

# Pacific salmon (*Oncorhynchus* spp.) runs and consumer fitness: growth and energy storage in stream-dwelling salmonids increase with salmon spawner density

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**Abstract:** We examined how marine-derived nutrients (MDN), in the form of spawning Pacific salmon, influenced the nutritional status and  $\delta^{15}\text{N}$  of stream-dwelling fishes. We sampled juvenile coho salmon (*Oncorhynchus kisutch*) and Dolly Varden (*Salvelinus malma*) during spring and fall from 11 south-central Alaskan streams that ranged widely in spawning salmon biomass (0.1–4.7 kg·m<sup>-2</sup>). Growth rate (as indexed by RNA–DNA ratios), energy density, and  $\delta^{15}\text{N}$  enrichment in spring-sampled fishes increased with spawner biomass, indicating the persistence of spawner effects more than 6 months after salmon spawning. Point estimates suggest that spawner effects on nutrition were substantially greater for coho salmon than Dolly Varden (268% and 175% greater for growth and energy, respectively), indicating that both species benefitted physiologically, but that juvenile coho salmon accrued more benefits than Dolly Varden. Although the data were less conclusive for fall- than spring-sampled fish, they do suggest spawner effects were also generally positive during fall, soon after salmon spawned. In a follow-up analysis where growth rate and energy density were modeled as a function of  $\delta^{15}\text{N}$  enrichment, results suggested that both increased with MDN assimilation, especially in juvenile coho salmon. Our results support the importance of salmon runs to the nutritional ecology of stream-dwelling fishes.

**Résumé :** Nous examinons comment les nutriments d'origine marine (MDN), que représentent les saumons du Pacifique en fraie, influencent le statut nutritif et le  $\delta^{15}\text{N}$  des poissons des cours d'eau. Nous avons échantillonné des jeunes saumons coho (*Oncorhynchus kisutch*) et Dolly Varden (*Salvelinus malma*) durant le printemps et l'automne dans 11 cours d'eau du centre-sud de l'Alaska qui différaient considérablement par la biomasse de saumons en fraie (0,1–4,7 kg·m<sup>-2</sup>). Le taux de croissance (mesuré par les rapports ARN–ADN), la densité énergétique et l'enrichissement de  $\delta^{15}\text{N}$  chez les poissons prélevés au printemps augmentent tous en fonction de la biomasse des reproducteurs en fraie, ce qui indique une persistance des effets des reproducteurs plus de 6 mois après la fraie des saumons. Des estimations ponctuelles laissent penser que l'effet des reproducteurs sur la nutrition est substantiellement plus important pour le saumon coho que pour la Dolly Varden (respectivement 268 % et 178 % supérieur pour la croissance et l'énergie), ce qui indique que les deux espèces profitent du point de vue physiologique, mais que les jeunes saumons cohos accumulent plus d'avantages que les Dolly Varden. Bien que les données soient moins claires chez les poissons échantillonnés à l'automne que chez ceux du printemps, elles indiquent que les effets des reproducteurs sont aussi généralement favorables durant l'automne, peu après la fraie des saumons. Lors d'une étude subséquente, nous avons modélisé le taux de croissance et la densité énergétique en fonction de l'enrichissement de  $\delta^{15}\text{N}$ ; les résultats indiquent que les deux augmentent avec l'assimilation des MDN, particulièrement chez les jeunes saumons cohos. Nos résultats soulignent l'importance des montaisons de saumons pour l'écologie de l'alimentation chez les poissons qui habitent les cours d'eau.

[Traduit par la Rédaction]

Received 18 October 2010. Accepted 15 September 2011. Published at www.nrcresearchpress.com/cjfas on xx December 2011. J2011-0134

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## Introduction

Ecosystems are linked through movements of material, and these spatial subsidies can greatly affect community interactions and enhance productivity (Polis et al. 1997; Wipfli and Baxter 2010). Many subsidies are characterized by infrequent periods of high availability, and ecologists now recognize that ephemeral resource pulses can have persistent ecological effects on multiple trophic levels (Yang et al. 2008). Pulsed resources are features of many ecosystems, and examples include mast fruiting by trees (Ostfeld et al. 1996), synchronized insect emergence (Williams et al. 1993), season- and storm-induced litter fall (Lodge et al. 1991), and anadromous fish spawning runs (Willson and Halupka 1995).

Pacific salmon (*Oncorhynchus* spp.), the dominant epipelagic consumers throughout the northern Pacific Ocean (Larkins 1964), gain substantial body mass foraging at sea prior to returning to fresh waters where they spawn and die. Marine-derived nutrients (MDN) delivered to riverine systems in the form of salmon excreta, eggs, and carcasses represent a seasonally pulsed subsidy that enhance productivity of freshwater and riparian ecosystems (Gende et al. 2002; Naiman et al. 2002; Janetski et al. 2009). Juvenile salmonids can consume large quantities of MDN (Scheuerell et al. 2007), and their growth rates (Bilby et al. 1996; Wipfli et al. 2003; Giannico and Hinch 2007), body condition (Bilby et al. 1998), and energy storage (Heintz et al. 2004, 2010) have been shown to increase in association with MDN. However, prior studies investigating fish nutritional responses to MDN have generally been conducted in experimental settings or in natural streams with little or no replication, which limits the extent to which these findings might apply to a range of natural systems. Understanding the effects of pulsed MDN subsidies on freshwater consumers across heterogeneous landscapes could lead to informed strategies for conserving and managing salmon and their ecosystems.

In this study, we examined effects of MDN from spawning salmon on the nutritional status of coho salmon parr (*Oncorhynchus kisutch*) and juvenile Dolly Varden (*Salvelinus malma*), generalist consumers that capitalize on MDN (Bilby et al. 1998; Denton et al. 2009). We sampled fish during spring and fall from 11 streams that represented nearly two orders of magnitude in range in salmon spawner abundance, in addition to variation in geomorphic features, ambient nutrient levels, and species composition of spawning salmon. We measured total energy density ( $\text{kJ}\cdot\text{g}^{-1}$  wet mass), which largely reflects variation in lipid storage (Shearer 1994; Anthony et al. 2000), and muscle RNA–DNA ratios, an index of recent growth rates commonly used for salmonids (e.g., Ferguson and Danzmann 1990; Wang et al. 1993; MacLean et al. 2008). In a follow-up analysis, we tested nitrogen stable isotope signatures ( $\delta^{15}\text{N}$ ) as a potential proxy for fitness-based measures. We predicted that (i) growth rates, energy density, and  $\delta^{15}\text{N}$  would increase with spawner abundance, but that the rate of increase would diminish at high resource abundance; and (ii) spawner effects would be greater in fall, just after salmon spawning, than in spring, more than 6 months after spawning.

## Materials and methods

### Study area and salmon streams

This study was conducted in 11 clear-water streams on the

Kenai Peninsula, south-central Alaska, that vary widely in the abundance of spawning salmon (Fig. 1, Table 1). The study area spanned three ecoregions that differed in topography, climate, vegetation, and dominant salmon species, and our aim was to select study sites across broad environmental conditions representative of the region. Across the study area, streamflow peaks with snowmelt during June, after which smaller discharge peaks occur during periods of rainfall; discharge is low from November through March when precipitation generally falls as snow (Brabets et al. 1999).

Five of the study streams — Bear, Glacier, Moose, Ptarmigan, and Quartz creeks — are located in the Chugach–St. Elias Mountains ecoregion (Nowacki et al. 2001). The climate is continental with approximately 64 cm of annual precipitation (Brabets et al. 1999). Streams in this ecoregion are typified by gently sloped mainstem channels that drain mixed spruce–birch (*Picea* spp. and *Betula papyrifera*) forest and steep tributaries that drain rugged alpine basins (Nowacki et al. 2001). Channel slope of the study streams (measured from 1:63 000 digital topographic maps) averaged 2.7% (Table 1). Sockeye salmon (*Oncorhynchus nerka*) are the dominant species of spawning salmon in these five streams. Most spawning occurs between late July and early September, and fry migrate downstream to rear in lakes. We sampled fish from 1 to 3 km upstream of the receiving lake in each of these streams.

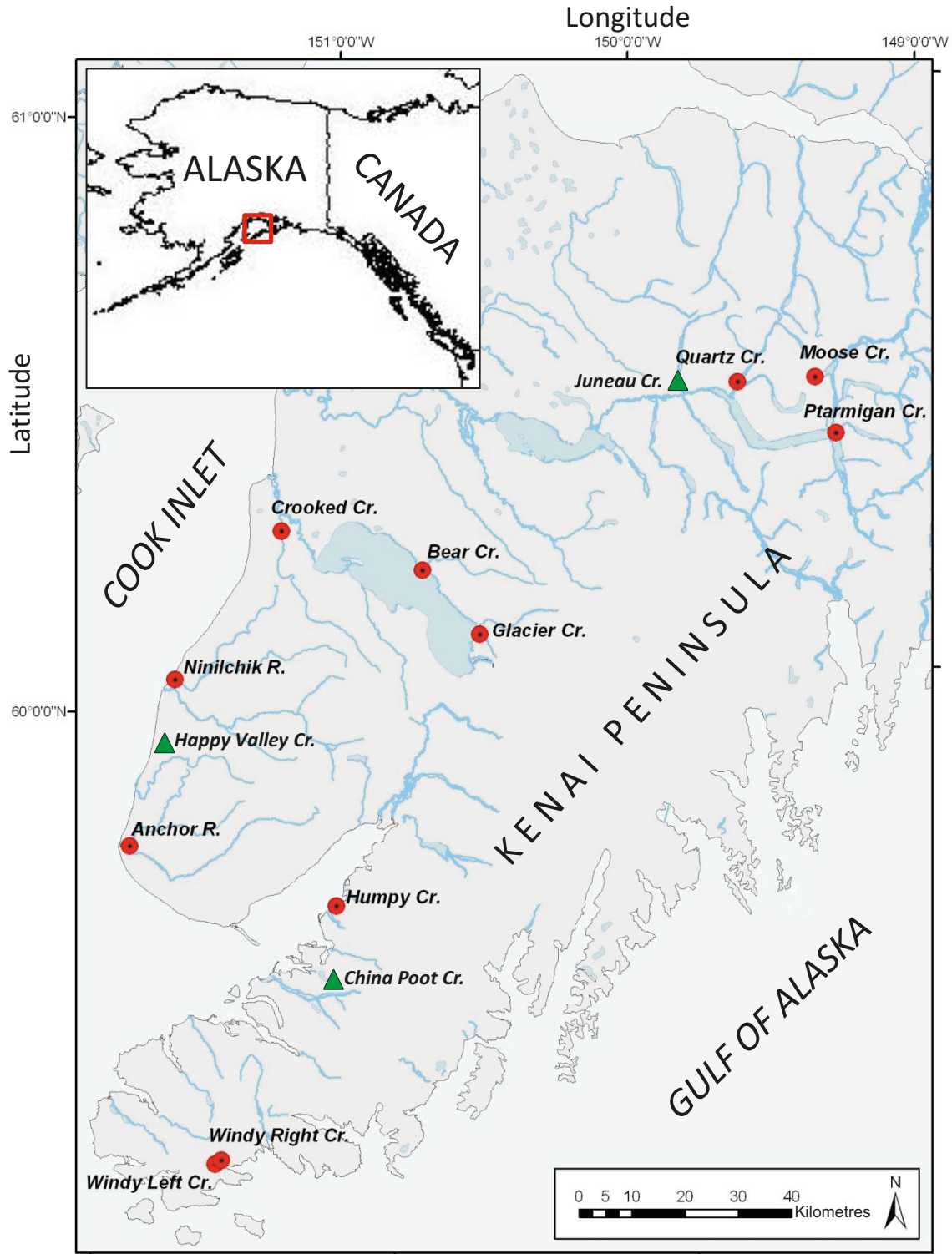
Three streams, Anchor and Ninilchik rivers and Crooked Creek, are in the Cook Inlet Basin ecoregion (Nowacki et al. 2001). Here, the climate is transitional between maritime and continental, with approximately 57 cm annual precipitation (Brabets et al. 1999). Streams in this ecoregion have low- to moderate-gradient meandering channels that drain a rolling landscape of white spruce (*Picea glauca*) forests. Channel slope of the study streams averaged 0.6% (Table 1). Because of the lowland topography in this region, streams here tend to have warmer summer temperatures than those in the other two ecoregions, which drain mountainous landscapes (Kyle and Brabets 2001; Mauger 2005). Each of these streams supports runs of Chinook salmon (*Oncorhynchus tshawytscha*) that spawn primarily during June and July and coho salmon that spawn primarily during September and October. We sampled each of these streams in the lower reaches (i.e., within the first 2 km above the Sterling Highway).

The remaining three study streams — Humpy, Windy Left, and Windy Right creeks — are in the Gulf of Alaska Coast ecoregion (Nowacki et al. 2001). This region has a maritime climate, with approximately 140 cm annual precipitation (Brabets et al. 1999). Watersheds in this area are typically short and drain rugged mountains. Channel slope of the study streams averaged 1.8% (Table 1). Vegetation is dominated by white spruce and Sitka spruce (*Picea sitchensis*), giving way to dense alder (*Alnus* spp.) stands at higher elevations. The study streams receive modest runs of chum salmon (*Oncorhynchus keta*), which spawn primarily during July and August, and sizeable runs of pink salmon (*Oncorhynchus gorbuscha*), which spawn primarily during August and September. We sampled each of these streams within 1 to 3 km above tidewater.

### Salmon spawner density estimates

In addition to representing a range of ecological condi-

**Fig. 1.** Kenai Peninsula, Alaska, USA, with the 11 salmon streams (circles) and 3 salmon-free streams (triangles) used in this study.



tions, these particular 11 streams were selected because the Alaska Department of Fish and Game (ADF&G) monitors their salmon escapements, and they exhibit a wide range of spawner densities (Fig. 1, Table 1).

On the Anchor and Niniichik rivers and Crooked Creek, ADF&G counted migrating spawners at weirs in the lower reaches. The Anchor River weir was coupled with a DID-

SON sonar for high-flow periods that rendered the weir ineffective (Kerkvliet et al. 2008). Chinook counts were complete for the three streams, but some coho counts required extrapolation from early returns or estimation from harvest rates (Michael Booz, ADF&G, Homer, Alaska, personal communication, 2007).

In Humpy, Windy Left, and Windy Right creeks, ADF&G

**Table 1.** Channel slopes and estimated spawning salmon densities for study streams.

Study streams by ecoregion	Channel slope (%)	Spawning reach length (km)	Average stream width (m)	2005		2006		Dominant species
				Abundance (no.·km <sup>-1</sup> )	Biomass (kg·m <sup>-2</sup> )	Abundance (no.·km <sup>-1</sup> )	Biomass (kg·m <sup>-2</sup> )	
<b>Chugach–St. Elias Mountains ecoregion</b>								
Bear Creek	5.7	19	5	4 441	1.8	3 345	1.3	Sockeye
Glacier Creek	1.1	2	3	1 938	1.3	2 407	1.6	Sockeye
Moose Creek	2.5	3	3	119	0.1	324	0.2	Sockeye
Ptarmigan Creek	3.4	5	8	608	0.2	692	0.2	Sockeye
Quartz Creek	0.8	19	8	824	0.2	3 542	0.9	Sockeye
<b>Cook Inlet Basin ecoregion</b>								
Anchor River	1.0	106	9	283	0.1	262	0.1	Chinook–coho
Crooked Creek	0.1	39	8	111	0.1	137	0.1	Chinook–coho
Ninilchik River	0.6	29	8	155	0.1	184	0.1	Chinook–coho
<b>Gulf of Alaska Coast ecoregion</b>								
Humpy Creek	1.7	5	7	18 896	4.1	10 004	2.4	Pink
Windy Bay Left Creek	0.7	8	5	9 043	2.7	8 183	2.6	Pink
Windy Bay Right Creek	3.0	2	4	11 998	4.7	8 855	3.7	Pink

personnel conducted periodic ground surveys (five or six surveys per season) throughout the salmon spawning reaches. They applied a stream life factor of 17.5 days to both salmon species present (pink and chum) to estimate total spawner abundance (Hammarstrom and Ford 2008; Ted Otis, ADF&G, Homer, Alaska, personal communication, 2007).

In the remaining streams — Moose, Ptarmigan, Quartz, Bear, and Glacier creeks — ADF&G personnel counted spawning salmon with one or more ground surveys in periods of relatively low streamflow during peak spawning of the dominant sockeye salmon populations (David Westerman, ADF&G, Soldotna, Alaska, personal communication, 2006). In cases where more than one survey was conducted, we used the highest spawner count.

We calculated the total spawner biomass for each stream (for both 2005 and 2006) using the year-specific average mass for individuals of each salmon species sampled from local commercial catches (Hammarstrom and Ford 2008). We measured the approximate length of each stream used by spawning salmon from ADFG's interactive fish distribution database (<http://gis.sf.adfg.state.ak.us/FlexMaps/fishresourcemonitor.html?mode=awc>), which enabled stream-specific estimates of spawner biomass densities. For Quartz and Bear creeks, however, we used the length of the actual spawner survey to express the length of stream used by spawning salmon. These estimates were coupled with estimates of average stream width throughout the spawning reach to yield estimates of spawner biomass per unit area of stream bed (i.e., kg·m<sup>-2</sup>) within the sampling reach.

Our escapement estimates undoubtedly contained different levels of observational error. Weir counts, which probably provided the most accurate estimates, were used on the three streams with the lowest spawner densities (i.e., Anchor and Ninilchik rivers and Crooked Creek), making it unlikely that spawner abundance at the low end of the spectrum was grossly underestimated. Underestimation was probably greatest among those streams where escapement estimates relied on a single foot survey (i.e., Moose, Ptarmigan, Glacier,

Quartz, and Bear creeks). Despite these limitations, spawner densities observed during field sampling were consistently in agreement with estimates derived from ADF&G data, and given the nearly two orders of magnitude in range in estimated spawner densities, observational error should have little or no influence on the overall results. As a post hoc test of this assertion, we doubled the spawner densities at sites where underestimation was expected and found negligible changes in relationships between spawner abundances and dependent variables.

### Sampling

We conducted field sampling in early May 2006 to examine the prolonged effects of the previous year's spawning runs and again in September or October 2006 to examine effects immediately following spawning runs. During each sampling bout, we used baited minnow traps to collect a target of five coho salmon parr and five juvenile Dolly Varden at each stream. Fish of both species were not always captured from all streams on both dates. Fish were quickly killed by anesthetizing with an overdose of MS-222 (tricaine methanesulfonate) and were stored at -70 °C until processed. We removed a small piece of white dorsal muscle (~0.05 g) for RNA–DNA and homogenized the remaining material for energy density and stable isotope analyses. This work was conducted under the University of Alaska Fairbanks IACUC protocol No. 06-04.

### Energy density

Energy density analyses were conducted at the National Marine Fisheries Service laboratory in Auke Bay, Alaska. The energy density (kJ·g<sup>-1</sup> dry mass) of most fish, including all fish <3.5 g total wet mass, was determined with a Parr 1425 semi-micro bomb calorimeter. The energy density of some fish, including most of larger individuals, was determined from the calorific equivalents for lipid (36.43 kJ·g<sup>-1</sup>) and protein (20.10 kJ·g<sup>-1</sup>) (Brett 1995). Lipid and protein were measured as in Heintz and Vollenweider (2010). For 12

samples, energy density was estimated by both bomb calorimetry and the calorific equivalents of lipid and protein. These samples indicated that energy content estimates from calorific equivalents were highly correlated with the calorimetric estimates ( $R^2 = 0.91$ ) but that calorific equivalents consistently underestimated energy density by approximately  $2 \text{ kJ}\cdot\text{g}^{-1}$ ; all calorific estimates were adjusted accordingly.

### RNA–DNA

RNA–DNA analyses were conducted at the University of Southern Mississippi following the protocol described in Wang et al. (1993). Total DNA was measured using the diphenylamine procedure (Burton 1956), and total RNA was measured using a modified Schmidt–Thannhauser procedure (Munro and Fleck 1966). All RNA and DNA analyses were conducted in duplicate, and the two values were averaged. Duplicate RNA values differed by an average of 3.3%, whereas DNA duplicates differed by an average of 3.6%.

### Nitrogen stable isotopes

Stable isotope analyses were performed at the US Geological Survey Stable Isotope Laboratory in Denver, Colorado. The nitrogen stable isotope composition was determined by continuous flow – isotope ratio mass spectrometry using a Carlo Erba NC1500 elemental analyzer interfaced to a Micro-mass Optima mass spectrometer (Fry et al. 1992). Results are reported in  $\delta$ -notation as deviations in parts per thousand (‰) relative to a standard as follows:

$$(1) \quad \delta^{15}\text{N} = (R_{\text{sample}}/R_{\text{standard}}) - 1$$

where  $R$  is the isotope ratio  $^{15}\text{N}/^{14}\text{N}$  of the sample and monitoring gas, respectively. Nitrogen isotopic compositions ( $\delta^{15}\text{N}$ ) were normalized to the internationally accepted scale (air) using L-glutamic acid standards, USGS 40 ( $\delta^{15}\text{N} = -4.52\text{‰}$ ) and USGS 41 ( $\delta^{15}\text{N} = 47.57\text{‰}$ ). Analytical error was  $\pm 0.2\text{‰}$ , based on replicate analyses of samples and in-house standards.

Because baseline  $\delta^{15}\text{N}$  varied across the study area (Rinella 2010), we used a  $\delta^{15}\text{N}$  enrichment index that accounted for ecoregional variation as opposed to using raw  $\delta^{15}\text{N}$  values. Thus, we expressed fish  $\delta^{15}\text{N}$  relative to that of scraper macroinvertebrates (i.e., primary consumers) collected above a salmon-blocking waterfall within the respective ecoregion, as we expected these organisms to reflect the isotopic composition of the ambient dissolved nitrogen pool (Vander Zanden and Rasmussen 1999). We chose the simplified  $\delta^{15}\text{N}$  enrichment index over established methods, like trophic positions (Vander Zanden and Rasmussen 1999), because we were primarily interested in the relative isotopic enrichment among the streams. For macroinvertebrates, we used composite samples ( $\geq 10$  individuals each) of the caddisfly (*Glossosoma* spp.) and the mayfly (*Drunella doddsi*) collected during spring, summer, and fall from three widely dispersed sites on each salmon-free stream. The streams were Juneau Creek, Happy Valley Creek, and China Poot Creek for the Chugach–St. Elias Mountains, Cook Inlet Basin, and Gulf of Alaska Coast ecoregions, respectively (Fig. 1); salmon-free scraper  $\delta^{15}\text{N}$  values (mean  $\pm$  standard deviation, SD) were  $2.8\text{‰} \pm 1.4\text{‰}$ ,  $6.7\text{‰} \pm 1.5\text{‰}$ , and  $-0.1\text{‰} \pm 0.4\text{‰}$ , respectively. These values make sense given the landscape context

of the ecoregions. Salmon-free scrapers were the most enriched in the Cook Inlet Basin ecoregion, where finer soils associated with the meandering stream channels may foster denitrification and, in turn, an isotopically enriched nitrogen pool (Pinay et al. 2003). Salmon-free scrapers were the most depleted in the Gulf of Alaska Coast ecoregion, where depleted inputs from extensive stands of nitrogen-fixing alder may dominate the nitrogen pool (Compton et al. 2003; Shaf-tel et al. 2010). Additional post hoc support for the magnitude of these ecoregional baselines came from our study streams, where our model predicted that in a stream with zero spawners, coho salmon and Dolly Varden would be enriched by about 5.4‰ and 4.7‰, respectively, over grazer macroinvertebrates. This level of enrichment is consistent with expectations for consumers (Vander Zanden and Rasmussen 1999) and indicates that the baselines produced appropriate values.

### Statistical analyses

Our analyses were based on this mixed model:

$$(2) \quad y_i \sim N[\alpha_{1,j(i)} + \alpha_{2,j(i)}x_{1,i} + \beta_1x_{2,i} + \beta_2x_{3,i} + \beta_3x_{1,i}x_{3,i} + \beta_4x_{2,i}x_{3,i} + \beta_5x_{1,i}x_{2,i}x_{3,i} + \beta_6x_{4,i} + \beta_7x_{2,i}x_{4,i}, \sigma]$$

where  $y_i$  is the response (RNA–DNA ratio, energy density, or  $\delta^{15}\text{N}$  enrichment) for fish  $i$ , and  $N(\text{Mu}, \text{Sigma})$  is the normal distribution with mean  $\text{Mu}$ , standard deviation  $\text{Sigma}$ . The  $j(i)$  terms map data points to streams. For example, if  $j(5) = 4$ , then the 5th observation is on stream 4. The  $\alpha_{1,j}$  terms are stream effects. If  $y_i$  was sampled in spring,  $x_{1,i} = 1$ ; otherwise  $y_i$  was sampled in fall and  $x_{1,i} = 0$ . If  $y_i$  was measured from a Dolly Varden,  $x_{2,i} = 1$ ; otherwise  $y_i$  was measured from a coho salmon and  $x_{2,i} = 0$ . The vectors of spawner densities and fish lengths are given by  $x_3$  and  $x_4$ , respectively. We used 2006 salmon spawner data as predictors for MDN measures in fish collected during the fall of that year. Since our spring samples were collected prior to the onset of the 2006 spawning runs, we used 2005 spawner data as predictors for these samples. Replacing spawner densities with  $\delta^{15}\text{N}$  values in  $x_3$  gives the model we used for exploring relationships between  $\delta^{15}\text{N}$  and RNA–DNA ratios and  $\delta^{15}\text{N}$  and energy density.

We used Bayesian methods to estimate parameters of eq. 2. This required assigning prior distributions to model parameters. We used standard, noninformative priors (Gelman et al. 2004). Specifically, we used  $\alpha_{1,j} \sim N(\mu_{\alpha_1}, \tau_{\alpha_1})$  and  $\alpha_{2,j} \sim N(\mu_{\alpha_2}, \tau_{\alpha_2})$  with  $\mu$  and  $\tau$  assigned uniform priors. The priors for  $\beta_1$ ,  $\beta_2$ ,  $\beta_3$ , and  $\beta_4$  were uniform and for the random error variance was  $p(\sigma^2) \propto \frac{1}{\sigma^2}$ . We constructed a Gibbs sampler in FORTRAN and used it to simulate the posterior distribution (Intel Corporation 2011). We based conclusions on posterior modes and 95% Bayesian confidence intervals (CI).

Previous studies suggest that MDN assimilation and nutritional benefits can saturate with increasing spawner density (Bilby et al. 2001; Wipfli et al. 2003; Heintz et al. 2004). Therefore, it was important to assess the eq. 2 assumption that dependent variables were linearly related to spawner densities across the range of studied spawner densities. Predicted versus observed graphs strongly suggested assuming a linear model was reasonable. To more formally test the adequacy of the linear model, we used posterior predictive checking. The

basic idea behind posterior predictive checking is that synthetic data generated from the fitted model should be consistent with the observed data (Gelman et al. 2004). To test the assumption that dependent variables were linearly related to salmon biomass, we calculated  $d = \bar{y}_H - \bar{y}_L$ , where  $\bar{y}_H$  and  $\bar{y}_L$  are mean response values for study streams with the highest and lowest salmon densities, respectively. Next we simulated 1000 data sets from the fitted model and computed  $d_{\text{sim}} = \bar{y}_{H,\text{sim}} - \bar{y}_{L,\text{sim}}$  for each simulated data set. If the response variables saturated with increasing salmon densities across the range of our data, we would expect a very high percentage of  $d_{\text{sim}}$  values to exceed  $d$ . Instead, only between 15% and 80% of  $d_{\text{sim}}$  values were more extreme than  $d$  for every response variable and season, demonstrating that the linear model adequately characterized relationships between response variables and salmon biomass.

## Results

All point estimates of spawner effects and  $\delta^{15}\text{N}$  enrichment effects were positive for both fish species in both seasons (Figs. 2 and 3), and CI values indicate many of these estimates had a high probability of being  $>0$  (Table 2). CIs were wider for fall-sampled fishes because of smaller sample sizes. Fish lengths and values of the response variables are summarized by stream (Table 3). Throughout the Results section, model parameters are presented as a point estimate followed, parenthetically, by the bounds of the 95% CI.

### Effects associated with spawner biomass

An increase in spawner biomass of  $1 \text{ kg}\cdot\text{m}^{-2}$  corresponded with estimated RNA–DNA increases of 1.69 (0.73–2.57) and 0.63 (–0.20–1.52) for spring-sampled coho salmon and Dolly Varden, respectively, and 0.43 (–1.23–1.92) and 0.17 (–1.86–2.14) for fall-sampled coho salmon and Dolly Varden, respectively (Fig. 2a). Among spring-sampled fish, the spawner effect was estimated to be greater for coho salmon than for Dolly Varden by 1.04 (0.39–1.67).

An increase in spawner biomass of  $1 \text{ kg}\cdot\text{m}^{-2}$  corresponded with energy density increases of  $0.77 \text{ kJ}\cdot\text{g}^{-1}$  (0.32–1.17  $\text{kJ}\cdot\text{g}^{-1}$ ) and  $0.44 \text{ kJ}\cdot\text{g}^{-1}$  (0.03–0.82  $\text{kJ}\cdot\text{g}^{-1}$ ) for spring-sampled coho salmon and Dolly Varden, respectively, and  $0.95 \text{ kJ}\cdot\text{g}^{-1}$  (0.07–1.80  $\text{kJ}\cdot\text{g}^{-1}$ ) and  $0.92 \text{ kJ}\cdot\text{g}^{-1}$  (–0.20–1.97  $\text{kJ}\cdot\text{g}^{-1}$ ) for fall-sampled coho salmon and Dolly Varden, respectively (Fig. 2b). For spring-sampled fish, the spawner effect for coho salmon was estimated to be  $0.32 \text{ kJ}\cdot\text{g}^{-1}$  (0.00–0.63  $\text{kJ}\cdot\text{g}^{-1}$ ) greater than that for Dolly Varden.

An increase in spawner biomass of  $1 \text{ kg}\cdot\text{m}^{-2}$  corresponded with increases in the  $\delta^{15}\text{N}$  enrichment index of 1.7‰ (0.9‰–2.8‰) and 1.7‰ (0.9‰–2.7‰) for spring-sampled coho salmon and Dolly Varden, respectively, and 1.4‰ (–0.6‰–3.3‰) and 1.1‰ (–1.0‰–3.1‰) for fall-sampled coho salmon and Dolly Varden, respectively (Fig. 2c).

### Effects associated with $\delta^{15}\text{N}$ enrichment

A 1‰ increase in  $\delta^{15}\text{N}$  corresponded with RNA–DNA increases of 0.85 (0.39–1.19) and 0.28 (–0.06–0.56) for spring-sampled coho salmon and Dolly Varden, respectively, and 0.73 (0.18–1.39) and 0.52 (0.05–1.18) for fall-sampled coho salmon and Dolly Varden, respectively (Fig. 3a). For spring-

sampled fish, the  $\delta^{15}\text{N}$  effect for coho salmon was estimated to be 0.56 (0.24–0.87) greater than that for Dolly Varden.

A 1‰ increase in  $\delta^{15}\text{N}$  corresponded with energy density increases of  $0.24 \text{ kJ}\cdot\text{g}^{-1}$  (0.04–0.47  $\text{kJ}\cdot\text{g}^{-1}$ ) and  $0.01 \text{ kJ}\cdot\text{g}^{-1}$  (–0.21–0.19  $\text{kJ}\cdot\text{g}^{-1}$ ) for spring-sampled coho salmon and Dolly Varden, respectively, and  $0.54 \text{ kJ}\cdot\text{g}^{-1}$  (0.23–0.81  $\text{kJ}\cdot\text{g}^{-1}$ ) and  $0.19 \text{ kJ}\cdot\text{g}^{-1}$  (–0.08–0.46  $\text{kJ}\cdot\text{g}^{-1}$ ) for fall-sampled coho salmon and Dolly Varden, respectively (Fig. 3b).  $\delta^{15}\text{N}$  effects were estimated to be greater for coho salmon than for Dolly Varden by  $0.23 \text{ kJ}\cdot\text{g}^{-1}$  (0.07–0.38  $\text{kJ}\cdot\text{g}^{-1}$ ) for spring-sampled fish and  $0.34 \text{ kJ}\cdot\text{g}^{-1}$  (0.13–0.55  $\text{kJ}\cdot\text{g}^{-1}$ ) for fall-sampled fish.

## Discussion

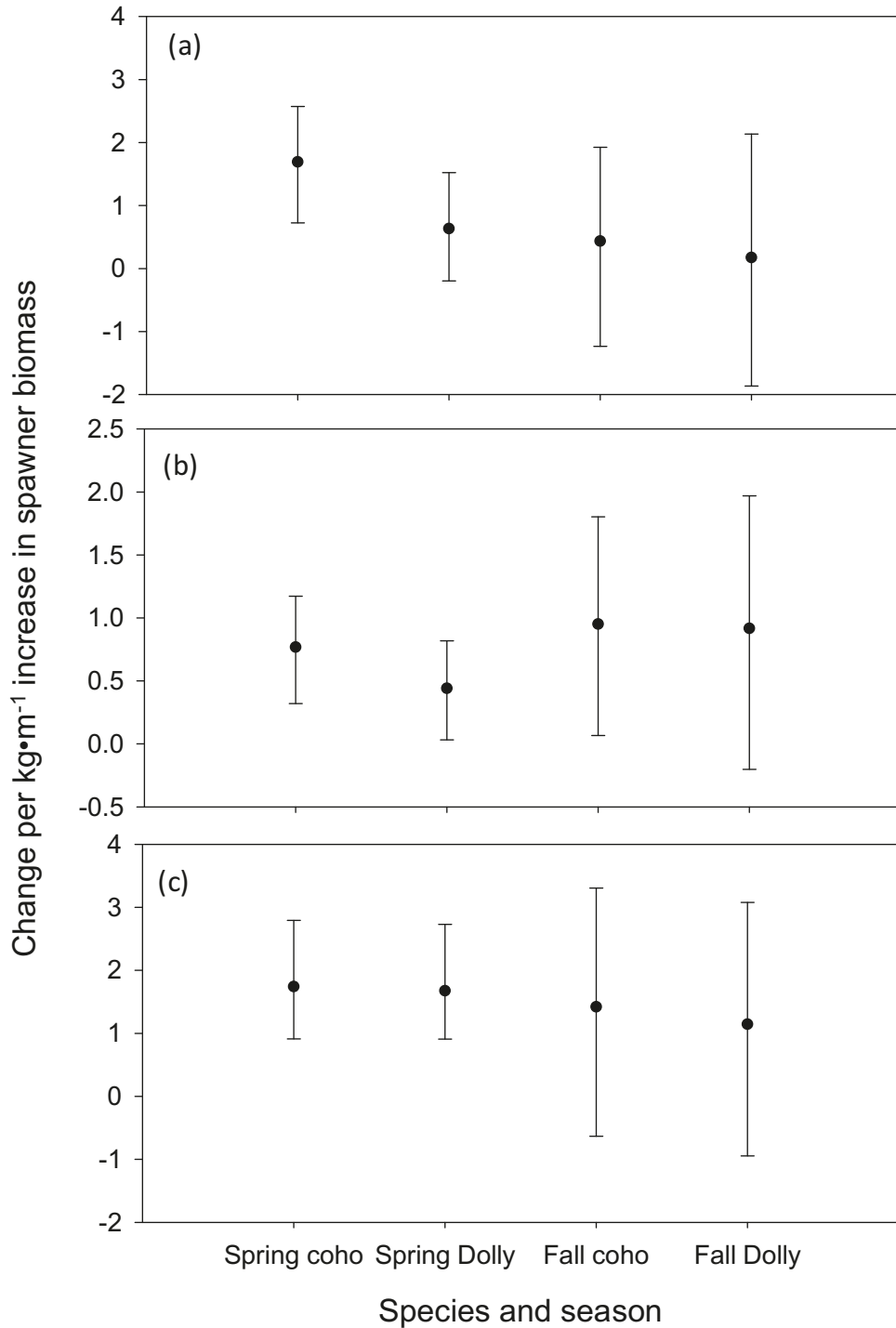
The nutritional status of stream-dwelling coho salmon and Dolly Varden increased with spawning salmon biomass across our study area, as predicted. Counter to our expectations, though, spawner effects were not consistently greater in the fall. Relationships between spawner biomass and energy density had high ( $\geq 0.95$ ) probabilities of being positive for both seasons and fish species, as did the relationship between spawner biomass and RNA–DNA ratios for spring-sampled coho salmon.  $\delta^{15}\text{N}$  enrichment also increased with spawner biomass, most clearly among spring-sampled fishes, adding support for MDN as a causal mechanism explaining observed increases in nutritional status. Through increased growth and energy, MDN supply may then contribute to increased fish survival during winter and at sea (Holtby et al. 1990; Quinn and Peterson 1996; Biro et al. 2004).

Our conclusion that MDN contributed to the enhanced nutritional status of fishes is further supported by the positive associations of  $\delta^{15}\text{N}$  enrichment with growth and energy, especially for coho salmon. These findings also support the use of  $\delta^{15}\text{N}$  as a proxy for nutritional status in ecologically based fisheries management strategies. One strategy uses  $\delta^{15}\text{N}$  enrichment in juvenile coho salmon as an indicator of adequate MDN supply (Bilby et al. 2001; Michael 2005; Shaff and Compton 2009), and this study supports the implicit assumption that  $\delta^{15}\text{N}$  enrichment corresponds to nutritional status.

To our knowledge, this is the first study to show linkages between salmon spawner biomass and the nutritional status of fishes in natural streams at a landscape scale. To date, studies indicating nutritional benefits associated with MDN have been experimental (e.g., Bilby et al. 1998; Wipfli et al. 2003; Heintz et al. 2004) or have been considerably more limited in geographic scope (e.g., Lang et al. 2006; Scheuerell et al. 2007). A number of stable isotope studies, however, have indicated increasing MDN assimilation with increasing salmon abundance over relatively large spatial scales (e.g., Bilby et al. 2001; Gregory-Eaves et al. 2007; Reichert et al. 2008). Our study strongly suggests that spawner biomass is an important factor in determining growth and energy among stream-dwelling fishes and that spawner effects were evident across a landscape that varied in terms of geomorphic features, ambient nutrient levels, and species composition of spawning salmon.

Here we present model estimates for our spring-sampled coho salmon to illustrate the magnitude of effect across a range of spawner biomass. We chose  $0.1 \text{ kg}\cdot\text{m}^{-2}$  as a low spawner biomass and  $4 \text{ kg}\cdot\text{m}^{-2}$  as a high spawner biomass,

**Fig. 2.** Point estimates (dots) and 95% Bayesian confidence intervals (bars) quantifying the effect of spawner biomass on (a) RNA–DNA ratio, (b) energy density, and (c)  $\delta^{15}\text{N}$  enrichment in coho salmon and Dolly Varden sampled during spring and fall.

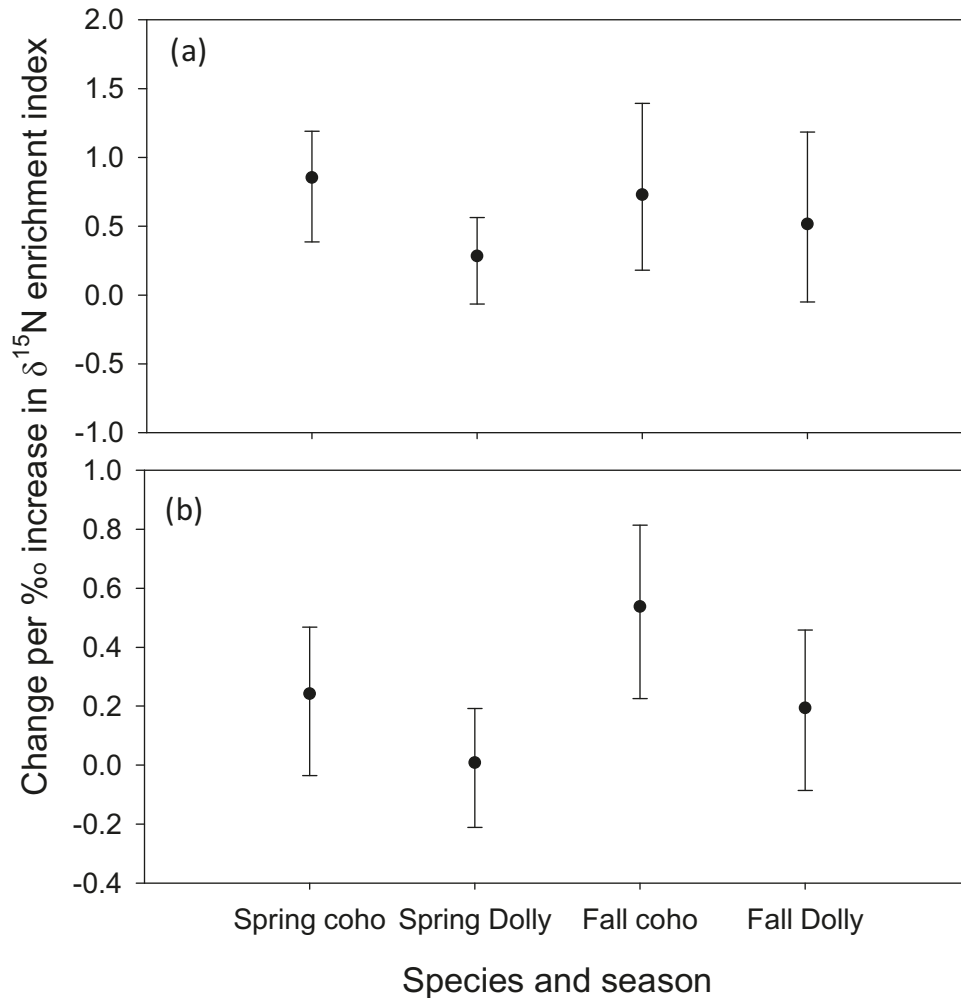


and this range was similar to that in the study streams. Under this scenario, RNA–DNA ratio was predicted to increase from 11.0 at low spawner biomass to 17.8 at high spawner biomass. Since RNA–DNA ratios above 3 to 4 indicate actively growing fish (Wang et al. 1993; Weber et al. 2003 and citations therein; MacLean et al. 2008), growth is clearly positive at the lowest spawner biomass, and a further increase is predicted to correspond with increasing spawners. Energy density was predicted to increase from 19.7 kJ·g<sup>-1</sup> at low spawner biomass to 22.7 kJ·g<sup>-1</sup> at high spawner biomass, cor-

responded to a 15% increase in total energy.  $\delta^{15}\text{N}$  enrichment index was predicted to increase from 5.2‰ at low spawner biomass to 12‰ at high spawner biomass. Since the  $\delta^{15}\text{N}$  enrichment index represents isotopic enrichment relative to salmon-free primary consumers (i.e., scraping macroinvertebrates), the enrichment observed at low spawner abundance is within the range expected by stepwise trophic-level enrichment alone (e.g., 1.3‰–5.3‰; Minagawa and Wada 1984) and suggests that fish assimilated little MDN in streams with few spawners. At high spawner biomass, by contrast, fish

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**Fig. 3.** Point estimates (dots) and 95% Bayesian confidence intervals (bars) quantifying the effect of  $\delta^{15}\text{N}$  enrichment on (a) RNA–DNA ratio and (b) energy density in coho salmon and Dolly Varden sampled during spring and fall.



**Table 2.** Probability that spawner effects and  $\delta^{15}\text{N}$  effects on respective dependent variables are  $>0$ .

Species, season	Spawner effects on:			$\delta^{15}\text{N}$ enrichment effects on:	
	RNA–DNA ratio	Energy density	$\delta^{15}\text{N}$ enrichment	RNA–DNA ratio	Energy density
Coho salmon, spring	$>0.99$	$>0.99$	$>0.99$	$>0.99$	0.95
Dolly Varden, spring	0.94	0.98	$>0.99$	0.94	0.50
Coho salmon, fall	0.73	0.98	0.94	$>0.99$	$>0.99$
Dolly Varden, fall	0.58	0.95	0.89	0.96	0.92

were clearly enriched relative to salmon-free primary consumers, indicating assimilation of MDN (Kline et al. 1990; Bilby et al. 1996; Chaloner et al. 2002).

Increasing growth, energy, and  $\delta^{15}\text{N}$  enrichment in relation to spawner biomass were evident during spring, indicating that these effects carried over through winter, an important energetic bottleneck (Giannico and Hinch 2007). The difference between spring and fall growth rates may have been underestimated by RNA–DNA ratios because fish sampled from warm habitats have lower RNA–DNA ratios than fish with similar growth rates sampled from cold environments (Bulow 1987; Ferguson and Danzmann 1990). These results imply overwinter storage of MDN, but the mechanism for that is not clear. One possibility is that fish assimilated

MDN and associated benefits during the salmon spawning period (i.e., summer and fall), presumably through direct consumption of salmon eggs and flesh (Moore et al. 2008; Denton et al. 2009), and that energetic demands and tissue turnover during the winter months was low enough for these nutritional and isotopic patterns to be maintained into the following spring. For example, the stable isotope composition of whitefish (*Coregonus* spp.) muscle reflected summer growth year-round, and the effect of tissue turnover during fall and winter was negligible (Hesslein et al. 1993; Perga and Gerdeaux 2005). Another possibility, not mutually exclusive of the former, is that MDN was stored in the stream environment and fish continued to consume it through the winter and spring. Possible direct pathways for stored MDN



**Table 3.** Mean values (including sample size (*n*) and standard deviation (SD)) for fork length, energy density, RNA–DNA ratios, and  $\delta^{15}\text{N}$  enrichment index in juvenile coho and Dolly Varden collected in spring and fall from the 11 study streams.

Stream	Spring						Fall					
	Coho			Dolly Varden			Coho			Dolly Varden		
	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD
<b>Fork length (mm)</b>												
Anchor River	5	69	2.6	5	130	12.3	5	95	4.8	5	96	8.1
Bear Creek	5	82	2.9	5	87	5.5	5	86	4.2	5	87	5.4
Crooked Creek	5	53	2.2	1	71	—	5	88	10.6	5	99	11.7
Glacier Creek	5	78	16.6	5	86	5.1	5	81	3.5	5	98	9.8
Humpy Creek	—	—	—	3	76	9.3	—	—	—	—	—	—
Moose Creek	5	61	4.5	5	72	16.3	3	80	4.6	5	74	6.1
Ninilchik River	5	61	4.5	—	—	—	5	90	6.6	—	—	—
Ptarmigan Creek	5	56	1.3	2	84	5.7	4	83	4.3	3	110	17.0
Quartz Creek	5	53	4.4	5	59	5.9	5	77	5.1	5	87	21.5
Windy Left Creek	5	52	1.5	3	92	16.1	—	—	—	—	—	—
Windy Right Creek	3	66	15.9	4	98	11.2	5	74	15.4	—	—	—
<b>Energy density (kJ·g<sup>-1</sup> dry mass)</b>												
Anchor River	5	19.0	0.4	5	21.9	1.4	5	21.9	1.3	5	21.3	0.5
Bear Creek	5	22.2	0.9	5	21.8	0.1	5	25.3	1.2	5	26.0	1.9
Crooked Creek	5	19.8	1.0	1	19.9	—	5	21.0	1.3	4	22.8	1.4
Glacier Creek	5	21.8	1.7	5	22.6	0.8	5	23.7	0.7	5	24.6	0.3
Humpy Creek	—	—	—	4	21.9	0.9	—	—	—	—	—	—
Moose Creek	5	21.5	0.8	5	20.6	0.8	3	22.6	0.5	5	21.7	1.1
Ninilchik River	5	19.6	0.3	—	—	—	5	21.0	1.1	—	—	—
Ptarmigan Creek	5	21.9	0.6	2	20.2	0.3	4	23.7	0.2	3	25.1	2.5
Quartz Creek	5	21.1	0.4	5	21.8	0.4	5	24.2	0.3	5	22.9	1.7
Windy Left Creek	5	23.9	0.3	3	22.9	0.3	—	—	—	—	—	—
Windy Right Creek	3	23.6	0.5	4	23.1	1.3	5	24.7	1.0	—	—	—
<b>RNA–DNA ratio</b>												
Anchor River	5	9.3	0.8	5	8.2	1.3	5	7.1	1.5	5	6.2	1.4
Bear Creek	5	13.5	1.2	5	12.1	4.2	5	8.6	2.0	5	9.9	3.6
Crooked Creek	4	5.1	0.6	1	7.0	—	5	5.2	0.5	4	10.0	3.2
Glacier Creek	5	10.8	1.8	5	9.0	2.1	5	9.9	0.7	5	8.8	1.5
Humpy Creek	—	—	—	4	10.0	2.8	—	—	—	—	—	—
Moose Creek	5	11.2	1.5	5	10.2	2.0	3	7.3	1.5	5	8.3	2.7
Ninilchik River	5	5.3	1.0	—	—	—	5	5.8	1.2	—	—	—
Ptarmigan Creek	5	12.8	1.3	2	7.1	1.5	4	8.5	1.8	3	9.6	2.4
Quartz Creek	5	9.6	1.3	5	11.2	2.0	5	6.7	1.5	5	8.6	2.8
Windy Left Creek	5	14.7	1.4	3	11.4	2.1	—	—	—	—	—	—
Windy Right Creek	3	16.0	2.2	4	12.6	1.0	5	9.4	2.9	—	—	—
<b><math>\delta^{15}\text{N}</math> enrichment index (‰)</b>												
Anchor River	5	3.5	0.5	5	3.8	0.3	5	3.5	1.7	4	4.2	1.0
Bear Creek	5	6.8	0.5	5	7.1	0.8	5	4.5	1.2	2	6.1	0.3
Crooked Creek	4	3.7	0.8	—	—	—	4	2.7	0.7	4	4.0	1.0
Glacier Creek	4	7.5	0.5	3	6.6	1.4	4	7.4	0.3	4	6.5	1.6
Humpy Creek	—	—	—	3	10.0	4.2	—	—	—	—	—	—
Moose Creek	5	5.9	0.6	4	6.0	1.7	2	5.7	0.3	2	6.1	1.7
Ninilchik River	4	3.1	0.6	—	—	—	5	2.6	0.6	—	—	—
Ptarmigan Creek	5	5.8	0.3	2	5.9	2.3	—	—	—	1	6.5	—
Quartz Creek	4	4.9	0.3	4	4.1	1.0	5	7.6	0.8	2	7.0	1.2
Windy Left Creek	2	9.2	0.1	3	11.5	1.1	—	—	—	—	—	—
Windy Right Creek	2	10.7	0.1	4	9.9	1.6	—	—	—	—	—	—

include consumption of dead salmon eggs, flesh, and emerging salmon fry, while possible indirect pathways include consumption of invertebrates that have been subsidized by MDN (Chaloner et al. 2002; Walter et al. 2006). Carbon stable isotopes may have helped resolve the relative importance of direct consumption and indirect food web pathways, but we did not extract lipids prior to analyses, and our  $\delta^{13}\text{C}$  data were highly variable and showed no relationship with spawner abundance.

Point estimates suggest spawner effects on growth and energy, respectively, were 268% and 175% greater for coho salmon than Dolly Varden. This finding is consistent with earlier work indicating that juvenile coho salmon consistently derive nutritional benefits from the direct consumption of MDN (Heintz et al. 2010), but that Dolly Varden typically receive transitory or delayed benefits through bottom-up pathways (Heintz 2009). A similar nutritional dichotomy was observed for rainbow trout (*Oncorhynchus mykiss*), which consumed MDN directly, and Arctic grayling (*Thymallus arcticus*), whose diets were supplemented indirectly by benthic macroinvertebrates dislodged by spawning salmon (Scheuerell et al. 2007). Our results further confirm that fish species can vary in the extent to which they benefit from MDN subsidies.

One weakness of this study is that spawner biomass was confounded with ecoregion. While sampling across ecoregions allowed us to achieve a large gradient in spawner biomass, it exacerbated the possibility that intrinsic differences in stream productivity or the physical environment (Janetski et al. 2009; Armstrong et al. 2010), rather than variation in spawner biomass, determined the observed patterns. Ecoregional differences in temperature and ambient nutrient levels, however, can be ruled out to some extent. Nutrient data from salmon-free streams (collected spring, summer, and fall simultaneous to the macroinvertebrate sampling; Rinella 2010) indicated that ambient levels of total nitrogen and total phosphorus were higher (by 2- and 20-fold, respectively) in the Cook Inlet Basin stream than in the others. Since spawning salmon can substantially increase dissolved nutrient levels (Johnston et al. 2004; Mitchell and Lamberti 2005), data from salmon-free streams provided a nonconfounded comparison of potential productivity, but required the assumption that they are representative of the other study streams in the respective ecoregions. Summer water temperatures were also likely higher in the Cook Inlet Basin than in the other regions (Kyle and Brabets 2001; Mauger 2005), as streams in the former drain lowlands and streams in the latter drain mountains. Despite this evidence that ambient nutrient levels and temperature were more amenable to fish growth in the Cook Inlet Basin, fish in these streams had the lowest growth and energy, which appear to instead be related to the low abundance of spawning salmon.

The observed patterns in growth and energy could also be explained simply by per-capita differences in food resources and not necessarily spawner effects, if abundances of stream-dwelling fishes were inversely proportional to spawner biomass. We cannot rule out this possibility, since differences in trapping effort precluded comparisons of catch per unit effort across the sites. Further, Lang et al. (2006) found fish were reluctant to enter baited traps when natural spawners were abundant, so our catch rates likely did not reflect the true

fish abundance. Despite our lack of data on fish densities, positive relationships with  $\delta^{15}\text{N}$  enrichment support MDN as a causal mechanism for both growth and energy.

Our data suggest both fish species benefitted from increasing spawner biomass across the entire range studied. This finding contrasts with a controlled experiment where isotopic enrichment (Chaloner et al. 2002), growth rate (Wipfli et al. 2003), and lipid content (Heintz et al. 2004) of juvenile coho salmon increased with the lowest salmon carcass treatment ( $1.9 \text{ kg}\cdot\text{m}^{-2}$ ) and leveled off with higher carcass treatments. Our findings also contrast with a study of 26 streams in Washington state where MDN assimilation (as indexed by  $\delta^{15}\text{N}$  enrichment) saturated at a spawner biomass of approximately  $0.15 \text{ kg}\cdot\text{m}^{-2}$  (Bilby et al. 2001). While these differences in the functional relationship between spawner biomass and MDN effects are intriguing, understanding their basis would require further investigation.

This research confirms the importance of MDN inputs to the trophic ecology of riverine systems and ecosystem function where salmon spawn. Our results demonstrate the positive relationships between salmon spawner biomass and the growth rate and energy density of stream-dwelling fishes across a broad spatial scale with considerable landscape heterogeneity. Further, our results show that increases in resident fish fitness associated with increasing spawner biomass persist for months following the period of salmon spawning. This study highlights the importance of maintaining strong salmon escapements in systems where the maintenance or recovery of stream-dwelling fish populations is a management priority.

## Acknowledgements

Thanks go to the Gulf Ecosystem Monitoring program (Exxon Valdez Oil Spill Trustees Council) for funding this project. Coowe Walker, Steve Baird, and Megan Murphy with the Kachemak Bay Research Reserve gave invaluable help in the field. Thanks also go to Ted Otis, David Westerman, Mike Booz, and Jeff Breakfield for help with Alaska Department of Fish and Game spawner counts and to Cayce Gulbransen for performing the isotope analyses. Advice from Hal Geiger and two anonymous reviewers greatly improved the manuscript. The US Forest Service Forest Health and the Kachemak Bay Research Reserve provided laboratory and bunkhouse space in Cooper Landing and Homer, respectively. Finally, thanks are extended to the University of Alaska Anchorage's Environment and Natural Resources Institute for supplemental funding during analysis and writing. The use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the US Government.

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