Columbia (Reimchen 2000).

Our results also revealed that the frequency of transporta-

**Table 4.** Number of adult sockeye salmon (*Oncorhynchus nerka*) that returned to Hansen Creek annually from 1999 to 2008, estimates of the proportion of those salmon that were transported into the forest based on missing tagged salmon, mean mass of killed salmon (whole), and estimated biomass transported after partial consumption by bears.

| Year | Count |         | Proportion of tagged fish missing | Mean mass (kg) of killed salmon |         | Total mass (kg) transported |
|------|-------|---------|-----------------------------------|---------------------------------|---------|-----------------------------|
|      | Males | Females |                                   | Males                           | Females |                             |
| 1999 | 7 265 | 12 239  | 0.318                             | 2.10                            | 1.79    | 9 121.5                     |
| 2000 | 1 557 | 1 903   | 0.232                             | 2.54                            | 2.12    | 1 429.2                     |
| 2001 | 1 082 | 894     | 0.254                             | 2.87                            | 2.49    | 1 050.0                     |
| 2002 | 3 684 | 4 755   | 0.178                             | 2.18                            | 1.87    | 2 329.4                     |
| 2003 | 4 869 | 6 273   | 0.254                             | 2.01                            | 1.76    | 4 084.8                     |
| 2004 | 1 298 | 2 169   | 0.118                             | 2.26                            | 1.88    | 639.8                       |
| 2005 | 1 933 | 1 995   | 0.217                             | 1.84                            | 1.84    | 1 209.1                     |
| 2006 | 7 053 | 13 387  | 0.260                             | 1.71                            | 1.54    | 6 528.2                     |
| 2007 | 2 801 | 5 049   | 0.230                             | 1.96                            | 1.73    | 2 522.2                     |
| 2008 | 1 492 | 2 643   | 0.163                             | 1.81                            | 1.62    | 877.7                       |
| Mean | 3 303 | 5 131   | 0.222                             | 2.13                            | 1.86    | 2 979.2                     |

tion of salmon carcasses to the riparian forest was strongly correlated with salmon density. We do not know how many bears preyed on salmon in any of these streams, so the mechanism associated with this process is uncertain. However, interaction among bears is a plausible explanation for these results. Salmon spawn throughout the small streams that we studied, even at low densities. As salmon density increases, the spatial distribution of fish, and thus areas that bears could fish for salmon, does not increase significantly. Thus, higher numbers of spawning salmon may attract more bears to a similar area, resulting in more frequent antagonistic interactions, as have often been recorded on salmon streams (e.g., Frame 1974; Chi 1999). At the streams in southeastern Alaska, dominance directly influenced the probability that bears would take carcasses into the forest. On average, subdominant bears carried their kills three times as far from the stream (close to 10 m) as dominant bears, and at all salmon densities, subdominant bears spent less time foraging for salmon on the streams than dominant bears (Gende and Quinn 2004). Together, these results suggest that higher salmon densities attract more bears, resulting in more fish being killed and dragged to the forest; however, we presently have no direct link between the densities of salmon and bears on our streams. There is, however, likely an upper limit to the number of bears that a stream can support before it is more advantageous for bears to forage elsewhere for less nutritious prey than risk interacting with other bears along that stream (Gende and Quinn 2004; Ben-David et al. 2004). This result is seen in the asymptote of predation level at streams as salmon density increases (Quinn et al. 2003). However, we did not detect an asymptote in the relationship between salmon density and the proportion carried into the forest. Regardless of the mechanism connecting salmon density to transportation rate, this phenomenon is important because bears tend to eat a smaller fraction of the carcass when salmon are more dense (Gende et al. 2001), further increasing the carcass biomass being transported into the forest.

The increased transportation of salmon from the stream with increasing salmon density has implications for nutrient flow. Salmon-derived nutrients from carcasses have been

found in virtually every trophic level in riparian forests, entering via both direct (consumption) and indirect (nutrient recycling) mechanisms (Gende et al. 2002). Recent experiments have shown that nutrients from salmon carcasses do not leach very far horizontally, and that elevated nutrient levels in soils are found only within 10–20 cm of the carcasses (Gende et al. 2007). Thus the availability of nutrients from salmon depends on the spatial distribution of the carcasses.

The tests of the null hypothesis that salmon killed and consumed on site would be similar in sex and spawning status to those transported yielded mixed results. First, neither the direct observations nor the tag data showed a strong, consistent tendency for bears to transport male salmon more than female salmon, though a statistically significant tendency to transport males was evident at Hansen Creek. Similarly, male salmon were not consistently killed more often than female salmon, though this was sometimes the case (Quinn and Buck 2001). We conclude the sex of the salmon does not strongly affect predation patterns, though it does affect patterns of consumption (Gende et al. 2001).

Work in the Queen Charlotte Islands revealed that black bears preferentially transported ripe chum salmon into the forest, relative to those consumed or dropped at the stream (Reimchen 2000). Our observations of bears in southeastern Alaska also showed a tendency to transport ripe salmon, but our tagging data were less clear. The numbers of days the salmon had been in the stream were similar for transported salmon and those that were consumed at the stream itself. In general, bears selectively prey on newly arrived fish but can accomplish this only in small creeks that facilitate predation (Gende et al. 2004a). The data from the present study corroborated this finding; in deeper and wider sites (e.g., Pedro Bay ponds and Pick Creek) the salmon were seldom killed in the first few days, whereas at the smaller creeks (e.g., Hansen and A) they were often killed within the first few days. Thus in the small creeks salmon are easy to catch and, because they are killed shortly after they arrive prior to expending their lipid reserves, are high in energy content. In contrast, at larger creeks salmon are harder to catch and thus live longer and use up more of their energy prior to preda-

tion, and so are less rewarding to the bears. The fact that transportation rates tended to be higher in the deeper sites (Fig. 3) implies that the difficulty of catching the fish may be more important than its energy content in determining how the bear handles it.

By way of conclusion and to quantify the role of bears in transferring nutrients to the forest, we estimated the overall salmon biomass and associated nutrients transported annually from Hansen Creek to the riparian forest. We used the total count of salmon of each sex in each year and the proportion of tagged salmon seen in the creek and then missing (and so presumed to have been transported) to estimate the number of salmon of each sex that were transported (Table 4). We then took the mean length of bear-killed salmon of each sex in each year and calculated the mean mass of these fish based on length–mass relationships of pre-spawning fish from multiple years (males:  $n = 1010$ ,  $r^2 = 0.87$ ; females:  $n = 654$ ,  $r^2 = 0.81$ ). To estimate the biomass eaten by the bears we used data collected in 1997 at Hansen Creek, where we determined the mass–length relationship, and then weighed and measured carcasses ( $n = 991$  females and 717 males) after partial consumption by bears (see also Gende et al. 2001). These data yielded estimates of 22% consumption of female salmon and 24% of male salmon carcasses by bears. After these adjustments, we estimated that bears transported a mean of 2979 kg per year into the forest adjacent to the 2 km of Hansen Creek, ranging from 9122 kg in 1999 to 640 kg in 2004.

Applying mean nutrient content of these fish at the mid-point of spawning (3% N, 0.4% P wet mass; Gende et al. 2004b) equates to approximately 89 kg of N and 12 kg of P annually to a riparian area of approximately 40 000 m<sup>2</sup> (10 m from the stream bank and 2000 m along each side of the stream). This fertilization,  $\sim 2.2$  g·N·m<sup>-2</sup>·year<sup>-1</sup>, approaches the range of silvicultural applications (3–5 g·N·m<sup>-2</sup>·year<sup>-1</sup>; Thomas et al. 1999). Bears do not distribute carcasses uniformly throughout the riparian zone, and thus some areas will exceed these nutrient loading rates, while others sites will not have any measurable effects because nutrients tend not to leach very far from the carcasses (Gende et al. 2007). Nevertheless, these estimates indicate the magnitude of marine-derived nutrients made available to riparian systems by bears. These estimates do not include salmon in the stream itself or the immediate vicinity that were seen on our surveys. Commercial fisheries in the region had removed on the order of 60% or more of the salmon prior to arrival in the stream (Alaska Department of Fish and Game data), and the bears themselves are hunted. Thus the biomass of salmon transferred by bears to the forest would have been much greater in past centuries.

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