

Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, U.S.A.

Robert E. Bilby, Brian R. Fransen, Peter A. Bisson, and Jason K. Walter

Abstract: Availability of organic matter and nutrients transported from the marine environment to streams by spawning salmon was increased in two small streams in southwestern Washington, U.S.A., by adding salmon carcasses from a nearby hatchery. Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) rearing at these sites was compared with nearby streams where few salmon spawned. Densities of age 0⁺ coho salmon and age 0⁺ and age 1⁺ steelhead increased following carcass additions to the treated streams. A similar increase in density was not observed at the reference sites. Condition factors in treated streams increased following carcass addition and remained at high levels while carcasses were present whereas no similar pattern was observed at the reference sites. Stomach contents of fish in streams to which carcasses had been added consisted primarily of salmon eggs and carcass flesh when carcasses were present in the stream. Stable isotope analysis indicated that the proportion of marine-derived nitrogen in the muscle tissue of juvenile salmonids increased as much as 39% following carcass placement. Results suggest that eggs and carcasses of adult salmon provide a very important resource during a period when other food items are often scarce.

Résumé : La disponibilité de la matière organique et des matières nutritives transportées du milieu marin à celui des cours d'eau par les saumons pendant le frai a été augmentée dans deux petits cours d'eau du sud-ouest du Washington (É.-U.) par l'ajout de carcasses de saumons provenant d'une pisciculture voisine. La réaction de juvéniles de saumon coho (*Oncorhynchus kisutch*) et de truite arc-en-ciel (*O. mykiss*) en croissance dans ces deux endroits a été comparée à celle de poissons de cours d'eau avoisinants où peu de poissons avaient frayé. Les densités de cohos d'âge 0⁺ et de truites d'âges 0⁺ et 1⁺ s'est accrue suite à l'ajout des carcasses et ce phénomène n'a pas été noté dans les cours d'eau témoins. Les facteurs de condition se sont améliorés dans les cours d'eau suite à l'ajout de carcasses et sont demeurés élevés pendant les carcasses étaient encore présentes, cela n'a pas été observé dans les sites témoins. Le contenu stomacal des poissons des cours d'eau où des carcasses avaient été ajoutées était surtout représenté par des oeufs de saumon et de la chair provenant des carcasses, lorsque ces dernières étaient présentes. Une analyse des isotopes stables a montré que la proportion d'azote d'origine marine dans les tissus musculaires des salmonidés juvéniles avait augmenté d'une valeur pouvant atteindre 39% suite à la mise en place des carcasses. Les résultats obtenus portent à croire que les oeufs et les carcasses des saumons adultes constituent une très importante ressource pendant la période où les autres ressources alimentaires sont souvent rares.

[Traduit par la Rédaction]

Introduction

Pacific salmon (*Oncorhynchus* spp.), which die after spawning, are an important source of organic matter and nutrients for the watersheds where these fishes spawn. Nitrogen (N) provided by spawning coho salmon (*Oncorhynchus*

kisutch) comprised 18% of the N in foliage of riparian vegetation along a small stream in western Washington, U.S.A. (Bilby et al. 1996). Nutrients provided by spawning kokanee salmon (*Oncorhynchus nerka*) enhanced algal productivity in a tributary of Lake Tahoe, California (Richey et al. 1975). Many species of terrestrial and aquatic invertebrate and ver-

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R.E. Bilby,¹ B.R. Fransen, and J.K. Walter. Weyerhaeuser Co., Western Forestry Research, WTC 1A5, Tacoma, WA 98477-0001, U.S.A.

P.A. Bisson. USDA Forest Service, Pacific Northwest Research Station, Olympia Forestry Sciences Laboratory, 3625 93rd Avenue SW, Olympia, WA 98512-9193, U.S.A.

¹Author to whom all correspondence should be addressed. Current address: Northwest Fisheries Science Center, 2725 Montlake Blvd. East, Seattle, WA 98112-2097, U.S.A. e-mail: Bob.Bilby@noaa.gov

Table 1. Characteristics of the study sites and availability of material from spawning salmon.

	Chehalis River		Willapa River	
	Treatment Salmon Creek	Reference Big Creek	Treatment A400 Creek	Reference Wasberg Creek
Channel width (m)	8.0	7.0	3.0	2.5
Gradient (%)	2.5	2.0	2.5	1.5
Predominant bed material	Gravel, cobble	Gravel, cobble	Gravel, cobble	Gravel
Length of study reach (m)	500	500	500	500
Carcasses added (no.)	450	0	400	0
Carcasses added (weight, kg)	2251	0	959	0
Naturally spawning fish (no.)	0	2	55	5
Carcass tissue available (kg·m ⁻²)	0.56	0.003	0.71	0.01

tebrate species consume fish carcasses or eggs (Nicola 1968; Brusven and Scoggin 1969; Johnson 1981; Cederholm et al. 1989; Parmenter and Lamarra 1991; Piorkowski 1995; Bilby et al. 1996; Eastman 1996; Hilderbrand et al. 1996; Minikawa 1997).

The extent to which N and carbon (C) from spawning salmon are incorporated into the trophic systems of streams has recently been quantified through the use of stable isotope analysis (Kline et al. 1990, 1994; Bilby et al. 1996; Johnston et al. 1997). Adult salmon are enriched with ¹⁵N and ¹³C relative to sources of N and C delivered to streams from the terrestrial environment in the Pacific Northwest. As a result, stable isotope ratios can be used to trace marine-derived N and C through the food webs of the freshwater systems where salmon spawn. Using this technique, Kline et al. (1990) found that virtually all the N in rainbow trout (*Oncorhynchus mykiss*) and aquatic insects in a southeastern Alaska stream was derived from spawning pink salmon (*Oncorhynchus gorbuscha*). Spawning coho salmon in a small stream in western Washington contributed from 20 to 40% of the N and C in cutthroat trout (*Oncorhynchus clarki*) and juvenile coho and up to 30% of these elements in aquatic insects and epilithon (Bilby et al. 1996). The proportion of spawner-derived N in aquatic insects in headwater tributaries of the Stuart River system in British Columbia, over 1000 km from salt water, ranged from 15 to 60% and was positively related to the density of spawning sockeye salmon (Johnston et al. 1997).

Although the application of the stable isotope method has enabled quantification of the N and C contributed by spawning salmon to the streams where they spawn, behavioral and growth responses of juvenile salmonids to availability of this material have not been thoroughly examined. Nearly all studies to date have been conducted in streams with high densities of spawning salmon (Kline et al. 1990, 1994; Bilby et al. 1996). The influence of spawner-derived nutrients and organic matter on fish has been inferred by the temporal correspondence between changes in population density, growth rate, or condition factor and the onset of spawning and comparison with fish in streams without spawning salmon (Bilby et al. 1996).

The effect of spawning salmon on fish communities can be examined much more directly by deliberately increasing the availability of carcasses in a stream and comparing the response with that of a nearby stream with comparable species composition and initial density. In this study, abundance

of carcasses was augmented by distributing spawned-out coho salmon from a hatchery. This project was designed as a case study to intensively examine the pathways and processes responsible for uptake of marine-derived nutrients and organic matter by the biota of these streams rather than as a replicated experiment (Conquest and Ralph 1998). Our objectives were to examine the extent to which juvenile coho and steelhead utilized salmon carcasses as a food source and to determine whether increased availability of this material had any impact on growth, population density, or condition factor in these streams. As only two sites were examined, we cannot determine whether the responses we observed at our sites are generally applicable to other systems. However, an improved understanding of how material from spawning salmon is utilized by stream-dwelling fishes will enable experiments to be designed to assess the generality of these results.

Study sites and methods

Experiments were conducted on third-order tributaries of the Chehalis and Willapa rivers in the Willapa Hills of southwestern Washington, U.S.A. (46°30'N, 123°30'W). All study sites were underlain by the Crescent Formation, a combination of marine sediments and volcanic rock including columnar and pillow basalt, tuff breccia, and siltstone (Wells 1981). This geology results in steep topography with streams flowing through V-shaped valleys. Mean annual precipitation in the Willapa Hills ranges from 180 to 250 cm, with the majority of it falling as rain from November through April. Summers are cool and dry.

Two pairs of 500-m-long stream reaches were examined, one pair in the Chehalis River watershed and one pair in the Willapa River watershed. Study sites in the Chehalis River watershed (Salmon Creek and Big Creek) were larger than those in the Willapa River watershed (A400 Creek and Wasberg Creek) (Table 1). However, all sites were comparable in gradient and substrate characteristics. The lower ends of the study reaches were within 100 m of the confluence of the study stream with the mainstem. Riparian forests at all sites were composed of 30- to 50-year-old mixed hardwood and conifer trees. Dominant overstory species included Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), and red alder (*Alnus rubra*).

The fish community during autumn and winter at the Big Creek and Salmon Creek sites consisted almost entirely of steelhead and torrent sculpin (*Cottus rhotheus*). A few juvenile coho salmon and cutthroat trout were captured, but their densities were too low to evaluate the response of these species to carcass addition. The fish communities at A400 and Wasberg creeks were more diverse and

included juvenile coho salmon, steelhead, cutthroat trout, torrent sculpin, and riffle sculpin (*Cottus gulosus*). We examined the response of steelhead at the Chehalis River sites and coho and steelhead at the Willapa River sites.

The experiment at Salmon and Big creeks was conducted during the autumn and winter of 1994–1995. A400 and Wasberg creeks were examined during the autumn and winter of 1995–1996. Coho salmon carcasses were placed in Salmon Creek (Chehalis River drainage) on November 22 and 23, 1994. The carcasses were obtained from the Satsop Springs Hatchery, located within the Chehalis River watershed, about 85 km downstream from the treatment site. Carcass decomposition at Salmon Creek required about 8 weeks and all carcasses were gone by early February. Carcasses placed in A400 Creek (Willapa River drainage) on November 18, 1995, were obtained from Forks Creek Hatchery, located in the Willapa River watershed about 3 km downstream from the study site. Rate of carcass decomposition at this site was more rapid than at Salmon Creek, likely due to the smaller size of the carcasses (Table 1). All carcasses were gone from the A400 Creek study site by late December. The carcasses added to the study sites had been spawned prior to placement in the stream. However, small quantities of eggs remained in the body cavities of some females and were added to the treated sites along with the carcasses.

Caudal fins were removed from all carcasses prior to placement in the treated streams to enable differentiation of hatchery carcasses from naturally spawning fish. Carcasses were weighed with a spring balance after removal of the caudal fins. Carcasses were added to the entire 500-m length of the study site at Salmon and A400 creeks. They were tethered in place with sisal cord passed through the gills and tied to streamside trees or logs in the channel to ensure that they would not be rapidly flushed from the study site. Numbers of carcasses added to the two streams (Table 1) were comparable with the number observed in streams that support large populations of naturally spawning coho salmon (Bilby et al. 1996). Carcasses added to Salmon Creek averaged 5.0 kg. The carcasses added to A400 Creek averaged 2.4 kg. Loading of hatchery carcass biomass on an areal basis was approximately equal at the two sites (0.56 kg·m⁻² at Salmon Creek and 0.62 kg·m⁻² at A400 Creek).

All sites were surveyed every 2 weeks during the study period to determine the number of naturally spawning fish. Natural spawning did not occur or occurred at very low levels at our reference sites (Table 1). The five carcasses found at Wasberg Creek appeared in January and February, 2 months after the peak of natural spawning and carcass addition to A400 Creek. Two carcasses were found in Big Creek in late November. Fifty-five naturally spawning coho utilized the study section of A400 Creek from early November through mid-December 1995, increasing total loading of carcass tissue at this site to 0.71 kg·m⁻². No natural spawning by salmon occurred in Salmon Creek during 1994.

Electrofishing was used to determine fish population densities and size and to collect fish for stomach content and stable isotope analysis. The lower 100 m of each study site was isolated with blocking nets and three passes were made through the reach. Fish captured on each pass were held in separate buckets. Standard length of each fish was measured to the nearest millimetre and weight determined to the nearest 0.1 g with a portable electronic balance. Fish population densities were estimated for each species and age-class using a removal–summation calculation modified for small population size (Carle and Strub 1978). Length–frequency distribution of steelhead was used to determine age.

The large size and high flows of Big and Salmon creeks relative to the two Willapa River streams prevented determination of population densities during most of the study period. Quantitative sampling was possible only during October, a month prior to carcass placement, and March, well after carcasses had fully decomposed. However, sufficient numbers of steelhead were captured throughout the study period for the determination of condition factor. The

smaller A400 Creek and Wasberg Creek sites were selected for study in 1995–1996 to enable population density estimates to be obtained throughout the winter and to examine the response of a more diverse fish community to carcass addition. Population density was estimated at these sites monthly from October 1995 through March 1996.

Comparison of condition factor between treatment and reference sites was made only when at least five individuals of a species or age-class were included in the sample at both sites for all sample dates. Thus, values are presented only for coho for A400 and Wasberg creeks and only age 0⁺ steelhead at Salmon and Big creeks. Condition factor (*K*) was calculated for each fish captured as

$$(1) \quad K = 100W/L^3$$

where *W* is weight (grams) and *L* is standard length (centimetres) (Weatherley and Rogers 1978). Significance of differences in population size, condition factor, and body size before and after carcass placement at the treated sites and between the treated and reference sites was evaluated with a *t*-test at a *P* ≤ 0.05.

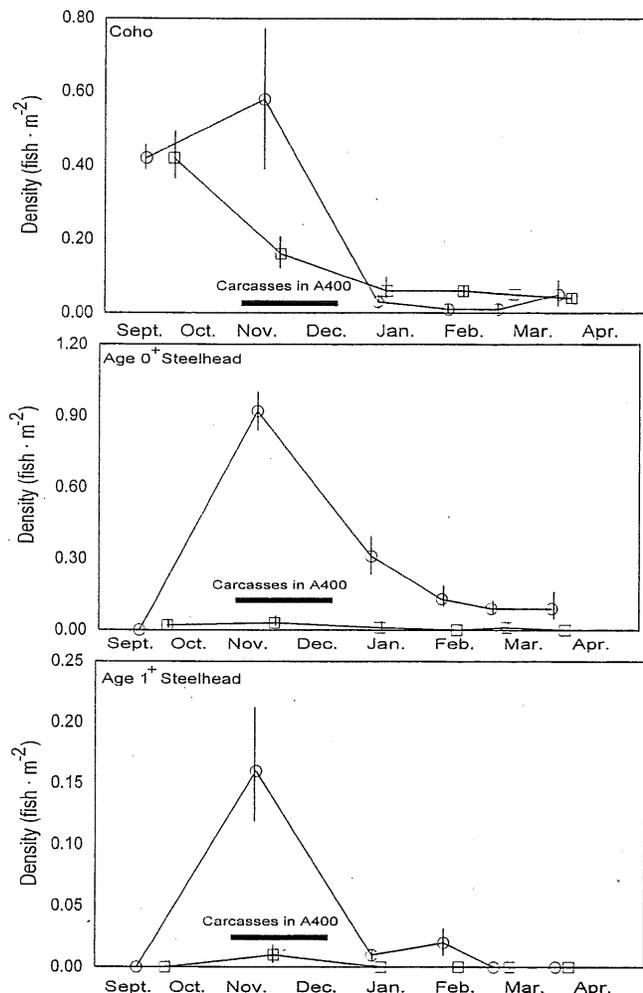
At A400 and Wasberg creeks, stomach contents were collected from fish of each species and age-class on each sample date. Stomachs of all captured individuals were sampled on most sample dates. However, when more than 30 individuals of a species and age-class were captured, only the first 30–35 fish were sampled. Results are reported only when more than five individuals of a species and age-class were sampled. Stomach contents were collected by gastric lavage, a nonlethal technique that enables recovery of over 90% of the stomach contents (Meehan and Miller 1978; Bowen 1983). This method entails the insertion of a large-gauge blunt hypodermic needle or small pipette (used for larger fish) down the throat into the gut. Water is slowly injected into the gut, flushing the stomach contents out of the mouth. Material was washed onto a 250-µm Nitex screen. Material collected for each species and age-class was consolidated for each sample date and stored in 70% ethanol. Stomach samples from steelhead at the Salmon Creek and Big Creek sites were obtained only from those fish sacrificed for stable isotope analysis; thus, very few stomach content samples were obtained from these sites and these data are not reported.

Stomach contents were separated into four categories; carcass tissue, salmon eggs, invertebrates, and miscellaneous material. The miscellaneous category included fine gravel, sand, plant fragments, and unidentifiable material. After sorting, the material was dried at 50°C and weighed.

We sacrificed one to three fish of each species and age-class on each sample date for stable isotope analysis. In addition, dorsal muscle tissue and eggs from coho salmon carcasses placed in the treatment streams were analyzed. We also collected cutthroat trout above blockages to anadromous fish at both study sites. Samples from the cutthroat were used to represent the isotope ratio for fish in these watersheds without access to marine-derived N and C. Samples were stored on ice for transport to the laboratory and then frozen until they could be prepared for analysis. After thawing, dorsal muscle tissue was cut from each fish. Samples were rinsed in a 10% solution of HCl to remove any inorganic C and then distilled water. Each sample was dried at 50°C and stored over silica gel desiccant in a sealed vial. Coastal Sciences Laboratories, Austin, Texas, conducted isotope ratio analyses. Samples were ground to a powder and combusted to generate CO₂ and N₂ gas and isotope ratios in the evolved gases were measured with a mass spectrometer.

Stable isotope ratios are expressed as δ¹⁵N and δ¹³C 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 are calculated as

Fig. 1. Density of juvenile salmonids at the A400 Creek (circles) and Wasberg Creek (squares) study sites. Salmon carcasses were added to the A400 Creek site. Vertical lines associated with each data point represent ± 1 SE. Values without error bars indicate that no fish were captured on that date. The heavy horizontal bar indicates the period during which carcasses were present at the treated site.



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

where R is the ratio of heavy isotope to light isotope. Standards are air for N and Peedee Belemnite for C. Higher values of $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ indicate higher proportions of heavier, marine-derived isotopes in the sample. Significance of differences in $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ values before and after carcass placement at the treated sites and between the treated and reference sites was evaluated with a t -test at a $P \leq 0.05$.

Kline et al. (1990), Bilby et al. (1996), and Johnston et al. (1997) have used similar isotope mixing models to determine the proportion of marine-derived nutrients in the tissues of juvenile fish. We used this method to quantify the proportion of spawner-derived N in the tissues of juvenile coho and steelhead at our study sites. This technique requires calculation of the quantity of a marine-derived element needed to elevate the isotope value from that exhibited by fish of similar age and trophic position in areas inaccessible to anadromous fish to the level observed in the juvenile fish at the study sites. Isotope ratios for fish without access to carcass material were obtained by analyzing muscle tissue from

cutthroat trout collected above a barrier to the passage of anadromous fish in each study watershed. An estimate of the isotope ratio that a juvenile fish would display if it fed only on material from spawning salmon is also required for the model. Isotope ratios of N increase with each trophic exchange, a process termed "fractionation." Thus, a fish eating salmon eggs or carcass flesh would exhibit a $\delta^{15}\text{N}$ value about 3‰ higher than that of their diet (Minigawa and Wada 1984). If fish were eating invertebrates that had fed on carcass tissue, two trophic exchanges would be involved and the juvenile salmon would exhibit a $\delta^{15}\text{N}$ value 6‰ higher than the carcass tissue. We assumed that uptake of marine-derived N occurred 50% through direct consumption of salmon eggs and carcass flesh and 50% through consumption of invertebrates containing N derived from the spawning fish.

Results

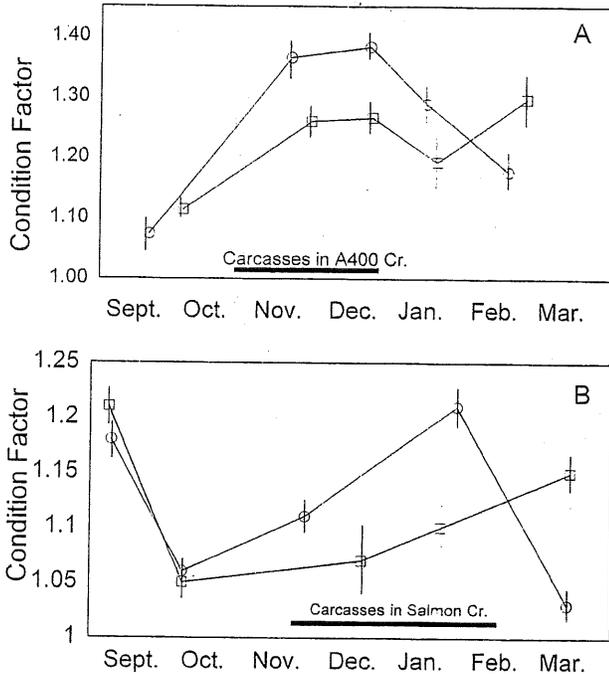
Population densities of all species and age-classes of fishes examined at A400 Creek increased following addition of coho salmon carcasses. Population densities of juvenile coho salmon at A400 and Wasberg creeks were not significantly different in September 1995 (Fig. 1). Densities declined rapidly at Wasberg Creek between September and November. Coho populations in headwater streams (Peterson 1982; Bilby and Bisson 1987; Hartman and Scrivener 1990) commonly exhibit this seasonal change in density. However, coho population density increased in A400 Creek over this time period and was significantly higher than that in Wasberg Creek during the November population census. Coho in A400 Creek declined to levels comparable with Wasberg Creek by early January after carcasses had disappeared from the site and remained at low levels through the late winter and spring at both sites.

Age 0+ steelhead were rare in Wasberg Creek and absent from A400 Creek during September and early October 1995 (Fig. 1). However, density of underyearling steelhead increased dramatically in A400 Creek at the time carcasses became available. Steelhead density in A400 Creek declined after carcasses had decomposed. However, density remained significantly greater in A400 Creek than in Wasberg Creek through early spring.

Age 1+ steelhead in A400 Creek exhibited a response in density similar to that seen for age 0+ steelhead (Fig. 1). Neither stream contained these fish in September. Large numbers of age 1+ steelhead appeared in A400 Creek at the time that salmon eggs and carcass material became available. A few age 1+ steelhead were captured in Wasberg Creek at this time, but density was significantly greater, by almost 10-fold, in A400 Creek. Density of yearling steelhead in A400 Creek decreased after carcasses had decomposed and remained at low levels through February. Age 1+ steelhead were not found at the study site on Wasberg Creek from January through April.

Condition factor of age 0+ steelhead at both Salmon and Big creeks decreased from early September to early October, but no significant differences existed between the two sites on either date (Fig. 2). Condition factor of steelhead increased rapidly following carcass addition to Salmon Creek in November. By January, age 0+ steelhead condition factor in Salmon Creek was significantly greater than it was in October and greater than that exhibited by the fish in Big Creek in January. After carcasses in Salmon Creek had decom-

Fig. 2. (A) Condition factor of juvenile coho salmon at the A400 Creek (circles) and Wasberg Creek (squares) study sites. Salmon carcasses were added to the A400 Creek site. Values are shown ± 1 SE. Insufficient numbers of steelhead were captured at the Wasberg Creek site to enable calculation of condition factor (less than five fish). (B) Condition factor of age 0⁺ steelhead at the Salmon Creek (circles) and Big Creek (squares) study sites. Salmon carcasses were added to the Salmon Creek site. Values are shown ± 1 SE. Insufficient numbers of age 1⁺ steelhead were captured at the Big Creek site after October for condition factor to be determined (less than five fish). The heavy horizontal bar indicates the period during which carcasses were present at the treated sites.

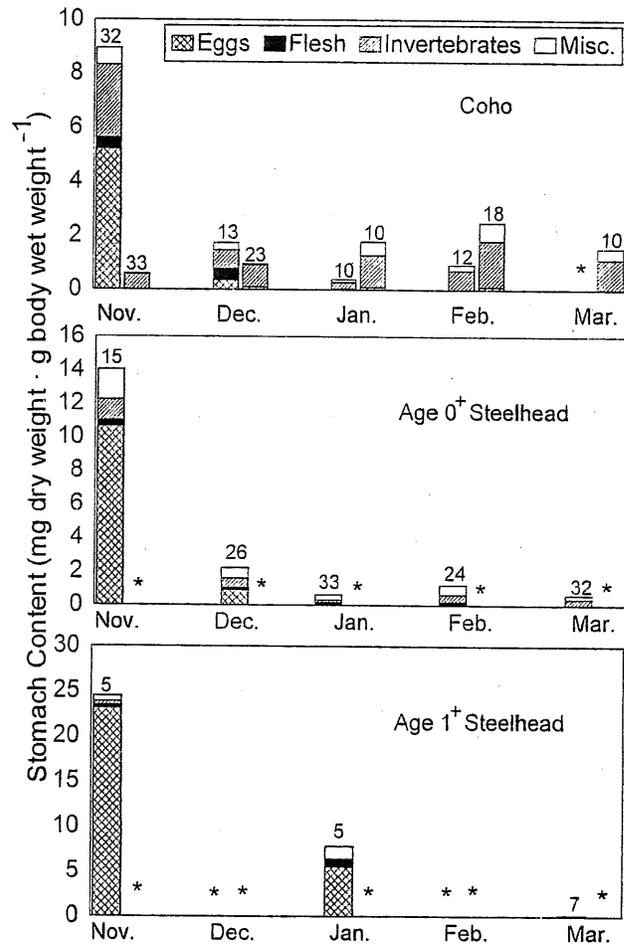


posed, condition factor of age 0⁺ steelhead decreased to levels comparable with those observed before the addition of carcasses. Condition factor of the age 0⁺ steelhead in Big Creek was significantly higher than in Salmon Creek in early March.

There was no significant difference in condition factor of juvenile coho in A400 and Wasberg creeks prior to the addition of carcasses to A400 Creek (Fig. 2). Condition factor of coho increased significantly in A400 Creek after carcasses became available and values remained significantly greater than those displayed by the fish in Wasberg Creek while carcasses were present. Coho in Wasberg Creek also exhibited a significant increase in condition factor between the October and November samples, but the increase displayed by the fish in A400 Creek was much greater. Condition factor of coho in A400 Creek decreased after carcasses decomposed and exhibited values lower than those at Wasberg Creek in late February.

Changes in average body weight of juvenile coho at the A400 Creek and Wasberg Creek sites suggested that a significant amount of growth occurred over the winter. However, as growth could not be determined for individual fish, the effect of factors such as size-dependent mortality or size-

Fig. 3. Amount and type of material removed from the stomachs of juvenile coho and age 0⁺ and age 1⁺ steelhead at the A400 Creek and Wasberg Creek study sites. The first bar of each pair represents A400 Creek, and the second bar represents Wasberg Creek. The number above each bar indicates the number of fish sampled. The categories are salmon eggs (Eggs), flesh from salmon carcasses (Flesh), whole invertebrates or invertebrate parts (Invertebrates), and plant parts, inorganic matter, and unidentifiable material (Misc.). Values are shown only for those dates when five or more fish were sampled. Instances when insufficient numbers of fish were captured are indicated with an asterisk. Amount of material is expressed as the dry weight of the stomach contents per unit wet body weight of the fish from which the material was collected to normalize for any differences in fish body size between the sites.



dependent immigration or emigration on observed changes in average body weight could not be determined. Age 0⁺ coho in A400 Creek increased from 2.3 g in late September to 7.2 g by December, a 215% increase in weight. Age 0⁺ coho in Wasberg Creek increased from 2.8 g in early October to 5.0 g in December, an increase in weight of 78%. There was no significant difference in average coho body weight between the two sites in our initial sample. However, body weight increased more rapidly at A400 Creek than Wasberg Creek and weight was significantly greater at the site with the carcasses in the November and December samples. Body size of the fish was not compared after December

Table 2. $\delta^{15}\text{N}$ values for cutthroat trout collected above barriers to passage by anadromous fish in the study watersheds and hypothetical $\delta^{15}\text{N}$ values for fish eating a diet containing 100% marine-derived N.

	$\delta^{15}\text{N}$	
	Big and Salmon creeks	A400 and Wasberg creeks
0% marine derived		
Age 0 ⁺ cutthroat trout	5.6±0.61 (4)	5.6±0.59 (4)
Age 1 ⁺ cutthroat trout	5.3±0.50 (4)	5.4±0.55 (3)
Salmon eggs/carcass flesh	12.8/11.9	11.4/13.2
100% marine derived, one trophic exchange	15.4	15.3
100% marine derived, two trophic exchanges	18.4	18.3

Note: Values for cutthroat are presented ±1 SE with the number of fish sampled in parentheses. The values for 100% marine-derived N were based on the average of stable isotope values for salmon eggs and carcass flesh and assumed a fractionation rate of 3‰ per trophic exchange (Minigawa and Wada 1984). Values are presented for one trophic exchange (juvenile fish eat salmon eggs and carcass tissue directly) and two trophic exchanges (fish eat invertebrates that have fed only on eggs and carcass). These values were used in calculating the proportion of marine N in the tissues of juvenile fishes at the study sites (Table 4).

due to the low number of juvenile coho captured after this date.

Stomachs of coho at the A400 Creek site during the period when carcasses were present contained more than the stomachs of coho in Wasberg Creek (Fig. 3). Over 60% of the stomach contents were derived from adult salmon, mostly eggs. The coho at the A400 Creek site during November also contained almost five times as much invertebrate biomass as the fish at the Wasberg Creek site. Material derived from carcasses still comprised about 40% of the stomach contents of the coho in the December sample, but total amount of material in the stomachs was much reduced from the November sample. Stomach contents of juvenile coho in Wasberg Creek were composed primarily of invertebrates through the winter. However, salmon eggs were found in the stomachs in the January and February samples. These eggs were provided by a small number of coho that spawned in the study reach of Wasberg Creek at this time. Total amount of material in the stomachs of the coho at Wasberg Creek was greater than that of the fish in A400 Creek after the carcasses had decomposed.

Stomach contents of age 0⁺ steelhead in A400 Creek consisted of 78% eggs and flesh from adult salmon in the November sample (Fig. 3). Material from adult salmon remained an important component in the diet of age 0⁺ steelhead in A400 Creek during December, although total weight of material in the stomachs at this time was much reduced from the November sample. Flesh from carcasses was found in the stomach samples through February despite the fact that the carcasses were fully disintegrated by late December. Small pieces of flesh remaining undecomposed within the streambed may have been the source of this material. Insufficient age 0⁺ steelhead were captured in Wasberg Creek to enable a comparison between the sites.

Age 1⁺ steelhead in A400 Creek utilized material from adult salmon as a food source very heavily during November

(Fig. 3). Material from salmon comprised 96% of their diet at this time. The fish sampled in January contained flesh as well as developing alevins (included as eggs in Fig. 3). Insufficient numbers of age 1⁺ steelhead were captured in Wasberg Creek to enable a comparison with the treated site.

Nearly all the invertebrates ingested by the fishes we sampled were aquatic. Terrestrial invertebrates comprised only 0.7% of the total biomass of material collected from the stomachs for all species at all sites and less than 6% of the total invertebrate biomass.

The consumption of carcass-derived products by juvenile salmon and steelhead at the treatment sites can be further evaluated by examining the change in stable isotope ratios in the tissues of juvenile fish following carcass additions. Eggs and muscle tissue of salmon carcasses added to the streams exhibited $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values much higher than values obtained from cutthroat trout collected in stream reaches inaccessible to anadromous fishes (Table 2). Values for cutthroat trout reflect the isotope ratio of N and C delivered to the system from nonmarine sources. Samples from coho and steelhead collected in stream reaches accessible to spawning salmon exhibited isotope values higher than those measured in cutthroat trout, indicating that some level of salmon-derived N and C was available in both the treated and reference study stream reaches. Addition of carcasses to the treated stream reaches resulted in an increase in $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, or both values, indicating that sufficient amounts of material from the carcasses were ingested by the fish to alter the isotopic composition of their muscle tissue (Table 3).

C and N stable isotope ratios in age 0⁺ steelhead were similar in Big and Salmon creeks prior to the placement of carcasses in Salmon Creek. $\delta^{15}\text{N}$ values of age 0⁺ and age 1⁺ steelhead collected when carcasses were present in Salmon Creek were significantly higher than in samples collected when carcasses were absent and higher than in samples collected at the reference site (Table 3). Less response was seen for $\delta^{13}\text{C}$, but values for age 0⁺ steelhead were significantly higher in Salmon Creek than in Big Creek when carcasses were present.

Juvenile coho collected from A400 Creek while carcasses were present in the stream exhibited $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values significantly higher than those in Wasberg Creek (Table 3). In addition, $\delta^{15}\text{N}$ values for coho at A400 Creek increased significantly when carcasses were present. This increase was not observed for $\delta^{13}\text{C}$. $\delta^{15}\text{N}$ values for age 0⁺ steelhead in A400 Creek when carcasses were present were higher than in Wasberg Creek (Table 3). $\delta^{13}\text{C}$ values for age 0⁺ steelhead when carcasses were present in A400 Creek were greater than values for this site when carcasses were absent and greater than the values displayed by the age 0⁺ steelhead in Wasberg Creek.

Carcass addition to A400 Creek had the greatest effect on the isotope ratios of age 1⁺ steelhead (Table 3). $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for age 1⁺ steelhead in A400 Creek when carcasses were present were significantly greater than at the reference site as well. By January, age 1⁺ steelhead exhibited isotope values comparable with those seen in the muscle tissue and egg samples taken from the salmon carcasses placed in the stream.

The addition of carcasses to both study sites caused a dramatic increase in the proportion of marine-derived N in the

Table 3. Stable isotope values for fish collected from the study sites.

	Salmon and Big creeks		A400 and Wasberg creeks	
	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
Age 0 ⁺ steelhead				
Reference site	5.8±0.5 (6)	-24.2±0.7 (6)	8.9±1.5 (5)	-23.7±0.7 (5)
Treatment site				
Carcasses absent	6.0±0.5 (3)	-23.5±0.8	9.8±2.2 (2)	-22.6±0.6 (2)
Carcasses present	7.3±0.6 ^{a,b} (4)	-22.9±0.9 ^a (4)	10.9±0.7 ^a (4)	-21.3±0.5 ^{a,b} (4)
Age 1 ⁺ steelhead				
Reference site	5.5±0.6 (7)	-23.1±1.0 (7)	10.1±0.8 (3)	-23.5±0.9 (3)
Treatment site				
Carcasses absent	5.7±0.4 (5)	-24.1±1.2 (5)	9.8±0.1 (2)	-22.5±1.1 (2)
Carcasses present	7.4±0.4 ^{a,b} (3)	-22.8±0.7 (3)	13.5±0.2 ^{a,b} (2)	-20.6±0.2 ^{a,b} (2)
Coho				
Reference site	—	—	7.8±0.8 (6)	-24.8±0.6 (6)
Treatment site				
Carcasses absent	—	—	8.8±0.8 (3)	-23.9±0.4 (3)
Carcasses present	—	—	10.6±0.7 ^{a,b} (3)	-23.3±0.6 ^a (3)

Note: Values for treatment sites are averages for samples collected when carcasses were present in the stream and absent. Values are shown ±1 SE with the number of samples in parentheses.

^aSignificant difference between values with carcasses present at the treated site and the reference site.

^bSignificant difference between values with and without carcasses at the treated site.

muscle tissue of the juvenile fish (Table 4). Prior to addition of salmon carcasses, juvenile steelhead contained less than 5% marine-derived N in both Salmon and Big creeks. Following carcass addition to Salmon Creek, proportion of marine-derived N in both age 0⁺ and age 1⁺ steelhead increased to over 17%. The addition of carcasses to A400 Creek caused a larger increase in the proportion of marine-derived N in juvenile salmonids than that observed at Salmon Creek, 13% for age 0⁺ steelhead, almost 20% for coho, and nearly 40% for age 1⁺ steelhead.

Discussion

We observed increased densities of juvenile fish, increased body weight, and improved condition factor in the stream reaches to which salmon carcasses were added. As the experiments were not replicated, we cannot be certain the increased density we observed at the treated sites was due to the presence of carcasses. However, the response in growth and condition factor can be directly associated with the addition of salmon carcasses. Sixty to 96% of the material in the stomachs of juvenile coho and steelhead during the period when carcasses were present at the treated sites consisted of eggs and carcass flesh. The total amount of material in the stomachs of the juvenile coho salmon at the treated sites was ninefold greater than at the reference sites shortly after carcass placement. The importance of this material in the diets of juvenile coho and steelhead was further supported by the observed shift in stable isotope values in the muscle tissue of these fish following addition of salmon carcasses to the treated sites.

Density of juvenile coho salmon and steelhead increased at the time coho salmon carcasses became available in A400 Creek. Density of juvenile coho salmon in Wasberg Creek declined from early October through January (Fig. 1), a behavior that has been reported in other studies in western Washington (Peterson 1982; Bilby and Bisson 1987). Juve-

Table 4. Proportion of marine-derived N in juvenile salmonid fishes in the treatment and reference stream reaches.

	% marine-derived N	
	Salmon and Big creeks	A400 and Wasberg creeks
Age 0 ⁺ steelhead		
Reference site	2.0	25.5
Treatment site		
Carcasses absent	2.1	33.2
Carcasses present	17.3	46.9
Age 1 ⁺ steelhead		
Reference site	1.0	36.3
Treatment site		
Carcasses absent	3.1	34.3
Carcasses present	17.5	71.9
Coho		
Reference site	—	16.6
Treatment site		
Carcasses absent	—	25.1
Carcasses present	—	44.1

Note: We have assumed that uptake of marine-derived N occurred 50% through direct consumption of salmon eggs and flesh and 50% through consumption of invertebrates containing N derived from the spawning fish. Coho did not occur at the Salmon Creek and Big Creek sites.

nile coho at this time of year typically move from headwater stream reaches to more sheltered locations lower in the watershed (Peterson 1982; Brown and Hartman 1988). However, coho populations in A400 Creek increased at the same time the decline was occurring in Wasberg Creek. Age 0⁺ and 1⁺ steelhead did not rear in either A400 Creek or Wasberg Creek during the late summer and early autumn. However, densities of both age-classes increased dramatically after salmon carcasses became available at A400 Creek. Cederholm and Scarlett (1982) reported autumnal movement of steelhead into small streams in response to periods of ele-

vated flow. Elevated flow may have contributed to the density response in steelhead we observed in A400 Creek, but the absence of a corresponding response in Wasberg Creek suggests that other factors were also involved.

Condition factor of juvenile coho salmon in A400 Creek and age 0⁺ steelhead in Salmon Creek increased after addition of carcasses to these streams. The fact that condition factor remained elevated at the treated sites while carcasses were present and then declined rapidly after carcasses had decomposed suggests that the availability of the carcasses was responsible for the elevated condition factor. This conclusion is further supported by the large quantity of salmon eggs and carcass flesh ingested by the fish in A400 Creek (Fig. 3) and the alteration in stable isotope ratios in the muscle tissues of the fish at both treated sites. Condition factor of fish at the Wasberg Creek site increased between the January and the February samples, at the time that condition factor at the treated A400 Creek site was declining. The presence of several spawning coho salmon in late January and early February at the Wasberg Creek site may have contributed to this increase.

Juvenile coho and steelhead in A400 Creek at the time carcasses were present in the system consumed large amounts of carcass-derived material (Fig. 3). The total amount of material in the stomachs of juvenile fish at this time was greatest shortly after carcasses had been added to the stream. The greater abundance of salmon eggs versus carcass tissue in the stomachs suggests that eggs are eaten preferentially to flesh. At A400 Creek, some eggs remained in the hatchery carcasses and a considerable amount of natural spawning occurred, increasing the availability of eggs. The stomachs of some age 1⁺ steelhead were so full of eggs that the walls of the body cavity were distended. Relatively little flesh was found in the stomachs of the fish at A400 Creek despite the fact that it was readily available. Salmon eggs became an important item in the diets of juvenile salmonids at Wasberg Creek during January and February when several coho salmon spawned at this study site. Flesh was never recovered from the stomachs of fish at Wasberg Creek. Selecting salmon eggs over other food sources is energetically efficient. The caloric content of sockeye salmon eggs in Alaska was about 4450 cal·g wet weight⁻¹ (1 cal = 4.1868 J) compared with 645 cal·g wet weight⁻¹ for flesh from the carcasses of the spawning fish (Eastman 1996). Caloric values for invertebrates are about 15% lower than for salmon eggs (Curry et al. 1993).

Juvenile coho at the A400 Creek site also contained more invertebrates in their stomachs during November than at any other time at this site or at Wasberg Creek. Invertebrate abundance often decreases following spawning by salmon, presumably due to physical disruption of the streambed during the process of redd construction (Hildebrand 1971; Field-Dodgson 1987; Minikawa 1997). Invertebrates displaced from the streambed by redd excavation may have become more readily available to the fish. Biomass of invertebrates collected from the stomachs of juvenile coho at the Wasberg Creek site increased in January and February, when a few spawning coho were present at this site (Fig. 3). Steelhead contained relatively few invertebrates in their stomachs at A400 Creek while carcasses were present in the stream.

Studies in Alaska have reported that high proportions of the invertebrates found in the stomachs of juvenile salmonids are of terrestrial origin (Eastman 1996). However, we found that nearly all the invertebrates in the stomachs of the fish we sampled were aquatic. It is likely that few terrestrial invertebrates were active at the time of year when we conducted these studies, reducing their importance in the diet of the fish.

Juvenile coho grew more rapidly at the A400 Creek site than at the Wasberg Creek site. By December the coho at the treated site were 44% larger than the coho at the reference site. Larger body size can have a dramatic effect on survival of coho salmon and steelhead. Overwinter survival of juvenile coho salmon improves with increased body size (Hartman and Scrivener 1990; Quinn and Peterson 1996). Survival from smolt to adult is also positively correlated with body size of smolts (Bilton et al. 1982; Ward and Slaney 1988; Holtby et al. 1990). Therefore, availability of eggs and carcass tissue, and the resultant increase in body size of juvenile fish, may positively impact survival rates through the remainder of their life.

The increase in the C and N stable isotope values in the fish at the treated study sites following addition of carcasses further indicates that materials derived from spawning salmon are readily ingested by juvenile salmonids (Table 3). The increase in $\delta^{15}\text{N}$ values at both Salmon and A400 creeks following carcass addition is consistent with the stomach content data, indicating that large amounts of carcass-derived material were ingested by the fish at the treated sites. Change in $\delta^{13}\text{C}$ values was not as consistent as for $\delta^{15}\text{N}$, but significant increases were observed at A400 Creek for both age-classes of steelhead and at Salmon Creek for age 0⁺ steelhead. The less consistent response in $\delta^{13}\text{C}$ is likely due to the fact that the carcass and salmon egg $\delta^{13}\text{C}$ values were only slightly higher than those exhibited by the juvenile fish prior to addition of carcasses to the site. Therefore, only a small response in $\delta^{13}\text{C}$ values would be expected.

The dramatic increase in the proportion of marine-derived N in the muscle tissue of the juvenile fish at the treated sites (Table 4) indicates the dominant role of carcass-derived material in the winter diet of juvenile salmonids. The proportion of marine-derived N in juveniles at the A400 Creek and Wasberg Creek sites was higher than at Salmon and Big creeks both before and after addition of the carcasses (Table 4). Higher densities of naturally spawning salmon at the A400 Creek and Wasberg Creek sites are likely responsible for the elevated values prior to carcass addition. Following carcass addition, the increases in the proportion of marine-derived N were greater at A400 Creek than at Salmon Creek, especially for age 1⁺ steelhead. The difference in response may have been related to greater salmon egg availability at A400 Creek due to the presence of spawning salmon at this site. Salmon eggs were the dominant item in the diet of age 1⁺ steelhead shortly after addition of the carcasses to A400 Creek, comprising over 90% of the material recovered from their stomachs.

Habitat restoration should include not only measures to ensure the protection and enhancement of physical attributes of a stream but should also consider the nutritional health of the system. Our results coupled with information published

over the last 7 years (Kline et al. 1990, 1994; Michael 1995; Bilby et al. 1996; Johnston et al. 1997) make it increasingly apparent that adequate levels of spawning salmon are an important component of healthy stream habitat in the Pacific Northwest. Unfortunately, levels of naturally spawning salmon throughout the region have declined precipitously over the last several decades as a result of a variety of factors (Nehlsen et al. 1991; Nickelson et al. 1992; Washington Department of Fisheries 1993; National Research Council 1996; Slaney et al. 1996). It is likely that the decreased numbers of returning salmon have decreased the capacity of the freshwater habitats where they spawn to support juvenile salmon and other aquatic biota.

Distribution of salmon carcasses from hatcheries may be used to increase the availability of carcass material in watersheds where population levels are severely depressed. However, this technique cannot replace all the ecological functions provided by naturally spawning fish. Spawning fish remove sediment from streambed gravels (Montgomery et al. 1996) and alter the community composition and productivity of invertebrate populations (Piorkowski 1995; Minikawa 1997). Adult salmon also enter streams and spawn over an extended period of time. Therefore, carcass material would be present in the channel for a longer period than would be the case with hatchery carcasses added on a single date. Although hatchery carcasses could be added to a site several times throughout the spawning season, the logistics of making multiple releases at numerous sites make this option a daunting proposition. Distribution of carcasses of hatchery-spawned salmon should be viewed as a procedure to be utilized in situations where disease introduction and water quality concerns are deemed minimal and are monitored and where the abundance of spawning salmon cannot be increased sufficiently through restrictions on harvest rate.

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