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Preliminary Evaluation of the Use of Nitrogen Stable Isotope Ratios to Establish Escapement Levels for Pacific Salmon

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Preliminary Evaluation of the Use of Nitrogen Stable Isotope Ratios to Establish Escapement Levels for Pacific Salmon

ABSTRACT

Research over the last decade has established the ecological significance of the nutrients and organic matter deposited by Pacific salmon in the freshwater habitats where they spawn. A large proportion of the nitrogen in plants and animals in streams where salmon are abundant may be derived from spawning fish, and juvenile salmonids exhibit higher growth rates at locations where carcasses are available. Currently, no method is available to establish salmon escapement goals that meet the nutritional needs of streams. We examined the relationship between the abundance of spawning coho salmon (*Oncorhynchus kisutch*) and the nitrogen stable isotope ratio of coho salmon parr to determine whether a saturation level for salmon-derived nitrogen could be identified. Coho parr were collected from 26 sites in western Washington in late winter. The isotope ratio in the coho parr was related to the abundance of salmon spawning at that site the previous autumn. The amount of carcass-derived nitrogen increased with increasing abundance of carcass tissue up to 0.15 kg of carcass/ m² of streambed area but exhibited no increase above this level. These preliminary data suggest that relationships between stable isotope values and carcass abundance may provide a useful supplement to traditional methods of establishing escapement goals for Pacific salmon.

The role that Pacific salmon play in nutrient and organic matter transfer between marine and freshwater ecosystems has received considerable attention over the last several years (Cederholm et al. 1999; Gresh et al. 2000). The five species of Pacific salmon native to northwestern North America perform this function as a result of two unusual life histories traits—they are anadromous and return to their natal stream to spawn and they are semelparous (die after spawning once). More than 95% of the body mass of Pacific salmon accumulates in the marine environment (Groot and Margolis 1991). This material is transported and deposited in freshwater habitats where the salmon spawn and die, providing an important nutrient and organic matter subsidy to freshwater and terrestrial ecosystems in the Pacific Northwest (Kline et al. 1990; Bilby et al. 1996; Ben-David et al. 1997).

The biological significance of this subsidy has long been recognized for sockeye salmon rearing lakes (Juday et al. 1932; Donaldson 1967). However, until recently, little quantitative evidence that marine-derived materials affected stream productivity was available. Over the last 10 years, application of stable isotope analysis

to this subject has enabled direct quantification of marine-derived nutrients in streams (Kline et al. 1990; Bilby et al. 1996; Johnston et al. 1997). Spawning salmon are enriched with the heavier isotope of nitrogen and carbon (¹⁵N and ¹³C) relative to contributions of N and C to the stream from other sources (Kline et al. 1990; Bilby et al. 1996). As a result, the proportion of N or C of marine origin in aquatic organisms, riparian vegetation, benthic organic matter, wildlife or dissolved in stream water can be determined (Bilby et al. 1996; Hilderbrand et al. 1996; Ben-David et al. 1997). These studies have firmly established that salmon often make a substantial contribution of nutrients to the stream where they spawn, to the vegetation bordering the channel and to various species of wildlife.

The organic matter and nutrients that spawning salmon provide have been shown to affect stream productivity at all trophic levels. Kokanee salmon (landlocked *O. nerka*) carcasses added 44.6 kg of phosphorus to a small tributary of Lake Tahoe, California, raising the phosphate concentration of the water by 4–6 µg/L and increasing algae production (Richey et al. 1975). Heterotrophic activity, as indexed by ¹⁴C uptake, was over 10X greater in the section of stream containing kokanee salmon carcasses than a section without carcasses. Schuldt and Hershey (1995) found that adding 25 chinook salmon carcasses to a tributary of Lake Superior elevated concentration of both N and P and resulted in increased chlorophyll *a* in the epilithic organic matter layer on the streambed.

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Elevated nutrient availability and the consequent increase in primary production causes increases in invertebrate and fish production. Total invertebrate density and biomass from late spring through early autumn was higher in a stream where coho salmon spawned than it was in a nearby stream with comparable physical characteristics but inaccessible to salmon (Minakawa 1997). Increased food availability, due to higher invertebrate production and the presence of carcass flesh and eggs during spawning, causes increased growth of stream fishes. Artificially increasing availability of salmon carcass flesh and eggs by adding carcasses of hatchery coho salmon to a small stream in southwestern Washington doubled the growth rate of juvenile coho salmon at this site relative to a nearby stream reach with low availability of carcasses (Bilby et al. 1998). Rapid increases in the amount of carcass-derived N in the juvenile fish at the treated site and the abundance of eggs and flesh in their stomachs clearly indicated that the material derived from the carcasses was responsible for the accelerated growth rate. In the Wood River watershed in Alaska, char and trout grew very rapidly while carcasses of sockeye salmon were present (Eastman 1996). The body weight of one tagged char increased 58% in 36 days.

Increases in the body size of juvenile salmonids can raise survival rates. Larger body size has been positively correlated with overwinter survival of juvenile coho salmon (Hartmann and Scrivner 1990; Quinn and Peterson 1996) and larger smolts enjoy a considerable advantage in survival upon entering the marine environment (Bilton et al. 1982; Ward and Slaney 1988; Holtby et al. 1990). Thus, the influence spawning salmon have on the growth of juvenile salmon in freshwater may be reflected in increased rates of survival thorough their entire life history.

Decreases in the abundance of salmon over the last century have been well documented for California, Oregon, Idaho, and Washington (Nehlsen et al. 1991; Nickelson et al. 1992; WDFW and WWTIT 1993). Salmon have been eliminated from about 40% of their historic range in these states and population levels are considered to be stable in only 16% of the area (NRC 1996). Some stocks in British Columbia and Alaska also have exhibited decreased abundance, although most stocks north of the U.S.-Canada border are in better condition than those to the south (Baker et al. 1996; Slaney et al. 1996).

Declines in salmon abundance have caused a corresponding decrease in the amount of nutrients and organic matter delivered by salmon to the freshwater ecosystems. Gresh et al. (2000) reported that delivery of nutrients by salmon to watersheds in Washington, Idaho, Oregon, and California is about 6% to 7% of historic levels. Even where declines in salmon populations have not been as drastic as for the northwestern United States, reductions in nutrient subsidies have occurred. An

extensive survey of nutrient delivery by spawning salmon to British Columbia streams documented large decreases in watersheds where populations have not been enhanced by hatchery supplementation, stream fertilization, construction of spawning channels, or other mitigating action (Larkin and Slaney 1997).

There is increased interest in the Pacific Northwest in developing escapement goals that account for the nutrient and organic matter subsidy provided by spawning salmon (Larkin and Slaney 1997; Michael 1998; Gresh et al. 2000). However, there is relatively little information on which to base escapement targets that will meet this objective. Ideally, estimates of the number of spawning salmon required to meet the nutritional needs of freshwater ecosystems would be determined by experimentally altering escapement levels for each stock and evaluating the impact on system productivity. Conducting such an experiment on thousands of watersheds is a daunting prospect and would not provide usable results for many years. A



possible alternative to this approach is to develop a relationship between the density of spawning salmon and the level of marine-derived nutrients in the tissues of juvenile fish or other stream or riparian biota. This type of relationship may enable a "saturation level" for marine nutrients to be established. We propose a method for establishing this "saturation level" using stable isotope analysis. Stable isotope data collected for coho parr in western Washington are provided as an illustration of how this information could be used to aid in developing escapement goals.

Methods

To determine if such a relationship exists, we collected coho parr from 26 stream reaches (Table 1) in 12 large watersheds in western Washington (Figure 1) from 1991 through 1997. The parr were collected from stream reaches where coho were the only species of Pacific salmon that spawned and

Increased food availability, due to higher invertebrate production and the presence of carcass flesh and eggs during spawning, causes increased growth of stream fishes, like these coho salmon fry.

where records of spawning salmon abundance were available for the years when the samples were collected. We restricted our samples to sites where only coho salmon spawned to reduce the complications introduced by multiple species of salmon spawning over an extended period of time. Coho salmon typically spawn from late October through early January in western Washington.

Stable isotope analyses enables the determination of the level of some salmon-derived nutrients in samples collected from streams where these fish spawn. Stable isotope ratios of nitrogen (N) are most commonly used for this purpose (Kline et al. 1990; Bilby et al. 1996; Johnston et al. 1997). Use of N stable isotope ratios to represent the uptake of salmon-derived nutrients does not imply that N is limiting aquatic productivity. In some systems, phosphorus or some other nutrient provided by the salmon may be more important. However, N exists in 2 isotopic forms, ^{14}N and ^{15}N , and returning adult salmon contain much higher levels of ^{15}N relative to N provided to the stream from other sources (Kline et al. 1990). Due to the difference in the stable isotope ratio between these sources of N, the stable isotope ratio provides a good indication of the proportion of salmon-derived N in a sample. This

estimate cannot be made for most other elements.

N stable isotope ratios are expressed as $\delta^{15}\text{N}$ values (Peterson and Fry 1987). These values represent the difference in the ratio of ^{15}N to ^{14}N in a sample and the ratio in air. Values are calculated:

$$\delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where R_{sample} = the ratio of $^{15}\text{N}/^{14}\text{N}$ in the fish tissue sample and R_{standard} = the ratio of $^{15}\text{N}/^{14}\text{N}$ in atmospheric N (Peterson and Fry 1987). Higher values of $\delta^{15}\text{N}$ indicate higher proportions of the heavier isotope in the sample.

Juvenile fish were collected in late February and early March by seining or electrofishing. We did not sacrifice more than three coho parr at any site to minimize impacts on smolt output. We were unable to collect three fish from a few locations (Table 1). In addition, we collected age 0⁺ cutthroat trout from the same watershed upstream of a barrier impassible to salmon. Fish were killed immediately after capture.

Stable isotope values from the cutthroat trout were used to represent background isotope ratios for that watershed. Variability in background N stable isotope ratio among watersheds can be caused by a

Table 1. Average $\delta^{15}\text{N}$ values for juvenile coho salmon and cutthroat trout and carcass abundance for each study reach. Juvenile coho were collected at the sites where counts of spawning salmon were made. The cutthroat trout were collected from the same watershed, upstream from an impassable barrier to returning salmon. $\delta^{15}\text{N}$ values are shown \pm one standard error followed by the number of fish in the sample.

Watershed	Stream and year	$\delta^{15}\text{N}$ (‰)		Carcass abundance (fish/km)
		0 ⁺ Coho	0 ⁺ Cutthroat	
Chehalis	Big Creek 1996	7.0 \pm 0.2 (3)	6.0 \pm 0 (3)	39.1
Chehalis	Big Creek 1997	7.7 (1)	6.0 \pm 0 (3)	19.9
Deschutes	Huckleberry Creek 1996	7.1 \pm 0.2 (3)	6.5 \pm 0.3 (3)	9.9
Deschutes	Huckleberry Creek 1997	7.2 \pm 0.1 (3)	6.1 \pm 0.1 (3)	4.5
Deschutes	Johnson Creek 1996	7.4 \pm 0.3 (3)	6.5 \pm 0.3 (3)	1.2
Hoko	Cub Creek 1996	7.9 \pm 0.1 (3)	7.0 \pm 0.9 (3)	26.1
Hoko	Bear Creek 1996	6.3 \pm 0.4 (3)	7.0 \pm 0.9 (3)	21.7
Clallam	Charley Creek 1996	7.7 \pm 0.3 (3)	5.3 \pm 0.2 (3)	33.5
Skagit	Ennis Creek 1997	5.8 \pm 0.8 (3)	4.9 \pm 0.4 (3)	50.9
Skagit	Hilt Creek 1997	8.7 \pm 0.7 (3)	6.7 \pm 0.8 (3)	55.3
Skagit	Mouse Creek 1997	7.2 \pm 0.3 (3)	5.5 \pm 0.6 (3)	33.5
Skagit	Parker Creek 1997	6.8 \pm 0.5 (3)	4.5 \pm 0.1 (3)	59.0
Skykomish	Worthy Creek 1997	9.9 \pm 0.4 (3)	8.5 \pm 0.4 (3)	52.2
Snoqualmie	E.F. Griffin Creek 1991	11.7 \pm 0.4 (2)	8.5 (1)	968.0
Snoqualmie	E.F. Griffin Creek 1996	10.3 \pm 0.2 (3)	7.7 \pm 0.3 (3)	331.0
Snoqualmie	E.F. Griffin Creek 1997	10.0 \pm 1.6 (3)	7.7 \pm 0.3 (3)	201.0
Snoqualmie	Griffin Creek 1996	11.6 \pm 0.6 (3)	7.7 \pm 0.3 (3)	230.0
Snoqualmie	Griffin Creek 1997	10.4 \pm 0.5 (3)	7.7 \pm 0.3 (3)	332.0
Snoqualmie	Grizzly Creek 1992	12.4 (1)	8.1 \pm 0.2 (3)	304.0
Snoqualmie	Grizzly Creek 1993	11.3 \pm 3.0 (2)	8.2 (1)	646.0
Snoqualmie	Grizzly Creek 1997	10.7 \pm 0.7 (3)	7.7 \pm 0.3 (3)	234.0
Dickey	Colby Creek 1996	9.4 \pm 0.3 (3)	7.5 \pm 0.3 (3)	3.7
Bogachiel	Hemphill Creek 1996	8.4 \pm 0.3 (3)	7.2 \pm 0.5 (3)	63.4
Soleduck	Redoubt Creek 1996	8.5 \pm 0.1 (3)	6.5 \pm 0.5 (3)	78.3
Hoh	Winfield Creek 1996	8.8 \pm 0.2 (3)	5.9 \pm 0.1 (3)	14.9
Willapa	Wasberg Creek 1996	8.9 (1)	6.5 (1)	10.0

variety of factors including variation in denitrification rates, a process that increases levels of ^{15}N (Delwiche and Steyn 1970). Stable isotope ratios in juvenile coho salmon and age 0^+ cutthroat trout are similar when they are found in the same stream reach, indicating similar diets (Bilby et al. 1996). Thus, the difference between the coho parr and the age 0^+ cutthroat trout represented the level of enrichment with marine-derived N in the coho. Samples of dorsal muscle tissue from the carcasses of recently deceased, adult coho salmon also were collected from most watersheds where juvenile fish were captured (Table 2). These samples were taken in November and December. Carcass samples were not obtained from the Clallam River, the Hoh River, the Dickey River, or the Soleduck River. Isotope ratios from carcasses in the nearest watershed where samples were collected were used to represent the values for these unsampled water-

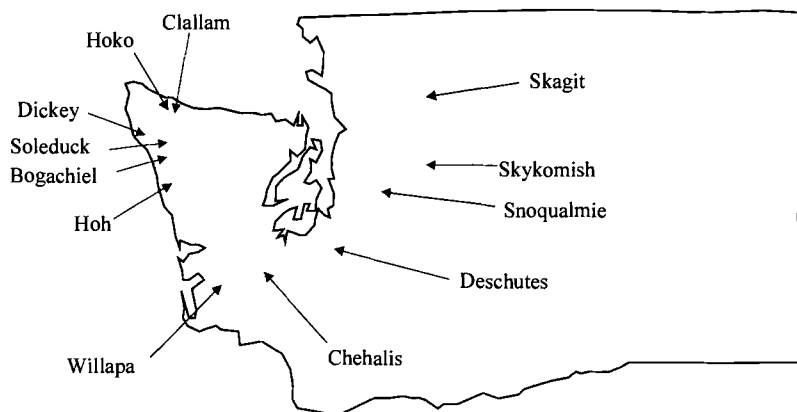
Table 2. Average $\delta^{15}\text{N}$ values coho salmon carcass muscle tissue collected from watersheds where juvenile coho were sampled. $\delta^{15}\text{N}$ values are shown \pm one standard error followed by the number of fish in the sample.

Watershed	Carcass $\delta^{15}\text{N}$
Chehalis	12.0 ± 0.3 (4)
Deschutes	13.5 ± 0.1 (4)
Hoko	14.0 ± 0.3 (36)
Skagit	14.2 ± 0.3 (16)
Skykomish	14.4 ± 0.6 (23)
Snoqualmie	14.1 ± 0.4 (18)
Bogachiel	14.5 ± 0.1 (4)
Willapa	14.5 ± 0.8 (28)

sheds. Bogachiel River values were applied to the Soleduck, Dickey, and Hoh Rivers and Hoko River values were used for the Clallam River site. All samples were stored on ice and transported to the lab. Samples were frozen prior to preparation for stable isotope analysis.

Approximately 10 g of dorsal muscle tissue was sampled from juvenile fish and carcasses for stable isotope analysis. The tissue was rinsed with a 10% solution of HCl then with distilled water and dried at 50°C (Bilby et al. 1996; 1998). Dried samples were placed in a small, glass vial and inserted into a scintillation vial containing a small amount of silica gel desiccant. The vials were then placed in a desiccator until they were submitted for analysis.

Stable isotope analyses were performed at the University of Alaska, Fairbanks. Analytical procedures followed those described in Ben-David et al. (1998). Samples were ground to a fine powder and 1–1.5 mg was combusted. The evolved N_2 gas was introduced into a continuous flow, isotope ratio, mass spectrometer to determine $\delta^{15}\text{N}$ values. Duplicates of each sample were analyzed and the average used to represent the isotope value for that sample.



Densities of spawning coho salmon in stream reaches where we collected samples were determined from counts conducted by the Washington Department of Fish and Wildlife or one of the western Washington Indian tribes. Spawning salmon abundance during a year was estimated from the counts of live fish using the area-under-the-curve method (Ames 1984). Abundance of spawning salmon at the study sites ranged from slightly over 1 fish/km to 968 fish/km (Table 1). Bank full channel width was measured at each sample site to enable determination of surface area per km of channel length. Average weight of spawning coho salmon was assumed to be the same as the average weight of hatchery fish collected that year at the nearest hatchery facility (data provided by H. Michael, Washington Department of Fish and Wildlife). As hatchery reared coho salmon contribute a large proportion of the spawning salmon at many of the sampled sites, these weight estimates are representative of the carcass weight. Deposition of carcass material at each site was expressed as kg wet-weight/ m^2 of streambed surface area.

Figure 1. The location of the watersheds in western Washington from which samples were obtained.



A decomposing salmon carcass lies in a tributary of the Chehalis River, Washington.

Relative level of enrichment of coho parr with ^{15}N was expressed as:

$$^{15}\text{N enrichment of parr} = (\delta^{15}\text{N parr} - \delta^{15}\text{N cutthroat}) / (\delta^{15}\text{N carcass} - \delta^{15}\text{N cutthroat}).$$

This value provides an index of isotopic enrichment in the coho salmon relative to cutthroat trout of the same age without access to carcass-derived N and relative to the isotopic ratio in the tissues of the returning adult salmon. The higher the index value, the higher the level of carcass N in the muscle tissue of the juvenile coho salmon. However, the index values do not represent the proportion of carcass-derived N in the coho parr, as this calculation does not account for isotopic fractionation (change in isotope ratio caused by trophic exchange). Models have been developed to account for fractionation occurring

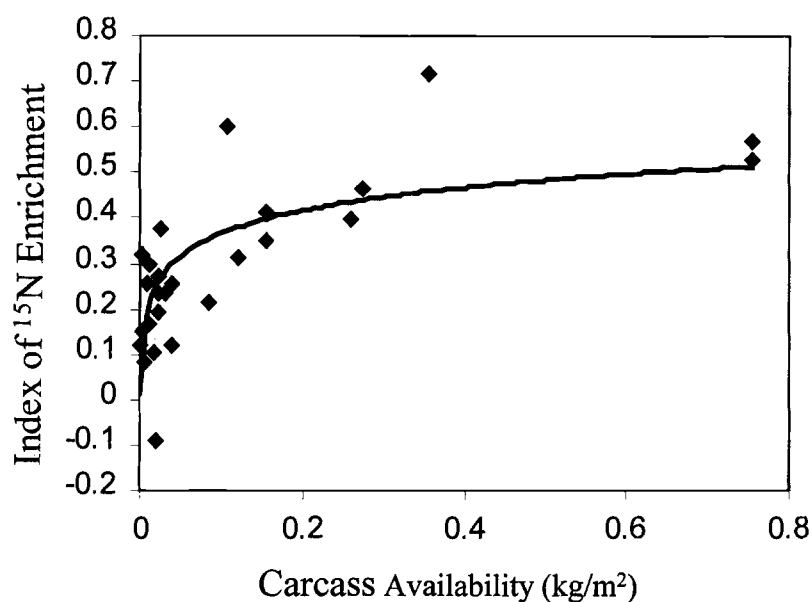


Figure 2. The relationship between the level of enrichment with ^{15}N in the muscle of coho parr and the abundance of carcass material at that site. Carcass abundance is presented as kg wet-weight carcass tissue per m^2 streambed surface area. Calculation of enrichment index is described in the text. Regression statistics: enrichment index = $0.073 \ln(\text{carcass abundance}) + 0.534$; $R^2 = 0.49$; $p = 6.16 \times 10^{-5}$.

with trophic exchanges (Kline et al. 1990). However, we had no direct information on the rate of fractionation for our study sites. Therefore, we elected to represent the level of enrichment using this index.

Results and discussion

$\delta^{15}\text{N}$ values for cutthroat trout collected from above salmon barriers ranged from 4.5‰ to 8.5‰ (Table 1). The range in background stable N isotope values emphasizes the need to understand watershed-specific background isotopic ratios when determining enrichment levels. Juvenile coho salmon $\delta^{15}\text{N}$ values ranged from 5.8‰ to 11.7‰ and were higher than those for cutthroat trout from the same system in all cases but Bear Creek. The isotope values for the juvenile coho salmon and cutthroat trout were very consistent at each site (Table 1). The coefficient of variation exceeded 10% at only 3 of the 23 sites for coho parr and 2 of 23 sites for cutthroat trout. The low variability in the $\delta^{15}\text{N}$ values at a site suggests that the relatively small sample

(3 fish) provided a reasonable representation of the isotope ratio for that location. Carcass $\delta^{15}\text{N}$ values also varied among watersheds but were more consistent among sites than those for juvenile fish, ranging from 12.0‰ to 14.5‰ (Table 2).

Enrichment with marine-derived N increased with increasing abundance of carcass tissue up to values between 0.10 kg/m^2 and 0.15 kg/m^2 -wet weight (Figure 2). At carcass abundance levels above 0.10 kg/m^2 , ^{15}N -enrichment index values were variable, ranging from about 0.20 to 0.70. However, ^{15}N enrichment at the sites with carcass abundance over 0.10 kg/m^2 was consistently high, with enrichment index values below 0.30 at only 1 site, and little increase with increasing carcass tissue abundance. Average index of enrichment for locations with carcass tissue abundance less than 0.10 kg/m^2 (\pm one std. error) was 0.19 ± 0.11 ($n=17$); those sites with carcass tissue abundance over 0.10 kg/m^2 exhibited average enrichment index of 0.48 ± 0.13 ($n=9$).

The decline in rate of increase in the enrichment index value with increasing abundance of carcass tissue (Figure 2) could be produced if juvenile coho salmon ingested enough carcass flesh and eggs that their N stable isotope ratio approached that of their food source (Figure 3). In this case the inflection in the curve would not represent a saturation level but an asymptotic effect as the $\delta^{15}\text{N}$ of the parr approached that of the carcasses. The average $\delta^{15}\text{N}$ value for salmon carcasses collected at our study sites was 13.9‰ (Table 2). Juvenile fish will exhibit a $\delta^{15}\text{N}$ value approximately 3‰ higher than that of their food source due to isotopic fractionation (Minigawa and Wada 1984; Kline et al. 1990). Therefore, if juvenile coho salmon ate the carcass tissue directly, they would exhibit a $\delta^{15}\text{N}$ value of 16.9‰ . However, the maximum $\delta^{15}\text{N}$ level we observed in coho parr ($\delta^{15}\text{N} = 11.7\text{‰}$) was well below the level at which the enrichment index would be greatly affected by convergence with the isotopic value of the food source. Therefore, the inflection in the relationship between isotopic enrichment of coho parr and carcass deposition (Figure 2) represents a limitation on incorporation of marine-derived N by the coho parr; a saturation point for this trophic interaction.

We believe that the level of enrichment with ^{15}N in coho parr observed at our sample locations was largely a product of direct consumption of salmon flesh and eggs by the juvenile fish the preceding autumn and early winter. The coho parr also incorporated salmon-derived N during the summer, deposited by salmon spawning in previous years. However, the isotopic ratio in muscle tissue of rapidly growing fish is indicative of recent diet (Hesslein et al. 1993). Coho salmon parr in a stream reach to which carcasses were added grew very rapidly during the time the carcasses were in the stream, increasing in body weight 4.9 g in approximately 70 days, a rate of approximately 2% per day (Bilby et al. 1998). The N isotope ratio of the muscle tissue of these

fish increased dramatically over this period of time. This growth rate is comparable to those obtained for juvenile salmon in hatcheries at low water temperatures, where food availability is generally not limiting (Weatherley and Gill 1995). Thus, the inflection in the relationship between enrichment with ^{15}N and carcass deposition may reflect the point at which the availability of carcass tissue or eggs fully meets the dietary needs of the rearing coho salmon. However, as we collected no information on rate of growth of the coho parr at our study sites, we can draw no direct relationship between growth and deposition of carcass tissue.

Recent abundance of adult coho salmon in many of the watersheds we sampled is well below the carcass deposition levels at which we observed diminished rate of incorporation of salmon-derived N (Figure 4). We expressed carcass abundance as kg/m^2 streambed surface area in our study (Figure 2) but spawning salmon abundance is reported as total number of fish per watershed (WDFW and WWTIT 1993). Using published information on the length of

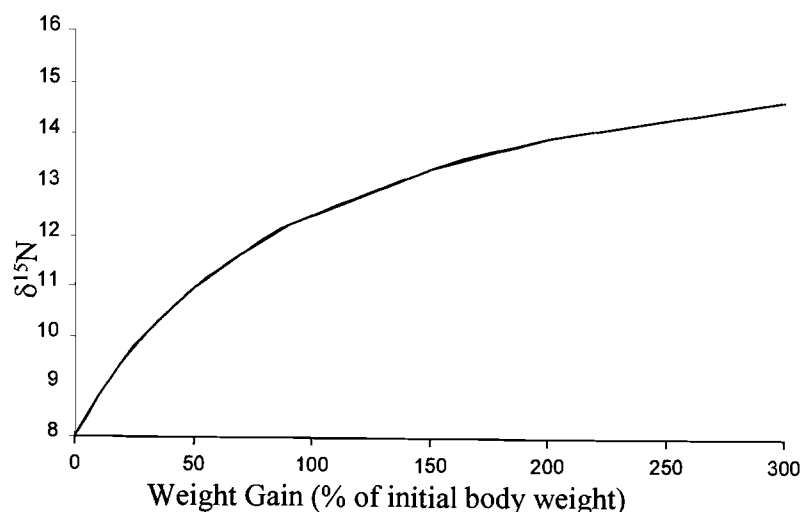


Figure 3. Change in the isotope ratio of a coho parr with growth. This example assumes all growth by the coho parr is due to ingesting carcass tissue. Starting coho $\delta^{15}\text{N}$ was assumed to be 8.0, the approximate value observed at the Griffin Creek sites prior to the arrival of spawning salmon (Bilby et al. 1996). The carcass $\delta^{15}\text{N}$ of coho salmon carcasses was assumed to be 13.9, the average value for carcasses analyzed for this study.

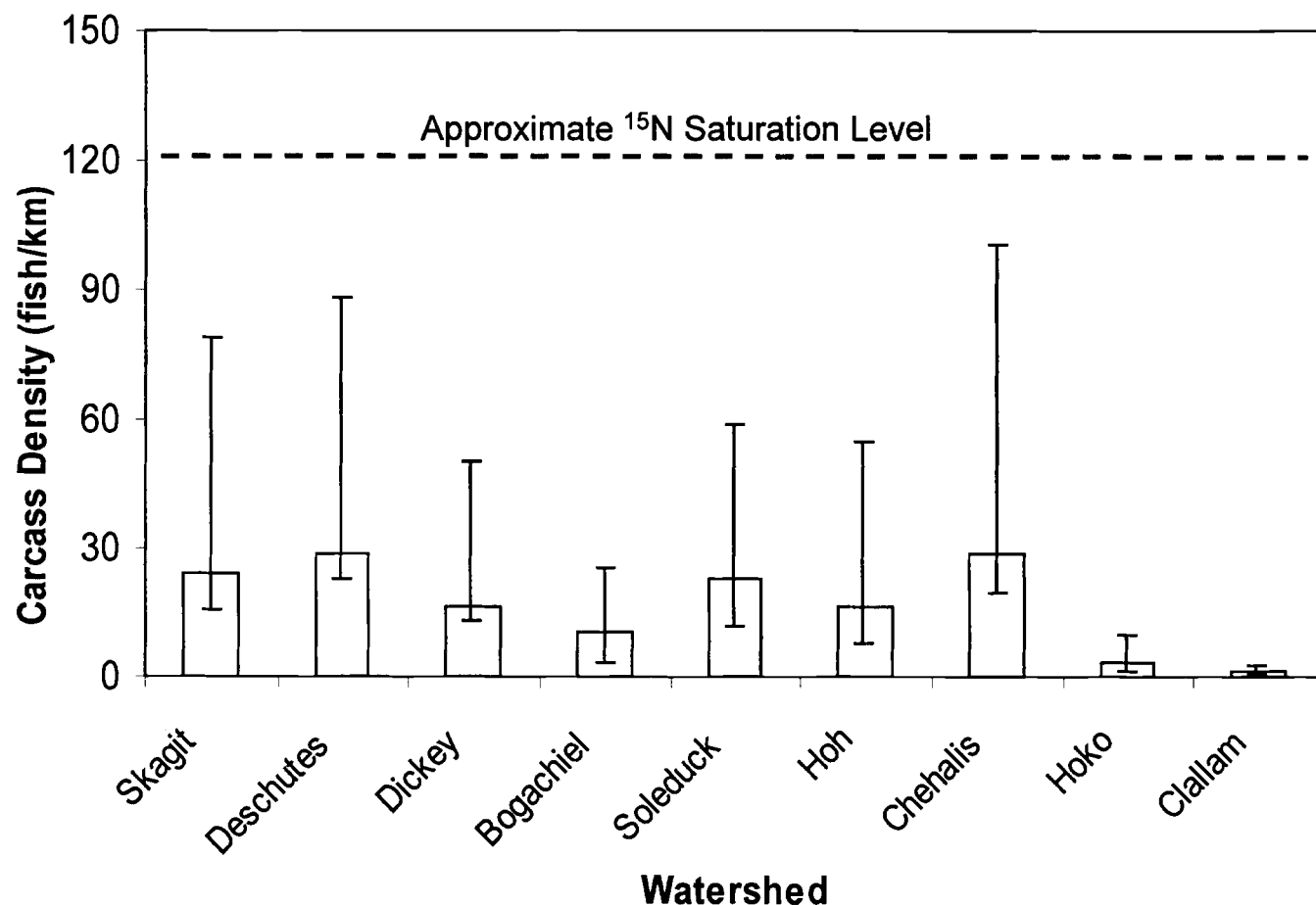


Figure 4. Comparison of the approximate level at which we observed diminishing rates of incorporation of salmon-derived N in our study with spawning coho salmon abundance from the late 1960s through the 1990s in some of the watersheds we sampled. The bars represent the average spawning coho salmon abundance over the period of record and the error bars represent the range in abundance over that time period. Length of the data record varies by watershed: Skagit, 1967–1991; Deschutes, 1979–1991; Dickey, 1980–1991; Bogachiel, 1980, 1982, 1984–1991; Soleduck, 1980–1991; Hoh, 1980–1991; Chehalis, 1984–1991; Hoko, 1984–1991; Clallam, 1984–1991 (WDFW and WWTIT 1993). Escapement data or stream length data were not available for the Skykomish, Snoqualmie, or Willapa watersheds.

Caddisfly larvae feed on salmon carcasses in a tributary of the Chehalis River, Washington.

stream channel accessible to anadromous fish (Phinney and Bucknell 1975) we were able to calculate the average number of spawning coho salmon/km for some of the watersheds we sampled. Average densities ranged from 1 fish/km to 30 fish/km. We estimated the number of salmon/km required to provide 0.1 kg/m² wet weight of carcass biomass by using the average channel width and average coho body weight values for our study stream reaches; approximately 120 salmon/km. This level of coho salmon abundance was not achieved for any of the watersheds during any year of record (Figure 4). This comparison suggests that many streams in western Washington are capable of incorporating substantially more marine-derived nutrients than they have received over the last several decades.


The relationship displayed in Figure 2 should be considered preliminary due to some of the assump-



tions that we made in conducting this analysis. We do not know whether the coho parr we collected had spent the entire winter at the site where they were captured, although significant movement towards saltwater by smolts usually does not occur until April (Cederholm and Scarlett 1982), well after we had collected our samples. Actual availability of carcass material at a site may not be accurately represented by the total biomass of fish spawning at that location. Retention of carcasses in the channel may vary considerably among sites as a result of differences in removal from the stream by scavengers and differences in transport during high flows due to the presence of structures in the channel to catch and retain carcasses (Cederholm et al. 1989). Some of the potential sources of among site variability in carcass retention may have been minimized by the similarity among the sample sites in stream size and physical characteristics of the chan-

nel. The accuracy of the counts of spawning salmon also may have varied among sites owing to differences in availability of hiding cover, water clarity, stream size, flow levels, experience of the observer and other factors. Regardless of these potential sources of variability, our data clearly indicate a relationship between degree of enrichment with ¹⁵N and abundance of spawning salmon.

The limitations we placed on sample site selection in order to reduce variation in the relationship between spawner abundance and isotopic enrichment also limit the application of the relationship presented in Figure 2 to establishment of salmon escapement goals. No samples were collected from locations where multiple species of salmon spawn. In addition, we have examined only the relationship between coho parr $\delta^{15}\text{N}$ during late winter and carcass availability. The relationship may vary seasonally for juvenile coho salmon. Responses of plants, invertebrates, other fishes or wildlife may differ. Some evidence that this relationship varies is provided by Johnston et al. (1997) who found $\delta^{15}\text{N}$ values in insects in tributaries of the Stuart River, British Columbia continued to increase with densities of spawning sockeye salmon up to 2 fish/m². Assuming an average weight of a sockeye salmon is 2 kg, the carcass deposition rates would be 4.0 kg/m², well above the levels at which we observed decreasing response in ¹⁵N enrichment for coho parr at our study sites.

It is evident that Pacific salmon are not only a product of the ecosystems where they spawn and rear but also make a critical contribution to the ecological health and productivity of these systems. As such, they should be considered part of any comprehensive approach to restore freshwater habitat in the Pacific Northwest. Many efforts at habitat restoration now underway are attempting to couple improvements in land use practices with deliberate manipulations of channel form to produce the physical habitat conditions preferred by target species. These efforts cannot be successful if the streams lack the capacity to generate sufficient food to support the rearing salmon. Restoration of freshwater habitat in the region will require that the role Pacific salmon play in maintaining the health of freshwater habitats be considered in establishing harvest levels and escapement goals for these fishes. More extensive data on the relationship between the abundance of spawning salmon and the incorporation of salmon-derived N into the various components of stream and riparian ecosystems are needed before isotopic enrichment can be used as a tool to aid in establishing escapement goals. Nonetheless, these initial data show promise that this technique may be useful for this purpose, especially as no other method of establishing escapement goals considers the important contribution these fishes make to the productivity of the habitats where they spawn and rear. 

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References

- Ames, J. 1984. Puget Sound chum salmon escapement estimates using spawner curve methodology. Pages 133–148 in P. E. K. Symons and M. Waldichu, eds. Proceedings of the workshop on stream indexing for salmon escapement estimation. Canadian Technical Report of Fisheries and Aquatic Sciences 1326.
- Baker, T. T., A. C. Wertheimer, R. D. Burkett, R. Dunlap, D. M. Egers, E. I. Fritts, A. J. Gharrett, R. A. Holmes, and R. L. Wilmot. 1996. Status of Pacific salmon and steelhead escapements in southeastern Alaska. *Fisheries* 21(10):6–19.
- Ben-David, M., M. Flynn, and D. M. Schell. 1997. Annual and seasonal changes in the diet of martens: evidence from stable isotope analysis. *Oecologia* 111:280–291.
- Ben-David, M., T. A. Hanley, and D. M. Schell. 1998. Fertilization of terrestrial vegetation by spawning Pacific salmon: the role of flooding and predator activity. *Oikos* 83:47–55.
- Bilby, R. E., B. R. Fransen, and P. A. Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. *Canadian Journal of Fisheries and Aquatic Sciences* 53:64–173.
- Bilby, R. E., B. R. Fransen, P. A. Bisson, and J. K. Walter. 1998. Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*O. mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, U.S.A. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1909–1918.
- Bilton, H. T., D. F. Alderdice, and J. T. Schnute. 1982. Influence of time and size at release of juvenile coho salmon (*Oncorhynchus kisutch*) on returns at maturity. *Canadian Journal of Fisheries and Aquatic Sciences* 39:426–447.
- Cederholm, C. J., D. B. Houston, D. L. Cole, and W. J. Scarlett. 1989. Fate of coho salmon (*Oncorhynchus kisutch*) carcasses in spawning streams. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1347–1355.
- Cederholm, C. J., M. D. Kunze, T. Murota, and A. Sibitani. 1999. Pacific salmon carcasses: essential contributions of nutrients and energy for aquatic and terrestrial ecosystems. *Fisheries* 24(10):6–15.
- Cederholm, C. J., and W. J. Scarlett. 1982. Seasonal immigrations of juvenile salmonids into four tributaries of the Clearwater River, Washington 1977–1981. Pages 98–110 in E. L. Brannon and E. O. Salo, eds. *Salmon and trout migratory behavior*. Fisheries Research Institute, University of Washington, Seattle.
- Delwiche, C. C., and P. L. Steyn. 1970. Nitrogen isotope fractionation in soils and microbial reactions. *Environmental Science & Technology* 4:929–935.
- Donaldson, J. R. 1967. The phosphorus budget of Illiamna Lake, Alaska, as related to cyclical abundance of sockeye salmon. Ph.D. thesis, University of Washington, Seattle.
- Eastman, D. E. 1996. Response of freshwater fish communities to spawning sockeye salmon (*Oncorhynchus nerka*). M.S. thesis, University of Washington, Seattle.
- Gresh, T., J. Lichatowich, and P. Schoonmaker. 2000. An estimation of historic and current levels of salmon production in the northeast Pacific ecosystem: evidence of a nutrient deficit in the freshwater systems of the Pacific Northwest. *Fisheries* 25(1):15–21.
- Groot, C. and L. Margolis, eds. 1991. *Pacific salmon life histories*. University of British Columbia Press, Vancouver.
- Hartman, G. E., and J. C. Scrivener. 1990. Impacts of forestry practices on a coastal stream ecosystem, Carnation Creek, British Columbia. *Canadian Bulletin of Fisheries and Aquatic Sciences* 223.
- Hesslein, R. H., K. A. Hallard, and P. Ramlal. 1993. Replacement of sulfur, carbon and nitrogen in tissue of a growing broad whitefish (*Coregonus nasus*) in response to change in diet traced by $\delta^{34}\text{S}$, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$. *Canadian Journal of Fisheries and Aquatic Sciences* 50:2071–2076.
- Hilderbrand, G. V., S. D. Farley, C. T. Robbins, T. A. Hanley, K. Titus, and C. Servheen. 1996. Use of stable isotopes to determine diets of living and extinct bears. *Canadian Journal of Zoology* 74:2080–2088.
- Holtby, L. B., B. C. Andersen, and R. K.

- Kadowaki. 1990. Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 47:2181–2194.
- Johnston, N. T., J. S. MacDonald, K. J. Hall, and P. J. Tschaplinski. 1997. A preliminary study of the role of sockeye salmon (*Oncorhynchus nerka*) carcasses as carbon and nitrogen sources for benthic insects and fishes in the "Early Stuart" stock spawning streams, 1050 km from the ocean. British Columbia Ministry of Environment, Lands and Parks, Fisheries Project Report RD55, Victoria.
- Juday, C., W. H. Rich, G. I. Kemmerer, and A. Mean. 1932. Limnological studies of Karluk Lake, Alaska 1926–1930. *Bulletin of the U.S. Bureau of Fisheries* 47:407–436.
- Kline, T. C., Jr., J. J. Goering, O. A. Mathisen, P. H. Poe, and P. L. Parker. 1990. Recycling of elements transported upstream by runs of Pacific salmon: I. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ evidence in Sashin Creek, southeastern Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 47:136–144.
- Larkin, G., and P. A. Slaney. 1997. Implications of trends in marine-derived nutrient influx to south coastal British Columbia salmonid production. *Fisheries* 22(11):16–24.
- Michael, J. H., Jr. 1998. Pacific salmon escapement goals for the Skagit River watershed as determined by nutrient cycling considerations. *Northwest Science* 72:239–248.
- Minigawa, M., and E. Wada. 1984. Stepwise enrichment of $\delta^{15}\text{N}$ along food chains: further evidence and the relationship between $\delta^{15}\text{N}$ and animal age. *Geochimica et Cosmochimica Acta* 48:1135–1140.
- Minakawa, N. 1997. The dynamics of aquatic insects associated with salmon spawning. Ph.D. thesis, University of Washington, Seattle.
- NRC (National Research Council). 1996. Upstream: salmon and society in the Pacific Northwest. National Academy Press, Washington, DC.
- Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries* 16(2):4–21.
- Nickelson, T. E., J. W. Nicholas, A. M. McGie, R. B. Lindsay, D. L. Bottom, R. J. Kaiser, and S. E. Jacobs. 1992. Status of anadromous salmonids in Oregon coastal basins. Oregon Department of Fish and Wildlife, Corvallis.
- Peterson, B. J., and B. Fry. 1987. Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics* 18:293–320.
- Phinney, L. A., and P. Bucknell. 1975. A catalog of Washington streams and salmon utilization. Washington Department of Fisheries, Olympia.
- Quinn, T. P., and N. P. Peterson. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. *Canadian Journal of Fisheries and Aquatic Sciences* 53:1555–1564.
- Richey, J. E., M. A. Perkins, and C. R. Goldman. 1975. Effects of kokanee salmon (*Oncorhynchus nerka*) decomposition on the ecology of a sub-alpine stream. *Journal of the Fisheries Research Board of Canada* 32:817–820.
- Schuldt, J. A., and A. E. Hershey. 1995. Effect of salmon carcass decomposition on Lake Superior tributary streams. *Journal of the North American Benthological Society* 14:259–268.
- Slaney, T. L., K. D. Hyatt, T. G. Northcote, and R. J. Fielden. 1996. Status of anadromous salmon and trout in British Columbia and Yukon. *Fisheries* 21(10):20–35.
- Ward, B. R., and P. A. Slaney. 1988. Life history and smolt-to-adult survival of Keogh River steelhead trout (*Salmo gairdneri*) and the relationship to smolt size. *Canadian Journal of Fisheries and Aquatic Sciences* 45:1110–1122.
- WDFW and WWTIT (Washington Department of Fish and Wildlife and Western Washington Treaty Indian Tribes). 1993. 1992 Washington state salmon and steelhead stock inventory. Appendix 1 and 2. Washington Department of Fisheries Information and Education Division. Olympia.
- Weatherley, A. H., and H. S. Gill. 1995. Growth. Pages 101–158 in C. Groot, L. Margolis and W. C. Clarke, eds. *Physiological ecology of Pacific salmon*. University of British Columbia Press, Vancouver.