

Do bears facilitate transfer of salmon resources to aquatic macroinvertebrates?

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Abstract: In coastal areas of the Pacific Northwest bears (*Ursus* spp.) prey heavily on spawning Pacific salmon (*Oncorhynchus* spp.) and selectively kill energy-rich individuals that are the most recent arrivals on spawning grounds. Pacific salmon eventually die in spawning habitats anyway, albeit with considerably lower energetic content. We investigated whether foraging activities of bears facilitate growth of stream invertebrates by increasing the duration of salmon carcass availability and the nutritional value of carcasses for scavengers. Our survey in southwest Alaska showed that carcasses are highly colonized by caddisfly (Trichoptera) larvae. Caddisflies show a strong preference for bear-killed over senescent carcasses, which may be a result of extended temporal availability, improved accessibility of consumable tissue, and higher energetic content of bear-killed fish. Isotope analyses further indicate uptake of marine-derived nutrients in caddisflies during the salmon run, which, however, does not extend into subsequent generations. Thus, species with life histories linked to the annual marine derived nutrient pulse gain the biggest advantage from the salmon resource subsidy. A long-term survey in several creeks in this region showed that bear predation intensity varied greatly among creeks and years, therefore indirect effects of bear predation on aquatic scavengers are likely highly patchy in time and space.

Résumé : Dans les régions côtières pacifiques du nord-ouest américain, les ours (*Ursus* spp.) font une forte prédation sur les saumons du Pacifique (*Oncorhynchus* spp.) lors de la fraye et tuent de préférence les individus riches en énergie qui sont le plus récemment arrivés sur les sites de reproduction. Les saumons du Pacifique meurent sur les habitats de fraye de toute façon, bien que leur contenu énergétique soit alors considérablement réduit. Nous avons examiné si les activités alimentaires des ours améliorent la croissance des invertébrés des cours d'eau en prolongeant la période de disponibilité des carcasses de saumons et en augmentant la valeur nutritive des carcasses pour les charognards. Notre inventaire dans le sud-ouest de l'Alaska montre que les carcasses sont fortement colonisées par les larves de phryganes (Trichoptera). Les trichoptères montrent une forte préférence pour les carcasses tuées par les ours par rapport aux carcasses sénescences, ce qui peut s'expliquer par une disponibilité prolongée dans le temps, une accessibilité accrue de tissu consommable et un contenu énergétique supérieur des poissons tués par les ours. Les analyses d'isotopes indiquent de plus une accumulation de nutriments d'origine marine chez les trichoptères durant la montaison des saumons, qui, cependant, ne se prolonge pas dans les générations qui suivent. Ainsi, les espèces dont le cycle biologique est relié à l'apport ponctuel annuel de nutriments d'origine marine retirent un avantage maximal de la contribution des saumons aux ressources du milieu. Un inventaire de longue durée dans plusieurs ruisseaux de la région montre que l'intensité de la prédation par les ours varie considérablement d'un cours d'eau à un autre et d'une année à l'autre; les effets indirects de la prédation des ours sur les charognards aquatiques sont donc vraisemblablement très variables dans l'espace et le temps.

[Traduit par la Rédaction]

Introduction

Large carnivores have considerable influence on the structure and function of lower trophic levels by directly regulating the abundance of their prey, which in turn may indirectly

affect other species with which carnivores do not interact directly. Well-known examples of such trophic cascades include predation by wolves on ungulates (moose) (Post et al. 2002), which in turn has strong effects on fir trees (McLaren and Peterson 1994), or predation by killer whales on sea ot-

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ters, which in turn strongly affects urchin densities and kelp production (Estes et al. 1998). Large carnivores can also cause physical and chemical changes to environments, thereby altering habitats used by other organisms and controlling the availability of resources for scavengers (Rose and Polis 1998; Wilmers et al. 2003). In coastal areas of the Pacific Northwest the foraging behavior of brown and black bears (*Ursus arctos* and *Ursus americanus*, respectively) on spawning anadromous salmon (*Oncorhynchus* spp.) modifies the structure of riparian areas (Frame 1974; Gende et al. 2002). Salmon populations and subsequent bear predation are especially remarkable in coastal Alaska and British Columbia, where bears kill large quantities of salmon when they are available (Hilderbrand et al. 1996; Reimchen 2000), and carry partially consumed carcasses into riparian forests (Reimchen 1994; Gende et al. 2001, 2004b). In some regions, rates of bear predation on salmon are so high that a large fraction of the total salmon run are killed after only a few days in spawning creeks (Quinn and Buck 2000). Bears show a strong preference for energy-rich fish (those that had not spawned) and target energy-rich body parts including the brain and gonads (Gende et al. 2001, 2004a; Quinn et al. 2003). As a consequence, bear-killed salmon carcasses serve as an important resource for aquatic and terrestrial scavengers, including birds (Schindler et al. 2003).

The nutrient and energy subsidies to coastal ecosystems represented by spawning migrations of anadromous salmon have gained considerable attention from the aquatic sciences during the last decade (Cederholm et al. 1999; Gresh et al. 2000; Naiman et al. 2002). The salmon that return annually to Pacific Northwest freshwater systems are an important source of nutrients for aquatic biota (Bilby et al. 1996; Naiman et al. 2002; Ito 2003) and riparian plants and consumers (Kyle et al. 1997; Helfield and Naiman 2001; Ben-David et al. 2004). Studies using stable-isotope tracers such as nitrogen (^{15}N) and carbon (^{13}C) demonstrate that salmon nutrients are incorporated into stream biota and riparian plants at various trophic levels (Bilby et al. 1996), and that marine-derived N can represent 30%–75% of the N in fishes and aquatic invertebrates (Naiman et al. 2002). This fertilization process provides high-energy food for resident fishes, juvenile salmon, and invertebrates, and can increase aquatic- and riparian-ecosystem productivity (Wipfli et al. 1998, 1999) through either direct consumption of salmon body tissue and gametes (Chaloner et al. 2002; Minakawa et al. 2002), increases in prey quality and abundance, or leaching of nutrients from decaying salmon carcasses (Bilby et al. 1996).

Upon entry into fresh waters, salmon cease feeding, which can be several months before spawning commences. During freshwater migration and spawning, salmon lose 80%–90% of their lipid and about 40%–50% of their total energy (Hendry and Berg 1999; Gende et al. 2004a). Salmon live generally for less than 3 weeks on the spawning grounds (Quinn et al. 2001a), but this varies among populations. The physiological deterioration associated with prolonged migration and spawning leads eventually to death. Therefore, the nutritional value of salmon carcasses depends strongly on the timing of death relative to the timing of entry into fresh water (Gende et al. 2002). Salmon killed immediately after entering spawning creeks (either by bears or through being

stranded naturally because the water level is low) have a higher nutritional value than those senescing after many days in the creek (Gende et al. 2004a).

The decomposition of salmon carcasses can take several months to complete, because although the rate of decomposition is initially high, it declines over time (Chaloner et al. 2002). As with terrestrial carrion (Hanski 1987), scavengers are important agents in the decomposition of salmon carcasses (Britton and Morton 1994; Chaloner et al. 2002; Meehan et al. 2005). Avian and other vertebrate scavengers often remove chunks of salmon tissue and may carry some carcasses into riparian areas. Carcasses remaining in creeks are colonized by a range of terrestrial and aquatic invertebrates (Kline et al. 1997; Chaloner et al. 2002; Nakajima and Ito 2003) that scavenge salmon tissue. Caddisfly (Trichoptera) larvae are often the numerically dominant insect group associated with salmon carcasses (Minakawa et al. 2002), although many other insect taxa have been identified on salmon carcasses. Invertebrates likely facilitate the transfer of nutrients and energy from salmon carcasses to other components of the food web and therefore the transfer of marine-derived nutrients (MDN) to higher trophic levels (Bilby et al. 1998).

The objective of this study was to investigate whether brown bear predation on sockeye salmon (*Oncorhynchus nerka*) facilitates the growth of aquatic scavengers. We hypothesized that bear-killed salmon carcasses represent high-quality food resources for aquatic scavengers, which, in turn, opportunistically and preferentially feed on these carcasses as a means to maximize their own growth and development rates. Specifically, we surveyed the impact of bear predation on sockeye salmon over the season in Hidden Lake Creek, southwest Alaska, and investigated the colonization of salmon carcasses by caddisfly larvae. We monitored the energetic and nutritional response of caddisfly larvae to the presence of sockeye salmon carcasses that accumulated over the course of seasonal spawning activities of this population. In addition, we used a long-term data set of carcass counts in several creeks in this region to estimate the temporal and spatial variation of bear predation on migrating sockeye salmon, which allowed us to extend the survey from Hidden Lake Creek to a broader spatial and temporal scale. Our results highlight the importance of terrestrial predators for facilitating the propagation of MDN and energy into freshwater food webs.

Study site and methods

This study was conducted in the Wood River system located in the Wood-Tikchik State Park, southwest Alaska (59–60°N, 158–159°W) (for a map see Quinn et al. 2001b). Streams used as spawning grounds for salmon range in width from 1.7 to 15.7 m and are described in detail in Marriott (1964). Sockeye salmon dominate the spawning runs of this region between late July and mid-October, with peak runs in late July to early September. Live and dead salmon were surveyed in 25 creeks throughout the Wood River system during peak spawning (August) by walking upstream from the mouth of the creek until a barrier to migration or a region with unsuitable habitat for salmon was

reached. Carcasses in the stream channel and riparian zone were categorized by mode of death (i.e., senescent or bear-killed). Sampling frequency varied among creeks and resulted in 4–17 years of data for each creek. Based on these annual surveys the proportion of bear-killed sockeye salmon in each of these creeks was calculated according to Quinn et al. (2001b, 2003) as the average of the following ratios: bear kills/all dead and bear kills/(live + all dead). The average of these two predation levels takes into account the seasonal variation of bear-killed sockeye salmon in relation to sockeye salmon density and is an accurate estimate throughout most of the salmon run (Quinn et al. 2003).

In 2003, a 400-m reach of Hidden Lake Creek was surveyed over the course of the salmon run to monitor changes in the densities of salmon carcasses available to aquatic scavengers. The section of the creek was, on average, 0.5 m deep and 3 m wide. Sockeye salmon carcasses were counted and categorized by their mode of death (stranded, senescent, bear-killed) once a week from 27 July to 25 August. Muscle tissue from the middorsal area of fresh carcasses (bear-killed or stranded; $N = 27$) and senescent carcasses ($N = 10$) was taken at the end of July and middle of August, frozen, and later freeze-dried for 18 h to determine energy density and stable-isotope characteristics. In terms of composition, dorsal muscle is a good representative of the entire soma (Hendry and Berg 1999). Each sample was ground and the calorimetric value was determined using a 1425 Semimicro Bomb Calorimeter (Paar Instrument Company, Moline, Illinois). According to Hendry and Berg (1999) a water content of 71% and 83% was assumed for fresh and senescent carcasses, respectively. In addition, isotope ratios of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were measured for each of the carcasses (for descriptions see below).

To estimate the biovolume of bear-killed salmon carcasses and the proportion of bear-killed carcass remnants in the creek, we measured the weight and snout length of fresh bear-killed carcasses (36 females and 28 males) and of live ripe (20 males and 20 females) sockeye salmon. From the snout length – weight regression for live sockeye salmon (females: $r^2 = 0.79$, $P < 0.001$; males: $r^2 = 0.90$, $P < 0.001$), the original weight of the carcasses was estimated and the average proportion of biomass consumed per carcass calculated.

In the same section of Hidden Lake Creek, the abundance of caddisfly (Trichoptera, Limnophilidae, mainly *Ecclisomyia* sp.) larvae (Wiggins 1977) on carcasses was determined on each survey date by rotating the carcasses on the stream bed in shallow water or gently lifting them onto a submerged tray in deeper water to prevent loss of caddisfly larvae from them. Our visual inspection suggested that this method was effective on both types of carcasses and did not bias our estimates of higher densities of caddisflies on bear-killed carcasses. Both external and exposed internal body parts were carefully observed for caddisflies, and carcasses were assigned to the fresh (bear-killed, stranded) or senescent category. Carcasses are distinguishable as follows: bear-killed carcasses have holes from canine teeth and a varying amount of tissue has been removed; stranded carcasses are intact and fresh, with negligible wear on the fins; senescent carcasses are emaciated and have dried and tattered fins and tails as a result of nest-digging, and fungus on the body. Selection by

caddisfly larvae of bear-killed carcasses was quantified by Chesson's selectivity coefficient, α (Chesson 1983), which is a measure of preference for bear-killed over senescent carcasses. This index was calculated as

$$(1) \quad \alpha = \frac{r_i/n_i}{\sum r_j/n_j}$$

where r_i is the proportion of caddisfly larvae on bear-killed carcasses, n_i is the proportion of bear-killed carcasses in the creek, and r_j and n_j are the proportion of caddisfly larvae on bear-killed and senescent carcasses, respectively. Stranded carcasses were excluded from the analysis because of their rare occurrence. In our study, α values of 0.5 represent random colonization (1/number of types of food available) and α values greater or less than 0.5 represent selection and avoidance of bear-killed carcasses, respectively.

In addition to those that were collected from the carcasses, caddisfly larvae were also collected from the creek bed using a Surber sampler (30.5 cm \times 30.5 cm) from 4 July to 25 August. Caddisflies were preserved in 70% ethanol for growth, energy-content, and isotope analyses. Caddisfly larvae from two nearby non-salmon creeks (N-4 and Upper Pick) were also collected for isotope analyses between 21 July and 4 September.

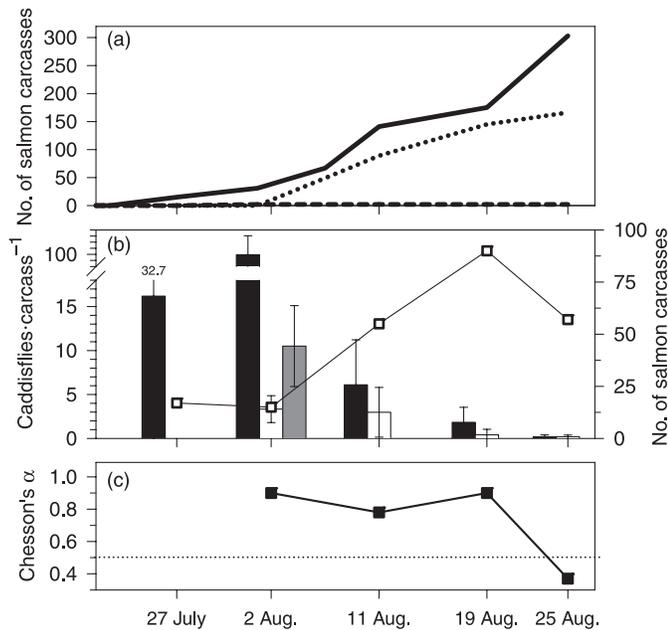
In the laboratory, caddisflies were removed from their cases, measured to the nearest 1 mm of length, dried for 18 h in a freeze-dryer, and weighed to the nearest 0.001 mg. Growth rates for caddisflies were measured as the difference in dry weight (DW) over time ($N = 26$ –125 individuals per date). On each sampling date, the energetic densities of individual caddisflies sampled from the creek and from carcasses were measured by bomb calorimetry ($N = 5$ individuals per date; on 4 July only three individuals were available). Further, we used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios to measure the input of salmon-derived C and N in caddisflies ($N = 5$ –6 individuals per date) collected from the creek bed and carcasses. Dried caddisflies were ground and enclosed in tin capsules. Isotope analysis was conducted at the Stable Isotope Facility, University of California Davis. Stable-isotope ratios are expressed as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Peterson and Fry 1987). These values represent the level of enrichment or depletion of the heavier isotope of N or C relative to a standard. Values were calculated as follows:

$$(2) \quad \delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \times 1000$$

where R is the ratio of heavy isotope to light isotope. Standards are air for N and Pee Dee Belemnite for C. Higher $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ values indicate higher proportions of the heavier isotope in the sample. Because salmon are enriched in ^{13}C and ^{15}N relative to freshwater and terrestrial systems, elevated $^{13}\text{C}:^{12}\text{C}$ or $^{15}\text{N}:^{14}\text{N}$ ratios in freshwater systems are generally indicative of marine (salmon) enrichment (Schoeninger et al. 1983; Owens 1987).

The observed isotope values in the caddisflies were converted to percentages of marine-derived N using a two-source mixing model (Bilby et al. 1996). This model calculates the percentage of marine-derived N as

Fig. 1. Sockeye salmon (*Oncorhynchus nerka*) carcasses and caddisfly (Trichoptera) larvae in Hidden Lake Creek over the summer season in 2003. (a) Cumulative abundance of salmon carcasses in the creek characterized by their mode of death (bear killed (—), senescent (---), or stranded (- - -)). (b) Number of caddisfly larvae per sockeye salmon carcass characterized by the mode of death of the salmon (bear-killed (solid bars), senescent (open bars), or stranded (shaded bars)) and the number of salmon carcasses counted (□). Values are shown as the mean ± standard error. (c) Mean Chesson's selectivity coefficients, α , for bear-killed carcasses by caddisfly larvae (■). The dotted line indicates random feeding ($\alpha = 0.5$). Values >0.5 represent positive selection of bear-killed carcasses; values <0.5 represent avoidance.



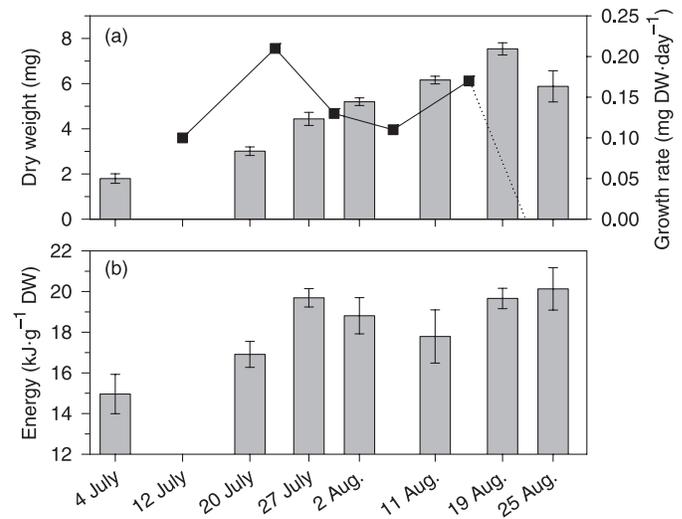
$$(3) \quad \%MD-N = \frac{(\delta^{15}N_{\text{caddis}} - 3.4) - (\delta^{15}N_{\text{base}} - 3.4)}{\delta^{15}N_{\text{salmon}} - (\delta^{15}N_{\text{base}} - 3.4)} \times 100$$

where %MD-N is the percentage of marine-derived N; $\delta^{15}N_{\text{caddis}}$ is the observed isotope value of the sample; $\delta^{15}N_{\text{salmon}}$ is the marine end member (i.e., isotope values representing 100% marine-derived N from average salmon isotope values); $\delta^{15}N_{\text{base}}$ is the caddisfly baseline (i.e., isotope values representing 0% marine-derived N; this is the average value for caddisfly larvae sampled from two nearby non-salmon creeks); and 3.4 is the assumed increase in $\delta^{15}N$ per trophic level (DeNiro and Epstein 1981; Vander Zanden and Rasmussen 1999).

Results

In Hidden Lake Creek, sockeye salmon were first observed on 27 July (Fig. 1a). Almost all of the early carcasses were produced via bear predation and a few carcasses were stranded. No carcasses of senescent salmon were observed until 2 August. From early August onwards, the number of bear-killed and senescent carcasses increased, with bear-killing being always the dominant mode of death. On average, bear-killed carcasses retained 80% of their original body

Fig. 2. Condition of caddisfly larvae in Hidden Lake Creek over the summer season in 2003. (a) Seasonal dry weight (DW; bars (mean ± standard error)) and instantaneous growth rate (■) for caddisfly larvae. The dotted line denotes a rapid decrease in growth rate, which was probably driven by pupation of the larvae. (b) Seasonal energy content of caddisfly larvae (mean ± standard error).



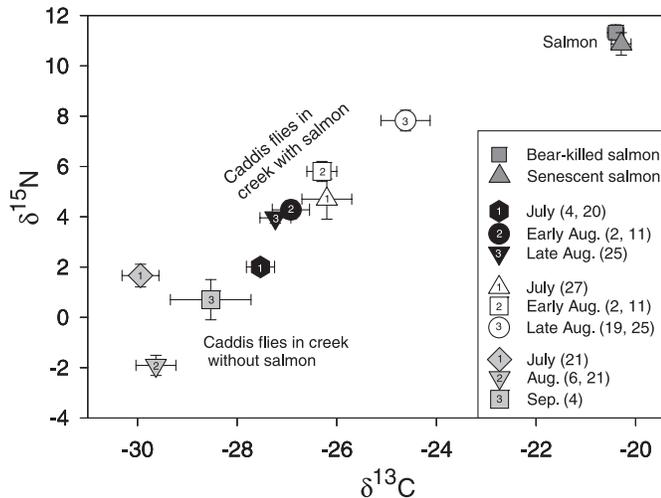
mass and the biomass of bear-killed carcasses in the creek ranged from 4.8 to 39.2 g DW·m⁻² during the salmon run.

In Hidden Lake Creek, sockeye salmon carcasses were heavily colonized by caddisfly larvae, which reached the highest densities in early August (average density 68-carcass⁻¹, maximum density 300-carcass⁻¹). Caddisflies were found on the carcass surface, buried within carcass tissue, in gill, mouth, and brain cavities, and in cavities created by bear bites. Based on the survey in Hidden Lake Creek, we found more individual caddisflies on body fragments of carcasses (i.e., bear-killed carcasses) (average ± standard error (SE) = 24.6 ± 17.1) than on senescent (1.7 ± 1.5) or stranded carcasses (2.1 ± 1.2) (Fig. 1b). Chesson's selectivity coefficients (bear-killed : senescent carcasses) calculated for caddisfly larvae indicated a strong preference for bear-killed over senescent carcasses from July until mid-August and random feeding on carcasses in late August (Fig. 1c).

The energetic content of bear-killed carcasses was significantly higher than that of senescent carcasses (analysis of variance (ANOVA), $F_{[1,35]} = 1962.1$, $P < 0.001$) with a value of 6.55 ± 0.04 (average ± SE) kJ·g⁻¹ wet weight in bear-killed ones and 3.68 ± 0.03 kJ·g⁻¹ wet weight in senescent ones. In contrast, the stable-isotope ratios $\delta^{15}N$: $\delta^{14}N$ and $\delta^{13}C$: $\delta^{12}C$ did not differ between bear-killed and senescent carcasses (Fig. 3).

The average DW of individual caddisfly larvae increased progressively over the season from 1.8 mg in early July to a peak value of 7.5 mg in mid-August (Fig. 2a). Average caddisfly biovolume ranged from 2.3 to 6.3 mg DW·m⁻² in the creek and from 0.3 to 5.3 mg DW·m⁻² on the carcasses. The biomass of caddisflies on bear-killed carcasses represented only a small proportion of that of the carcass (always less than 0.14%). By the end of July, the caddisfly growth rate peaked and was relatively high throughout the rest of

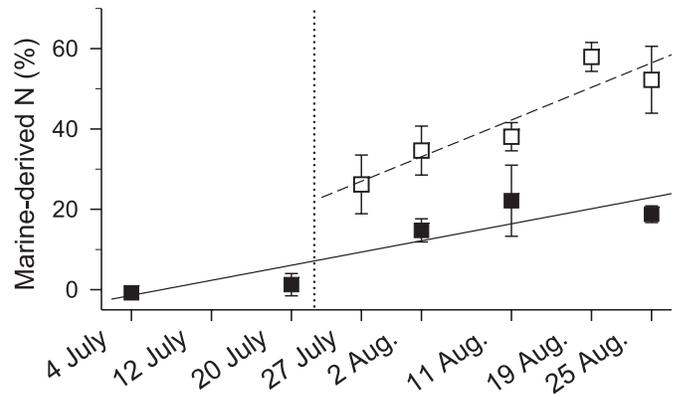
Fig. 3. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios (mean \pm standard error) of caddisfly larvae before and during the salmon run and in muscle tissue of bear-killed (fresh) and senescent sockeye salmon in Hidden Lake Creek over the summer season in 2003. In addition, isotope values from two nearby non-salmon creeks (Upper Pick and N-4) are shown before the salmon entered the system on 27 July, and in N-4 during the whole period of the salmon run. Isotope values for caddisflies in Hidden Lake Creek are shown before and over the course of the salmon run (solid symbols represent caddisflies sampled from the creek bed and open symbols represent caddisflies sampled directly from carcasses). Numbers in parentheses are days of the month.



the summer (Fig. 2a). The energy content increased from 14.96 ± 0.97 (average \pm SE) to 20.13 ± 1.04 $\text{kJ}\cdot\text{g}^{-1}$ DW during the summer (Fig. 2b). In addition, the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signal in caddisflies from the creek increased progressively over the summer after salmon entered the creek, but decreased again in late August (Fig. 3). Stable-isotope values were always higher in caddisflies taken from carcasses than in those collected from the creek bed during the salmon run (ANOVA, $\delta^{15}\text{N}$: $F_{[1,30]} = 22.37$, $P < 0.001$; $\delta^{13}\text{C}$: $F_{[1,30]} = 9.71$, $P < 0.005$; this includes dates when samples were taken simultaneously from the creek bed and carcasses). The stable-isotope ratio for caddisfly larvae in Hidden Lake Creek approached that measured in salmon carcasses over the month of August, but did not increase for caddisfly larvae in a nearby non-salmon creek (Fig. 4). Consequently, the percentage of marine-derived N in caddisflies increased progressively over the season, with a maximum of about 58% in individuals sampled from the carcasses and 22% in individuals sampled from the creek (Fig. 4). The energy content and DW of caddisflies did not differ between individuals sampled simultaneously from the carcasses and creek bed (ANOVA, energy: $F_{[1,34]} = 0.91$, $P = 0.35$; DW: $F_{[1,264]} = 0.43$, $P = 0.51$; data not shown).

A long-term survey of 25 creeks in the Wood River system indicated that the impact of bear predation as the primary mode of death of migrating sockeye salmon varied considerably in both space and time. The average proportion of bear-killed salmon carcasses ranged from 5% to 82% among creeks between 1970 and 2003 (Fig. 5), and also varied greatly among years within a single creek, especially in

Fig. 4. Percentages of marine-derived N in caddisfly larvae sampled from the creek bed (■) and from salmon carcasses (□) over the summer season in 2003 in Hidden Lake Creek, showing linear regression lines. The dotted line indicates the date when salmon were first observed in the creek. Values are given as the mean \pm standard error.



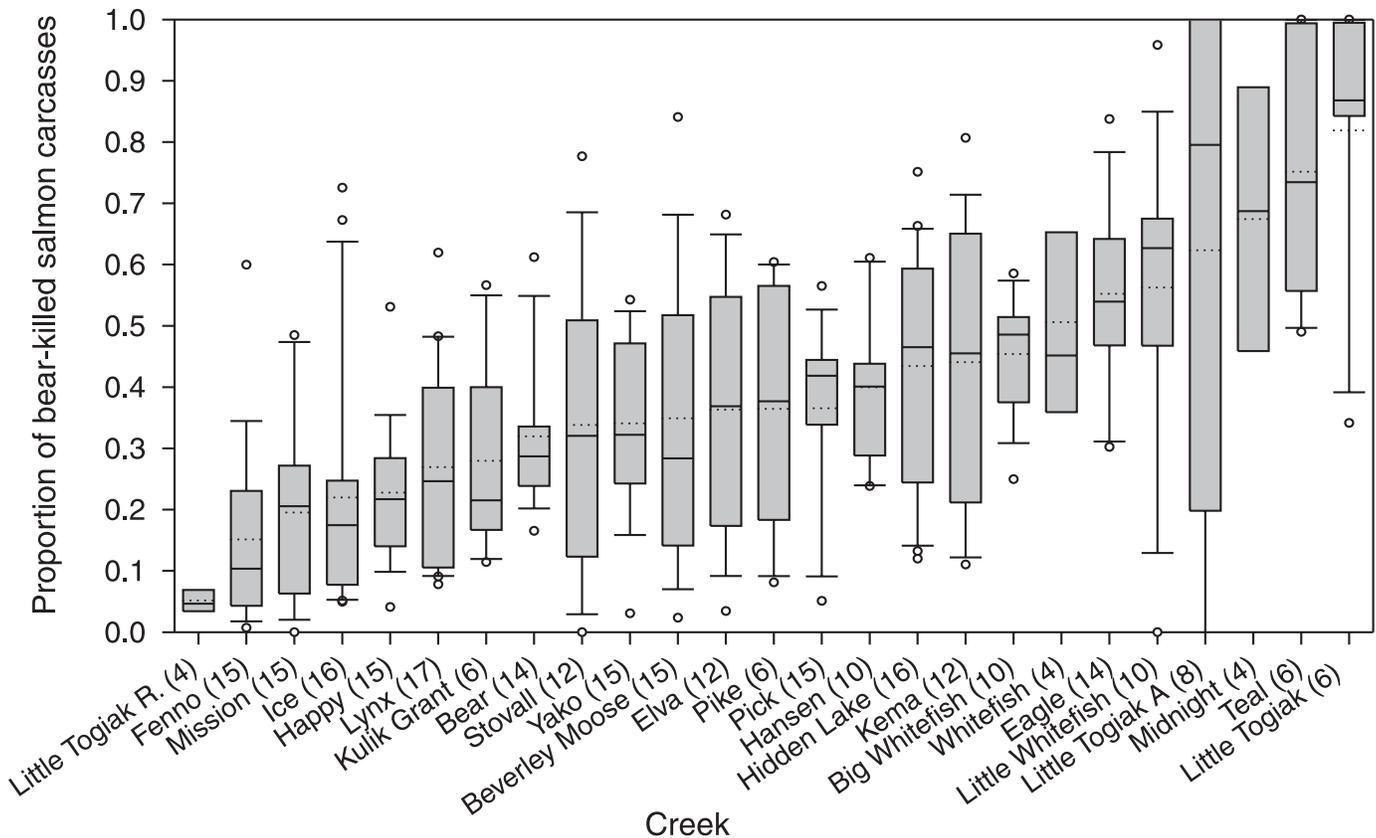
creeks with moderate bear predation. However, some creeks always had relatively low or high rates of bear predation across the entire survey period.

Discussion

The foraging behavior of brown and black bears can have a strong impact on the mode of death of migrating salmon (Quinn and Buck 2000; Gende et al. 2001). Our survey supports the results of Quinn et al. (2003) and Gende et al. (2004a), showing that nearly all salmon arriving early in the spawning run were killed by bears, and that the number of senescent carcasses increased later in the season with increasing salmon density. In Hidden Lake Creek bear-killed sockeye salmon carcasses were available to aquatic scavengers about a week before the carcasses of senescent individuals were observed. Throughout the salmon run the proportion of bear-killed carcasses was always slightly higher than that of senescent ones. A similar pattern with a relatively high proportion of bear-killed carcasses was reflected, on average, over 16 years (~45% bear-killed carcasses) in Hidden Lake Creek. In this creek sockeye salmon carcasses were colonized by caddisfly larvae (mainly *Ecclisomyia* sp.) especially between late July and early August, with a maximum density of 300 individuals per carcass. The association of caddisflies and other macroinvertebrates with salmon carcasses has been also shown in other studies throughout the Pacific Northwest (Chaloner et al. 2002; Minakawa et al. 2002).

Our study shows that caddisfly larvae selectively prefer the carcasses of bear-killed salmon, especially until mid-August, while later in the course of the salmon run, bear-killed and senescent carcasses were colonized equally. Two mechanisms may drive this preference for bear-killed carcasses. First, since bears often target specific body parts (Gende et al. 2001) and therefore open up salmon carcasses, improved accessibility of consumable tissue (i.e., muscle, brain, and viscera) may explain the dominant colonization of

Fig. 5. Box plots showing the proportions of bear-killed sockeye salmon carcasses in 25 creeks in the Wood River system in southwest Alaska. Plots indicate the variation of counts in August across time series between 4 and 17 years (the number of years is given in parentheses). Creeks are ordered from low to high bear predation rates. Each box represents the 25th and 75th percentiles; the dotted line indicates the mean, the solid line indicates the median, the vertical bars indicate the range excluding outliers, and the circles outside the bars indicate outliers.



bear-killed remains. Gaining access to muscle tissue of stranded or senescent carcasses is more difficult because caddisflies have to first penetrate the tough salmon skin. Second, bear-killed carcasses may also be a resource that provides a higher energetic and nutritional level than senescent carcasses (Hendry and Berg 1999). Therefore, in the Pacific Northwest, bears, but also other mammals and birds that kill and consume salmon (Jauquet et al. 2003), indirectly facilitate the growth of scavengers by altering the temporal availability, accessibility, and quality of an important food resource. In areas where bears are absent, the foraging activities of other salmon predators like wolves, mink, eagles, and gulls are expected to have a similar function to those of bears and may also indirectly affect the growth of scavengers.

In sites with low salmon densities and high bear-activity levels it is likely, however, that bears reduce salmon resource subsidies available to macroinvertebrates, especially if bears consume high proportions of salmon and carry them into the riparian zone (Reimchen 1994; Meehan et al. 2005). However, in the Wood River system salmon runs are usually high (Hilborn et al. 2003) and the proportion of salmon removed by predators from the creek bed is usually low (Meehan et al. 2005), except for very small creeks, where bears may remove up to 50% of carcasses from the creek bed. In addition,

when salmon densities are high, bears usually consume only a small fraction (20%, on average, as shown in our study) and thus provide a resource subsidy to scavengers by provisioning them with the remains of their kills.

The incorporation of MDN in caddisfly larvae was indicated by the immediate increase in $\delta^{15}\text{N}$ coincident with the arrival of sockeye salmon in Hidden Lake Creek and by the gradual enrichment of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in caddisflies over the course of the salmon run, approaching levels measured in salmon carcasses. In contrast, caddisfly larvae from a non-salmon creek showed no enrichment in $\delta^{15}\text{N}$ during the course of the salmon run. The similarity in $\delta^{15}\text{N}$ values between caddisflies from two nearby non-salmon creeks and from Hidden Lake Creek before salmon arrived suggests that the background uptake of marine-derived N is negligible and that MDN likely do not extend into subsequent generations of caddisflies. This indicates that MDN are not retained long enough in the system to affect growth early in the season; this was also proposed by Lessard et al. (2003). The difference in caddisfly $\delta^{13}\text{C}$ value between the non-salmon creeks and Hidden Lake Creek may be driven by geomorphological and hydrologic factors, which can strongly influence the isotopic source of C available to consumers (Finlay et al. 2003), and the differences in $\delta^{15}\text{N}$ values between the creeks may reflect differences in feeding patterns. Our study indi-

cates that the increase of MDN in caddisfly larvae is temporary in this system and is strongly associated with the presence of salmon. The temporal increase in consumers' productivity during the course of the salmon run has also been shown in other invertebrates and fish (Wipfli et al. 1998; Zhang et al. 2003). Thus, species with life histories linked to the annual MDN pulse may gain the biggest advantage from the salmon resource subsidy. Invertebrates with autumnal reproduction have access to a particularly rich food resource to prepare for pupation and reproduction, and the reproductive success of these consumers may be strongly affected or even be limited by the availability of salmon-derived resources.

The enrichment of marine-derived N and C in caddisfly larvae sampled from the creek at large and from carcasses indicates that some MDN are incorporated indirectly via detritus or direct uptake by scavenging on carcasses. Incorporation of marine-derived N in caddisflies ranged up to 58% and the enrichment of N was always higher in caddisflies sampled directly from carcasses than in individuals sampled from the creek bed, although the energy content did not vary between these two classes of caddisflies. In addition, leaf litter fall may also contribute to the increase in caddisflies' isotope signature (Helfield and Naiman 2001). The progressive increase in energy content and isotope values shows that salmon subsidies not only increase resource availability, but also improve food quality. The C:N ratio of caddisflies decreased with increasing salmon density and therefore also the nutritional value of caddisfly larvae and their value as prey increased. Therefore, salmon not only represent a highly nutritional prey source, but also increase the nutritional value of other components of the ecosystem (e.g., in prey species for resident fishes and juvenile salmon). Because foraging activities by bears increase the availability of the highest quality salmon carcasses, bears indirectly facilitate consumption of salmon by, and increase growth rates of, caddisflies and possibly other aquatic scavengers.

The life cycle of the caddisfly *Ecclisomyia* sp. in Hidden Lake Creek appears to be timed to coincide with the seasonal availability of salmon, with most larval growth occurring in midsummer at the time when salmon start to arrive, are killed by bears, and decompose. The relatively strong increase of the growth rate of caddisflies in this creek after the arrival of salmon suggests that caddisfly growth is strongly influenced by the availability of salmon-derived energy. An increase in growth after the arrival of salmon has also been shown for resident fishes and juvenile salmon in southeast Washington (Bilby et al. 1998). In addition, a laboratory study showed that *Ecclisomyia* sp. grew faster when reared on salmon carcasses than when reared on alder leaves (Minakawa et al. 2002). Apparently these detritivores have the appropriate feeding morphology and behavior required to switch from a primarily detritus-based diet to salmon tissue (Anderson 1973). Since animal material provides high-quality food with proportionally more digestible protein and essential nutrients (Anderson and Cummings 1979), salmon carcasses may be an essential energy source for the completion of larval stages and pupation of invertebrate larvae (Wiggins 1977). The decline in DW and isotope signal in late August may be driven by pupation and emergence of individuals growing the fastest, while those that remain may

have fed less on salmon and achieved a slower growth rate and lower $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values.

Bears are an important agent in the transport of nutrients from salmon carcasses (Quinn et al. 2003), and consequently affect growth of macroinvertebrates on a large scale. As was shown by Quinn et al. (2003) and by our survey of several creeks over a longer time period in southwest Alaska, the proportion of salmon killed by bears shows both spatial and temporal variation, suggesting that the provision of marine-derived subsidies for scavengers is not homogeneous and can vary greatly among years and sites. The variation in the proportion of salmon killed among creeks depends strongly on the physical characteristics of the creeks, which influence the availability of salmon to bears, the overall salmon density in the creek, and the density of bears using the creek (Gende et al. 2001, 2004a; Quinn et al. 2003). In general, bear predation rates are highest in the narrowest and shallowest spawning streams and lowest in more complex larger streams (Gende et al. 2004a). Therefore, the amount of resource subsidies to macroinvertebrates provided by bear-killed carcasses varies greatly on temporal and spatial scales associated with creek morphology, salmon densities, and bear activities.

In the Pacific Northwest, bears serve as important vectors of salmon-derived nutrients into riparian ecosystems (Reimchen 1994; Hilderbrand et al. 1999; Helfield and Naiman 2006). In addition, our study suggests that bears are important agents affecting the availability, accessibility, and nutritional quality of resources, like salmon, for scavengers, including caddisfly larvae, and thereby indirectly facilitate their growth and increase their nutritional value as prey. These results further emphasize the importance of large carnivores as keystone species in coastal ecosystems.

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