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Magnitude and Fate of Salmon-Derived Nutrients and Energy in a Coastal Stream Ecosystem

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Ron Heintz[d], and Thomas M. Scott[e]

ABSTRACT

We quantified the energy and mineral (nitrogen, phosphorous) composition of live pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*), their eggs, and carcasses, and tracked the fate of chum salmon spawning in a small Alaskan coastal stream. On average, salmon entered streams with 5.3 kJ•g^{-1}, 3.3% N, 0.48% P. Much of the energy in female salmon was stored in the gametes because the gonads were both large (20% of their wet body mass) and high in energy density (11 kJ/g). Carcasses following senescent death had lower mass-specific energy and N (but not P) compared to fish at stream entrance. Bears removed nearly 50% of the salmon-derived nutrients and energy from the stream by capturing salmon and dragging the carcasses from the stream. Much of the salmon biomass was made available to riparian scavengers because bears partially consumed the fish. Nutrients bound in salmon tissue at senescent death were quickly exported to the estuary after only a few days because of periodic high flows and low rates of scavenging by bears.

INTRODUCTION

In Alaska and coastal British Columbia, a fundamental characteristic of stream ecosystems is the return of spawning salmon, and subsequent congregation of organisms to feed on them (Cederholm et al. 1989, Willson and Halupka 1995). Pacific salmon gain at least 99% of their adult weight while foraging in the ocean but migrate to freshwater systems to spawn and die, which results in a net flow of marine-derived nutrients in the form of salmon tissue (Juday et al. 1932, Lyle and Elliot 1998, Cederholm et al. 1999, Gende et al. 2002). Salmon often return to these streams in very high densities, and because the recipient systems tend to be nutrient poor, the influx of salmon can serve as a significant contributor to the nutrient capitol of stream and lake ecosystems (Juday et al. 1932, Donaldson 1967).

There is a growing interest in the ecological role of these nutrients and energy because indices of stream productivity, such as growth rates and population densities, are correlated with the availability of salmon for many organisms that feed on salmon tissue (e.g., Bilby et al. 1996, Hilderbrand et al. 1999b, Wipfli et al. 1999) and because salmon-derived nitrogen and carbon has been traced to many trophic levels in both aquatic and riparian food webs (Bilby et al. 1996, Hilderbrand et al. 1999a). However, whether the nutrients and energy provided by salmon influence food web or ecosystem productivity depends upon many factors, including the ability of stream (or riparian) systems to retain the salmon nutrients, the magnitude and types of nutrients

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provided, and the pathways by which nutrients are incorporated into different food webs (Gende et al. 2002).

For example, following senescent death, salmon carcasses may be flushed out of the stream to a lake or ocean before their nutrients can be incorporated into the stream food web via invertebrate scavenging or microbial breakdown (Gende et al. 2002). Thus, retention mechanisms, such as large woody debris, play an important role as to whether the nutrients are accessible to stream biota or lake or estuarine food webs (Cederholm et al. 1989). The foraging behavior of large vertebrates, particularly bears, may also play a key role in distributing the salmon nutrients. Bears congregate at salmon streams, often in high densities (Barnes 1989), resulting in predation rates that can exceed 90% in some small systems (Quinn et al. 2001 and 2003, Quinn and Kinnison 1999).

To date very few studies have examined the magnitude of nutrients and energy in salmon tissue while on the spawning grounds. For example, existing studies of the biochemical composition of salmon generally describe the nutrient levels of pen-reared salmon fed artificial diets, boneless-skinless filets, or analyzed ocean-dwelling juvenile or adult salmon (reviewed by Haywood-Farmer 1996), none of which is indicative of the biochemical composition of salmon on the spawning grounds. Furthermore, few studies have described the fate of the salmon tissue once salmon arrive on the spawning grounds (Cederholm et al. 1989, Reimchen 2000), rather relying primarily on indirect measures such as use of stable isotopes, to track the presence of salmon nutrients within food webs (Rand et al. 1992, Bilby et al. 1996). Stable isotopes are useful tools for studying fate of salmon nutrients (Kline et al. 1997) but are subject to many untested assumptions (Kline et al. 1997, Gende et al. 2002) and so should complement direct measures of the fate of salmon nutrients.

Our objectives include the following. We quantified the nitrogen, phosphorous, and energy of pink and chum salmon tissue in each of three primary forms used by stream and riparian biota -- live fish just entering streams, eggs, and carcasses. We quantified the total-body composition of salmon at stream entrance (first day in fresh water), after 5 days on the spawning grounds, and at senescent death (after approximately 10 days: carcasses), as well as the composition of salmon gonads. We also examined the fate of chums salmon tissue, including the role of bear foraging activities in distributing the salmon nutrients. We used direct observations and carcass surveys to quantify the number of salmon captured and consumed by bears, the number of females that successfully spawned, and the removal of salmon carcasses from the stream by scavenging bears.

METHODS AND MATERIALS

Study site

The study site was Bear Creek, on northeast Chichagof Island, Alaska. Bear Creek is a small, third-order stream that flows directly into the ocean across a large intertidal area exposed twice daily by tides that fluctuate as much as 7 m. This creek is relatively free of anthropogenic influence. The lowest reach of Bear Creek was determined by the extent to which salmon were able to spawn; at low tide, the lowest reaches of the main channel becomes braided and too shallow to support fish. Bear Creek contained 0.55 km of spawning habitat, of which about 0.09 km was tidally influenced on a daily basis. Flows were not regularly influenced by tides in the stream sections where most spawning occurred. The upper extent of spawning was determined by a large barrier falls created by a woody debris jam. Streamside vegetation was dominated by old-growth Sitka spruce (*Picea sitchensis*) and western

hemlock (*Tsuga heterophylla*) with enclaves of streamside alder (*Alnus* spp.) and a spectrum of fleshy-fruited understory shrubs such as blueberry (*Vaccinium* spp.) and salmonberry (*Rubus spectabilis*).

Nutrient and energy composition

Over the course of the run, shoaling pink and chum salmon were seined at the mouth of Bear Creek at low tide to capture fish that had not yet entered the stream. Upon capture, each fish was measured for length, weighed, and marked with a numbered 4 cm Floy® disc tag placed in the dorsal musculature for individual identification during daily foot surveys. At least two observers walked the stream twice a day and recorded the presence of tagged fish to determine the in-stream age and count the total number live salmon and carcasses. Three males and three females of each species were collected using dip nets after the fish were in fresh water for 1, 5, and 10 days. Since senescent death for both species occurred after an average of 10.4 d, fish captured at 10 days were either dead or moribund. Each fish was measured, weighed, and dissected into gonad and soma tissue. Tissues were then frozen for subsequent analysis. The body masses of individuals used in analysis ranged from 0.6 kg to 1.2 kg for female pink salmon, 1.2 to 2.3 kg for male pink salmon, 1.5 to 3.4 kg for female chum salmon, and 2.3 to 5.1 kg for male chum salmon. Samples were shipped from the study site and stored at -80°C in the laboratory.

We estimated the energy and mineral (N, P) composition of salmon tissue by first quantifying the major chemical constituents (lipid, protein, water, ash) of each sample. All samples were partially thawed and homogenized and then re-frozen. Dry mass was estimated after drying an aliquot to a constant weight at 110°C. Dried samples were then ground using a mortar and pestle and stored in sealed 20 ml vials at room temperature for further analysis. Ash content was estimated upon combustion at 500°C.

Lipids were extracted from frozen wet homogenate following a modified method described in Schafer (1998) and using a Dionex ASE 200 accelerated solvent extractor. Lipid extraction was with a 2:1 mixture of chloroform and methanol at 120°C under pressure of 500 PSI. Protein content was calculated by subtraction (100 - % lipid - % ash). Energy composition was then estimated by multiplying lipid and protein by standard energy equivalents (36.4 kJ/g for lipid, 20.1 kJ/g for protein; Brett 1995, Hendry and Berg 1999). Carbohydrate content is very low in salmon tissue (Brett 1995, Jonsson et al. 1997) and was thus ignored. Total nitrogen was quantified with a combustion gas analyzer (FP-2000, LECO Corp., St. Joseph, MI) according to AOAC (2002). Phosphorous was estimated from ash samples with an inductively coupled plasma emission spectrophotometer (Jarrel-Ash AtomComp, Fisher Scientific, Walham, MA; Shearer et al. 1994).

Magnitude and fate of salmon nutrients and energy

To determine the total number of salmon that entered Bear Creek, at least two observers walked the stream and counted the number of live salmon of each species and sex for each day that salmon were present. Fish were resurveyed if observer counts were not within 5% of each other. Total run size was determined by summing the total number of dead plus the number of live salmon on the last day of the salmon run. To estimate the total N, P, and energy (kJ) that entered Bear Creek, we multiplied the average salmon mass (determined during tagging) by the respective mass-specific nutrient composition and the total number of fish entering the stream.

At Bear Creek and many other small coastal streams, spawning of pink and chum salmon overlap both spatially, and to a lesser degree, temporally.

Our initial goal was to estimate the fate of both species but in 2000 only 25 pink salmon returned to spawn. Consequently, in addressing the ultimate fate of salmon in Bear Creek, we focus on chum salmon.

Fate of salmon tissue

Once in the stream, almost all salmon died from either senescence or bear predation. Bear-killed fish may be carried to the gravel bars or into the riparian forest where they are partially consumed (Gende et al. 2001). Following senescent death, the carcasses may become stranded on shallow gravel bars, hung up on large woody debris, settle in deep pools, or wash into the estuary. Other predators such as wolves (*Canis lupus*) and bald eagles (*Haliaeetus leucocephalus*) are either absent or do not kill live fish in significant numbers in this area. Here we are concerned primarily with differentiating among habitats that receive the salmon tissue (terrestrial riparian, stream, estuarine), so we did not quantify which consumer utilized the tissue once available in these respective habitats.

To record the number of salmon that died of senescence or were killed by bears, we used carcass surveys and direct observations. Carcass surveys occurred during daily counts of live salmon. When a carcass was found, we designated the mode of death as either senescence or bear killed. Bear-killed salmon were easily distinguished from senescent dead salmon by bite marks and loss of tissue. For each carcass we measured the lower jaw and mass and used lower jaw-body mass regression equations (Gende et al. 2001) to estimate the initial mass of the fish. During surveys we also searched within 20 m of the stream bank, as bears often drag carcasses from the stream prior to consumption (Reimchen 2000, Gende et al. 2001). Most carcasses were carried 10 m or less from the stream, although we did find carcasses 100 m or more from the stream.

Bear-killed females were further labeled as ripe or spawned-out, based on the presence of eggs near the carcass or in the body cavity. Bears often selectively consume the eggs of females (Frame 1974, Reimchen 2000, Gende et al. 2001) and preferentially kill ripe fish when possible (Gende et al. in press). Female salmon often spawn their eggs over several days and bears may kill them any time during this period (Gende et al. in press). We designated all females that had eggs as fully ripe because we had no estimates of the number of eggs that had been successfully spawned; all other females were designated as spawned-out and assumed to have deposited all their eggs into the creek gravel. To avoid repeated measures on the same carcass, the lower jaw was either cut in half or fit with an individually numbered metal jaw tag to track the scavenging rate by bears.

We also recorded bear predation by directly observing the bears. Each day following surveys of live salmon and carcasses, bears foraging on salmon were directly observed from streamside tree stands, as part of a related study of bear foraging behavior (Gende and Quinn in press). We observed bears from dawn to late evening, and mapped where bears carried salmon. We visited each carcass following observation periods to record species, sex, length, mass, and spawning status. Combining the direct observations and carcass surveys gave us an accurate estimate of the number of chum salmon that were killed by bears, the amount of biomass moved from the stream and consumed by bears, and the number of females that successfully spawned their eggs.

We estimated the scavenging rate by bears by placing jaw tags on 61 senescent dead salmon throughout the run. A carcasses was tagged the day we observed a fish die and revisited each day until it was no longer present or completely consumed by bears, other scavengers, or microbially decomposition. We searched the stream and riparian forest each day for jaw-tagged salmon

and recorded the locations of the carcasses and distances they may have moved from their original tagging locations, and whether or not scavenging by bears occurred. If a carcass was not found in the stream, we searched the riparian zone within a 15 m radius of the previous location, focusing on the prominent bear trails where bears were observed consuming many captured salmon. We also used dip nets to retrieve carcasses that were at the bottom of deep pools. This increased our accuracy of our estimates of carcass fate but probably facilitated further physical breakdown of the tissue. Carcasses were returned to the pool following measurement.

RESULTS

Form of salmon-derived nutrients

Mass-specific total-body energy, N, and P were similar among males and females for both pink and chum salmon (Fig 1). On average, fish entered the stream with about 3.3% N, 0.48% P, and 5.3 kJ·g^{-1}. Males averaged about 15% larger than females, and chum salmon were up to twice as large as pink salmon. Thus, the absolute amounts of nutrients and energy varied with sex and species (Table 1).
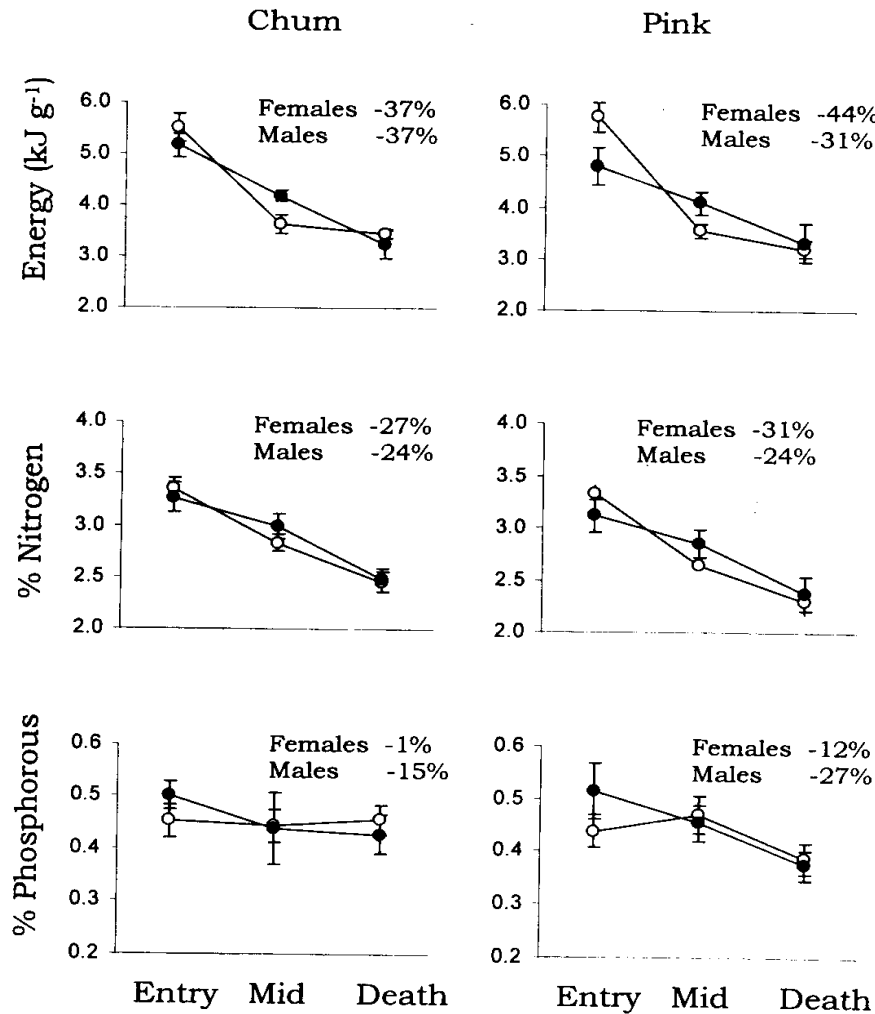

Figure 1. Energy, N, and P composition of female (o) and male (•) chum and pink salmon at stream entrance (Entry), after five days on the spawning grounds (Mid), and the carcasses at senescent death (Sen). Values are presented as percent (± SE) of total wet mass.

The eggs in females were high in energy, averaging 9.25 kJ•g^{-1}, and gonadal tissue represented about 20% of the wet mass at stream entrance (Fig. 2, Table 1). Consequently, the eggs represented about 33% of the total energy, 25% of the total N, and 17% of the total P in each female fish. Females deposited nearly 100% of their eggs into the stream gravel during spawning as only a few residual eggs were found in the body cavities of senescent females. Male testes were comparatively low in energy ($\bar{x}$ = 4.7 kJ•g^{-1}) and N ($\bar{x}$ = 4.4%), although they were high in P ($\bar{x}$ = 1.0%; Fig. 2). Because testes were relatively small, they represented only 4% of the total energy, 6% of the N, and 10% of the P. The testes in males at death averaged 26% (± 9%; N = 8) of their initial mass. Carcasses weighed less than fish at stream entrance due to the expulsion of gametes during spawning and metabolic loss. Averaging both species and sexes, mass-specific N, P, and energy for senescent dead salmon was 2.4%, 0.41%, and 3.31 kJ•g^{-1}, representing a loss of 26%, 14%, and 38%, respectively (Fig. 1).

Table 1. Mass, nutrient (N, P), and energy (kJ) composition of whole fish at the stream entrance, in the gonads at spawning, and in the carcasses at senescent death of male and female pink and chum salmon spawning in Bear Creek, southeastern Alaska in 2000.

		Chum		Pink	
		Males	Females	Males	Females
Whole fish at stream entry (including gonads)	$\bar{x}$ mass (Kg)	3.94 ± 0.05	3.25 ± 0.05	1.63 ± 0.03	1.49 ± 0.02
	$\bar{x}$ energy (kJ)	20620 ± 262	17903 ± 165	7861 ± 241	8520 ± 114
	$\bar{x}$ N (g)	130.0 ± 1.7	107.3 ± 1.0	52.2 ± 1.6	49.2 ± 0.7
	$\bar{x}$ P (g)	20.1 ± 0.3	14.6 ± 0.3	8.3 ± 0.1	6.4 ± 0.1
Gonads at spawning	$\bar{x}$ mass (g)	149.7 ± 0.2	685.8 ± 0.9	88.0 ± 0.5	283.1 ± 0.2
	$\bar{x}$ energy (kJ)	704 ± 8.9	6322 ± 58.4	414 ± 12.7	2610 ± 35.0
	$\bar{x}$ N (g)	6.4 ± 0.1	28.8 ± 0.3	3.8 ± 0.1	11.9 ± 0.2
	$\bar{x}$ P (g)	1.5 ± 0.02	2.1 ± 0.02	0.9 ± 0.03	0.8 ± 0.01
Whole fish at senescent death	$\bar{x}$ mass (Kg)	3.40 ± 0.06	2.26 ± 0.04	1.45 ± 0.04	1.16 ± 0.02
	$\bar{x}$ energy (kJ)	11433 ± 202	7781 ± 138	4993 ± 139	3761 ± 65
	$\bar{x}$ N (g)	85.0 ± 1.5	56.5 ± 1.0	34.8 ± 1.0	27.8 ± 0.5
	$\bar{x}$ P (g)	14.6 ± 0.3	9.9 ± 0.2	5.9 ± 0.2	4.8 ± 0.1

Magnitude and fate of salmon-derived nutrients

Chum salmon first entered Bear Creek on 21 July (26 fish), and abundance continued to increase until 2 August (543 fish), and ended on 18 August when only 14 live salmon were counted (Fig. 3). Total run size was 674 chum salmon; only 25 pink salmon entered Bear Creek in 2000. Multiplying the average body mass and nutrient content by the number of chum salmon revealed that Bear Creek received a total of 80.2 kg of N, 11.6 kg of P, and 1.2 x 10^7 kJ of energy in the form of chum salmon tissue. As there were about 2200 m^2 of stream area, this equated to about 37g of N, 5.3g P, and 5455 kJ of energy per m^2 of stream area.

Brown bears were observed killing 262 chum salmon throughout the run: 104 females and 158 males. Carcass surveys revealed an additional 56 bear-kills (24 females, 32 males), for a total of 318 bear-killed chum salmon. Ultimately bears killed 47% of the chum salmon that entered Bear Creek in 2000. Of the female salmon that we observed being killed by bears 65% (68) had most of their eggs present, and 67% (16) of the females found during carcass surveys had some eggs in the body cavity or near the area of the carcass. Combining the observed kills and carcass surveys, we estimated that 84 females (26% of the total females) were killed prior to spawning.

Bears carried salmon an average of 4.5 m (± 3 m; N = 302) from the stream bank (range 0-221 m). Most carcasses were carried above the high water bank several meters from the stream. Bears consumed an average of 34% (± 9%) of the tissue from each captured salmon. Combining the nutrient

values and biomass of fish killed prior to and after spawning, bears removed a total of 34.8 kg of N (43% of total entering), 5.6 kg of P (48%), and 5.2 x 10⁶ kJ (40%) of salmon-derived energy from the stream.

Given that 84 females were killed prior to spawning, a total of 253 females (75%) successfully completed spawning, resulting in 7.3 kg of N, 0.7 kg P, and 1.5 x 10⁶ kJ energy made available to stream biota in the form of salmon eggs. The remaining nutrients were extruded as metabolic waste products or bound in carcasses. Although loss of N and energy was precipitous from stream entrance to death, carcasses still contained 5-15g of P, 28-85g of N, and 3700-11433 $kJ \cdot g^{-1}$ of energy (Table 1).

Bears scavenged 18% (11) of the senescent salmon and moved the fish an average of 0.3 m. Despite low scavenging rates, carcasses did not remain in the stream for very long. Average stream residence time of jaw-tagged carcasses was 4.5 days, but varied with stream flows. For example, a few carcasses, particularly those that had spawned at the upper reaches of the stream, were present 16 or more days *post mortem*, and completely decomposed. However, 43% of the tagged carcasses washed into the estuary after three days or less.
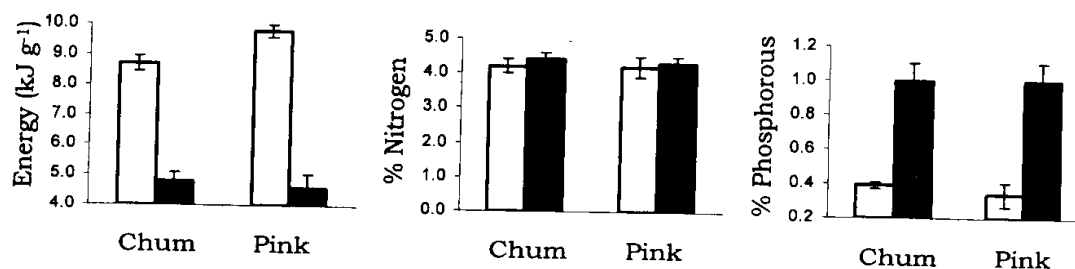

Figure 2. Energy, N, and P composition of female (□) and male (■) gonads in chum and pink salmon at spawning. Values are presented as percent (± SE) of total wet mass.

DISCUSSION

Much recent work has focused on the ecological importance of salmon-derived nutrients to stream ecosystems, particularly their effects on the productivity of in-stream biota (Bilby et al. 1996, Bilby et al. 1998, Wipfli et al. 1998, Wipfli et al. 1999, Cederholm et al. 1999). Our data on the nutrient and energy composition of salmon and associated counts of fish entering a small coastal stream are consistent with the idea that the return of spawning Pacific salmon can represent a major influx of marine-derived N, P, and energy to stream ecosystems. However, our results also demonstrate that, with the exception of egg deposition by female salmon, most of the nutrients may ultimately end up outside the stream system.

Bears killed a large fraction (almost 50%) of the chum salmon that entered this stream, carried many of the fish to the riparian forest, and only partially consumed the carcasses, resulting in a large amount of biomass made available to riparian scavengers. High predation rates, carcass dragging, and partial consumption are common foraging traits at small streams in coastal British Columbia and Alaska. In a survey of 13 creeks over 10 years, Quinn et al. (2003) found that annual predation on sockeye salmon was high, averaging 35%, with the smallest streams averaging 48%. At several creeks and ponds smaller than Bear Creek, the rates of predation were up to 90% (Quinn and Kinnison 1999). The rate of predation on salmon by bears is generally a decreasing function of stream width (Quinn et al. 2001), and Bear Creek, like many small coastal streams, is quite narrow.

Other studies have found that salmon-derived nutrients, made available via bear foraging activities, are utilized by riparian trees and shrubs, suggesting that bear foraging activities are important at other streams. In southwestern Alaska, much of the salmon-derived N detected in foliage of white spruce was a product of bear foraging activities when they dragged carcasses into the forest and excreted digested fish waste (Hilderbrand et al. 1999a). Likewise, the distribution of marine-derived nitrogen in riparian shrubs and terrestrial invertebrates was closely linked to the activities of bears in southeast Alaska (Ben-David et al. 1998) and British Columbia (Reimchen et al. 2003). Plant growth may be elevated in riparian reaches along salmon streams, particularly in areas where bears drag carcasses for consumption (Helfield and Naiman 2001).

Of the salmon that avoided predation and died a senescent death, most did not remain in the stream for very long. Despite losses of energy and nutrients due to excretion and gamete expulsion, these carcasses still contained up to 11,433 kJ of energy, 85g of N and 15g of P, and thus represented an important source of nutrients and energy. As salmon approached death, they lost their ability to maintain their position in the stream and drifted many meters downstream from their spawning site before dying. Fish that spawned in the upper reaches of the stream were more likely to become entangled in woody debris, or settle into a deep pool that formed behind the debris (Cederholm and Peterson 1985). These carcasses tended to remain in the stream and completely decompose following processing by invertebrates or microbes, or from physical abrasion. However, most of the spawning occurred < 250 m above stream reaches that were influenced by daily high tides. Fish that spawned and died in these areas had only one large tangle of woody debris and one deep pool where the carcasses could come to rest; if carcasses drifted past these areas they usually washed onto gravel bars and were swept into the estuary during the next period of high flows or large outgoing tide. In western Washington, Cederholm et al. (1989) found that carcasses generally moved less than 600 m downstream, and remained in the stream for extended periods due to the retention by large woody debris. We also found that woody debris was an important retention mechanism and that many consumers (both aquatic and terrestrial) scavenged the carcasses when present. However, because Bear Creek contained less than 500 meters of spawning habitat, there were comparatively fewer opportunities for carcasses to be retained long enough for complete decomposition. Heavy precipitation periodically raised stream flows for periods lasting only several hours, but this was long enough to flush most of the carcasses from the gravel bars. On one
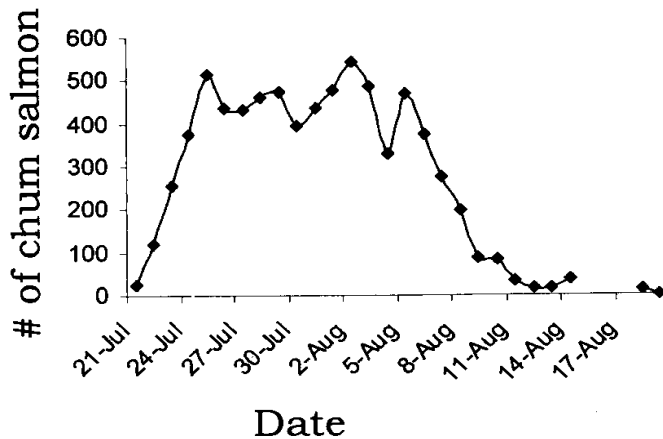

Figure 3. Total number of live salmon, carcasses and bear killed salmon on each day of the salmon run, 2000.

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occasion following three days of heavy precipitation, almost every carcass, including those in deep pools, was washed into the estuary. Richey et al. (1975) also noted that high flows washed almost all carcasses from a small subalpine stream. Likewise, most salmon carcasses were deposited in the estuary at Sashin Creek, Alaska (Brickell and Goering 1970).

By extension, then, the influence of carcasses on estuarine productivity and community structure needs further investigation (Sugai and Burrell 1984). Nearly half of the salmon that entered the stream died naturally, and many of these carcasses would wash into the estuary shortly thereafter, so many of the nutrients would ultimately be exported to the estuary. Fujiwara and Highsmith (1997) suggested that salmon-derived nutrients from spawning-adults may influence estuarine productivity to the benefit of juvenile salmon by increasing the amount of organic material available to estuarine algae, which are fed upon by harpacticoid copepods, which in turn serve as the primary prey for juvenile salmon. Reimchen (1994) also noted the presence of salmon carcasses in an estuary in British Columbia, and recorded many species utilizing the tissue.

Perhaps the most important mechanism by which salmon-derived nutrients and energy were made available to stream biota was through the deposition of eggs into the gravel by spawning females. Mortality rates of pink and chum salmon eggs have been estimated between 87 and 93% (Chapman 1988, T.P. Quinn, unpublished data), with a large source of mortality from aquatic organisms eating or scavenging the eggs, including invertebrates (Nicola 1968), juvenile salmonids (*Oncorhynchus* spp.; Bilby et al. 1998), and a variety of other opportunistic consumers (Moyle 1966, Willson and Halupka 1995, Obermeyer et al. 1999, Cederholm et al. 1999). In Iliamna Lake, Alaska, sculpins (*Cottus* spp.) could consume up to 130 eggs over a seven-day period and were estimated to consume over 600,000 eggs, constituting nearly 16% of the eggs laid by beach-spawning sockeye populations (Foote and Brown 1998). Eggs may be more important than the carcasses to freshwater food webs because they were comparatively much higher in energy and nitrogen content, and because they are buried in the gravel following deposition, serving as a mechanism by which the eggs are retained in the stream. We did not collect data on how long the eggs were retained in the gravel, but we assume they were available for a longer period than the carcasses.

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